Common Eiders *Somateria mollissima* in the Netherlands:

The rise and fall of breeding and wintering populations
in relation to the stocks of shellfish

Nederlandse titel:	Fluctuaties van broedende en overwinterende populaties Eidereenden in Nederland in relatie tot schelpdieren
Layout and figures:	Dick Visser
Cover:	Sandra Meerlo
Pictures:	Alterra (pages 86, 168, 180, 181, 184, 185, 189, 202, 226, 316), Bram Fey (pages 18, 136, 189), Martin de Jong (pages 184, 188), Romke Kats (page 50), Andre Meijboom (pages 8, 254), Jeroen Reneerkens (page 188), Pim Wolf (page 66), Ingrid van der Spoel (pages 62, 177, 284, 320, 324, 328, 332)

RIJKSUNIVERSITEIT GRONINGEN

Common Eiders *Somateria mollissima* in the Netherlands:
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PROEFSCHRIFT

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
vrijdag 20 april 2007
om 14.45 uur

door

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geboren op 25 maart 1970
te Harlingen

voor mijn liefjes, Sandra, Sverre en Meinte
en familie, Henk, Minke en Jelliena

Contents

Chapter **1**

General introduction

The NWO research program 'Sustainable use and conservation of marine living resources'

The seas and coastal areas of the world have a long history of human exploitation, which contributed to the degradation, alteration, destruction and collapse of marine ecosystems (Jackson *et al.* 2001). At present, marine living resources are still declining all around the globe coinciding with an increase in damage to marine ecosystems (Roberts 1997). Although management systems for sustainable exploitation of natural resources have been developed, only a few of them have actually been put into practice (Hilborn *et al.* 1996). These alarming observations result from a combination of three causes:

1. lack of understanding of essential ecological processes in the sea, resulting in a mismatch between scales of ecological processes and scales of human exploitation systems;
2. deficiencies in the international legal regime, resulting from a spatial mismatch between the distribution of legal authority over jurisdictional (geographical) zones and ecological subdivisions, in combination with limited possibilities to oblige states to comply with internationally agreed management policies;
3. the fact that human behaviour is traditionally based on self-interest and short-term goals (i.e., a mismatch between ecological and economic time scales) which tends to neglect environmental effects and external costs passed on to others and to the future.

Therefore, the multidisciplinary PRIORITEIT programme `Sustainable use and conservation of marine living resources´ (SUSUSE) was initiated and financed by the Dutch Organisation for Scientific Research (NWO) between 1998 and 2006. SUSUSE aims to fill up the gaps in knowledge on exploitation, conservation and management of marine living resources in the Wadden Sea area resulting in new guidelines for the practical application at sea.

The focus of the programme is on the 'mismatch of ecological and human processes' hypothesis that populations of marine organisms and human exploitation and management systems act at different spatial and temporal scales. The SUSUSE programme is an attempt to investigate the predicted mismatch and centred around three themes:

1. spatial scales of populations of marine organisms in relation to the spatial scale of human exploitations systems,
2. analysis of temporal scales of development of populations of marine organisms and the possible mismatch with the temporal scales of humans exploitation systems, and
3. integrated approach of marine biodiversity.

One of the central themes of PRIORITEIT and SUSUSE is the integration of biological and socio-economical sciences in order to develop new theoretical concepts for sustainable use and conservation of marine living resources. The outcomes of this programme should result in new guidelines for the practical application at sea by policy makers based on a workable and scientifically sound strategy for sustainable use and conservation of marine living resources.

The aim is to examine the temporal variations in marine bivalve stocks in relation to time scales of bird predation and shellfish fisheries, and investigate the economic and other consequences of the observed ecological time scales for exploitation and conservation of marine living resources in the Dutch part of the international Wadden Sea. The total effort of multidisciplinary research of SUSUSE theme 2 is focused on (Figure 1.1):

1. recruitment of shellfish (Bos 2005),
2. settlement of shellfish (Hendriks 2004),
3. long-term population dynamics of the main avian predator of shellfish, the Common Eider Somateria mollissima (this thesis), and
4. building bio-economic models for sustainable use and conservation of marine bivalves (Hoekstra in prep.).
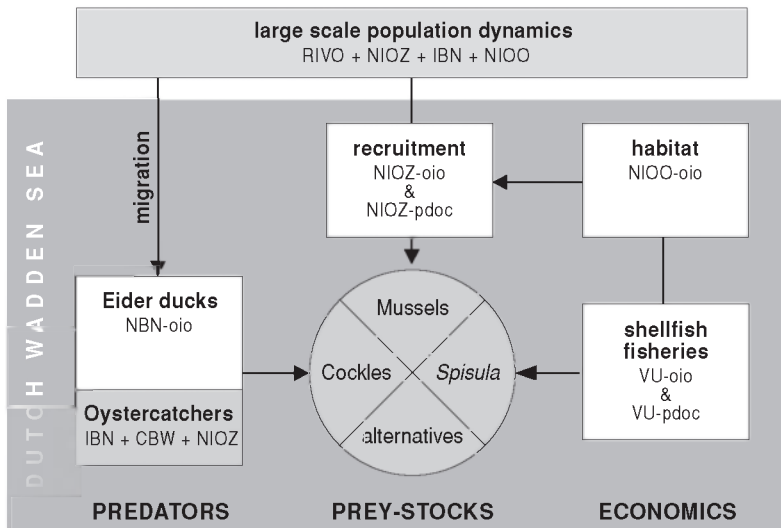
Figure 1.1 Schematic overview of the multidisciplinary research of SUSUSE theme 2 'Analysis of the temporal scales of development of populations of marine organisms, and the possible mismatch with scales of human exploitations' and their contributing partners in the Dutch Wadden Sea with respect to predators, prey stocks and economics. The shaded areas are the six participants within the four research fields of SUSUSE theme 2 project and non-shaded areas are recent and ongoing external research, for example continuous monitoring of populations of shellfish and oystercatchers within the project of the Evaluating the Effects of Shellfishery part II (EVA II), which is sponsored by the government and shellfishery. (Taken from SUSUSE-proposal).

Introducing the shellfish scene and its main players

The Wadden Sea area

The Wadden Sea area (including the adjacent North Sea) is an internationally important natural area, which is safeguarded for its characteristic habitats and inhabitants (i.e. the birds) by the EU Habitat and Birds Directives, and the Bonn and Bern Conventions on migrating animals. These habitats are important for a wide variety of bird species, such as terns, gulls, wildfowl and waders, which use the Wadden Sea area throughout their annual cycle for wintering, breeding, moulting or as a stopover site to refuel during migration from and to the breeding grounds (Van der Kam 1999). For some species of birds, the numbers exceed the level of 1 % of the total population indicating that the Wadden Sea area is of great importance for those species at a given moment in time.

The shellfish

The total stock of shellfish in the Dutch part of the Wadden Sea area is currently represented by only a few species of shellfish, mainly mussels *Mytilus edulis*, cockles *Cerastoderma edule*, Soft-shelled Clam *Mya arenaria* and Baltic Tellin *Macoma balthica* in the Wadden Sea (Beukema 1982, Beukema *et al.* 1993, Zwarts 1997, Van Stralen & Kesteloo-Hendrikse 1998, Van Stralen & Kesteloo-Hendrikse 1999, Bult & Kesteloo 2001, Beukema & Dekker 2005) and Cut-trough Shells *Spisula subtruncata* and American Razor Clam *Ensis directus* in the coastal zone of the North Sea (Craeymeersch & Perdon 2006). In general, shellfish undergo large natural fluctuations in numbers, relative densities and reproductive success (Van der Meer 1997). Most of these species of shellfish serve as the principle food for several species of shellfish-eating birds in the Wadden Sea and coastal North Sea, but some of them are also of commercial interest for the fishery.

The shellfish-eating birds

Shellfish are preyed upon by a variety of shellfish-eating birds and predation by birds differs in relation to the species of shellfish and/or size (small or commercial). In general, shellfish-eating birds swallow their prey whole, except for the Oystercatcher, and therefore the maximum size they can take is limited by their gape width. The list of bird species preying on small shellfish is long and includes for example Turnstones *Arenaria interpres*, Bar-tailed Godwits *Limosa lapponica* and Grey Plovers *Pluvialis squatarola*, but substantial reductions in the stocks of small shellfish was only documented for Herring Gulls *Larus argentatus* (Zwarts & Ens 1999) and predicted for Knots *Calidris canutus* (Van der Meer 1997). The birds preying upon large shellfish of commercial size are Common Scoter *Mellanitta nigra*, Common Eider *Somateria mollissima* and Oystercatcher *Haematopus ostralegus*. The Common Scoter specializes on *Spisula*, whereas Eiders and Oystercatchers primarily feed on mussels and cockles.

The shellfish-fishing industry

A long history of shellfish exploitation exists in the Wadden Sea area and involved shellfish species such as Periwinkle *Littorina littorea*, Whelk *Buccinum undatum*, European Flat Oyster *Ostrea edulis*, Blue Mussel *Mytilus edulis*, Cockle *Cerastoderma edule* and Cut-trough Shells *Spisula subtruncata* (Dijkema 1997, Wolff 2005). Two recently invaded exotic species of shellfish in the Wadden Sea area have also become of commercial interest, i.e. Pacific Oyster *Crassostrea gigas* and the American Razor Clam *Ensis directus* (Dijkema 1997, Wolff 2005). The mechanical shellfishery has primarily concentrated on Mussels, Cockles and S*pisula*.

Mussel cultures were introduced in the western part of the Dutch Wadden Sea in 1950 when a parasite (*Mytilicola intestinalis*) decimated the traditional mussel cultures in the SW Netherlands (Dijkema 1997). Each year seed mussels up to 65 million kg fresh weight were fished in the tidal (until 1993) and sub-tidal parts of the Wadden Sea to stock culture lots in both the Wadden Sea and SW Nether-lands (Ens 2003). The stocks of seed mussels experienced large annual fluctuations result-ing in a shortage of seed mussels, for example after three successive mild winters in 1988-1990. In order to stock the cultures lots, nearly all tidal mussel beds were fished in the Wadden Sea (Ens *et al.* 2004). To date, recovery is not yet complete.

Cockles were traditionally hand raked, but the cockle fishery was mechanised during the 1960's resulting in hydraulic suction dredging (Ens 2003) and as a con-sequence, the catch increased from 1–2 million kg fresh weight prior to 1960 to a maximum of 80 million kg fresh weight in 1989. An all-time low in the stock of cockles in the Wadden Sea was observed after the mild-winters in 1988-1990 due to intensive cockle fishery in previous years and low recruitment during subse-quent years (Smit *et al.* 1998). At the same time, large stocks of *Spisula* were dis-covered in the coastal areas of the North Sea, which served as a welcome replace-ment of the low stocks of Cockles. However, during the course of this thesis research, the Dutch government decided that some forms of the fishery were not sustainable and as a consequence the mechanised cockle fishery was terminated in 2005.

The shellfish policy

The extremely low stocks of both mussels and cockles in the Dutch Wadden Sea around 1990 were caused by unrestricted shellfishery. A heated public debate was triggered when increased mortality among shellfish-eating birds (Oystercatchers and Common Eiders) was observed and as a consequence new management rules were introduced in 1993 (LNV 1993) and further adjusted in 1998 (LNV 1998). In short, some tidal areas characterized by a high probability of re-settlement of mussel beds or eelgrass beds were closed to the fishery. Moreover, a food-reserva-tion policy was introduced for shellfish-eating birds (Oystercatchers and Common Eiders) designed to intervene in years with low stocks of shellfish. The aim was to ensure that shellfish stocks (post-fishery) would be adequate to support the birds.

The shellfish problem

The life history of shellfish eating birds differs in two important respects from the life history of their prey. First, the shellfish remain at a fixed location after settlement, while birds move between different feeding areas or move away when local conditions deteriorate. Second, comparing one year to the next, bird populations are much more stable than shellfish populations, due to the higher life expectancy of the birds and the much lower variability in their recruitment. As a consequence, the birds will experience years with an overabundance of food and years with poor food stocks. Local studies on bivalve exploitation by birds in the Dutch Wadden Sea confirm this prediction (Zwarts *et al.* 1996a, Van der Meer 1997). However, the extent to which the populations of the shellfish eating birds are hit by low stocks will depend on the geographical scale over which the shellfish stocks vary in synchrony. Winter weather is a large-scale phenomenon and severe winters often lead to mass mortality among the shellfish and high recruitment in the next year. As this applies to many shellfish species, despite differences in vulnerability, this means that shellfish stocks will vary in unison over a large geographical scale so that the shellfish eating birds will have limited possibilities for escape, despite their wings (Beukema *et al.* 1993). Low stocks of shellfish are a threat to both players in the shellfish-scene, because fishermen see their activities restricted and birds can only starve, migrate or ultimately die. Since the well-being of birds has been accorded priority in international treaties, the low stocks of shellfish should not be fished to a level that might become detrimental to the birds.

Outline of the thesis

Common Eiders are the most important consumers of commercially exploited shellfish in the Wadden Sea and coastal North Sea, and as a consequence potential conflicting demands exist between the shellfishery and Common Eiders. Quantitative knowledge on the dependence of Common Eiders on shellfish is lacking and is of crucial importance for the development of a management strategy in the Wadden Sea area, which attempts to reconcile the demands of both shellfishery and nature protection. This thesis is a first step to fill up these gaps in knowledge of the dependence of Common Eiders on shellfish during two important periods in the annual cycle, i.e. wintering and breeding.

Chapter 2 reviews the present status and most recent changes in the Baltic/ Wadden Sea Common Eider flyway population based on data on breeding, migrating, moulting, and wintering numbers in the flyway and summarises the causes of mortality observed in recent years throughout the flyway. Several geographic populations of Common Eider are present within the flyway throughout the annual cycle, and the Netherlands are used by two populations, i.e. wintering and breeding, which are presented separately.

The diet and prey preferences of Common Eiders in the Wadden Sea (Chapter 3 and 4) provide the background for the analysis of the wintering population (Chapter 5–8) and breeding population (Chapter 9–10) in the Netherlands. Chapter 3 provides an overview on the actual diet and prey preferences of Common Eiders. The reconstruction of the diet of the ingested shellfish was based on the analysis of shell fragments found in stomachs of oiled scoters, and in faeces from eiders roosting on an offshore sandbank. The primary prey in the diet of Common Eiders in the Wadden Sea area is the mussel followed by cockles and *Spisula*. Common Eiders are selective with respect to size and take only those sizes with the highest energy return indicating that not all prey species and sizes can be taken. Chapter 4 shows that Cut-trough Shells *Spisula subtruncata* and American razor Clams *Ensis americanus* are the staple food in the diet of Common Eiders, but also in Common Scoters *Melanitta nigra*, wintering along the coastal North Sea in the Netherlands.

Chapter 5 describes the patterns of mass mortality observed among Common Eiders in the Dutch Wadden Sea area in the winter of 1999/2000, when approximately 21,000 individuals died. Data on the dissection of beached birds, number and distribution of wintering eiders and the available food stocks was presented and it was hypothesised that over-fishing of mussels and cockles in the Wadden Sea in the early 1990s resulted in drastically reduced food resources. These reductions in food had impacts on the eiders causing mortality, shifts in distribution, and increased use of secondary prey.

Chapter 6 investigates the role of two parasites, *Profilicollis botulus* and *Amidostomum acutum*, in the recent mortality events of the Common Eider (1999/2000 and 2001/02). Three hypotheses were advanced to test whether mortality was caused by food shortage, parasite outbreak or that food shortage increased mortality among heavily parasitized individuals. Parasite loads were compared in beached (starved) and shot (healthy) eiders in order to test whether body condition was dependent on parasite loads. Evidence indicated that mass mortality was not caused due to an outbreak of parasites and the parasite outbreak hypothesis was rejected.

Chapter 7 analyses the size of the wintering population, the shift in distribution and mortality in relation to the total stocks of tidal and sub-tidal mussels, cockles, *Spisula* and *Ensis*, and winter severity in the Dutch Wadden Sea area. Although variation in the total wintering population in the Wadden Sea was related to the Winter Severity Index (explained by influxes of birds from the Baltic Sea area during severe winters) mortality was closely related to the stocks of sub-tidal medium-sized mussels. Variations in this primary food stock also explained shifts of wintering Eiders to the North Sea.

Chapter 8 links the distribution at various scales of wintering Common Eiders to the distribution of the tidal and sub-tidal shellfish in the Wadden Sea and evaluates the importance of sub-tidal cultured mussels.

Chapter 9 reveals the existence of widespread non-breeding by adult females, which was observed in 1990-1993 and 2003, and was calculated in a population trajectory for a single breeding colony (Vlieland) using data on annual number of breeding females and fledglings, and estimates on the probability of breeding in 2nd and 3rd year old females, and annual survival of juvenile, immature and adult females, using 25-year data of ring recoveries.

Chapter 10 investigates the relationship between the Dutch breeding population and the dependence on the local feeding conditions near the breeding colony. The importance of local feeding conditions is indirectly revealed by showing that at colony saturation the number of nesting females was related to the tidal area near the breeding colony. For Vlieland, the incidence of non-breeding was found to be negatively related to the total density of profitable food. For a series of years when cockles of appropriate size were lacking, breeding numbers on both Vlieland and Rottum were shown to be related to the stocks of tidal mussels near the colony.

Chapter 11 contains a general discussion of the main findings of this study and discusses future threats and perspectives. Although quantitative insights on the relationship between Eider populations, demography and distribution in relation to the stocks of shellfish have been obtained, there are still important gaps in our knowledge of the feeding ecology of the Common Eider. Until these gaps have been filled, we will be unable to implement a realistic science-based management plan in the Wadden Sea.

Chapter **2**

Status of the Baltic/Wadden Sea population of the Common Eider *Somateria m. mollissima*

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Abstract

A dramatic decline in the number of wintering Common Eiders from *c*. 800,000 to *c*. 370,000 occurred in Danish waters between 1990 and 2000. Denmark represents the most important wintering area for Eiders from the Baltic/Wadden Sea flyway, and mid-winter counts suggest the total population could have fallen from *c*. 1.2 million individuals in 1991 to *c*. 760,000 in 2000, implying major (*c*. 36%) overall declines. However, although declines of similar magnitude have been detected in breeding numbers at some resorts (e.g. Saltholm in Denmark), such a dramatic decline is not generally evident amongst breeding numbers monitored throughout the flyway. Five hypotheses are offered to explain this discrepancy, two of which are considered likely to contribute to the differences. These relate to shortcomings in our ability to monitor adequately breeding and wintering numbers in both time and space, as well as to an unknown buffering effect of non-breeders (which are counted on the winter quarters, but which do not appear amongst assessments of breeding abundance). Parameters known to contribute to declines in population size include low duckling survival caused by viral infections, mass adult mortality due to Avian Cholera, and reduced adult annual survival rates due to mass mortality events on the wintering grounds. The population continues to be a quarry species in Denmark, Sweden, Norway and Finland. It is strongly recommended that the national monitoring schemes should be more standardised and synchronised, in order to better establish future population abundance and change. It is further recommended that population modelling is undertaken to fully understand the relationships between the numbers of Common Eiders in the Baltic/Wadden Sea flyway population and the different factors affecting their abundance.

Introduction

The Baltic/Wadden Sea flyway population of Common Eider *Somateria m. mollissima* comprises breeding populations from Finland, Estonia, Sweden, Denmark, southern Norway, Germany and the Netherlands. Birds nesting in Denmark, Germany, western Sweden and The Netherlands are resident or partly migratory whereas those in southern Norway, eastern Sweden, Finland and the Baltic countries are completely migratory (Cramp & Simmons 1977). Eider of eastern provenance mix on the wintering areas in the western Baltic Sea, Kattegat, inner Danish waters, and in the Wadden Sea from Denmark to The Netherlands (Swennen 1990, Noer 1991, Fransson & Petterson 2001). The Common Eider has been widespread and common throughout its range in the Baltic and Wadden Sea countries for most of the 20th century (Cramp & Simmons 1977). Numbers have fluctuated throughout the 20th century, but increased continuously between the late 1940s to the 1990s (Almkvist *et al.* 1974, Hario & Selin 1988a, Camphuysen 1996 and references therein).

The Baltic/Wadden Sea flyway population was estimated to comprise 1.35–1.70 million birds in 1991 based on extrapolation from midwinter counts and was considered to be stable at that time (Rose & Scott 1997). However, since the late 1980s, increasing reports have documented marked declines in specific breeding populations within the Baltic/Wadden Sea flyway (e.g. Hario & Selin in 2002, Hollmén 2002, Christensen & Noer 2001), and hence, growing concern for the population has been expressed. To obtain better information about the Baltic/Wadden Sea Eider population, the Seaduck Specialist Group of Wetlands International arranged a workshop in Estonia during 17–21 April 2002 to compile information on the status and distribution of Eiders from all range states along the flyway. This paper summarises the outcome of the workshop, reviews the present status and most recent changes in the Baltic/Wadden Sea Common Eider flyway population based on data on breeding, migrating, moulting and wintering numbers in the range states and briefly summarises the causes of mortality reported in recent years.

Methods

Because all the range states have used different methods to count Eiders at different stages in the annual cycle, in the following country accounts, we attempt to briefly define the sources of data considered and presented here. Where possible, we assess their quality, suitability and compatibility and hence reliability to generate time series and trends.

Denmark

In Denmark, breeding pairs have been surveyed at least once every decade since the 1960s (Paludan 1962, Joensen 1973, Franzmann 1989, Lyngs 2000, Lyngs in prep.). Generally, most breeding sites were visited once during early May and numbers of nests/nesting females were counted. In some areas, colony size was estimated from numbers of males present around breeding islands during the pre-breeding period.

No long-term systematic counts of migrating birds at specific Eider locations have taken place in Denmark, but aerial surveys of moulting Eiders in Danish waters were carried out in August 1987, 1988 and 1989 covering coastal waters and offshore shoals and reefs down to 10m depth (Laursen *et al.* 1997).

Since the 1970s, seven extensive aerial surveys have been conducted to estimate the total mid-winter population of Common Eiders in Danish waters (Joensen 1974, Laursen *et al.* 1997, Pihl *et al.* 1992, Pihl *et al.* 2001). Each aerial survey was conducted during 5 January – 11 March, covering all Danish coastal waters and Kattegat (56°51'N, 10°57'E) with waters shallower than 10 m (the area considered to support all Danish wintering Eiders; Joensen 1974, Laursen *et al.* 1997, Pihl *et al.* 1992, Pihl *et al.* 2001). In the latest national survey (winter 1999/2000) the offshore part of Kattegat was covered by transect surveys (i.e. not the normal systematic total count method). Only birds observed on transect line were included from these flights, since the methods for density estimation are still in the process of development. In theory, these transect counts must have underestimated the Kattegat wintering numbers, but this source of error was judged to be of minor importance, since the distance between flight tracks was 2-3 km in both the total count method and the transect method. Eiders are easily detected at long distance, since they concentrate in large flocks and the white male plumage attracts observer attention. See Laursen *et al.* (1997) and Pihl *et al.* (2001) for more detailed descriptions and comparisons of the aerial survey methods.

In 1996 and 2001, outbreaks of Avian Cholera epidemics caused mass mortality amongst breeding females at several breeding colonies (Christensen *et al.* 1997, NERI unpublished data). The National Veterinarian Laboratory undertook necropsies of dead Eiders from wintering areas and breeding colonies, while NERI co-ordinated counts of dead Eiders in most of the affected breeding colonies.

Eiders are hunted in Danish waters from 1 October to 28 February. The number of Eiders shot by hunters has been monitored by the Danish Bag Record Scheme since 1958 (Strandgaard & Asferg 1980, Asferg 2001), while sex and age composition of the bag has been recorded through the Danish wing survey since 1982 (Clausager 2002 and references herein). Based on these data, specific analyses of factors affecting the Danish Eider bag have been undertaken (Noer *et al.* 1995, Christensen *et al.* in prep.).

A detailed population study of breeding Eiders on the island of Saltholm (55°39'N, 12°46'E) was carried out during 1993–2000 (Noer *et al.* 1993,

Christensen & Noer 2001). Based on parameters collected at Saltholm and other Danish colonies, a demographic model using Leslie matrices was developed to compare the observed changes in population size on Saltholm with that predicted based upon selected breeding parameters (Christensen & Noer 2001).

The Netherlands
Common Eiders first nested in 1906 in The Netherlands. Early breeding population censuses were crude estimates based on incidental sightings of breeding females. Until the early 1940s, Common Eiders only nested on Vlieland (53°15'N, 04°55'E), after initial breeding attempts on Terschelling in 1906. With most breeding Common Eiders in nature reserves, estimates of breeding numbers in the 1940s, 1950s and 1960s were usually from reserve wardens, often without indications of census methods. In the late 1950s, when the breeding population had increased to several thousands of breeding pairs, the "differentiated count" became established, notably on Vlieland (the largest and first established colony in The Netherlands; Hoogerheide 1950, Swennen 1976a). The differentiated count involved a census of Common Eiders roosting near the colony, after adult females had disappeared ashore to incubate eggs. Differentiating between adult males (Am), immature males (Im) and birds in female plumage (F; adults and immatures combined), and assuming a 1:1 sex ratio, the breeding stock (B in pairs) was estimated as

$$B = Am - (F - Im)$$

This method was developed to avoid disturbance in colonies, but it was criticised as early as the late 1950s as being inaccurate in a large colony such as on Vlieland (Hoogerheide 1958). Despite this, and with colonies meanwhile being established on all Dutch Wadden Sea islands, the differentiated method was employed on Vlieland between 1962 and 1988 and occasionally on Schiermonnikoog (53°30'N, 06°10'E). Reserve wardens monitored all other colonies, who produced annual "guesstimates", usually based on restricted nest searches and extrapolations. In the late 1980s and early 1990s, the monitoring programme on Vlieland was discontinued and breeding bird censuses entered a phase of uncertainty. Radically different methods between areas and between years were used, while the differentiated method was proved to be an inadequate tool to monitor the population crash on Vlieland (Duiven & Zuidewind 1995, Camphuysen 1996). On some small, easily covered islands, complete nest counts have been conducted, e.g. Griend (53°14'N, 05°15'E) (Oosterhuis & van Dijk 2002). Since 1991, breeding Eider numbers have been monitored annually by counting nesting females in selected sampling areas in the Wadden Sea area, covering *c.* 20% of the Dutch breeding population (Dijksen & Klemann 1992). However, the methods used were so different and census coverage was usually so incomplete in recent years, that reliable population trends

cannot be produced.

Along the Dutch North Sea coast, observers make systematic observations of migrating seabirds. The numbers counted along the North Sea coast reflect wintering numbers in the North Sea, but cannot be used to estimate the total number wintering in The Netherlands.

The first Wadden Sea aerial survey took place during severe winters in 1956 and 1963 and covered ice-free areas in the western Wadden Sea (Over & Mörzer Bruijns 1956, Verwey 1956, Zweeres 1963). Subsequent waterfowl surveys made by Swennen and co-workers between 1966 and 1991 concentrated on traditional Common Eider wintering grounds in the Wadden Sea, based on knowledge of areas with high Eider densities from field observations (Swennen 1976a, 1991a). Since 1993, a systematic aerial survey of Eiders in Dutch coastal waters has been undertaken, fully covering the Wadden Sea and the North Sea coastal zone during mid-winter (Koffijberg *et al.* 2001). In 2000, 2001 and 2002 three aerial surveys per winter were conducted, attempting complete coverage by flying along transects at high tide.

Beached bird surveys have been carried out along the entire Dutch coast, in 19 sub-areas, on a systematic basis since 1977 (Camphuysen *et al.* 2002). Before then, beached bird surveys were carried out in a less systematic manner. The census areas have been searched on a monthly basis, for all dead birds. Search effort (area covered) was highest during winter (November–April). Based on numbers found per one kilometre coastline searched, total numbers of beached birds in The Netherlands have been estimated (Chapter 5).

A number of detailed studies on breeding Eiders in The Netherlands have been undertaken during the last half of the 20th century. These studies have investigated population size and structure, dispersion, wintering numbers, foraging, reproductive success, adult and juvenile mortality, diseases, physiology and general ecology in both breeding and wintering Eiders (e.g., Everaarts *et al.* 1983, Hoogerheide 1950, Hoogerheide & Hoogerheide 1958, Swennen 1976a, 1983, 1990, Swennen & Smit 1991).

Germany
The numbers of breeding Common Eider throughout Germany were estimated for the period 1982–1999 by various methods, depending on size and accessibility of the areas involved (Hälterlein *et al.* 1995, Wilkens 1999). National breeding numbers are not yet available for 2000–2002. The breeding data allows discrimination between the northern and western parts of the German Wadden Sea. For several smaller areas longer time series are available, but they do not enable the compilation of a national estimate nor trend (Behm-Berkelmann & Heckenroth 1991, Berndt *et al.* 1993).

Eider migration has not been studied systematically in Germany, but the moulting concentrations during the post-breeding period (July/August) in the

German part of the Wadden Sea have been monitored by aerial survey at low tide (when Eiders concentrate in large flocks along tidal gullies) since 1987.

Aerial surveys of wintering Eiders have also been conducted annually since 1987 in the German Wadden Sea. In the Baltic, some aerial counts, combined with ground based counts, have taken place in most years (Nehls & Struwe-Juhl 1998).

The numbers of dead Eiders have been registered along a selection of German North Sea beaches for many years. Comparisons of numbers found can be made for the period 1992/93 to 2001/02 (Fleet 2001, Fleet & Reineking 2000, 2001). A selection of the beaches has been surveyed in winter (1 October – 31 March) with the same intensity and using the same methods since 1992/93 and can be used for the calculation of the number of dead birds found per kilometre. This in turn gives some indication of the relative annual mortality of this species in German North Sea waters.

Sweden
The total Swedish breeding population was estimated in 1973 (Almkvist *et al.* 1974) and again in 1983-1984 (Andersson 1985, Svensson *et al.* 1999). Aerial post-breeding censuses were carried out when males aggregate at traditional areas, prior to southward moult migration. The sex ratio was estimated during spring migration and on the breeding grounds, and was used to transform these male counts into breeding numbers. No national estimates of Eider breeding numbers exist for the last 18 years.

Regionally, trends in breeding numbers have been monitored at several sites along Swedish coasts. Boat based surveys of pre-breeding males have been carried out in the Stockholm archipelago (59°30'N, 19°00'E) in late April since 1985, when pairs are close to their breeding island. Each year several groups of islands in the northern and the southern parts of the outer Stockholm archipelago have been surveyed (Skärgårdsstiftelsen 2002). In the Bullerö archipelago (59°10'N, 18°52'E), systematic nest counts have been performed six times since 1971 shortly before hatching. In the Lygne archipelago (59°32'N, 19°28'E), Eider nests have been counted regularly by a private landowner and his heirs continuously since 1910. In the Baltic Småland archipelago (57°45'N, 16°40'E) the breeding numbers of Common Eiders were surveyed during 1990-2000 (Johansson & Larsson 2001). On Lilla Karlsö (57°19'N, 18°04'E) and Stora Karlsö (57°17'N, 17°58'E), Gotland, numbers of breeding pairs have been counted every year since 1990. In southern Sweden, land based counts of Eiders have been carried out annually in mid-September since 1976, the totals from which represent local breeders and their young.

At Kåseberga (55°25'N, 14°05'E) in southern Sweden, spring migration counts of Eiders have been conducted annually during 1992–2000. If we can assume that the percentage of the Baltic-breeding Eiders, which pass Kåseberga in spring each

year is constant, these counts could provide a representative measure of the annual total numbers passing. The Kåseberga data are the only such recent migration data that exist. The counts cover most of the spring migration period but there are some gaps in the coverage. In very recent years, these gaps are not very marked.

Volunteers in Sweden have conducted countrywide land-based winter surveys since 1991 covering the southern part of both the east coast and west coast.

In the Stockholm archipelago an experimental study of the effect of the non-native American Mink *Mustela vison* on the Eider population has been carried out between 1995–2001 at Bullerö-Långviksskär. Counts of male numbers, nests and studies of habitat preferences on Mink-inhabited and on Mink-free control islands have been carried out annually.

Finland

The size and extent of the Finnish archipelago makes complete breeding censuses impossible. Eider populations are monitored in sample areas within the framework of the national Archipelago Birds Censuses. These comprise 6 core areas where regular counts have been conducted for more than 50 years. Since 1984, an additional 27 areas (comprising 1550 islands along the entire coast) have also been counted. From these counts, indices are produced to describe the population trends. Koskimies & Väisänen (1991) present fieldwork procedures in detail.

The Hanko bird station (59°50'N, 23°00'E) at the southernmost tip of the mainland has generated long-term count data of migrating Eiders (from 1979 onwards), which are currently the subject of analysis.

During 1968–92, systematic winter counts have been conducted on four open-sea routes in the Åland Sea (Hario *et al.* 1993).

Detailed studies of breeding Eiders has been carried out in the Söderskär bird sanctuary (60°07'N, 25°25'E) in the Gulf of Finland since the 1950s. Data on breeding numbers, clutch size, timing of breeding, hatching success, female body weight and adult and duckling survival have been collected annually (Hario & Selin 1988a). Similar data have been collected at four other Eider nesting areas on the southern coast. Studies to develop methods for the evaluation of effects of diseases, food limitation, and contaminants have been conducted at all these locations since the mid-1990s (Hollmén 2002, Franson *et al.* 2000).

Other countries

The Norwegian Skagerrak winter population was estimated using land-based surveys in late 1980s (Nygård *et al.* 1988) and in 2002. The breeding numbers for this region have been estimated on the basis of aerial surveys of pre-/post-breeding males. Breeding and wintering numbers are monitored annually (Lorentsen 2001, Lorentsen & Nygård 2001).

Estonian breeding surveys have been performed annually based on nest searches 2–3 times each spring in the nature reserves which support 60–70% of the

national total (Onno 1970, Renno 1993, Kuresoo *et al.* 1998). The total national breeding numbers are based upon aerial and boat surveys of males in spring performed at a few colonies outside of the nature reserves.

In 1990–2002, annual winter ground counts of Estonian Eiders have been performed, with an aerial winter survey covering the whole coast in 1993.

In Latvia sporadic observations in possible breeding areas are performed regularly. The Latvian coast is counted every winter, and observations of migrating sea birds are performed annually during spring and autumn.

For Poland, wintering numbers used here are those reported to the Seaduck Specialist Group Database.

Statistical analysis

Statistical analyses were carried out using SAS for Windows. Spearman Rank Correlation Coefficients and their P-values were calculated to test for apparent correlations between variables.

Trends in the Finnish and Norwegian breeding populations and Norwegian wintering populations are analysed using TRIM software (Trends and Indices for Monitoring data), with stepwise models being used to identify significant changes in index trends (Pannekoek & van Strien 1998, Hario & Rintala 2002, Lorentsen 2001, Lorentsen & Nygård 2001).

Results

Denmark

The Danish breeding population of Common Eiders increased steadily from *c.* 1,200 pairs in 1935 (Spärck 1936) to a maximum of *c.* 25,000 pairs in 1990 (Lyngs 2000). In 2000, the population comprised *c.* 24,000 breeding pairs (Figure 2.1, Lyngs in prep.).

The similarity in numbers of breeding Eiders in 1990 and 2000 does not reflect a stable situation between or within colonies. During this period, a few old, large colonies have experienced marked decreases, while increases have occurred in a number of small and newly established colonies, especially in the innermost Danish waters (Lyngs in prep.). Danish breeding Eiders are resident or partly migratory (Lyngs & Christensen in prep). Females are highly philopatric as documented by ringing data (Lyngs & Christensen in prep.) and a DNA-study (Tiedemann & Noer 1998), but males show high natal dispersal.

Marked declines in numbers of breeding Eiders have been recorded at several Danish colonies during the 1990s. The most obvious declines were related to outbreaks of Avian Cholera in 1996 and most recently in 2001. Avian cholera, caused by the bacteria *Pasteurella multocida*, was recorded in Eiders from several colonies in southwest Kattegat (Stavns Fjord (55°54'N, 10°39'E), Hov Røn (55°54'N,
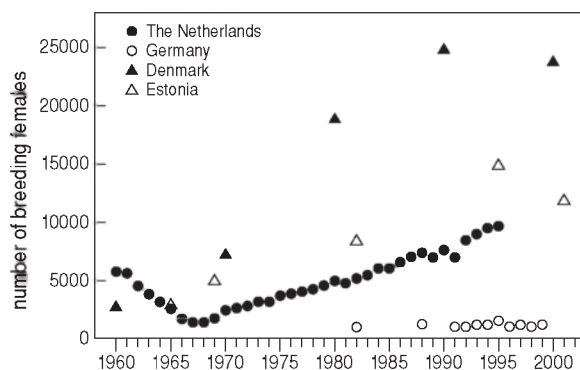
Figure 2.1 National annual total numbers of breeding Eider females in The Netherlands, Germany, Denmark and Estonia for 1960–2001 (see methods section for description of data collection techniques and constraints on interpretation). Each year is identified by the January of each count, hence "1986" refers to the winter 1985/1986 etc.

10°17'E), Svanegrund (55°50'N, 10°21'E), Alrø Polder (55°52'N, 10°07'E), Mågeøerne (55°35'N, 10°07'E), Søby Rev (55°53'N, 10°14'E)) in both 1996 and 2001, but was also recorded in one colony in eastern Denmark in 2001. The number of Eiders that succumbed to the Avian Cholera epizootics in 1996 and 2001 was estimated to total 3,500–4,000 females and *c.* 400 males (Christensen *et al.* 1997, NERI unpublished data). At individual colonies, the proportion of females dying ranged from 30% and 90%. On a national scale, the epizootics were estimated to have reduced the total breeding population in 1996 and 2001 by *c.* 8–10%.

In eastern Denmark, the Saltholm colony has decreased by 38% during 1993–2000 (Figure 2.2, Christensen & Noer 2001) without being affected by Avian Cholera. For this colony, population modelling showed that observed changes in breeding parameters (nest numbers, clutch size, hatching success, duckling production and duckling survival) during the study period could only account for a 3% decline in breeding female numbers. Thus, the observed decline did not result from observed reductions in reproductive performance. Given this result, the population model was used to assess the effect of potential changes in first time breeding distribution (age at first breeding) and changes in adult survival. Multiple model runs with reasonable parameter simulations showed that only a reduction in adult survival could result in a match between the observed and expected population decline, corresponding to a change in mean annual survival rate from 0.87 to 0.81 (Christensen & Noer 2001).

Counts of moulting Eiders in Danish waters during August in 1987–89 found total numbers between 70,000 and 135,000 individuals. The major moulting grounds were located in Kattegat, the Belts and in the Wadden Sea, and showed a similar distribution in all years (Laursen *et al.* 1997).
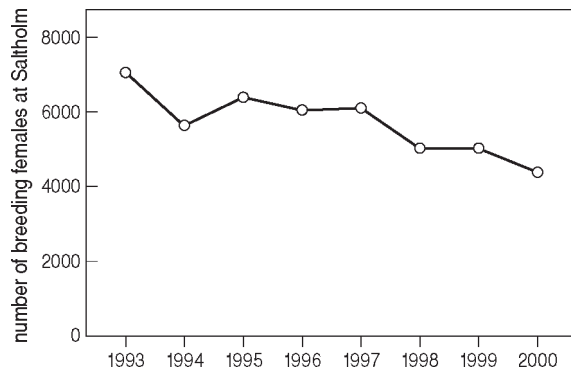
Figure 2.2 Annual numbers of female Eiders breeding at the Saltholm colony, in Øresund, SE Denmark, during 1993–2000. Estimates are based on extrapolation of sampled nest-search transects carried out using identical methods each year.

Eiders wintering in Danish waters comprise birds from Sweden, Finland, other Baltic countries and local Danish breeders (Noer 1991). Based on aerial mid winter surveys, the number of Eiders wintering in Danish waters was estimated in 1970/71 at 300,000–500,000 (Joensen 1974), increasing to *c.* 800,000 in the late 1980s and the early 1990s (Laursen *et al.* 1997). In 2000, the winter population was estimated to comprise *c.* 370,000 individuals (Figure 2.3, Table 2.1, Pihl *et al.* 2001), suggesting a dramatic decline in mid-winter numbers during the 1990s. Comparison of regional numbers shows that declines in wintering numbers have occurred most markedly in Kattegat (91%) and Great Belt (71%), while five other regions contributed a combined decrease of 30% (see Pihl *et al.* 2001). The overall decrease of *c.* 50% between 1990 and 2000 corresponds to an annual decrease of *c.* 5% over the last ten years.

Studies of the occurrence of intestinal Acanthocephalan parasites in Eiders shot by Danish hunters during 2000–2002 found high infestation rates (80–95%), with a mean of *c.* 170 parasites per bird, except in adult males, which on average harboured 25 parasites. Preliminary analyses of parasite loads and body condition showed no indication that body condition was affected by parasite infection in either adult or juvenile Eiders (NERI unpubl. data).

Denmark has a traditional sea duck hunt during autumn and winter. Eider numbers bagged by hunters increased during 1958–1970 from *c.* 100,000 to *c.* 140,000 per season. During the 1970s and 1980s, the size of the bag was relatively stable, but has declined during the 1990s to the present level of *c.* 80,000 individuals (Figure 2.4, Noer *et al.* 1995, Asferg 2001). Recent analyses from the period 1983–1999 showed that the annual Eider bag is mainly affected by the number of hunters, since variation in this parameter explains 78% of the variation
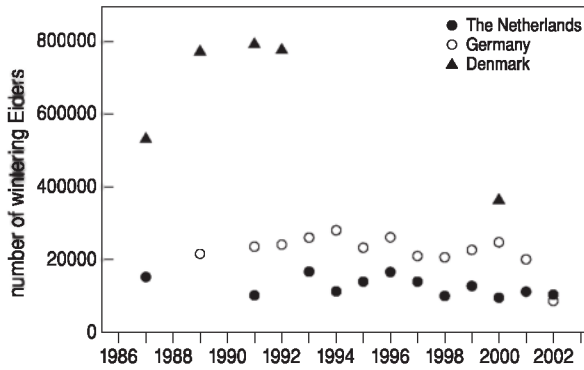
Figure 2.3 Annual mid-winter counts of Eiders in The Netherlands, Germany and Denmark from 1987–2002. Note that 'Germany' includes only data from the former West Germany, thus excluding Mecklenburg-Vorpommern. Each year is identified by the January of each count, hence "1987" refers to the winter 1986/1987 etc.

Table 2.1 Summary table showing available national estimates of winter (individuals) and summer (pairs) numbers of Eiders in the Baltic/Wadden Sea flyway population for 1991 and 2000.

	Winter		Summer	
	1991	2000	1991	2000
The Netherlands	103,299	97,657	7,621	?
Germany	236,451	248,663	971	1166
Denmark	797,000	370,000	25,000	24,000
Sweden	20,000	20,000	?	?
Norway	?	10,000	?	30,000
Finland	30	200	150,000-180,000	170,000
Poland	24,000	10,000	?	?
Estonia	100	100	12,000 *	12,000 *
Total flyway	1,180,850	756,620	215,592	237,166

* = extrapolated figure since no firm data exist for the given time period.

in bag size. Reproductive success of Danish breeding Eiders (the ratio of juvenile birds per adult female bagged in October) and number of days with hunting (affected by weather conditions) were found to explain an additional 8.1% and 5.0% of the variation, respectively (Christensen *et al.* in prep). Thus, a decline in the number of hunters reporting shot Eiders from *c.* 14,000 in the early 1980s to *c.* 7,000 in 1999 seems to be the main reason for the decline in Eiders shot in Denmark.
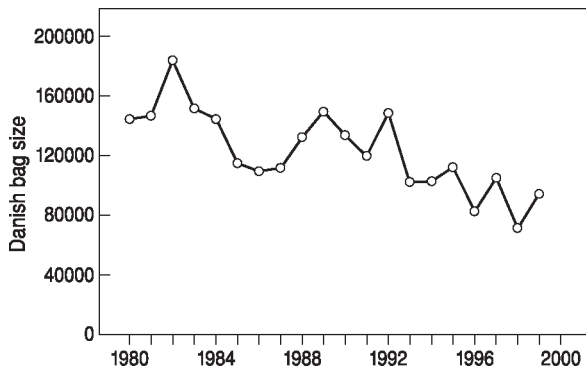
Figure 2.4 Estimated size of the annual Danish Eider bag during 1980–1999. Each year is identified by the January of each count, hence "1986" refers to the winter 1985/1986 etc.

The Netherlands
The number of breeding Eiders in The Netherlands increased markedly from c. 10 pairs in 1930 to *c.* 6,000 in the 1960s. In the mid-1960s the population declined due to pesticide discharges in the river Rhine causing heavy mortality among breeding Eiders and other bird species within the Wadden Sea (Swennen 1972, Koeman *et al.* 1996). After this die-off, the population recovered during the 1970s and 1980s (Figure 2.1). In the late 1990s and early 21st century, local population declines have been documented while the breeding population as a whole numbered probably between 5,000 and 10,000 breeding pairs.

The breeding population is sedentary staying generally within the Wadden Sea (cf. Swennen 1990), so its size cannot be determined using migration observations. Females are highly philopatric, but males show high natal dispersal.

The majority of Eiders wintering in The Netherlands originate from Baltic breeding areas, which mix with local breeders (Swennen 1991a). The total number of wintering Eiders has increased markedly from *c.* 10,000 during the 1950s to a peak of *c.* 170,000 in the early 1970s (Figure 2.3, Table 2. 1). Since then, numbers have ranged between *c.* 100,000 and 170,000. Despite large year to year variation, counts suggest a decline during the late 1990s (Figure 2.3).

During the 1970s and 1980s, wintering Eiders were mainly confined to the Wadden Sea with few recorded in North Sea coastal waters. In the early 1990s, the distribution of Eiders changed markedly, with a higher proportion of birds recorded along the North Sea coast, especially during the winters 1992–93 and in 2000–2002.

Normally *c.* 3000 beached dead Eiders are found each winter in beached bird surveys, but extremely high numbers occurred during the three most recent winters, 1999/2000, 2000/2001 and 2001/2002, with a peak of *c.* 22,000 during 1999/2000 (Camphuysen 2001, Chapter 5, Figure 2.5). Compared to the long-
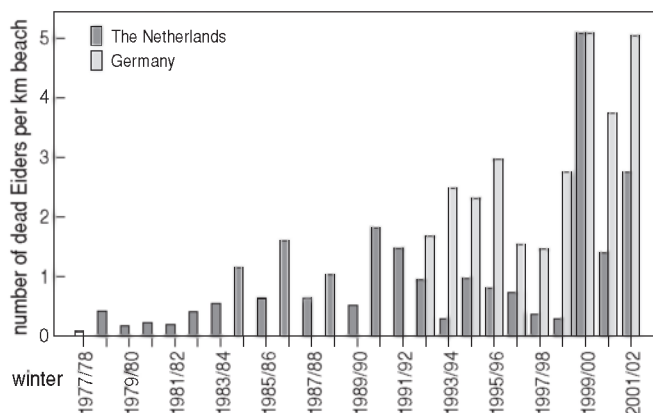
Figure 2.5 Total numbers of dead Eiders found in winter per km beach searched during the beached bird surveys in The Netherlands, 1978–2002 and in Germany, 1993–2002.

term average, relatively large numbers of beached Eiders were also recorded during the winters 1991/92 and 1992/93 (Figure 2.5).

Given the areas in which dead Eiders were found and recoveries of ringed birds (Camphuysen unpublished), it seems that a large proportion of the birds that died belonged to the Dutch breeding population. Recoveries of dead birds ringed in Denmark and Finland showed that these were mainly juveniles and immature birds (Lyngs in prep.). Thus, despite the fact that migrants outnumber local birds during winter, the migratory adult Eiders have seemingly avoided the massive die-offs in Dutch waters.

Examination of dead birds collected during the winter 1999/2000 and 2001/2002 showed that all were extremely emaciated and carried large numbers of intestinal acanthocephalan parasites (Kuiken 2001). There has been considerable discussion about the role of parasites in the mass die-off in The Netherlands (cf. Borgstede 2001, Smaal *et al.* 2001, Van den Berk *et al.* 2001). However, as heavy parasite infestation has also been found in 'healthy' Eiders shot by hunters in Denmark (see above), it seems that a general shortage of food (specifically bivalves) in the Wadden Sea is the most obvious explanation for the observed mass mortality. Documented overexploitation of the shellfish stock (blue mussel and cockles) in the Dutch Wadden Sea clearly occurred in the early 1990s. It was precisely at this time that Eiders began to occur in large numbers on *Spisula* banks in the North Sea, indicating a general food shortage in the Wadden Sea (Chapter 5). In the North Sea, however, *Spisula* is being increasingly exploited by humans (Smaal *et al.* 2001, Piersma & Camphuysen 2001) resulting in years when Eiders may have difficulties in obtaining adequate alternative food resources. In the winter of 1999/2000 hardly any large *Spisula* occurred along the entire Dutch North Sea coast.

Germany

The German Wadden Sea breeding population has been rather stable at 1000–1300 pairs since 1982 (Figure 2.1), but there were notable shifts from the northern to the western part in recent years (Hälterlein *et al.* 2000). At most, 19 breeding pairs have been recorded in the German part of the Baltic Sea, so the contribution from these birds is negligible in a flyway perspective.

The moult concentrations in the German Wadden Sea have shown a significant decrease from 258,000 in 1989 to 160,000 in 2001 ($r_s = -0.891$, $P = 0.001$, $n = 10$).

Excluding winter 2001/2002, the German winter population has been rather stable over the last 15 years, showing no long-term trends in any region (Figure 2.3, Table 2. 1, Bräger & Nehls 1987, Bräger *et al.* 1995, Nehls 1989, Scheiffarth *et al.* 2001). In winter 2001/2002, numbers of Eiders were the lowest seen since the start of regular aerial counts throughout all former West German coastal waters in 1987 (more than 100,000 less than the former minimum numbers).

Systematic aerial winter counts along the coast of Mecklenburg-Vorpommern (54°12'N, 12°05'E) started in the early 1990s (Nehls 1994, Nehls & Struwe-Juhl 1998) but have not been conducted on a yearly basis. Wintering numbers were constant around 70,000 Common Eiders during 1997/1998–2000/2001. However, no counts are available for the winter 2001/2002.

The numbers of dead Eiders registered along German North Sea beaches in winter increased tenfold from an average of 433 birds in the period 1991/92 to 1994/95 to 4265 birds in 2001/02. The increase began in 1997/98, two years after the extremely cold winter 1995/96 when 783 were found dead. Numbers found dead in 2000/01 were lower than the previous and the following winter, due to prevailing south-easterly winds that winter, which prevented birds being beached in the German Bight. Because awareness of the recent dramatic increase in Eider mortality could inflate the detection rate of this species, the numbers of dead Eiders registered in winter on only a selection of German North Sea beaches have been compared in this analysis. These are sites using the same methods at the same intensity of coverage since 1992/93. Numbers reported from these sites increased from 1.4 birds/km in 1992/93 to 4.6 birds/km in 2001/02 (Figure 2.5). The increase was greater in Niedersachsen (0.9 birds/km 1992/93; 7.6 birds/km 2001/02) than it was in Schleswig-Holstein (1.7 birds/km 1992/93; 3.2 birds/km 2002/01; Figure 2.5).

Sweden

The total Swedish breeding population was estimated at 170,000 pairs in 1973 and 270,000 pairs in 1983-1984, an annual increase of *c.* 6% over that ten-year period. The Swedish population is mainly migratory, wintering in Danish waters and the Wadden Sea (Fransson & Petterson 2001). In 1973, the Stockholm archipelago was estimated to support *c.* 50% of the Swedish breeding population.

Breeding numbers in the northern Stockholm archipelago have increased (r_s = 0.78, P = 0.0002, n = 17) but decreased in the south (r_s = –0.53, P = 0.03, n = 17) during 1985–2001 (Figure 2.6). Nest counts at Bullerö showed an increase from 1971 to 1989, followed by a decrease in the years from 1989 to the most recent count in 2001 (Figure 2.7). The Lygne islands in the Stockholm archipelago showed an increase from 1948 to 1979. During the last ten years (1992–2001) the breeding numbers at Lygne have decreased by *c.* 25% from 1,320 to 980 pairs (Figure 2.7). There was no significant trend in the Eider breeding numbers on the Småland archipelago between 1990–2000, although there were negative trends amongst 10 out of 39 other breeding avian species (Johansson & Larsson 2001).
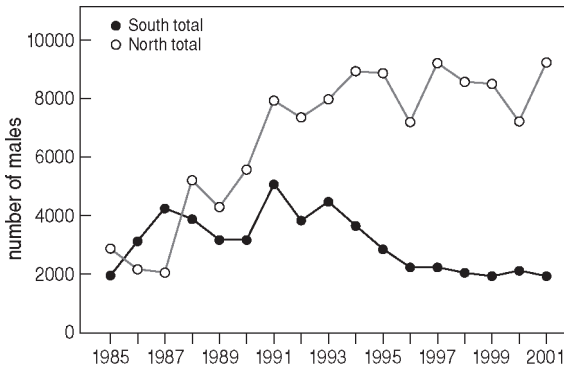
Figure 2.6 Trends in numbers of breeding Eiders in the northern and southern parts of the Stockholm archipelago, Sweden, as estimated from ship-based male surveys undertaken in late April. Five island areas were not surveyed in some single years and where this occurred, the average of the year before and immediately after were substituted.
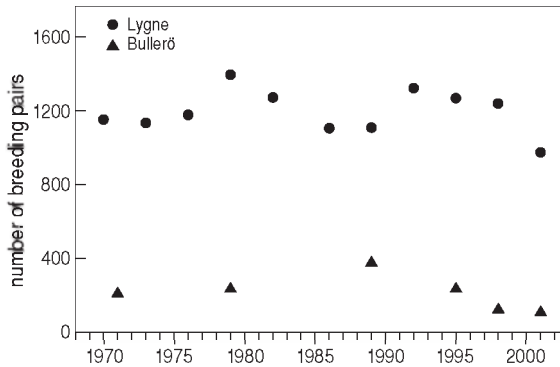
Figure 2.7 Eider nest counts at Bullerö and Lygne in the archipelago of Stockholm, Sweden, 1970–2001.

No significant trends in breeding numbers were found from the two islands near Gotland (P > 0.05). From the Swedish west coast, September counts of Eiders showed no significant trends between 1992–2001 ($r_s = -0.62$, P = 0.05, n = 10).

During 1992-2000, there was no overall significant trend in the time series of migration data from Kåseberga (Figure 2.8; rs = 0.067, P = 0.86, n = 9), although reported numbers have been lower in more recent years.

Since 1991, the peak in winter numbers along the southern coasts was *c.* 16,000 in 2000 (Figure 2.9, Table 2.1), with no significant trend over the whole period (Figure 2.9).
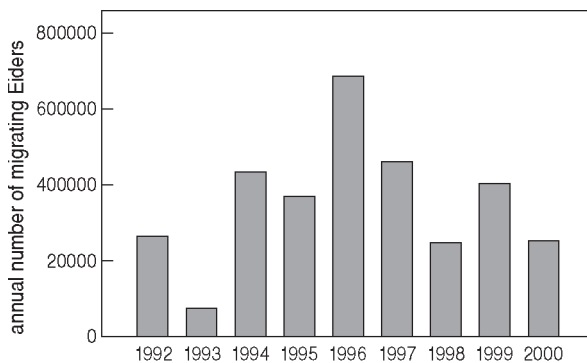
Figure 2.8 Number of spring migrating Eiders counted at Kåseberga on the southern coast of Sweden, 1992–2000.
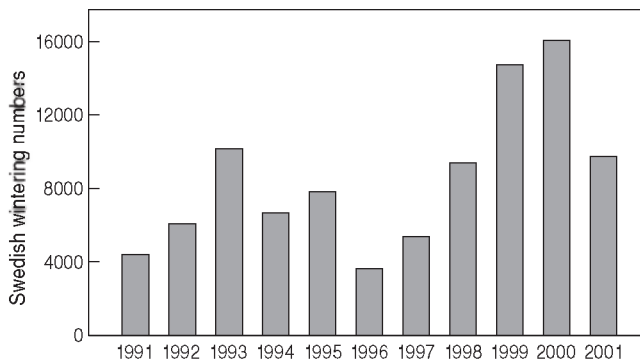
Figure 2.9 The number of wintering Eiders along the west coast and southern part of the east coast of Sweden, 1991–2001. Each year is identified by the January of each count, hence "1991" refers to the winter 1990/1991 etc.

In part of the Stockholm archipelago, the effects of the non-native American Mink on breeding Eider ducks have been followed since Mink first appeared in the early 1970s. The Mink mainly predate eggs but also take incubating females. In most areas of the Stockholm archipelago where the Mink has been present in high densities for 10–30 years there has been a substantial decrease in numbers of breeding Eider ducks. The choice of nesting habitats has also changed dramatically since the arrival of the Mink. Eiders have abandoned bushy and wooded islands and moved to gull colonies or joined solitarily nesting gulls on small open islets. In areas recently colonised by the Mink, the Eider population has shown stable or even increasing trends whilst areas without Mink show consistent increases in numbers of breeding Eiders.

The Swedish annual hunting bag amounts to 3–5,000 individuals.

Finland

The total Finnish breeding population is currently (2001) estimated to comprise 150,000–180,000 pairs. Greatest numbers (*c.* 150,000) breed in the SW archipelago, while *c.* 10,000–20,000 breed in the Gulf of Finland archipelago, and less than 10,000 breed in the Bay of Bothnia. The population is entirely migratory.

The index of breeding Eiders in Finland increased from the 1970s to the late 1990s. The increase was most rapid during the 1970s and 1980s, averaging 7–10% per year. In the late 1980s and 1990s this increase ceased, and presently the population is estimated to be declining at a rate of 8–16% per year (Figure 2.10). Decreases in numbers of nest were first reported from the Gulf of Finland in the late 1980s, whereas marked declines in nest abundance in the SW archipelago only started during the mid 1990s (Hario & Rintala 2002).
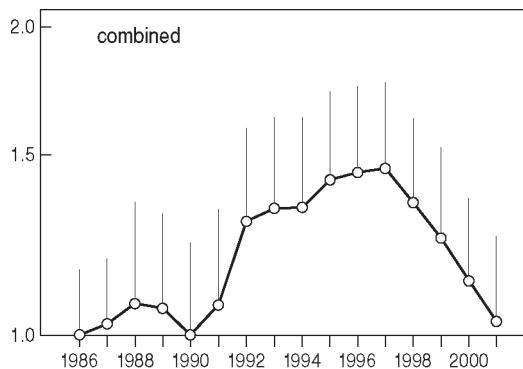
Figure 2.10 Indices of Eider population trends in Finland according to nest-count data, 1986–2001. Vertical lines show upper 95% confidence limits of the indices (from Hario & Rintala 2002).

Regular winter counts from the Åland Islands have shown that only 20–200 Eiders remain in ice-free areas, depending on the severity of the winter (Table 2.1). Owing to its harsh winter climate, and particularly the extent of sea ice, Finland lies in the northernmost extreme for wintering waterfowl in the Baltic, and there is no genuine tradition among Eiders to overwinter there.

Studies at the Söderskär bird sanctuary have documented poor duckling survival (fledging success) during the period of population decrease compared to the period of population increase, while adult mortality has remained stable throughout both periods (Hario & Selin 2002). Low duckling production has been related to viral infections in 1996 and 1999, causing mass mortality within the first weeks after hatch (Hollmén 2002). Intestinal infection with acanthocephalan parasites has been found in both adult female Eiders and ducklings in Finland, but the role of parasites as a mortality factor seems to be associated with other predisposing factors, such as impaired feeding ability or immunosuppressive viruses (Hario *et al.* 1995, Hollmén *et al.* 1999, 2000). A decrease in clutch size during the period of population decline cannot explain the population trajectory (Hario & Selin 2002), nor is it associated with the effects of gull predation on ducklings (Hario & Selin 1991). Predation by feral Mink has had only limited effect (Niemimaa & Pokki 1990), or no discernible effect at all, on the density of incubating hens (Nordström *et al.* 2002). On the other hand, the current recovery of the White-tailed Eagle *Haliaeetus albicilla* population is a subject of concern as Eagles seem to hunt incubating females in open terrain with comparative ease (Kilpi & Öst 2002). This development is ironic, since during the 1960s, various raptor populations decreased dramatically in size due to use of pesticides, including that of the White-tailed Eagle in north-western Europe. This species would have been the major aerial predator of adult Eiders throughout much of its range (although absent from the Wadden Sea). The crash in the Eagle population is likely to have resulted in lower predation rates of breeding females and wintering Eiders and could have contributed to increases in adult survival that was a potential factor involved in the expansion in numbers in the 20th century.

Common Eider is legal quarry in Finland in both spring and autumn. Spring hunting of Eiders is strictly licensed and is only permitted on males. Hunting practices differ between the mainland (coastal) Finland and the Åland Islands, due to differing legislation. On mainland Finland, *c.* 7000 males were formerly bagged in spring, but the current annual quota has been reduced to 2000 males. Another 10–12,000 Eiders are taken in autumn, of which *c.* 25% is male. On the Åland Islands, spring hunting takes 7,500–9,000 males, but there is no open season for females and yearlings. The total Eider bag amounts to 25,000–27,000 birds of which *c.* 18,000 (70%) are males. Contrary to the situation in Denmark, the Finnish bag size shows a strong correlation with the size of the breeding population (Hario & Selin 1987).

Other countries

The Norwegian Skagerrak population of breeding Eiders is estimated at 20–30,000 pairs based on male counts. The number of breeding pairs has shown an overall significant increase since 1988 (Lorentsen 2001), although breeding numbers since the mid 1990s seem to have stabilised. The wintering numbers have been stable at *c.* 10,000 Eiders (Table 2.1), with minor increases in some sub-areas. In Norway, a mean of 9108 individuals were bagged annually in the Skagerrak region from 1998 to 2001 (J.A. Rundtorn pers. comm.).

The Estonian breeding population has increased from *c.* 3,000 pairs in 1965 to *c.* 15,000 in 1995 (Leibak *et al.* 1994), and hereafter decreased to *c.* 12,000 pairs in 2001 (Eve Mägi, Arvo Kullapere and Andres Kuresoo pers. comm.). During 1990–2002, ground counts have shown that Estonia supported fewer than 100 wintering individuals annually (Table 2.1); winter aerial survey of the entire coast in early 1993 found only 75 Eiders. Common Eider has never been recorded breeding in Lithuania, due to lack of suitable nesting habitat. This species does not regularly winter there, although a few have occasionally occurred in recent years, never throughout the season. The species is a little more frequent during spring and autumn migration, but numbers are low, with no regular staging sites (R. Zydelis in litt.). Common Eiders have never been observed breeding in Latvia (Viksne 1983). The maximum count of wintering Eiders was 14 in 2001, with autumn and spring maxima of 5 and 50 Eiders respectively counted along the Latvian coast (A. Stipniece pers. comm.).

According to the Polish rarities committee, Eiders have bred only very sporadically in Poland. The Polish coast offers little wintering habitat for this species, which is usually present in numbers much less than 1000 (W. Meissner pers. comm.).

Assessing the overall size of the Baltic/Wadden Sea Flyway Population

For 1991 and 2000, reliable breeding estimates exist for Germany, Denmark, Estonia and Finland, whereas in contrast, there are no nationwide surveys for the numerous Swedish population from these two time periods and a reliable breeding estimate for The Netherlands is available only for 1991 (Table 2.1). Summing up the breeding figures excluding Sweden, Norway and Poland, results in *c.* 215,000 pairs for both periods.

Comprehensive winter surveys have been conducted in Denmark, The Netherlands, Germany and Norway. In 1991 the total number of wintering Eiders amounted to *c.* 1,200,000 birds and during the following 10-year period a decrease to *c.* 750,000 birds has taken place (Table 2.1). This decline is apparently due entirely to changes in the size of the Danish wintering population.

Discussion

Status of population and evaluation of methods

Although the Baltic/Wadden Sea Common Eider population increased steadily in numbers from the 1970s onwards, this review strongly suggests that the situation has begun to change during the last ten years. The total flyway estimate of the wintering population has decreased by *c.*36% between 1991 and 2000 (Table 2.1), although most national breeding trends show no equivalent marked decrease since the mid-1990s. Unfortunately, the lack of national breeding estimates precludes an overall assessment of changes in the total flyway breeding population between 1991 and 2000. There are no Swedish national breeding population estimates since the mid-1980s, a country known to host approximately one-third of the Baltic breeding population (Almkvist *et al.* 1974) and trends in breeding numbers at a few local areas may not be representative of those in the total population as a whole. Given that better count coverage is achieved in winter, we therefore consider that the *c.*36% decline in total numbers offers the best assessment of population change available and therefore gives some cause for concern.

Why the apparent mismatch between the reductions in wintering numbers and apparent general stability (and slight increases in some areas) in local breeding numbers? We suggest that this discrepancy could be explained by one or more of the following five (not necessarily competing) hypotheses:

A) That any decline in breeding numbers at a given nesting area is buffered by the availability of substantial numbers of young non-breeding birds. These normally non-breeding Eiders are able to recruit into the breeding population during periods of reduced competition for pre-nesting feeding habitat or breeding habitat (e.g. as a result of increased adult female mortality that contributes to the overall decline seen in wintering numbers). This would sustain (at least in the short term) stable local breeding numbers (e.g. by a simple decrease in age of first breeding) despite an overall decrease in total population number.

B) That the decline in flyway wintering numbers is caused by a significant (but currently undetected) decline in the Swedish breeding population.

C) That the recent winter surveys in Denmark have not detected and counted all the Eiders, either because of difference in coverage or due to inaccuracy in the wintering counting procedures.

D) That the earlier breeding counts have missed a large proportion of the breeding pairs detected in more recent years.

E) That the changes in winter distribution of Eiders has involved expansion into previously non-surveyed areas.

Let us consider the support for these hypotheses as follows:

Hypothesis A:
Alerstam & Högstedt (1982) were the first to propose that the relative extent of breeding habitat to those habitats used to survive between breeding seasons shaped the migratory and reproductive tactics of different bird species. They characterised the Common Eider as a species that exploits a highly limited breeding habitat, but a surplus of abundant and widespread non-breeding survival habitat (a classic "S-species" of Alerstam & Högstedt 1982). Because of strong competition for breeding habitats, Eiders show deferred breeding and high annual survival, because immatures and non-breeding adults can remain in the extensive offshore marine "survival" habitats where they can enjoy very high annual survival rates. This "buffer" element of the population of birds not participating in reproductive activity can constitute at least 20-30% of the total population (Almkvist *et al.* 1974, Alerstam *et al.* 1974, Coulson 1984). The "buffering" effect of the non-breeders was evident after the Danish outbreaks of Avian Cholera, which killed 90% of all breeding females in two colonies (Stavns Fjord (55°54'N, 10°39'E) in 1996 and Rønø (55°45'N, 11°50'E) in 2001). In the years following the outbreaks, breeding numbers fell by 75% and 65% at Stavns Fjord and Rønø, respectively (NERI unpublished data), i.e. less than would have been expected if there was no pool of non-breeders awaiting the opportunity to attempt to nest. Those case-studies suggest a potential pool of non-breeders exists that takes no part in reproduction under normal circumstances but which can recruit at an earlier age if competition for breeding habitat is, for whatever reason, reduced. In cases of less dramatic reductions in local breeding female number, competition for limited nest sites could result in a stable breeding population even during a period of overall population decline. These non-breeders contribute in number to the winter counts, but are not detected during normal breeding surveys. In this way, winter surveys would detect a general flyway population decline before this was ever apparent from counts of breeding birds. In addition to competition for suitable nesting sites, competition for food prior to breeding may have an even greater impact upon the success of a breeding attempt by first-year breeders or experienced breeders. Common Eiders are capital breeders (Meijer & Drent 1999) and females store large energy reserves (up to 20 % of body mass) for egg-formation, egg-laying, and for fasting during incubation. Prior to breeding, females need to feed intensively in order to reach the minimal body mass for a successful breeding attempt and, if not reached, the female may decide (i) not to breed, (ii) to breed and risk abandonment of the clutch or (iii) death. Local food supply and the level of competition may therefore affect the pre-nesting increase in body mass. The observed increase of first-breeding females in the year after the die-off of adult females could also indicate that feeding conditions (less competition, more available food) have improved for inexperienced and less competitive first-year breeders.

Hypothesis B:

Since no national breeding estimates exist from Sweden for the last ten years, this population could theoretically have decreased significantly without this trend being detected. Three out of four studies of local Eider breeding ecology in the Stockholm archipelago have shown negative population trajectories during the last ten years, whereas a fourth from the northern part of the archipelago showed stable numbers. The results from these local breeding studies, and the fact that the archipelago of Stockholm was formerly known to host *c.* 50% of the Swedish breeding population of 270,000 Eider pairs, indicate that hypothesis B theoretically could contribute to the observed differences in trends between breeding and wintering numbers.

Hypothesis C:

The geographical coverage of mid-winter Eider counts has not been changed between the surveys. The switch from "systematic" total coverage to a transect survey in the Kattegat offshore area in 1999/2000 cannot explain the magnitude of the dramatic decline in Danish wintering numbers between 1991/1992 and 1999/2000. In addition, all other areas in Danish waters outside Kattegat (covered using the same methods in both years) also showed significant declines. In general, the aerial survey method used for the Danish winter counts is considered to be reasonably robust, as suggested by the low variability between the three survey totals from 1989, 1991 and 1992, when total Danish Eider numbers ranged between 779,000 (in 1989) and 797,000 (1991, Figure 2.3). We therefore consider that factors relating to survey technique are highly unlikely to have contributed significantly to the dramatic decline in Danish wintering numbers of Common Eiders that was found in 1999/2000.

Hypothesis D:

No major changes in survey methods or extent have occurred or been reported for the breeding counts during the period, and hence, we consider that all figures from the ten year period are reasonably comparable. Hypothesis D is therefore considered unlikely to contribute to the explanation for the observed patterns.

Hypothesis E:

Since most wintering areas are surveyed regularly and because Eiders winter relatively close to coastlines easily covered from either land or aircraft, any significant changes in winter distribution should have been detected. Food supply and the energetic constraints of feeding in deeper water restrict the opportunities for large numbers of Eiders to winter offshore or elsewhere in the range. Although large numbers formerly wintering in the Wadden Sea have moved out into the North Sea in recent years, the probability of this occurring undetected elsewhere in the winter range remains small. Our contention would be therefore that hypothesis E

is unlikely to explain the observed patterns either. However, the relative low number of wintering Common Eiders in the German Wadden Sea in winter 2001/2002 coincided with a lack of mid-winter survey in the Mecklenburg-Vorpommern region. The Eiders missing from the Wadden Sea could theoretically have been present in the Mecklenburg-Vorpommern region in that season. This case involved *c*. 100,000 Eiders which, whilst perhaps not grounds to change our rejection of hypothesis E, does underline the need for a greater degree of co-ordination of winter counts throughout the flyway.

We therefore favour the conclusion that hypothesis A and B are the most likely explanations for the differences in trends between the wintering and breeding figures. Whatever the true explanation for the discrepancy between the breeding and wintering assessments, it is clear that if it is possible to effectively count birds on the wintering grounds, this is likely to be the best point in the annual cycle at which to measure and detect major changes in overall flyway population number. Birds on the wintering grounds show the greatest aggregation of any stage of the year, so if the problems of adopting common count techniques and co-ordinating international census effort can be overcome, this represents the most important monitoring goal for the future.

To understand the reasons for this decline in overall numbers and localise its origin geographically, it is necessary to undertake an analysis of the population trends on a national scale. However, since the different breeding sub-populations are mixed on the winter areas, it becomes difficult to achieve any geographically differentiated explanation for the overall flyway population decrease based on national winter survey data. The only significant and major decreases in winter numbers between 1991 and 2000 were seen in the Danish waters, and since most sub-populations are represented here, no firm conclusions can be drawn as to where and at what time in the flyway the Eiders experience problems.

If our hypothesis A above is the explanation for the lack of decline in monitored breeding numbers, we might expect that, once the pool of non-breeders is exhausted, declines will be detected on the breeding grounds as well as in winter numbers. At that stage, the Baltic/Wadden Sea Eider population will be even more sensitive to changes in annual adult survival, disease epidemics and winter and pre-breeding food shortage. For this reason, we also recommend continued vigilance on the breeding areas and urge some development of common standards for conducting breeding surveys that will be effective in tracking these changes in the future.

Even though no significant decreases in national total breeding numbers have been recorded between 1991 and 2000, several indications strongly suggest declines in local sub-populations. Amongst most countries in the Baltic/Wadden Sea flyway, a common trend in population trajectory is seen: an increase during the 20th century until the early or mid 1990s, followed by either stability, or in most cases, declines, either in breeding or wintering numbers (Figures 2.1, 2.6, 2.7,

2.8, 2.10). In Finland, the annual breeding index was not significantly different between the two breeding seasons of 1991 and 2000, but in the years between, numbers increased up to 1997, after which a steep decline ensued down to 2001. In winter 1999/2000 and 2001/2002, relatively large numbers of dead Eiders from the local breeding population have been recorded in the beached bird surveys in The Netherlands (Camphuysen pers. comm.).

In conclusion, we consider that the *c.* 36% decline in winter numbers between 1991 and 2000 reflects a significant population decrease which has occurred throughout the flyway, not distinguishable at present in the trends of national breeding numbers due to the buffering effects of the non-breeding element of the population.

Factors affecting population size

Besides the dramatic decline in the Danish wintering population from 1991–2000 it is becoming increasingly obvious that in other parts of the wintering range Baltic/Wadden Sea population Eiders have come under pressure. Substantial declines were observed during 2000–2002 at two large German wintering areas, the Wadden Sea, as well as in the Baltic off Schleswig-Holstein. In the Dutch Wadden Sea, a long-term decline in wintering numbers has occurred. Many local and small-scale population studies along the flyway suggest that the population dynamics of Eiders have been adversely affected by a variety of human induced and natural factors.

Modelling has shown that small changes in adult survival have far greater impacts on annual changes in the numbers of Common Eiders (Christensen & Noer 2001) compared to far greater changes in annual reproductive success (Swennen 1983). This is in agreement with the general life history theory concerning larger and long-lived bird species. Nevertheless, a prolonged decrease in recruitment rate due to either persistent low fecundity or low chick survival will eventually result in lower numbers of immature non-breeders, reductions in recruitment and will also finally reduce population size (Hario & Selin 2002).

In the breeding season, both adult survival and recruitment can be adversely affected by different factors, eventually precipitating a decline in the population. Intensive predation studies on the American Mink in Sweden have shown significant reductions in local densities of breeding Eiders. To what extent the American Mink presents a general problem to sustaining the current size of the Baltic/Wadden Sea Eider population and whether the Eiders are able to adapt to this invasion remains an open question. In Finland, long-term removal of Mink from two archipelago areas (125 km^2 and 72 km^2, respectively) did not alleviate declines in breeding Eider populations whereas it greatly enhanced re-colonisation by smaller waterfowl species that had been extinct from the areas since the Mink invasion (Nordström *et al.* 2002). Nevertheless, the fact that American Mink have spread to most parts of the Eider breeding range suggests that it is a potential

threat to the population and may have contributed to the present decline. Hence, Mink predation represents an important subject for study in coming years. Other ground predators also affect Eider nesting success, such as rats *Rattus* spp. and Red Foxes *Vulpes vulpes*. In spring 2002, considerable egg-predation by rats was observed at the breeding colony on Vlieland in The Netherlands (R.K.H. Kats unpublished data). The presence of Foxes at breeding areas on the mainland is also thought to contribute to declines in nesting density there. The observed shift from nesting in closed habitats to more open areas and to islands with the presence of gulls may improve adult survival, but may increase the predation of eggs and ducklings and as a consequence reduce reproductive output.

Diseases can lower both adult survival and recruitment during the breeding season, as reported for Avian Cholera in Denmark (Christensen *et al.* 1997), for intestinal occlusion in males in Finland (Grenquist *et al.* 1972), and the outbreaks of duckling virus in Finland (Hollmén 2001). Since we know so little about diseases and their effects on the Eider population dynamics, we need to monitor disease in Eiders better as a part of an international flyway-monitoring programme. As a first step, a study of the causes of death and an assessment of how many colonies are infected, when and where should be made an immediate priority. Studies found high levels of acanthocephalan parasite infestation in healthy wintering Danish birds, with no relationship between parasite numbers and individual body condition, suggesting that high parasite loads were not responsible for mass mortality events in the Wadden Sea. Amongst potential contaminants, lead exposure needs to be monitored over the entire range. Among nesting females in the Gulf of Finland, highest exposure rates were documented in areas of population declines. Severe or sub-clinical lead poisoning was diagnosed in 23% of females that died of emaciation after incubation (Franson *et al.* 2000, 2002, Hollmén 2002).

The Baltic/Wadden Sea population of Common Eider remains legal quarry in Denmark, Norway, Sweden and Finland, amounting to an annual total flyway kill of *c.* 115,000 individuals. Whether or not this level of hunting pressure is sustainable is at present unknown. Analysis of the Danish bag statistics indicates that the bag size is more related to the number of active hunters than to the size of the Eider population (Christensen *et al.* in prep.). This apparent lack of relationship between bag size and population size can be explained by the hunting method predominantly used in Danish waters, where hunters approaching a flock of Eiders in motor boats are bagging one or two individuals from each flock when they flush. In this way, the bag size will not change even though the flock sizes are changing, since a maximum of one to two Eiders are normally bagged independent of flock size. The fact that the kill used to be far greater in Denmark at a time when the population still increased dramatically, suggests that the Danish hunting activities were sustainable, at least at that time. Indeed, there was no relationship between the Danish bag size and the size of the Söderskär Eider population during the

years of the steep population increase (1973-84). Thus, there is no indication that the Danish hunting pressure responded to the Finnish population growth as much as it could have done (despite responding significantly to annual changes in recruitment rate at Söderskär, Hario & Selin 1987, Noer *et al.* 1995).

Other non-hunting human activities could potentially increase the mortality of full-grown Eiders unintentionally; e.g. by-catch in gill nets and collisions with high-speed vessels (which are travelling increasingly fast in inshore waters) and with off-shore structures such as bridges and wind turbines. These potential sources of mortality have increased in European offshore areas in recent years, but we know nothing about the magnitude of such mortality and their individual and cumulative effects on migratory bird populations such as Eiders.

The Common Eider in the Wadden Sea is at its southern limit of winter distribution where it is almost wholly dependent upon shellfish stocks for its food supply. The staple food items are the Blue Mussel *Mytilus edulis* and the Cockle *Cerastoderma edule*, as well as *Spisula* in some areas (Leopold *et al.* 2001a). However, food quality is crucial for these birds, in particular the relation between shell mass and flesh mass (Nehls 1995, 2001). Flesh mass is highly dependent upon winter temperatures and shows large fluctuations between years (Beukema *et al.* 1993, Zwarts 1991, Zwarts & Wanink 1993). Therefore sufficient stocks of alternative prey are important for long-term survival, as has been shown for the Oystercatcher (*Haematopus ostralegus*, Zwarts *et al.* 1996a). Since only a small fraction of the total shellfish stock is available for exploitation by Eiders (Nehls 1995), they are sensitive to large scale destruction of mussel and cockle beds as has occurred in several parts of the Wadden Sea in recent years (Piersma & Koolhaas 1997, Piersma & Camphuysen 2001). In combination with a series of mild winters with low food quality and poor shellfish recruitment in the subsequent summer, this human impact on food stocks can have substantial adverse effects on the Eider duck population. In addition to direct adult mortality caused by lack of food, studies have shown that the reproductive output may also be adversely affected by reductions in food resources (e.g. through delayed nesting, increased desertion rate and reduced hatchability, Oosterhuis & van Dijk 2002).

Among the strictly migratory Finnish Eiders (that mainly winter in Denmark), food-related parameters such as female body weight at the start of incubation, clutch size and egg size did not change during the extended period of population increase followed by recent decrease (based on data from individual females breeding both in 1982–85 and 1986–1991, Hario & Selin 2002). This is consistent with theory, since Eiders are capital breeders (Meijer & Drent 1999), determinant egg-layers (Swennen *et al.* 1993) and egg size varies with age and clutch size (Swennen & van der Meer 1992). This may suggest that the blue mussel stocks exploited in winter in Denmark have not changed drastically in quality nor size, as Finnish Eiders rely heavily on stored (subcutaneous) fat transported from Denmark to the northern breeding sites in spring. In contrast, food intake on the

breeding grounds, during the relatively unpredictable period between the ice break-up and laying, is mainly invested in female self-maintenance (Hario & Öst 2002). Further evidence for the importance of the Danish mussel stock to northern Baltic Eiders comes from the fact that the strong salinity-induced west-east decline in mussel abundance in the Gulf of Finland (Öst & Kilpi 1997, Westerbom *et al.* 2002) is not reflected in parallel trends in Eider breeding parameters along the Gulf. Since Eiders from the central Gulf of Finland (with poor mussel stocks) fare equally well than those in the western Gulf (with ample mussel stocks) during the early breeding season, this strongly implies that both these Eider "sub-populations" exploit the same winter food resources (i.e. those in Denmark) which are at least ample at the present time. On the other hand, Finnish breeding numbers have declined, suggesting perhaps that fewer females are able to feed and store sufficient nutrients in Denmark to fly to Finland and breed. Where are the females that failed to acquire sufficient stored nutrients to breed? Perhaps this could suggest that the food supply in Denmark has declined in quality or extent, and fewer females return to the colonies to breed (although those that do so, especially the experienced older birds, continue to return in good condition).

Despite the fact that several studies have shown that different local factors are having adverse effects on the breeding population, their relative importance is unknown. For this reason it is important that future research proposals include a modelling approach, which will enable a better understanding of the relative importance of, and potential sensitivity to, the different factors affecting the population size and hence enable a prioritisation of future remedial actions.

Recommendations for monitoring
During the compilation of this review it has become clear that national and local monitoring programmes are performed in many areas along the flyway of this Eider population. The usefulness of the compiled data would, however, be greatly enhanced if the methods used by different schemes were harmonised and were better co-ordinated in timing to a greater extent than is presently the case. We would particularly urge, for example, those countries, which survey the winter population every second or third year, to synchronise their counting years and increase the number of years in which the whole Baltic/Wadden Sea Eider population was surveyed simultaneously. A monitoring programme of winter numbers (involving co-ordinated extensive aerial survey where appropriate) on the flyway-scale for this population is of the highest priority, if the further future decline is to be adequately tracked and quantified.

The possible alternative options for future monitoring programmes to assess changes in abundance and distribution could include migration counts, breeding censuses or a combination of these two approaches. In general, censusing sea ducks such as the Baltic/Wadden Sea Common Eider population is difficult to achieve comprehensively and satisfactorily, due to the wide and often scattered dis-

tribution throughout the annual cycle. During winter, Eiders aggregate in coastal and near offshore waters, making assessment of numbers easier, if not particularly easy logistically. However, in summer they nest on thousands of islands scattered over vast areas, making complete surveys impossible. Designing census protocols that optimise coverage in both time and space to minimise the extent of unsurveyed habitat and avoid double counting due to poor coverage and/or redistributing individuals between counts will be difficult, but not impossible.

Monitoring the overall population trajectory through any form of direct breeding counts is unlikely to be feasible, for the reasons discussed above. If the breeding areas are to be the subject of a future monitoring scheme, the combination of post breeding aerial surveys of male numbers and sex ratio estimates, as performed in the Baltic in the 1970s, seems to be the best potential option. Searching for nests in a systematic or sampled fashion is both time consuming, disruptive and potentially suffers from many pitfalls, although a properly designed stratified sampling programme could be used to generate an index of relative breeding abundance and hence trends over time.

Another possibility, rather than attempting to count birds extensively on the breeding grounds, would be to focus count attention intensively in areas where a representative number pass through on migration. If counts of migrating Eiders could be used to monitor the size of the Baltic breeding stock, spring represents the best period because the spatial and temporal distribution is relatively limited then. Such a migration monitoring approach is only feasible for the truly migratory populations breeding in Finland and Sweden, and fails to account for changes in the numbers of resident Eiders in The Netherlands or the partial migrants in e.g. Denmark. The study by Alerstam *et al.* (1974) could form the methodological basis for developing such a migration monitoring scheme. A historical perspective is potentially available in the form of a radar dataset from the east coast of Sweden which is known to be available for the study period of this review (L. Nilsson pers. comm.).

The Baltic/Wadden Sea Eider population is a classic meta-population system with widely differing migratory and life-history strategies depending on breeding provenance. It is therefore unlikely, for instance, that the population processes of sedentary Dutch-breeding birds reflect those of the long-distance migratory Finnish birds. Local studies of the breeding biology of the Eider throughout the flyway cannot contribute directly to the monitoring of overall changes in population size. However, they are vital if we are to be able to understand and interpret the reasons for the observed changes in numbers and distribution. Local studies invariably include some assessment of local and relative abundance that can represent important time series for tracking local change in relation to flyway population changes. Although the wing ratios in the hunting bag from Denmark offer an index of annual reproductive success, we have no regular measure of breeding output in the population, so even simple measures of reproductive success would rep-

resent a major contribution to our understanding. Annual ringing of even relatively small numbers of females on nests, and their subsequent recapture histories can now be used to generate robust estimates of annual adult female survival (and other parameters, such as site fidelity, annual breeding probability). These are vital parameters to understanding population change in this long-lived species. Systematic ringing of ducklings also enables an assessment of long-term changes in age of first breeding, a vital parameter in understanding the dynamics of the recruitment, discussed above. However, in practice, this requires massive ringing programs due to the very high early mortality of ducklings; and even when recruited, the first-time breeders need to be located with confidence – a demanding task in the field. Measures of annual fluctuations in these local and regional breeding parameters among the different sub-populations are of enormous value if we are to be able to interpret population change overall. This becomes especially true if the studies are spread over larger areas and generate longer time series, and if study methods are standardised between the various different research groups. If we are to understand what is going on in the Baltic/Wadden Sea Eider population, we need to know a great deal more about the population dynamics in as many as possible of the different sub-populations, in order to identify critical processes in the annual life cycle. Nevertheless, it is important to remain cautious and consider pattern and scale, since in the Swedish studies, two adjacent study areas in the Stockholm archipelago showed very different population trends. Care should therefore be taken when extrapolating to a national or international scale from such local or regional studies.

Conclusions

To conclude, we believe that the monitoring mechanisms currently in use to track changes in abundance of the Baltic/Wadden Sea Common Eider population are uneven and partly inadequate. We must ensure more adequate monitoring programmes to track winter population trajectories in the future in a way that can verify changes over time. If remedial actions are to be implemented for this species, aimed at restoring the population to favourable conservation status, it is essential that the monitoring programmes can detect these changes. Establishment of such monitoring programmes needs international agreement, co-ordination and adoption of common standards.

The available evidence suggests that a number of factors are responsible for observed declines in the Baltic/Wadden Sea Common Eider population, several of which have adversely affected numbers on a local scale. It is known that disease has reduced adult female annual survival and duckling survival in specific areas, but this may have gone undetected elsewhere. Geographical shifts and mass-mortality events probably caused by starvation have been reported from parts of the wintering range, most notably in The Netherlands and the German Wadden Sea. Eiders are still hunted in annual numbers three times as high as the numbers of

Eiders known dying in the mass mortalities and it is still unknown whether the current level of hunting is sustainable. Other factors may also be involved which have not been fully considered here (such as the general increase in shipping and shellfish exploitation throughout the range). The multi-factorial explanation for the declines necessitates an appropriate understanding of the relative importance of these different factors if we are to effectively prioritise and target resources to restore favourable conservation status of Common Eiders. Modelling of population processes is needed to fully understand the relationship between the Common Eider population dynamics and the different factors affecting its abundance and distribution.

Diet (preferences) of Common Eider *Somateria mollissima*

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Introduction

Eiders are large sea ducks, which feed on a large variety of prey species. They usually specialize on one or more prey species in any one situation and the list of known prey species is long. The prey may be attached to a hard substratum or buried in the sand; it may occur singly or clumped; it may be small (i.e. smaller than 1 cm) or large (> 7 cm); it may be soft or hard-shelled or spiny; it may be taken while the bird is walking on dry land or it may be taken while submerged at tens of meters. This would suggest that eiders can live and survive under many different circumstances and indeed they do. They may live, for instance, on a mixed diet of sea-urchins and very small (< 1 cm) mussels in kelp-dominated areas (St Lawrence Bay, Canada; Guillemette *et al.* 1993) or on medium-sized mussels (10–40 mm) in northern Norway and the Baltic and Wadden Seas (Madsen, 1954, Bustnes & Erikstad 1990, Kallenborn *et al.* 1994). The ducks, particularly those in the Wadden Sea, may also prey on much larger mussels of up to 7 cm (Nehls 1991, 1995). In Norway, eiders have shown great versatility, living either on large clams of up to 5.4 cm or on tiny fish eggs, both at water depths of 25–50 m (Brun 1971, Gjøsæter & Sætre 1974). Notwithstanding this suite of possibilities globally, eiders usually focus on bivalve molluscs and on blue mussels in particular. In most situations, at least one other prey species is also important. In the Wadden Sea, cockles fulfill this role (reviews in Camphuysen 1996, Leopold *et al.* 2000), but it is largely unknown whether mussels and cockles are interchangeable for individual ducks and to what extent other prey species might supplement the diet when both primary species are scarce. The question remains as to which parts of mussel and cockle stocks can be utilized by the eiders. This is important information for the management of the Wadden Sea, for instance, for decisions regarding the amounts of mussels and cockles needed to be set aside for the ducks as both are fished on a large, industrial scale in the Wadden Sea (Ens 2000). This contribution aims at describing the known diet and dietary preferences of eiders. Because eiders have such a wide variety of possible staple diets, one might wonder if they are capable of utilizing any food source. In any case, food should be available within the right but wide size and correct depth ranges, be sufficiently abundant, and have a positive energy return meaning that hunting, catching and processing costs combined must be outweighed by the calorific contents and subsequent energy gains. Still, even if eiders could survive on very different foods under a given set of conditions, the energy expended during feeding might still make one type of food more favorable than another. Also, some energy rich foods may create problems. Crabs carry a potentially lethal parasite load, while the long and sharp razor clams, as well as very large mussels or mussels covered with barnacles may cause more direct physical damage or even kill the bird (Swennen 1976a, Jukema, 1979 Swennen & Duiven 1989). For these reasons, Swennen (1976a) considered that eiders prefer relatively small and smooth, and hence safe prey. Nehls (1995)

has added to this picture the notion that selection of certain size classes is also influenced by handling costs and energetic returns (flesh contents). Larsen & Guillemette (2000) and Leopold *et al.* (2000) found evidence that depth at which prey occurs, may also be limiting, and that depth interplays with prey size.

Actual Diet and Prey Preferences in the Wadden Sea: What Can and Cannot be Eaten?

The Wadden Sea is highly productive, but only a few species are particularly abundant. Most of the very abundant worm-species are of very little importance to eiders. Other abundant foods like the clams, *Mya arenaria* and *Ensis directus*, generally live too deeply buried or grow fast to sizes too large for the ducks to swallow, to be of much use to them. Some animals that live within reach and are superabundant in places are apparently too small to be profitable. These species include the mud snail *Hydrobia ulvae*, for example, while fish eggs are never available in large quantities. This leaves the eiders in the Wadden Sea with a limited number of prey species. Of these, mussels and cockles form the staple diet in most available studies, but these are supplemented by the Tellinid *Macoma balthica*, the starfish *Asterias rubens*, the crab *Carcinus maenas* and the periwinkle *Littorina littorea*. Recently, i.e. since about 1990, eiders have also moved to the North Sea coastal zone, to feed on the clam Spisula subtruncata.

Mussels and cockles.
Mussels and cockles have been found to be the staple diets in all major diet studies within the Wadden Sea proper. Eiders, as seen from aerial and ship-based surveys throughout the international Wadden Sea, mainly reside over mussel culture plots, natural mussel beds and sand flats with high densities of cockles (Nehls, 1989, 1995, Swennen 1991a, Baptist *et al.* 1997, Berrevoets *et al.* 2000, Laursen *et al.* ms, pers. obs.). However, mussel culture plots become of little importance to eiders in the breeding and molting season in summer (Swennen *et al.*, 1989) when the birds avoid areas that are often disturbed by working mussel fishermen. Many large-scale studies have shown that these two bivalves form the bulk of the diet throughout the entire Wadden Sea, but also that much variation exists between places, seasons and years (Pethon 1967, Swennen 1976a, Buuren, 1983, Nehls 1989, Asferg 1990, Kallenborn *et al.* 1994, Hilgerloh 1999, 2000, Laursen *et al.* ms). One of the two prey species alone may form over 90% of the diet at certain locations. For eiders feeding on cockles, this is hardly surprising, as they feed essentially in a one-prey species situation. Some small *Mya* or large *Macoma* that are encountered in the process of digging up cockles, are obviously not rejected as food and form most of the remainder of the diet in such situations. Likewise, mussels form the bulk of the biomass on natural mussel beds and on culture plots, but

associated crabs, starfish or periwinkles may also be eaten. From these results, it is not immediately clear that the ducks actually do prefer mussels and cockles. They obviously prefer locations with a high biomass of suitable prey, and in the Wadden Sea, this happens to be mussel and cockle beds. In other areas of the world, mussels and cockles are substituted by other species, if these are more readily available.

Macoma

The brightly colored Baltic Tellins are very obvious in faeces and are noted in many studies but *Macoma* was only once (Laursen *et al.* MS) found as an important source of food. Many *Macoma* will be too small to be profitable and most of the larger animals live relatively deep in the sediment, especially in winter (Zwarts & Wanink 1993). Parasite-infected *Macoma* crawl towards and over the surface, but eiders, like Oystercatchers *Haematopus ostralegus*, may dislike such individuals (Hulscher 1982). On top of this, large *Macoma* are very hard-shelled and thus take a relatively high amount of energy to be broken down in the birds' stomachs (Camphuysen *et al.* 2002).

Mya

Sand Gapers quickly become an unsuitable prey for eiders in that they become too deeply buried for the birds to dig them up and too large to swallow. In general, only young animals are suitable prey. We know very few studies where feeding on *Mya* was observed on more than a very limited scale. Nyström *et al.* (1991) found that (juvenile) eiders ate young *Mya* (< 2 cm shell length), in the Baltic. Kallenborn *et al.* (2000) also found *Mya* in drowned eiders in the Baltic. Very little is known of *Mya* as eider food in the Wadden Sea. Swennen (1976a) did not find this species in 4441 faeces samples.

Ensis

Razor Clams seem an unsuitable food at first because of their shape and burying capacity (Swennen *et al.* 1985), but they are apparently eaten in certain situations. In autumn 2000, a flock of several hundred eiders was seen, apparently feeding, on a site off Vlieland in the North Sea coastal zone, where *Ensis directus* was commercially fished and presumable the only abundant biomass (J. van Dijk, pers. comm.). Laursen *et al.* (MS) actually found *Ensis* in stomachs of shot birds. From 1986-88, it constituted over 50% of all prey items in one of their study areas.

Littorina

Periwinkles have often been found in faeces and stomachs of eiders in the Wadden Sea, but are rarely considered as an important food source. In one study in Canada, periwinkles were found to be important prey to juvenile eiders (Cantin *et al.* 1974). For the Wadden Sea there is also evidence that at least some individuals

may focus on this prey, possibly after they have become severely infested with the parasite *Proficollis botulus* (Swennen 1976a). There is some anecdotal evidence that in times of food shortage, more eiders may switch to eating periwinkles (Swennen in Abrahamse & Revier 1991, Cadée 1991). *Littorina* is probably predominantly eaten in the high intertidal zone and on rocky shores, i.e. on dikes at the fringes of the Wadden Sea, where juvenile and sick, adult eiders are the most abundant (Swennen 1976a). Eiders may not be able to break down the opercula of *Littorina* in their stomachs and more than likely must regurgitate these remnants, possibly making *Littorina* a less preferred prey of healthy eiders (Swennen 1976a, but see Laursen *et al.*, MS: *Littorina* also found in healthy adults). The problems of removing these parts may also explain why *Littorina* is often recorded as prey in stomachs of starved eiders.

Asterias rubens
Starfish are eaten regularly, particularly on sublittoral mussel beds and mussel culture plots. It is unclear whether starfish are merely 'bycatch' to mussel-feeding eiders, or if some birds actually focus on this prey. One study (Buuren 1983) found starfish and crabs (the two species are placed together in this study) to be the dominant prey in winter, indicating that such prey gain importance when mussels reach a low flesh content at that particular time of year.

Carcinus maenas
Crabs are regularly taken by most eiders in the Wadden Sea, as most eiders carry at least some of the parasites that have these crabs as their first intermediate host (Swennen & Van den Broek 1960, Camphuysen *et al.* 2002). Crabs are dangerous prey, both during handling (pincers!) and after digestion, as many carry parasites, which are potentially lethal to the ducks. Eating crabs is thus often seen as a sign of poor feeding capability, and mostly observed in juvenile, inexperienced or otherwise impaired birds that feed in shallow, near shore waters, or as a sign of a lack of more suitable food (Camphuysen *et al.*, submitted). In this respect, it is interesting to note that at least one other bird has, like eiders, shown mass die-offs in connection with a presumed switch from preferred prey (fish) to crabs. Great Northern Divers (or Common Loons) *Gavia immer* have shown several such mass die-offs around Florida, USA, and their stomachs and guts were found to contain unusual quantities of crab-associated parasites (McIntyre 1988, Forrester *et al.* 1997). In contrast to the notion that crabs are prey to be avoided, Swennen (1976a) considered that eiders actually like eating crabs. Laursen *et al.* (MS), however found crabs in the stomachs of juvenile eiders in particular, suggesting that adult birds prefer to, or are better able to, feed on other prey, i.e. mussels and cockles.

Fish eggs

Different species of soft-bodied prey have been noted as food sources for eiders in the Wadden Sea, but never in great quantities. Fish eggs are rarely available in large amounts in the Wadden Sea. Swennen (1976a) only mentions that eiders (rarely) took eggs of Bull-rout *Myoxocephalus scorpius*, a bottom dwelling fish that spawns among rocks and other hard substrates, e.g. mussel beds.

Spisula subtruncata

Through Shells are a new and important prey species for eiders in the Netherlands. In 1989/90, large numbers first took to the Dutch North Sea coastal waters, which was apparently in response to a structural food shortage of mussels and cockles in the Wadden Sea (Leopold *et al.* 1995, 2001a) and a simultaneous increase of Spisula in the North Sea. Spisula became the staple diet of eiders in the (Dutch) North Sea (Den Hollander 1993, Leopold 1996). All things considered, Spisula would have good returns compared to the other important burying bivalve, the cockles. In a comparison of shell mass, shell strength and flesh contents, Camphuysen *et al.* (submitted) demonstrated Spisula to be a profitable prey species, provided that large specimens can be eaten. In fact, eiders were demonstrated to be able to live only on large (> 1.5 cm, preferably even > 2.5 cm) specimens (Leopold *et al.* 1998, 2000). However, all things are not equal, in that cockles can be found in very shallow waters, while Spisula occur at water depths of 5-15 meters and considerable effort must go into diving, which is needed to find and catch these bivalves. Without energetical measurements of eiders feeding on different prey at different water depths, the question whether Spisula could be a preferred prey or just a secondary prey in times of shortage of mussels and cockles, remains unresolved. There is some evidence both ways. Non-oil related eider mortality was highest in 1990/91 and 1999/2000, when prey in the Wadden Sea was apparently in short supply (Camphuysen *et al.* 2002). However, mortality was normal in 1992/93, when the highest numbers of eiders frequenting the North Sea Spisula banks was recorded.

Size or Quality Selection in Different Prey Species

Given that mussels and cockles, and possibly *Spisula* are the most important prey, the next question is whether eiders prefer a certain size or quality. The birds may do so in a two-step process: first, by selecting a feeding site where prey size or quality are generally profitable and second, by selecting the most profitable prey from within that site. In the Wadden Sea, subtidal, cultured mussels are the most profitable (Camphuysen *et al.* 2002) and therefore, the vast majority of eiders in the Dutch Wadden Sea (where most culture plots are located) reside over these mussels, if they are made available (no ice, no disturbance by fishermen,

Berrevoets *et al.* 2000, Leopold *et al.* 2000). Depth, however, may be a limiting factor for feeding on mussels. Larsen & Guillemette (2000) found that eiders very much prefer natural beds at water depths shallower than 6 m, than beds at 6–12 m. Mussels on the culture plots have thinner shells and are less well attached to each other than intertidal ones, and for this reason only, should be the preferred food of eiders (Bustnes 1988, Bustnes & Erikstad 1990, Nehls 1995).

Size Selection in Mussels

Mussels from natural intertidal beds and subtidal culture plots differ greatly in their profitability, and studies of prey selection on natural mussel beds cannot simply be extrapolated to culture mussels. Unfortunately, most studies on size selection have been carried out on natural mussel beds. A further problem when trying to understand the process of size selection from data in these studies is that most studies only provide the range (smallest and largest) taken and do not compare the
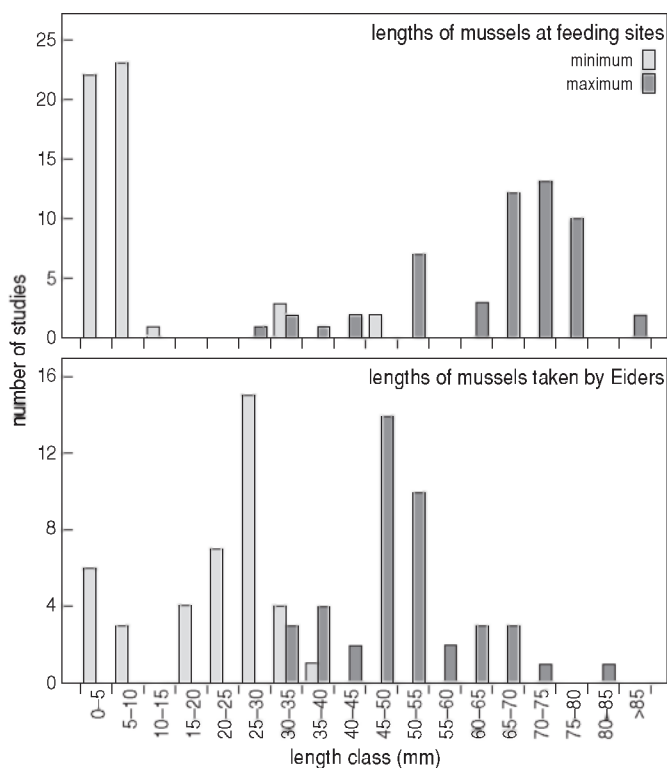
Figure 3.1 (top) Minimum and maximum lengths of Blue Mussels *Mytilus edulis* at eider *Somateria mollissima* feeding sites. (bottom) Minimum and maximum lengths of Blue Mussels taken by eiders. Along the Y-axis, the number of studies or substudies is given in which a particular minimum or maximum is given.

fraction taken from the prey on offer. An overview of size ranges of mussels taken worldwide is given in Figure 3.1. For the Wadden Sea, only a few studies are available. Swennen (1976a) concluded, from a wealth of field work conducted in the 1960's and 70's, that: eiders 'clearly took much smaller molluscs than were available on the flats', but gives no quantitative data on prey availability. He also suggests (in Swennen *et al.* 1989) that molluscs of 1–2 cm would be the preferred prey and speculates that the birds might deplete the stocks of small sized molluscs over winter, thus forcing the birds to gradually take larger and larger mussels until they must take mussels that are considered to be of 'commercial size' in late winter. Nehls (1995) agrees with the suggestion that size of ingested mussels increase during the winter, but he, and also Bustnes (1988) and Bustnes & Erikstad (1990), offers an explanation for this based on feeding energetic. Eiders maximize energetic returns, therefore subtle differences in flesh contents and shell masses between different size classes govern the birds' feeding decisions over winter. Nehls (1995) found, that on intertidal mussel beds in the German Wadden Sea, eiders selected a size range of 2–5 cm in summer and of 4–7 cm in winter (Figure 3.2A). A similar pattern of size selection was found in Canada (Hamilton *et al.* 1999), but within a size spectrum of much smaller mussels (Figure 3.2B). Laursen *et al.* (MS) found, that in shot birds in Denmark, mussels taken (range 3–5 cm) differed from those actually on offer (0.5–7 cm), indicating that the eiders did not select either the largest or the smallest mussels available. However, if the mussels on offer were on average small (mainly smaller than 3 cm) the eiders selected the largest mussels (3-5 cm) present. There are no data on size selection by eiders on the Dutch culture plots, which are the most important feeding sites of the Wadden Sea. Larsen
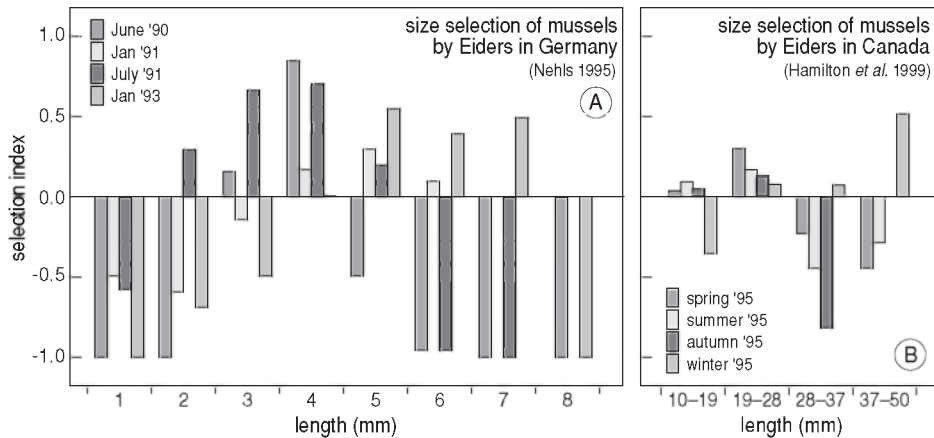
Figure 3.2 (A) Size selection of Blue Mussels *Mytilus edulis* by eiders *Somateria mollissima* feeding on natural intertidal mussel beds in the German Wadden Sea (after Nehls 1995). (B) Size selection of Blue Mussels by eiders feeding at Canadian rocky shores (Hamilton *et al.* 1999).

& Guillemette (2000) found, that on subtidal natural mussel beds in Denmark, the eiders mainly fed at depths of less than 6 m. Most culture plots fall within this range. They also argue that flesh to shell mass ratios are highly unfavorable in larger mussel sizes and observed that at depths greater than 6 m, the mussels could reach sizes that were too large to be profitable for the eiders, thus indicating a high predation pressure. Mussels in beds in deeper waters were thus unprofitable for two reasons: they occurred too deep and were too large.

Size Selection in Cockles

Surprisingly, even less is known about size selection in cockles, although selection in this rather uniform, intertidal prey would be much easier to study than in mussels. Both studies on distribution of eiders over the Wadden Sea and diet studies show cockles to be important prey, but just how they compare to mussels and which cockles are the most suitable prey remains unknown. An overview of ranges of size taken by eiders is given in Figure 3.3. Swennen (1976a) has provided eiders with cockles on unburied feeding trays and under these highly artificial circumstances, the eiders always took the smallest cockles from those on offer. This was especially true if large cockles were offered. There are no field studies that compare cockles taken with those locally present. There are only some general suggestions that cockles would be less profitable than mussels if flesh to shell masses were compared (Camphuysen *et al.*, submitted). Also, feeding on cockles seems to be restricted by the tidal cycle in that this prey is mainly taken when a little water is present on the feeding site. Cockles living in very muddy sediments are avoided (Nehls 1991, 1995).
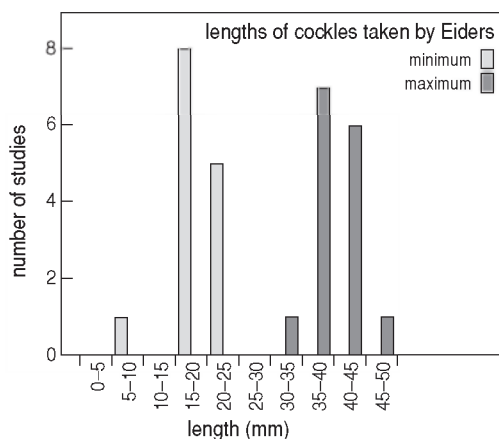
Figure 3.3 Minimum and maximum lengths of cockles *Cerastoderma edule* eaten by eiders *Somateria mollissima* in different studies.

Size Selection in Spisula

Size selection in *Spisula* has not been directly studied, through the comparison of sizes taken to sizes on offer. However, Leopold *et al.* (2000) compared eider distribution and size distribution of *Spisula* in the Dutch North Sea and found that eiders always selected sites with the largest *Spisula*. *Spisula* smaller than 1 or 1.5 cm seem to be too small. Eiders were also found to prefer *Spisula* banks at relatively shallow depths (< 10 m).

Discussion

Eiders can take many different prey items, but in the Wadden Sea, the mussel is probably the most important prey. Mussels are reliable prey as they are always present, unless the beds are grossly over fished, as happened in 1990 (Beukema, 1993, Camphuysen *et al.*, submitted). Cockles are the next most important prey and are also energetically profitable, but cannot be taken throughout the entire tidal cycle. These occur in very low densities after mass die-offs in severe winters and have thicker shells than (cultured) mussels. *Spisula subtruncata* is now the third most important prey, but has two main disadvantages: it occurs in relatively deep waters and the prey stock may be unreliable as evidence shows that mass die-offs have occurred in severe winters. Most prey sizes can be taken by eiders, but they seem to prefer medium sized prey. The most important piece of knowledge that we still lack in this respect is the feeding decisions eiders make, both on mussel seed and on culture plots, and on cockle beds. As we do not know what is present on the different culture plots (Smaal *et al.*, 2000), distribution of the birds over the range of plots available cannot be understood. Taking this one step further, we do not know what, if anything, the eiders select from within these plots. Neither size selection of mussels or the selection of mussels versus other prey present, such as starfish and crabs, within plots has been studied here. It is in this area that additional studies are most urgently needed to understand what exactly eiders do in the Wadden Sea. Opportunities are there, if fishermen and scientists can work together, as the constant stocking, restocking/relocating, growth and final removal of mussels from the plots form an immense feeding 'trial' for eiders. Tapping into this large-scale 'experiment' will be the challenge for the immediate future. Work on site and size selection in cockles is an easier task to address, as it can be done on foot and without information, which is currently only available to fishermen.

Identification and size estimation of *Spisula subtruncata* and *Ensis americanus* from shell fragments in stomachs and faeces of Common Eiders *Somateria mollissima* and Common Scoters *Melanitta nigra*

Mardik F. Leopold, Peter C. Spannenburg, Hans J.P. Verdaat & Romke K.H. Kats

Abstract

This study describes methods to reconstruct the size of ingested *Spisula subtruncata* and *Ensis americanus* in stomachs, guts and faeces of seaduck. These two bivalve species constituted staple foods of Common Eiders *Somateria mollissima* and Common Scoters *Melanitta nigra* in the SE North Sea. The ducks crush these shellfish in their muscular gizzards, leaving only tiny fragments in most samples that may be obtained in the field. We show that prey sizes (shell lengths) can still be estimated from such samples, by taking specific measurements from the shells' hinges or from the thickness of shell fragments. Even though the hinges of both bivalve species are the thickest parts of the shell, few remain pass the stomach of a sea duck undamaged. However, even broken hinges can be used to estimate prey size by regression analysis, using specific measurements of certain parts. Shell thickness is also related to shell size so this parameter can also be used to reconstruct shell size. In *Spisula* specific, recognizable parts of the shell can often be recognised in samples of crushed shells. In *Ensis* samples, such specific parts are harder to find, but average thickness of several fragments within a sample, or the thickness of the thickest or thinnest parts present in the sample may be used. Suggested measurements correlated well with shell length in reference material. The applicability of these correlations was tested in experimental feeding trials with captive ducks that were fed with *Spisula* of known size. These tests showed that not all measurements taken from hinges or shell thickness of fresh shells could reliably be taken from fragments of the shells as present in the faeces. From the hinges, the so-called chondrophores were the most frequently recovered parts (some 11.5 % of those ingested), and these were also the most resilient to wear. Shell thickness could be measured from relatively many shell fragments, particularly from the ventral region of the shell. Precision from any individual shell fragment was rather low, but average sizes of *Spisula* fed to the ducks could be estimated rather well, using either hinge or shell thickness measurements. The methods were tested on shell fragments in field samples where the available prey spectrum was known from benthos sampling programs. Reconstructed sizes of both *Spisula* and *Ensis* from shell fragments found in stomachs of oiled scoters or in faeces from eiders roosting on an offshore sandbank compared well with sizes of these prey available in the vicinity. Both seaduck species showed size selection when eating these two shellfish prey species in the field.

Introduction

Common Scoters *Melanitta nigra* are common seaducks in The Netherlands, where they occur in flocks of up to >100,000 in nearshore waters (Leopold 1993, Leopold *et al.* 1995, Bijlsma *et al.* 2001, ICES 2005). In the 1990s, the scoters were joined by tens of thousands of Common Eiders *Somateria mollissima* that were driven out of the adjoining Wadden Sea by a shortage of their principal food, blue mussels *Mytilus edulis* and edible cockles *Cerastoderma edule* (Leopold 1993, Camphuysen *et al.* 2001, Ens & Kats 2004). Both species of seaduck were usually found over banks of trough shells *Spisula subtruncata* in Dutch coastal waters and it was generally assumed that these bivalves formed their staple diet (Leopold 1993, 1996, Leopold *et al.* 1995). However, *Spisula* stocks have been decreasing lately, while another bivalve, the American razor clam *Ensis americanus* has increased dramatically in abundance (Armonies 2001, Bult *et al.* 2004a, Craey-meersch & Perdon 2004). These long-bodied razor clams may be hard to swallow or crush in the gizzard, but if this species takes over as the dominant bivalve in Dutch coastal waters, the ducks may be forced to change their diet, or leave. Observations on ducks feeding close to land (Photo 4.1) have shown that scoters can eat this prey (Leopold & Wolf 2003, Wolf & Meininger 2004). Eiders too have been noted to take *Ensis*, through stomach analyses (Swennen & Duiven 1989, Thingstad *et al.* 2000, Ens *et al.* 2002, Laursen *et al.* in prep., ICES 2005) direct observations on feeding ducks (e.g. Leopold 2002a) and faeces analysis (Nehls & Ketzenberg 2002) but information for Dutch waters is still very scanty.

Diet studies on seaduck in the area have been hampered by lack of suitable material. Direct observations are hard to conduct in the North Sea, where scoters and eiders mostly feed outside telescope range. Such observations may also be biased towards large prey that need a lot of handling time, such as large *Ensis*. Indirect methods, such as stomach or faeces analysis thus have to be used. Seaduck are protected birds in Dutch waters, making shooting ducks for e.g. stomach analyses a hard option to follow (cf. Madsen 1954, Aulert & Sylvand 1997, Laursen *et al.* in prep.). Set-nets as used other parts of these birds' range from which large numbers of drowned ducks may be obtained (cf. Durinck *et al.* 1990, Meissner & Bräger 1990, Kallenborn *et al.* 1994, Rumohr 2002, Žydelis 2000, 2002) are not abundantly deployed in areas where the ducks concentrate in the Netherlands either. Major oil incidents have not recently killed large numbers of seaduck in Dutch waters that could be used for obtaining stomachs (cf Hughes *et al.* 1996, 1997). Only the recent die-off of Common Eiders (Camphuysen *et al.* 2001), has been seized to conduct stomach analyses (Ens & Kats 2004). Both *Spisula* and *Ensis* were found in the stomachs, but obviously, a study of starved birds may yield results that are hard to interpret.

Prey can also be studied if faeces of the ducks can be collected. Faeces contain the crushed shells of the prey eaten and these fragments may be used to study

Photo 4.1 Female Common Scoter *Melanitta nigra* handling *Ensis directus* off the Brouwers-dam, SW Netherlands, 27 January 2004. Photo: Pim Wolf.

prey species taken and to reconstruct prey sizes. Such studies have been conducted on various species of shellfish eating birds in the Wadden Sea, where faeces can be collected with relative ease on tidal flats or on high tide roosts (e.g. Swennen 1976a, Nehls 1989, Dekinga & Piersma 1993, Hilgerloh 1999, 2000, Scheiffarth 2001, Nehls & Ketzenberg 2002). In these studies, prey size was assessed from the sizes of the hinges of ingested shells present in the faeces. The hinges are the thickest and hardest part of the shell and these sometimes remain intact even in badly fragmented shells. Empirical relationships between hinge size and shell size may than be used to back-calculate the original size of the ingested shells.

Faeces can only be collected where birds drop these on accessible places such as high tide roosts or mudflats used for feeding during low tide. Such studies have thus been limited to wildfowl, waders and gulls feeding in the intertidal. Seaduck, particularly scoters habitually rest at sea, and their faeces can not be collected here. Eiders however, often come ashore to rest, also when they feed in the North Sea. Exploratory observations on Eider droppings found along the Dutch mainland coast have indicated that *Spisula subtruncata* fragments were excreted in large quantities here (Leopold 1996).

Another problem for conducting diet studies on these birds is that information that relates hinge size to shell size for *Spisula* and *Ensis* is still lacking. Only Dekinga and Piersma (1993) used (small) *Spisula subtruncata* in feeding experiments with captive Red Knots *Calidris canutus*, but they found that the hinges of these shells usually got so damaged that shell size could not be estimated from faecal analysis. Likewise, the long and delicate *Ensis* hinges will probably mostly break up in a seaduck gizzard.

In this paper, we explore the possibilities to study the feeding habits of eiders and scoters, by analyzing shell fragments in faeces and stomachs. We focus on *Spisula subtruncata* and *Ensis americanus* as these are the most likely candidate staple foods in our study area. The feasibility to use hinges or shell thickness is explored in feeding experiments on captive Common Eiders and in field situations involving both species of seaduck and both species of prey. As hinges have used in many previous diet studies of molluscivores, we have first examined the possibility to use these in *Spisula* and *Ensis* as well. However, as the hinges of these shellfish may be very prone to breaking up in the muscular gizzard of a large seaduck (cf. Dekinga and Piersma 1993), we have also used shell thickness. Shell thickness is correlated to shell size (length), and therefore could, in theory, also be used to reconstruct original shell size. However, as opposed to the hinge which is a unique structure in a shell, shell thickness varies over the shell's length and width and unless clear reference points can be pinpointed that can still be identified in a sample of shell fragments, using this measure poses additional problems, which will be addressed.

Methods

Spisula subtruncata
Hinges
The first step in this study was to describe the hinges of *Spisula subtruncata* and *Ensis americanus*, to measure all parts that could conceivably be useful in faeces studies and relate these measurements, over a range of suitable prey sizes, to shell size. Hinges of *Spisula subtruncata* were examined under a stereo microscope fitted with an eye-piece micrometer. Nine measurements were taken: four from the right valve and five from the left valve. From the right valve we measured (Figure 4.1A): the maximum (diagonal) length (1) and maximal height of the chondrophore (2) and the lengths of the anterior and posterior lateral grooves (3 & 4). From the left valve we measured (Fig 4.1B and 1C): the maximum (diagonal) length (5) and maximal height (6) of the chondrophore, the distance between the two cardinal teeth (7) and the lengths of the anterior (8) and posterior (9) lateral teeth. Shell length (see Figure 4.2) was related to these measurements by linear regression (Table 4.1). Shell lengths (range: 15.24 to 32.31 mm) were distributed evenly over the total size range. Chondrophore and anterior lateral groove measurements resulted in the highest R^2- values.

Spisula shell thickness
Several reference points for measuring shell thickness were selected that would still be identifiable in samples of shell fragments. The first reference point is situated at the deepest point of the shell, near the top, directly under the hinge, along the
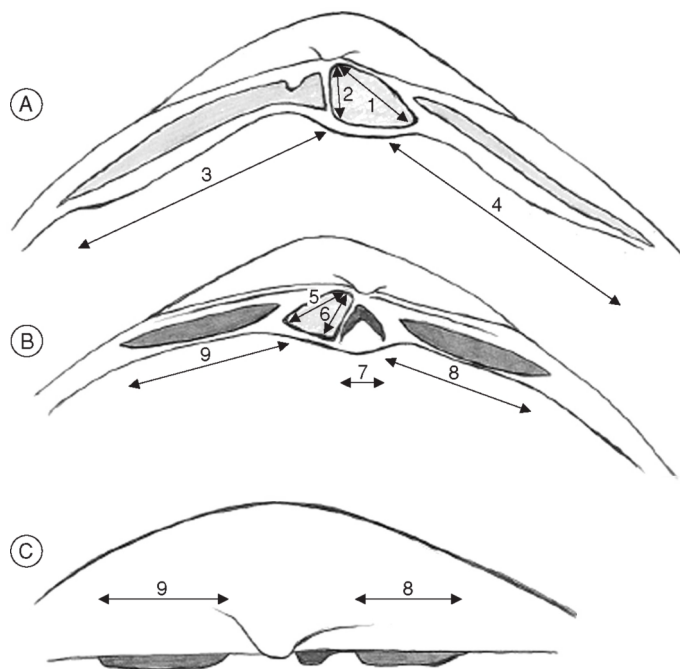
Figure 4.1 Right valve (A) and left valve (B & C) of *Spisula subtruncata*. Arrows and numbers indicate how measurements were taken of the different parts of the hinge. See text and Table 4.1 for the meaning of the numbers. Elevated teeth are depicted dark grey, depressions (grooves) light grey.

Table 4.1 Linear regression parameters used to estimate shell length (in mm) in Spisula subtruncata, from hinge measurements (numbers in left column refer to description given with Figure 1). All regressions for Spisula take the form: shell length = aX + b, with X = the specific measure in mm.

Spisula: Hinge measure	a	b	n	R^2
#1 chondrophore diagonal length right valve	7.36	8.26	41	0.94
#2 chondrophore maximal height right valve	9.41	7.93	41	0.93
#3 anterior lateral groove	3.45	0.54	41	0.95
#4 posterior lateral groove	3.32	2.51	41	0.87
#5 chondrophore diagonal length left valve	7.58	8.76	40	0.97
#6 chondrophore maximal height left valve	11.22	7.18	40	0.94
#7 distance between the cardinal teeth	21.51	2.06	40	0.57
#8 length of anterior lateral tooth	5.28	5.16	40	0.87
#9 length of posterior lateral tooth	5.30	4.73	40	0.80
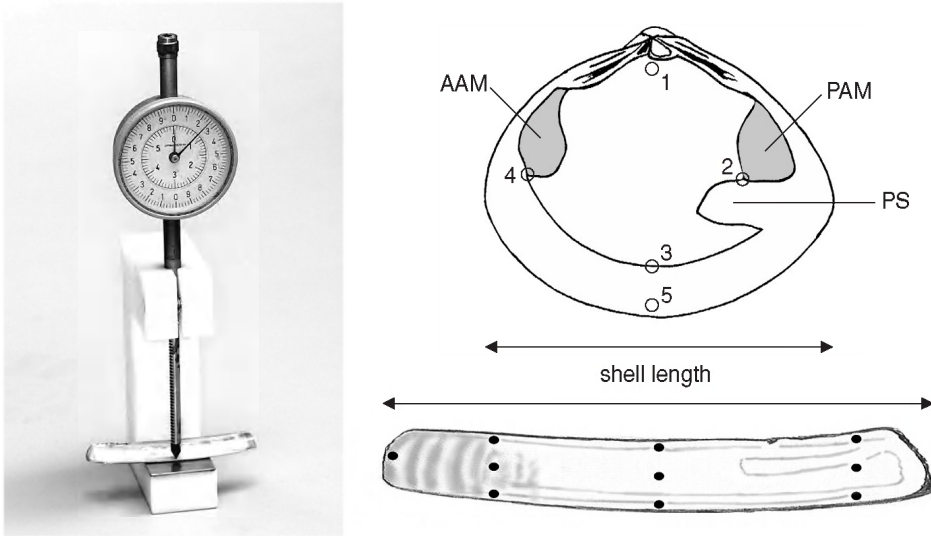
Figure 4.2 The micro thickness-meter that was used to measure shell thickness (photo left). Top-right: inside view of Spisula with reference points for measuring shell thickness (see Table 2). PL: pallial line with the pallial sinus (PS) and scars of anterior (AAM) and posterior (PAM) adductor muscles. Lower right: reference points in *Ensis*. Long horizontal arrows indicate how shell length was measured in either species.

dorsal-ventral median line (Figure 4.2). Points 2–4 lay along the dark 'pallial line' that runs along the outer margin of the shell and around the scars of the posterior and anterior adductor muscles. This pallial line (PL) marks the outer rim of the fleshy tissue of the living shellfish and is usually clearly visible in *Spisula*. It shows several characteristic bends that we could often pinpoint in samples of shell fragments. Point 2 sits at the ventral junction of the pallial line and posterior adductor muscle (PAM) imprint, point 3 sits at the ventral midpoint of the pallial line and point 4 at the ventral junction of the pallial line and anterior adductor muscle (AAM) imprint. Reference point 5 is between the ventral midpoint of the pallial line and the outer margin of the shell.

As fragments from left and right valves in stomach and faeces samples could not always be separated, we randomly selected left and right valves from our set of reference shells, thus keeping measurements within reference points independent. Again, shell length (range: 10.11 to 32.20 mm) was related to the different measurements (Table 4.2). All shell thickness measurements were taken with a micro thickness-meter from shells that were thoroughly air-dried, but still had the epidermis on (Figure 4.2).

Table 4.2 Linear regression parameters used to estimate shell length (in mm) in Ensis americanus, from measurements on shell thickness. All regressions for Ensis take the form: shell length = aX b, with X = shell thickness in mm.

Spisula shell thickness at:	a	b	n	R^2
Ref. point #1 (inner top):	26.10	0.210	63	0.51
Ref. point #2 (PAM):	21.39	0.428	63	0.67
Ref. point #3 (ventral PL):	21.58	0.410	63	0.71
Ref. point #4 (AAM):	23.75	0.399	63	0.60
Ref. point #5 (outer rim):	20.18	0.533	63	0.72

Ensis americanus

Hinges

Ensis americanus has a long and rather delicate hinge that is widest ventrally. The left side shows a prominent lateral gap here. From the left valve we measured: the maximum length (#1, A-D, Table 4.3 and Figure 4.3), the length from the anterior end to the gap (#2, A-B), the width of the gap (#3, B-C) and the length of the posterior 'island' (#4, C-D). Note that the length of (1) equals that of (2+3+4). From the right valve we measured: the maximum length (#5, I-F), the length without the posterior "head" (#6, I-H) and the width of the posterior head (#7, E-G). The precise manner in which these measurements were taken is depicted in Figure 4.3. Note that in measurement #5, the maximum length of the right valve was not measured to the ventral extreme (point F' in Figure 4.3), but to the midpoint of its ventral curve that was more often still intact in faecal samples (point F).

   Ensis hinges were measured under a Zeiss Stereo Microscope SV6, fitted with a Zeiss AxioCam MRc digital camera, connected to a computer via integrated Axiovision4 software. This system became available for our research during our study and allowed for measurements to be taken from a computer screen using the appropriate magnification. 34 hinges were selected from shells distributed evenly over a range of shell lengths from 34.8 to 179.8 mm. Shell length was regressed against the different measurements. R_ values were generally high (Table 4.3). It was noted, however that measurement #7 was prone to error, if the hinge was not put flat under the microscope.

Ensis shell thickness

In *Ensis* shells the pallial line is less clear than in *Spisula*, particularly in faecal samples and clear reference points could not easily be found. Over the entire shell width, the valves proved to be thinnest at the anterior end and thickest near the hinge. Therefore, 10 different measurements of shell thickness were taken per valve (Figure 4.2). One reference point was taken near the (thin) anterior margin of the valve (along the median line, 3 mm from the top). Six reference points were

Table 4.3 Linear regression parameters used to estimate shell length (in mm) in *Ensis americanus,* from hinge measurements (numbers in left column refer to description given with Figure 4.3). All regressions for *Ensis* take the form: shell length = aX b, with X = the specific measure in mm.

Ensis: Hinge measure	a	b	n	R^2
#1 (A-D) maximum length in left valve	17.45	0.853	33	0.93
#2 (A-B) anterior end to the gap in left valve	22.87	0.790	30	0.91
#3 (B-C) gap width in left valve	378.61	1.040	29	0.75
#4 (C-D) posterior island length in left valve	111.61	0.700	31	0.86
#5 (I-F) maximum length in right valve	17.67	0.880	34	0.94
#6 (I-H) length to posterior "head" in right valve	25.95	0.717	33	0.84
#7 (E-G) width of posterior "head" in right valve	81. 70	0.959	30	0.92
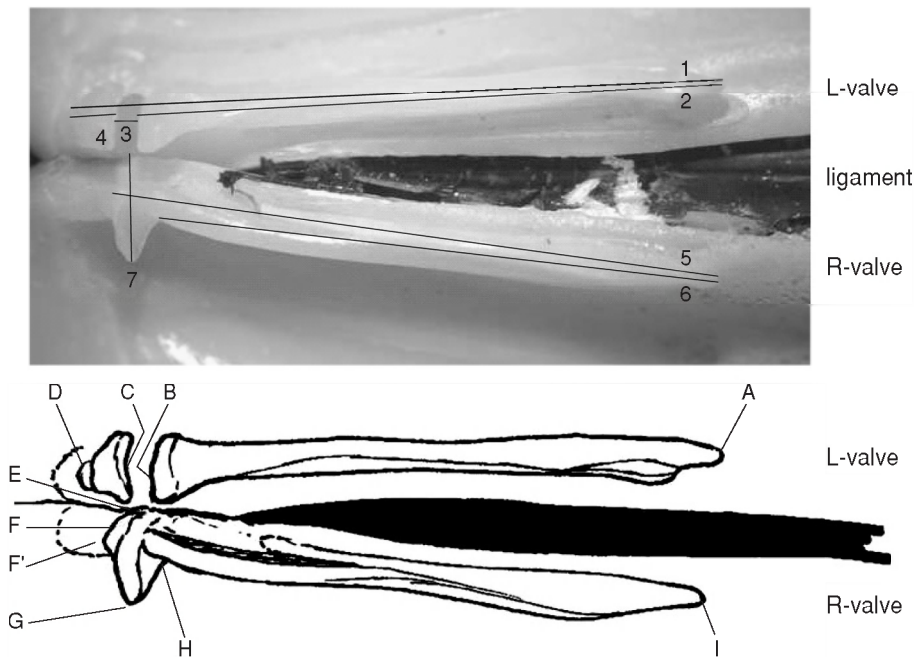
Figure 4.3 Pair of valves of *Ensis americanus,* joined by the outer ligament in between (black). In the photo (top) lines and numbers indicate how measurements were taken of the different parts of the hinge. See text and Table 4.3 for the meaning of the numbers. The lower panel shows a schematic drawing of an Ensis hinge, offering more contrast between the elevated (measured) ridges and the flat part of the valves below (inside view).

taken at 3 mm from the outer rim (evenly distributed over the length of the shell) and a final three along the median line of the shell. As reference material 19 *Ensis*-valves (ranging in length from 37.2 to 161.0 mm, left or right randomly selected) were used. Like in the reference *Spisula* shells, shell lengths were selected in such a way that this range of sizes was evenly covered. Shell length was regressed against shell thickness, using the largest values (the thickest part), the smallest values (the thinnest part), and the average thickness of all ten measurements (Table 4.4).

Table 4.4 Linear regression parameters used to estimate shell length (in mm) in *Ensis americanus*, from measurements on shell thickness. All regressions for *Ensis* take the form: shell length = aX + b, with X = shell thickness in mm.

Ensis shell thickness at:	a	b	n	R^2
thickest part	91.78	37.39	19	0.91
thinnest part	210.06	51.11	19	0.92
Average of all ten points	131.76	47.35	19	0.91

Feeding trials

Faeces of two captive Eiders were collected after these had been fed with live, intact *Spisula*. The Eiders were raised from the egg, and when they were full-grown, were kept on a diet of bivalves in outdoor cages with running seawater. The ducks were kept for experiments to determine the energetic costs of crushing and digesting bivalve prey. In each trial, one duck that had been kept without food for several hours was force-fed 8 to 15 live, intact *Spisula subtruncata* of the same size. The number of prey depended on prey size and *Spisula* used were: 24, 26, 28, 30, or 32 mm long. The duck was then kept in a metabolic chamber for energetic measurements and at the end of the experiment (lasting several hours), its faeces were collected. From these, all fragments that could be related to original shell size were sorted and the measurements as outlined above were taken. As the size of the prey was known, we could determine the reliability of the procedure of back-calculating prey size from faecal fragments.

These experiments were not repeated with *Ensis* as prey, as it was felt that force-feeding *Ensis* could be hazardous for the birds (see: Swennen & Duiven 1989).

Field samples

***Spisula*: scoter stomachs**

Stomachs were taken from oiled Common (n=23) and Velvet Scoters *M. fusca* (n=2), beached near a major *Spisula* bank off Terschelling in January 1995. These stomachs had been dissected out of the birds shortly after they were found and kept frozen until analysis. The stomachs were thawed for the present study and

rinsed with tap water to flush out all shell fragments. Samples were dried and *Spisula* shell fragments from which shell thickness measurements could be taken (no hinges were found) were sorted under a binocular microscope.

Ensis: Eider faeces

In December 2001 and in February 2003, Eider faeces were collected at the 'Razende Bol', a sandbank off Texel in the Dutch North Sea (52°58.50'N, 04°41.30'E). Here several thousands of Eiders were resting during high tide at the time. A total of 47 (2001) and 45 (2003) individual dropping were collected and kept frozen in plastic bags until analysis. After thawing, the faeces were washed and the shell fragments were sorted under a binocular microscope. The different species of prey present in the faeces were identified by comparison to a reference collection of shells. *Spisula* fragments were rare in this material, and no hinges of this species were found. The bulk of the shell fragments were *Ensis* and from each sample the thickest and thinnest shell fragment that could be found were sorted out, as well as 8 randomly chosen fragments, and the thickness of these 10 fragments were measured.

Results

Spisula feeding trials with captive Eiders

A total of 239 *Spisula* were fed to the ducks in the feeding trials. From the 478 hinge-halves that were thus potentially available, not a single one was recovered intact from the faeces. Only bits and pieces were found, like parts with one groove, tooth or chondrophore. Furthermore, most grooves and cardinal and lateral teeth were too damaged to be measured accurately (cf Dekinga & Piersma 1993). In total, 55 measurable parts (11.5 %) were recovered, from which 77 measurements were taken. In addition to the hinges, a total of 109 shell fragments were retrieved from the faeces, in which shell thickness could be measured at one of the pre-identified reference points (see Figure 4.2).

Spisula hinges

In total, 10 diagonal lengths (#1 in Figure 4.1) and 12 heights (#2) from 12 chondrophores from right valves and 14 diagonal lengths (#5) and 16 heights (#6) from 18 chondrophores from left valves could be measured. From 11 fragments the distance between the two cardinal teeth (#7) could be measured, while also the lengths of 8 anterior lateral teeth (#8) and of 6 posterior lateral teeth (#9) could be taken. The chondrophores were thus the parts most frequently recovered in a measurable state. Even so, of all chondrophores of the *Spisula* fed to the ducks, only 5.9 % were recovered (28 out of 478). For the cardinal teeth this percentage was 4.6, while only 2.9 % of the lateral teeth were recovered in such a state that they could be measured.

As the true sizes of the *Spisula* fed to the ducks were known, it was possible to calculate the errors that resulted from estimating shell size from the hinge measurements. Precision of any one estimate was rather low, and shell lengths could be underestimated by as much as 33.4% or overestimated by 26.0% (Table 4.5, Figure 4.4). The chondrophore measurements provided slightly better estimates than the cardinal and lateral teeth, as the overall bias was smaller. More important-

Table 4.5 Analysis of under- and overestimates (errors) of shell sizes estimated from different measures on hinge fragments found in faeces of Common Eiders *Somateria mollissima*, fed with *Spisula subtruncata* of known size. For measures (first column): see Figure 4.1.

Measure	AVG-%-error	range of errors	s.e.	N
#1 chondrophore diagonal length right valve	–4.0	–12.9 to 19.0 %	3.04	10
#2 chondrophore maximal height right valve	–3.9	–21.3 to 9.5 %	2.57	12
#5 chondrophore diagonal length left valve	3.4	–11.4 to 26.0 %	2.76	14
#6 chondrophore maximal height left valve	1.4	–19.1 to 17.5 %	2.32	16
#7 distance between the cardinal teeth	–7.7	–33.4 to 18.2 %	4.72	11
#8 length of anterior lateral tooth	–9.1	–19.3 to –1.4 %	2.46	8
#9 length of posterior lateral tooth	0.9	–16.2 to 17.2 %	5.20	6
Total	–2.2	–33.4 to 26.0 %	1.27	77
Total for chondrophores only	–0.3	–21.3 to 26.0 %	1.36	52
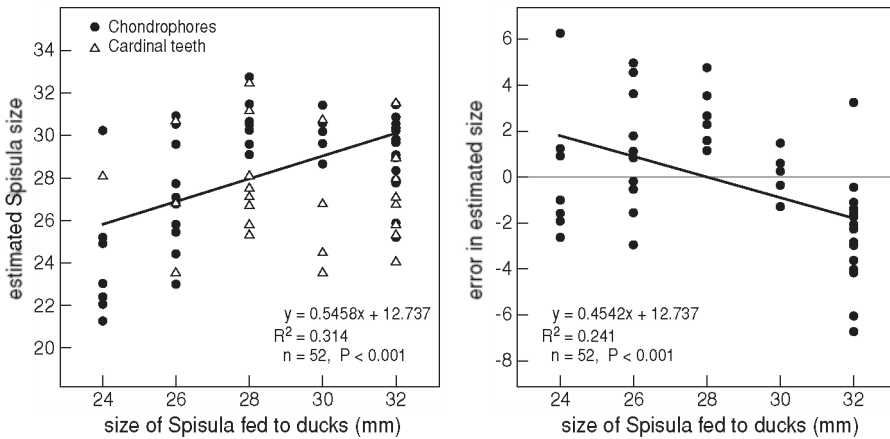
Figure 4.4 Estimated size of *Spisula subtruncata* as based on hinge-measurements, as a function of true shell size as fed to Common Eiders *Somateria mollissima* in the feeding experiments (left). A regression line is only given for chondrophore measurements (closed symbols; measurements #1-6 combined) as the measurements from the cardinal teeth (open symbols; measurements #7-9 combined) did not yield a significant correlation. Right panel: errors associated with the estimates (from chondrophores only) as: estimate–true size.

ly, over the size range studied here, there was no relationship between true shell size and shell size as estimated from the cardinal and lateral teeth, while this relationship was highly significant when chondrophore measurements were used (Figure 4.4). However, sample sizes were quite low and when all possible estimates were considered together, errors appeared to be distributed rather symmetrically, resulting in an average underestimate of shell size by only 2.2%. When only the chondrophores are considered, the average error is only –0.3%. It appears therefore, that the sizes of individual *Spisula* eaten by Eiders cannot be estimated with great reliability from hinges in faecal material, but if a sufficient number of hinges (hinge parts) can be obtained, the average size of the ingested prey can be estimated quite well, particularly from the chondrophores.

Spisula shell thickness

Shell length was also estimated from 109 shell fragments retrieved from the faeces, in which shell thickness could be measured at one of the pre-identified reference points (see Figure 4.2). Combining all measurements, a significant relationship was found between estimated shell size and true shell size (Figure 4.5). Errors again showed a negative relationship with true shell size, indicating that sizes of small *Spisula* were overestimated, while sizes of large *Spisula* were underestimated (Figure 4.5, right panel). Overall, the estimated sizes were more or less correct with an average error of only –0.76%, but with individual estimates being anywhere from –26 to +34% off (Table 4.6).
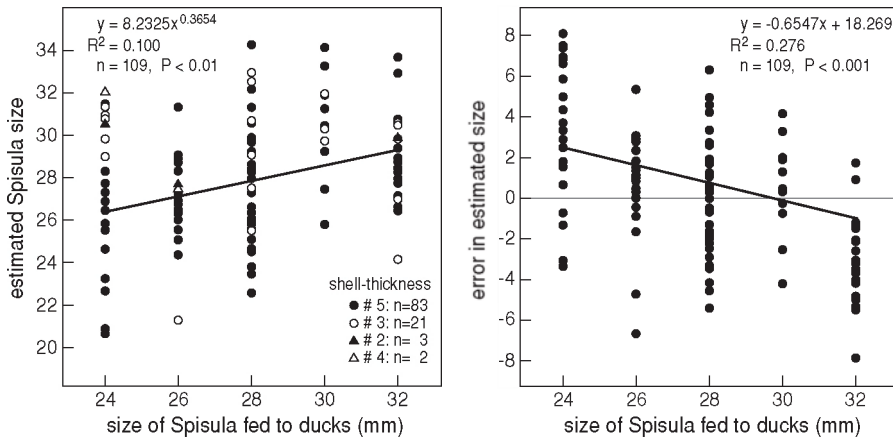

Figure 4.5 Estimated size of *Spisula subtruncata* as based on shell thickness measurements, as a function of true shell size as fed to the Common Eiders *Somateria mollissima* in the feeding experiments (left). The regression line is for all measurements combined. Right panel: errors associated with the estimates as: estimate–true size.

Table 4.6 Analysis of under- and overestimates (errors) of shell sizes estimated from different measures of shell thickness of fragments found in faeces, of Common Eiders *Somateria mollissima* fed with *Spisula subtruncata* of known size. For measures (first column): see Figure 4.2.

Measure	AVG-%-error	range of errors	s.e.	N
#2 PAM	9.2	–6.7 to 27.6 %	9.96	3
#3 Ventral PL	4.2	–24.7 to 30.5 %	3.59	21
#4 AAM	19.6	5.7 to 33.6 %	13.95	2
#5 Outer rim	–0.9	–25.8 to 31.1 %	1.19	83
Total	–0.76	–25.8 to 33.6 %	1.22	109

Spisula in scoter stomachs

Spisula remains were found in six stomachs of oiled Common Scoters and in one Velvet Scoter, beached at Terschelling in January 1995. No shell fragments with measurable hinges were present, but shell thickness measurements could be taken from a total of 31 shell fragments. At the time when the ducks beached, the Dutch coastal waters were surveyed for *Spisula subtruncata* and sea duck. Off Terschelling 50,000 Common Scoters and 1200 Velvet Scoters were found, as well as high *Spisula* densities (Leopold 1996). In 61 Van Veen bottom grabs taken off this island, 676 *Spisula* were found, mostly belonging to a single year-class (14–21 mm shell length). Very few *Spisula* of older year classes were found, but in the stomachs, *Spisula* of several year classes, including older ones, were found according to the reconstructed sizes from the shell thickness measurements (Figure 4.6). Note, however, that *Spisula* of around 20 mm shell length may be overestimated by some 5 mm from shell thickness measurements (Figure 4.5). Still, there is a suggestion that *Spisula* of 25–30 mm were taken disproportionably often by the ducks.

Ensis as Eider prey

Size distribution of *Ensis* available to Eiders roosting on the Razende Bol was determined in the same winters when the faeces were collected, by using a Van Veen bottom grab in nearshore waters off Texel, some 14 km north of the roost (Leopold 2002b, 2003). Although this grab may have missed some of the larger *Ensis* that have a higher probability to escape from this sampling device (Leopold 2002b), it is clear that in winter 2001/02 0-group *Ensis* (animals <65 mm long) dominated the population, while 0-group and 1-group animals (>65 <110 mm long) were present in more or less similar numbers in 2002/03 (Figure 4.7). *Ensis* was the dominant species in both winters, comprising 55% of bivalve biomass in 2002 and 95% in 2003. In the first winter a considerable proportion of the bivalve biomass was made up by Donax (26%) and *Macoma* (10%), but *Ensis* was apparently selected as food by the Eiders, as this was relatively more commonly present in the faeces (Table 4.7).
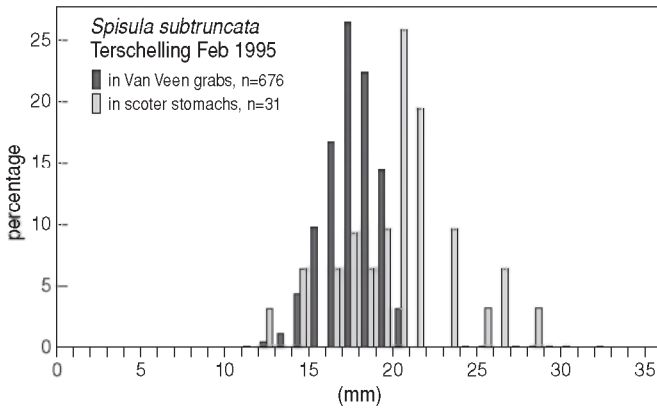
Figure 4.6 Size-frequency distributions of *Spisula subtruncata*, present off Terschelling in February 1995 (dark grey bars), compared to estimated sizes of *Spisula subtruncata* found in Common Scoter *Melanitta nigra* stomachs (light grey bars). A total of 29 sizes of ingested *Spisula* were derived from shell fragments found in Common Scoter stomachs and two more (24.3 and 25.6 mm estimated shell length, included in the graph) were found in a Velvet Scoter *Melanitta fusca*. Note that the apparent difference between the peaks in the two length distributions (at 18 and 21 mm respectively) was probably caused by overestimation of shell size from shell fragment thickness measurements (see Figure 4.5).

The faecal samples collected on the Razende Bol in December 2001 and in February 2003 contained 9 prey species in total, with *Ensis americanus* as the dominant prey species, in either winter (Table 4.7). In both winters combined, *Ensis americanus* was present in 87 out of 92 droppings (94.7%) and 78.3 % of the samples contained *Ensis* exclusively. *Spisula* remains were present in only 5 of the 92 samples and no measurable parts were found that could be used to estimate original shell length. Several other prey species were also identified in the faeces, but like *Spisula*, their contribution was marginal (Table 4.7).

Ensis hinges

Ensis hinges or parts of hinges were found in 12 of the 47 faecal samples collected in December 2001 and in 25 of the 45 samples collected in February 2003 (Figure 4.7). The left and right halves of the hinges were usually separated in these samples, making an estimation of total numbers of prey animals involved not possible. Measurements could be taken from 43 and 59 parts (left or right summed), for the first and second winter samples, respectively. As often more than one measurement per hinge-half could be taken, total numbers of measurements amounted to 188 (Table 4.8), for 102 hinge-halves. If more than one measurement for a given hinge-half could be taken, we used the average estimate for all these measurements as the final estimate for shell size (Figure 4.7).
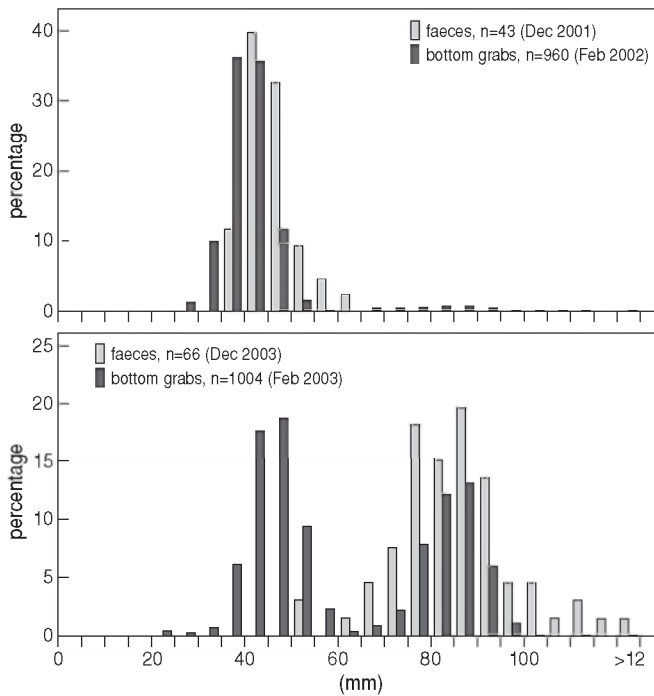
Figure 4.7 Length-frequency distributions of *Ensis americanus* as reconstructed from hinges in Common Eider *Somateria mollissima* faeces collected at the Razende Bol in December 2001(upper panel) and in February 2003 (lower panel), compared to sizes of *Ensis* found in bottom samples near the roost (dark grey bars) in the same winters. No growth is thought to occur in shellfish in midwinter, i.e. between December 2001 and February 2002. Shell lengths in mm, in 5 mm bins.

Table 4.7 Occurrence of different prey species in Common Eiders *Somateria mollissima* faecal samples collected in the field (Razende Bol) in two successive winters. 47 faeces were collected on 11-12-2001 and 45 on 26-02-2003. The numbers of samples containing each of the prey species are given.

Prey species	Dec 2001	Feb 2003	Total
Ensis americanus	45	42	87
Carcinus maenas	7	0	7
Mytilus edulis	0	5	5
Spisula subtruncata	4	1	5
Littorina littorea	2	0	2
Macoma balthica	1	0	1
Cerastoderma edule	1	0	1
Donax vittatus	0	1	1
Natica alderi	0	1	1

Shell lengths of *Ensis* were estimated using the equations given in Table 4.3. All *Ensis* taken in December 2001 probably were 0-group animals, with predicted lengths ranging from 40.9 to 64.4 mm. Reconstructed sizes of *Ensis* for February 2003 ranged from 52.6 to 139.8 mm and comprised three year classes (Figure 4.7). Presumed 1-group *Ensis* (n=53), with lengths from 65–110 mm predominated. Only two smaller *Ensis* were found (53 and 54 mm) and four *Ensis* with reconstructed shell lengths of 113-140 mm.

Sizes of 1-group *Ensis* present in the seabed and taken by the Eiders in February 2003 were not statistically different (Table 4.8, t-test, NS). However, the reconstructed shell lengths of the 0-group *Ensis* taken in December 2001 were some 5 mm larger than the lengths of the same animals sampled at sea two months later, in February 2002 (Table 4.8, t=5.88, P<0.01). The shape of the size distribution of *Ensis* present in the seabed and of *Ensis* found in the faeces is very similar, with an offset of 5mm (Figure 4.7). This suggests that the difference should not be attributed to selective sampling (either through size selection by the birds or by selectively missing relatively large *Ensis* in the grab samples). More likely, a systematic error was involved in estimating the size of these small 0-group *Ensis* from the hinges still present in the faeces. Without a feeding experiment in which sizes of prey fed to the birds are known (like in our experiments with *Spisula*), this cannot be further explored.

If we compare the estimates of *Ensis* shell length (Table 4.8) as derived from different parts of the hinge to the presumed "ground truth" (the average sizes of *Ensis* in the grab samples in either winter), we see that measurement #5 (IF = maximum length in right valve, see Table 4.3 and Figure 4.3) gives the best estimates of original shell length, in both year classes. All other measurements resulted in overestimates in the 0-group *Ensis*, and in more varied errors in the 1-group.

Table 4.8 Average lengths (with SD and sample size) of the dominant age group of *Ensis americanus* in Van Veen bottom grabs taken off Texel in two consecutive winters compared to average lengths of *Ensis* found in Common Eiders *Somateria mollissima* faeces at the Razende Bol roost, as reconstructed from the hinges present therein. All specimens smaller than 65 mm were considered to be 0-group *Ensis* (see Figure 8) and all specimen between 65 and 110 mm were considered to be 1-group. For measurements #2-7 see Figure 4.3 and Table 4.3.

		Bottom grabs	#2 (A-B)	#4 (C-D)	#5 (I-F)	#6 (I-H)	#7 (E-G)	Average est. prey size
0-group:	Avg	40.21	45.09	49.49	41.80	46.57	46.94	45.42
Feb 2002	SD	4.51	4.40	4.90	5.55	4.80	7.84	5.73
	N	923	13	8	30	38	15	43
1-group:	Avg	84.08	80.01	94.01	82.54	81.82	89.95	84.80
Feb 2003	SD	6.29	6.58	12.21	6.41	11.34	15.79	8.63
	N	438	24	24	7	18	11	53

Ensis shell thickness

From each sample that contained *Ensis* the thickest fragment was sorted out, as well as an anterior (thinnest) fragment and their thicknesses measured. Eight more randomly selected fragments per sample were sorted out and measured. For using this procedure, it had to be assumed that all *Ensis* in one sample were of the same size. Finding the thickest fragments from the faeces proved to be relatively easy, since these were generally the largest parts present. Sorting out the thinnest parts was sometimes a problem, since these parts were often severely fragmented.

Shell lengths of *Ensis* were estimated using the equations given in Table 4.4. The predicted lengths of *Ensis* for December 2001 ranged from 44.7 to 79.6 mm and from 65.8 to 107.8 mm for February 2003. Figure 4.8 depicts the frequency distributions of estimated shell lengths. The three estimation procedures produced similar results. 0-group *Ensis* was predominantly taken by the Eiders in December 2001 and one year olds in the next winter (Figure 4.8). However, shell size was overestimated when compared to the average sizes of 0-group and 1-group *Ensis* in the grab samples in either year (Table 4.8). Possibly, relatively thick shell parts (within or between shells) were better preserved in the faeces, resulting in a positive bias of 1.5 to 2.1 cm (37–53%) for the 0-group *Ensis* and of 0.2 to 1.0 cm (2–12%) for the 1-group (Tables 8 and 9).

Discussion

Prey identification

Sea ducks such as eiders or scoters ingest their prey whole and crush these in their muscular gizzards. Remaining shell fragments in stomachs or faeces provide clues on the prey species taken. Eiders and scoters mostly feed on hard-shelled molluscs (Leopold *et al.* 2001a, Fox 2003) that always leave such clues. Other prey such as crabs, worms or fish also contain hard parts that may be identified and only very rarely soft prey such as fish eggs will be taken (e.g. Gjøsæter & Sætre 1974, Bishop & Green 2001) that may be overlooked for the lack of suitable hard parts. From Eiders, faecal samples can be collected with relative ease and these can be processed rather quickly. Scoters rest at sea, and collecting scoter faeces seems impossible. Good field material may, however, also be obtained from stomachs, from shot, drowned or oiled birds and good opportunities to use such material should always be considered.

In samples collected in the field, prey species composition is *a priori* unknown, as opposed to the situation in our cage experiments. In most field studies however, some understanding of local prey availability is usually available, aiding identification of shell fragments. In situations where ducks are likely to feed on one super-abundant prey organism, as has been be situation in the SE North Sea lately, the prey may be easily identified. However, sea ducks may also feed in habitats with a
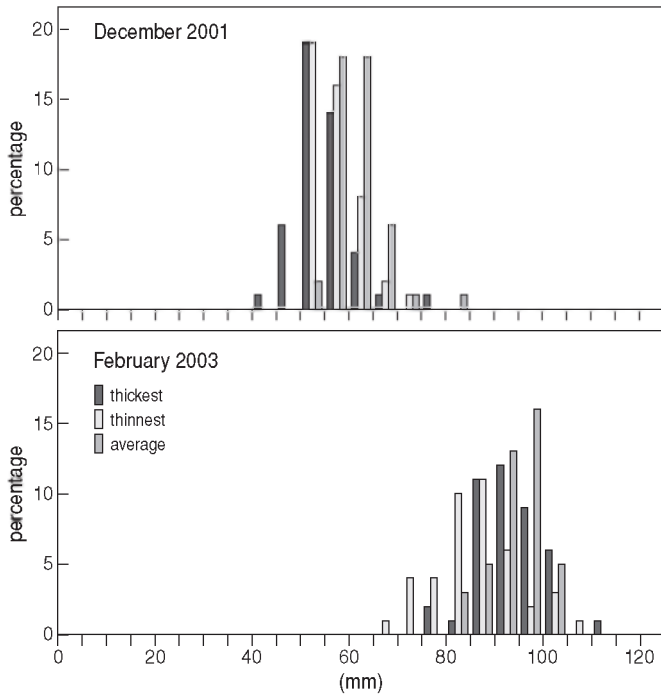
Figure 4.8 Estimated sizes (shell lengths, mm) of *Ensis americanus* taken as prey by Common Eiders *Somateria mollissima* resting on the Razende Bol in winter 2001/02 and in winter 2002/03. Shell lengths are estimated from the thickest fragment in each faecal sample, from the thinnest and from these plus 8 randomly taken fragments per sample (average).

much larger diversity of prey (*cf* Aulert & Sylvand 1997, Hughes *et al.* 1997, Thingstad *et al.* 2000, Rumohr 2002) and this could make identification of shell fragments more complex. In our own samples of eider faeces we found seven prey species, but one (*Ensis americanus*) was clearly the staple food.

Recognizing *Spisula* and *Ensis* fragments in sea duck stomachs or faeces proved to be rather straightforward. *Spisula* fragments are thick, and have a whitish inside and a light brown, rough outer surface with fine parallel lines. The shells are not clearly ridged like in *Cerastoderma* sp. (that are also much whiter and thicker). *Donax vittatus* shells are shiny brown on the outside without the fine lines that mark *Spisula*, and purple on the inside. The hinges of *Spisula* differ from those of Donax, by the presence of two lateral teeth on the left valve (and matching grooves on the right valve, Figure 4.1) and by having a chondrophore filled with a brown internal ligament. Donax lacks these features. *Spisula* hinges resemble those of the closely related *Mactra corallina*, but these shells are much thinner and their inside is purple, not white. *Ensis* is purple to pinkish-white on the inside and has a brownish skin on the outside of the valves. *Ensis* shell fragments are clearly thinner

than those of *Spisula* and much smoother. The purple to pink shells of *Mactra* are usually much darker than *Ensis* and lack an outer layer of skin as is present on *Ensis*. Some *Macoma balthica* are also pink but are so at both sides and these shells come in all sorts of bright colours, preventing misidentifications. Fragments of other bivalves like *Tellina* or *Abra* that may have been taken by scoters in Belgium waters (Degraer *et al.* 1999) superficially resemble *Spisula* or *Ensis* fragments, but are in fact different in both colour and texture. Mussel fragments are blackish blue and very different from *Spisula* or *Ensis*. *Mya* sp. are also important sea duck prey, particularly in the Baltic (Kirchhoff 1979, Stempniewicz 1986, Meissner & Bräger 1990, Kube 1996, Rumohr 2002, Žydelis 2002). *Mya* sp. are but is whiter than both *Spisula* and *Ensis* and have very different hinges. Shore crabs may be similar in coloration to both *Spisula* and *Ensis*, but are always given away by their claws that are their hardest parts.

Eiders and scoters take different *Spisula* species and razor clams in other parts of their range (see e.g. Stott *et al.* 1973, Hughes *et al.* 1997, Rumohr 2002) and identification could be more problematic if several similar species are taken simultaneously. Clearly, knowledge of the local benthic fauna helps to correctly identify badly broken-up prey remains. More information is needed on such prey species, but clearly, the methods presented in the current paper could also applied to these, or any other prey species with hard remains. Furthermore, using these methods is not necessarily restricted to seaduck studies, but could also be used on other animals that ingest shellfish whole, such as gulls (see e.g. Meijering 1954, Löhmer & Vauk 1969, Vauk & Löhmer 1969, Spaans 1970, Wietfeld 1977, Garthe *et al.* 1999, 2003, Kubetzki & Garthe 2003), waders (e.g. Dekinga & Piersma 1993, Scheiffarth G. 2001), or fish (Arntz 1972, Braber & de Groot 1973).

Estimation of prey numbers ingested

The number of measurable hinges that could be sorted out of the stomachs or faeces was low. No useful hinge-parts could be retrieved from 25 scoter stomachs. None were recovered intact from the faeces in our feeding experiments, only 55 bits and pieces were found after digestion and excretion of 239 *Spisula* (11.5 % of all available hinge-halves). From these 55 hinge-parts, 77 measurements could still be taken, mostly (n=52, Table 4.5) from the chondrophores. From the same 239 *Spisula* a total of 83 fragments from the outer rim were retrieved from the faeces (Table 4.6) that were suitable for thickness measurements, suggesting a slightly higher (17 %) recovery rate. However, since it cannot be excluded that more than one fragment per valve was measured, actual recovery rate was probably somewhat lower. The shells of *Spisula* appear to be quite brittle, and are crushed to small fragments in the ducks stomachs, destroying most measurable parts (cf Dekinga & Piersma 1993). *Ensis* provided even lower recovery rates. In our 92 Eider scats we found a total of 102 *Ensis* hinge-halves, with no clues that could be used to match left and right halves. Even if these 102 hinge-halves were from 102 different *Ensis*,

this would only represent about 1 razor clam per scat. Thickness measurements could not provide a better estimate of number of prey represented in a scat, as we used minimum, maximum or average values per scat (i.e. n=1). Field studies using faeces are, in any case unlikely to be of much use for direct estimations of numbers of prey ingested by birds that defecate many times a day. Thus, single scats only contain remnants of a fraction of the prey ingested during a day.

Prey size estimation

Based on both the feeding experiments and the field studies, we feel confident that the general size class (or age class) of both *Spisula* and *Ensis* was estimated correctly. However, within the size range of prey taken by eiders and scoters, sizes of small *Spisula* were overestimated, while sizes of large *Spisula* were underestimated, by about 2–5 mm on average (Figures 4.4, 4.5 and 4.6). Maximum errors for individual shells were about 8 mm (33%, Tables 4.5 and 4.6), these amounts of error were similar for reconstructions based on hinge and shell thickness measurements.

Based on field study comparisons, small, 0-group *Ensis*, of circa 40 mm length were over estimated by about 5 mm and 1-group *Ensis* of circa 84 mm by less than 1 mm in eider faeces, when hinges were used for reconstruction (Table 4.8). These errors were larger when shell thickness was used (positive biases of 15–21 mm in 0-group, and 2–10 mm in 1 group *Ensis*, respectively, Table 4.9). Still, again the dominant size (age) group was probably identified correctly in our eider faeces.

If a mixture of more than one year class of *Ensis* is ingested, using shell thickness will provide less accurate results. In contrast to *Spisula* in which particular parts of the inner shell could still be pinpointed in the fragments, we could only work with one (average or minimum or maximum) value per sample in *Ensis*. The fact that the faecal samples of the first winter showed a positive bias for estimated prey size could thus indicate that some 1-group *Ensis* were also taken, with a majority of 0-group prey. Some 1-group *Ensis* were present in the benthic samples,

Table 4.9 Average lengths (with SD and sample size) of *Ensis americanus* taken by Common Eiders *Somateria mollissima* off Texel, as reconstructed from the thickness of shell fragments present in their faeces collected at the Razende Bol roost. For measurements see Figure 4.2.

		Thickest part	Thinnest part	All ten parts
December 2001	Avg	55.20	57.14	61.44
	SD	5.58	4.32	4.81
	N	46	46	46
1-group: Feb 2003	Avg	93.21	86.07	94.34
	SD	7.22	9.34	5.17
	N	42	42	42

and if the ducks showed a strong preference for these larger preys, such a bias in estimated sizes could occur. Alternatively, a positive bias of ingested prey sizes may also occur if the probability of retrieving measurable shell fragments increases with shell size. There is also some evidence in support of the latter hypothesis. Given that smaller prey should be taken in larger quantities than larger prey, larger numbers of *Ensis* should have been found in the first winter samples when mainly 0-group *Ensis* were available. The opposite was found (Figure 4.7, Table 4.8), suggesting that many of 0-group *Ensis* hinges got broken to such an extent in the ducks' stomach that they could not be retrieved from the faeces.

Is the method accurate enough to study prey size selection by sea duck?
Fox (2003) has commented that: prey selection in Common Scoter has still to be demonstrated, as data on sizes of ingested prey and prey sizes available for ingestion in field situations have never been studied simultaneously. He also noted that scoters have been recorded to feed on a wide size range, and suggested that scoters may not be very selective when it comes to prey size. This suggestion is corroborated by the results of Durinck *et al.* (1990), who found the same sizes of ingested *Spisula subtruncata* in Common Scoters and the larger Velvet Scoters that were drowned in the same bottom set-nets, indicating that both species of sea duck simply took what was locally available. In contrast, many studies on the feeding ecology of Common Eiders (summarized in Leopold *et al.* 2001a) have shown that these ducks are selective, taking mussel sizes with the highest energy return, or prefer small or thin-shelled individuals or mussels with relatively few barnacles growing on their shells.

In our own work on *Ensis*-eating eiders, we unknowingly studied a situation in which mainly 0-group *Ensis* was available to –and taken by- the ducks in one winter, while both 0-group and 1-group *Ensis* was available in the next winter. When given this choice, the birds clearly selected the larger, 1-group prey, *Ensis* of 8–9 cm long (Figure 4.7). There is some evidence, both from direct observations and from stomach analyses, that eiders and scoters are capable of eating even larger *Ensis*, but as yet, optimal or maximum sizes (or indeed dangerous sizes) are not yet known.

Our small data set from stomach contents of scoters (Figure 4.6) suggests that they too, showed size selection. These ducks were feeding on a rich *Spisula* stand that was mainly composed of 14–21 mm long individuals. Although these were probably also mostly taken by the scoters, we found evidence that larger (older) *Spisula* of 25–30 mm were taken disproportionably often (Figure 4.6). According to Fox (2003) this is the first evidence for size selection in scoters.

Our study presents the first evidence for size selection in Common Eiders feeding on a new prey species, the American Razor Clam. Perhaps surprisingly, the eiders took relatively large *Ensis* when given the choice. Apparently, the better energy return out weighted the risk of injury in 1-group *Ensis* compared to 0-group

razor clams. In both situations, the *Ensis* was the staple food of the eiders, in a situation when the traditional prey species (blue mussel, edible cockle and *Spisula*) were in short supply. In the winters of 2001/02 and 2002/03 when our study was conducted, the *Spisula* stocks had just collapsed in the Netherlands, while stocks of mussels and cockles in the Wadden Sea were also very low. Tens of thousands of Common Eiders had died of starvation during the preceding winter (Camphuysen *et al.* 2001) and the ducks were hard-pressed to switch to alternative prey. *Ensis americanus* has colonized the eastern North Seaboard very successfully, and both eiders (this study) and scoters (Leopold & Wolf 2003, Wolf & Meininger 2004) have now learned to utilize this rather awkwardly shaped shellfish to their advantage.

Mass mortality of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance

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Abstract

Mass mortality of common eiders (*Somateria mollissima*) was observed in winter 1999/2000 in the Dutch Wadden Sea. Approximately 21,000 common eiders died. Dissected birds were severely emaciated and 94% were infected with the acanthocephalan parasite *Profilicollis botulus*. Green shore crabs (Carcinus maenas), intermediate hosts of the parasite, were slightly more 'available' than in other years, but parasite infections in the eiders were close to normal. Few eiders were oiled (5%), there were no toxicological, bacteriological, or virological explanations for the observed mortality.

In the Wadden Sea, a wetland of international importance, mussel (*Mytilus edulis*) cultures occur in sublittoral areas, while mechanical cockle (*Cerastoderma edule*) fisheries are licensed annually after evaluation of available resources. The wintering eiders in 1999/2000 required *c*. 3.1 million kg ash-free dry mass, while information on mussel and cockle stocks (irrespective of accessibility and profitability) suggested a resource 4.7x the requirement of common eiders only. Food shortage is suggested to have caused the observed mortality, involving both principal (mussels and cockles) and secondary (*Spisula*) prey.

Winter census reports showed shifts in wintering distribution of common eiders in the 1990s, indicating the utilisation of *Spisula* in the North Sea in poor food years in the Wadden Sea. Following particularly intense fisheries in summer 1999, attempts to feed on *Spisula* in winter 1999/2000 failed. It is hypothesised that overfishing of mussels and cockles in the Wadden Sea in the early 1990s resulted in structurally reduced food resources, contractions of the foraging area of common eiders, and increased use of secondary prey in the North Sea.

Introduction

The Dutch Wadden Sea is of vital importance to about 50 species of waterfowl, waders, gulls and terns, that depend on it for at least part of the year (Van de Kam *et al.* 1999). The internationally important wintering population of common eiders (*Somateria mollissima*; 1993–1997, 102,000–173,000 individuals) mainly originates from Baltic and Danish breeding colonies (Swennen 1990, Baptist *et al.* 1997). Small numbers migrate further south, effectively making the Wadden Sea the southern border of their distribution (Cramp and Simmons 1977).

In the mild winter and spring 1999/2000 mortality of common eiders was exceptionally high. All dead eiders showed signs of starvation, and most were infected with acanthocephalan parasites, of which green shore crabs (*Carcinus maenas*) are the intermediate hosts (Liat and Pike 1980). Common eiders are large, marine, molluscivorous ducks and are the main avian consumers of blue mussels (*Mytilus edulis*) and common cockles (*Cerastoderma edule*) in the Wadden Sea, together with the Eurasian oystercatcher (*Haematopus ostralegus*; Swennen 1976a, Smit 1981). In this paper we describe the mass mortality, using results of beached bird surveys, pathological studies of dead birds and winter population censuses. In addition, we sketch the conditions and (recent) historical background under which the incident took place. The main questions addressed are:

1. What factors could have contributed to the elevated mortality?
2. Were parasite loads abnormal, both in the common eiders and in green shore crabs (intermediate hosts of acanthocephalan parasites)?
3. Was there evidence for food shortage of common eiders in winter 1999/2000?
4. Could modern fisheries practices have contributed to this incident?

The post-hoc nature of the present study may be considered typical and perhaps inevitable for unexpected incidents such as the one described. The questions raised must be answered by utilising data sets that have not been collected exactly for that purpose. We provide this as a case study of what could be seen as a common problem (worldwide) that is seldom solved or explained satisfactorily: presumed or potential fishery effects mixed up with anomalous environmental conditions (Jennings *et al.* 2001). The available information is used to formulate a hypothesis of what may have caused the mortality and what the underlying mechanism could have been.

Materials and methods

To look back in time, and to place the results in an historical context, we have applied data that were collected during long-term study programmes. For example, the mortality was discovered and is described on the basis of systematic counts of corpses of birds (beached bird surveys), using a monitoring programme that start-

ed in the mid 1960s (Camphuysen 1998). Potential causes of death are compared with those of previous seasons or with studies and experiments elsewhere.

Study area
Data were collected in and around the Dutch Wadden Sea, between 52°40_ N, 04°35' E and 53°35' N, 07°07' E (Figure 5.1). This includes the northern part of the mainland coast of Noord-Holland, the mainland Wadden Sea coast and all islands. North Sea coasts were considered separately from coastal areas of the Wadden Sea itself. Eulittoral and sublittoral parts of the Wadden Sea were defined as areas respectively above and below the spring-tide low-water mark.

Examining common eider mortality patterns and scale
Beached bird surveys (BBS) were conducted by numerous volunteers in 19 subregions (Figure 5.1), seven of which are situated along the North Sea coast of the mainland (31 km total length; subregion 1) and the Wadden Sea islands (143 km; subregions 2–7). Seven subregions are in the western Wadden Sea (203 km; subregions 8–11, 14–16), another five in the east (96 km; subregions 12–13, 17–19). BBS were made on foot, walking the tide-line, by recording and describing every corpse. Notes included (sub) species, age, sex, and plumage of each bird, presence of oil in the feathers, and state of corpse (fresh, old, very old, complete or disintegrated). Corpses were marked by clipping the primaries of the wings to avoid double counts during later surveys.

For the present analysis, monthly BBS conducted between November 1999 and June 2000 were selected (336 counts, covering 1917 km in the Wadden Sea area). BBS have been centrally co-ordinated in the Netherlands with standardised methods since 1977, mainly covering the winter period (November–April). The annual total coast length surveyed in winter between 1977 and 1999 averaged 786.4±346.5 km (range 165–1615 km). A total of 1640 km were surveyed in winter 1999/2000. The fraction of oil-contaminated eiders of the total number found dead were logit-transformed and compared with the long-term trend fitted by least-squares estimation to check for abnormalities (Camphuysen 1998, C.J. Camphuysen unpublished data). In the subsequent analysis of seasonal patterns and between-year variations, oiled eiders were omitted to provide indices of 'non-oil-related mortality' over time. Many eiders were sexed and aged in the field and the proportion of adult males relative to all other birds found was used to illustrate shifts in age and sex composition.

Monthly BBS are sample counts and were used to estimate the total number of dead common eiders in the Wadden Sea by extrapolation for November 1999 until June 2000. With the spatial planning of counts it was attempted to sample monthly as much as possible of each of the 19 subregions; it was not intended to find as many stranded birds as possible by prioritising high density areas. All subregions were visited at least once, but coverage was rather poor at Terschelling
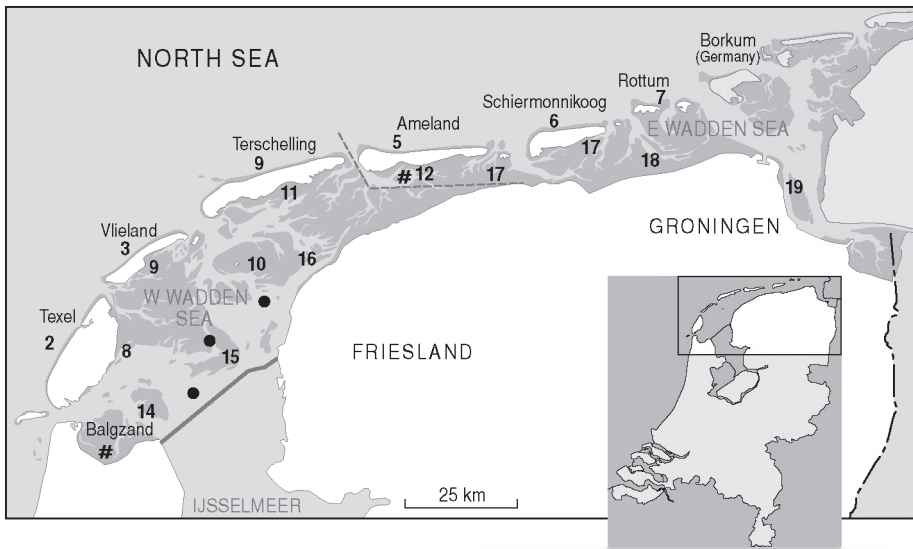
Figure 5.1 Northern part of the Netherlands showing Wadden Sea area with numbered subregions used in this study (see Table 5.1). Eulittoral macrobenthos study sites are indicated with #, sublittoral study plots with black dots. A dotted line separates the western from the eastern Wadden Sea.

(subregions 4, 11), Ameland (5, 12) and in the Balgzand area (14). Three log-linear Poisson models which assumed independence of the data were applied to input missing counts, as in Van der Meer *et al.* (1996). In each model, the expected value of beached birds was assumed to depend on a function of month and area (stretch of coast). The models differed in the extent to which they included interactions between these factors. Model parameters were estimated with the regression procedure of the Genstat 5.1 programme (Payne *et al.* 1987). Estimates of the monthly total number of dead common eiders in each of the coastal stretches (summarised per subregion) were obtained by extrapolation of observed or modelled (only where observations are missing) densities. Monthly surveys contained 62.8% missing values (n=584), a figure that was particularly high in May (79.4%, n=73) and June (83.6%, n=73), while mid-winter was better covered (40–60%).

Examination of collected eiders: dissections, histology, virology, parasitology
Between 27 December 1999 and 16 March 2000 100 common eiders were collected on Texel, and 13 corpses in December in Friesland. All birds were measured (basic biometrics) and weighed to the nearest 5 g. The birds were sexed and aged, using a combination of external (plumage) characteristic and gonadal development. The Texel batch was dissected to obtain an impression of the physical condi-

tion (fat reserves scored 0–3, i.e. depleted to very fat; breast muscle condition scored 0–3, severe atrophy to excellent condition), followed by a closer examination of the gizzard and the intestinal tract by a parasitologist. The gizzard was opened and the contents examined and removed. Empty gizzards were turned inside out and rinsed with water to score the presence of stomach nematodes *Amidostomum acutum*. Intestines were opened and the number of acanthocephalans was assessed as low (up to some tens), intermediate (some hundreds) or high (many hundreds to more than thousand worms). Samples of the contents of the intestines were examined with a stereomicroscope for other helminths. Samples of each type of parasite found were placed in 70% alcohol until later identification, and samples of severely affected tissue were placed in 5% formalin until later examination.

In the eiders from Friesland a more detailed necropsy was carried out, including examination of respiratory, digestive, urogenital, cardiovascular, nervous, haematopoietic, musculoskeletal, and endocrine systems. Five-micro-metre-thick sections of formalin-fixed, paraffin-embedded tissue samples were stained with haematoxylin and eosin and examined by light microscopy. The intestine was separated from the rest of the gastro-intestinal tract at the gastro-duodenal junction and at the colo-cloacal junction. Every 30 cm along the intestine, starting at the duodenum, 3-cm lengths of intestine were cut open. Acanthocephalans were counted, the width of the cut-open intestine was measured. The total acanthocephalan burden was calculated as the product of the average number of acanthocephalans per cm of intestine and the total length of intestine. Other parasites were sampled for subsequent identification as in the larger batch.

In addition to the birds collected, body mass was assessed for 44 freshly dead or dying common eiders in the field, mainly in December 1999, using Pesola spring and electronic balances.

Censuses of wintering eiders

Wintering common eiders were surveyed during aerial counts of the Wadden Sea and the bordering North Sea coastal zone. The first three surveys took place during ice-winters and concentrated on the limited areas of open water within the Wadden Sea. A subsequent 10 surveys were conducted between 1967 and 1991 by the Netherlands Institute for Sea Research (NIOZ), focussing on known concentrations of wintering common eiders (Swennen 1976a). The North Sea was seen as a secondary area and was covered only where eiders were known to occur. Since 1993, annual mid-winter surveys have been conducted by Rijksinstituut voor Kust en Zee (RIKZ) using a dense network of strip transects flown over the entire Wadden Sea (Baptist *et al.* 1997). In 1991, a transition year between the two programmes of aerial surveys, results from ship-based surveys indicated that large numbers of eiders had abandoned traditional wintering areas within the Wadden Sea to stay in North Sea coastal waters. These waters were included in all

subsequent aerial surveys (1993–2000; Berrevoets *et al.* 2000). Additional sources of information were the Dutch Seabird Group seawatching monitoring programme (1972–present) and ship-based surveys conducted since 1985 in Dutch coastal waters (Camphuysen and Leopold 1994, Platteeuw *et al.* 1994) to check for the occurrence of common eiders along the North Sea coast before the 1990s.

Shellfish abundance and quality

Long-term observations on the abundance and body condition of macrozooben-thos in the western Wadden Sea have been carried out in eulittoral areas at Balgzand since 1969 and at Piet Scheveplaat since 1978 (# in Figure 5.1). In addition, three sublittoral sections of the western Dutch Wadden Sea have been monitored since 1989 (black dots in Figure 5.1). The areas were surveyed twice a year (February–March and August–September). At Balgzand, 15 fixed locations were used scattered over the entire 60 km^2 area. Fixed transects were situated at Piet Scheveplaat and in the sublittoral part of the western Dutch Wadden Sea. Eulittoral areas were sampled with corers during low tide up to 30 cm deep. Samples were washed over 1-mm mesh screens in the field and sorted alive shortly afterwards in the laboratory. Sublittoral areas were sampled from a ship using a Reineck box-corer, penetrating about 20–25 cm into the sediment. Molluscs were identified and aged on board, densities were estimated, and individual length and biomass [g ash free dry mass (AFDM) after incineration at 560°C] was determined (Beukema 1988). Shellfish quality is expressed as Body Mass Index (BMI): individual biomass divided by the third power of the maximum shell length (in g mm^{-3}x106). Adult and juvenile mussels were treated separately because in this species, BMI tends to vary with age.

Crab abundance and cystacanth infection levels

The relative abundance of green shore crabs in winter 1999/2000 was described using results of the long-term macrozoobenthos monitoring programme (see earlier), including data from 10 previous years. A second set of data comprised standard catches in a long-term fish trap programme (1966–present; NIOZ). In a tidal inlet at the southern tip of Texel, fish and larger mobile epibenthic invertebrates were and still are caught, counted and measured on a daily basis (Van der Veer *et al.* 1992). Assessments of green shore crab abundance in autumn (1 September–15 November 1989–1999) were derived from this programme. In response to the observed parasite infection in eiders, samples of green shore crabs were taken, from eulittoral and sublittoral areas near Texel (February–March 2000). The presence of cystacanths (total number) was assessed after opening the carapace.

Results

Eider mortality

Unusually large numbers of dead eiders were first reported in November 1999 (overall density 3.3x long-term average, 1977–1998; Figure 5.2). Numbers of dead and dying eiders increased markedly in December (9.6x long-term average) and declined again in January 2000 (4.5x long-term average). A second episode of elevated mortality commenced in February (5.8x) and mortality levels peaked in March (12.8x) and April (12.4x), to decline again in May (9.6x) and June (5.8x long-term average). Between 1 November 1999 and 30 June 2000, 8745 casualties were recorded. After corrections for missing values, total numbers stranded between November 1999 and April 2000 were estimated at 18,150 (Table 5.1), with particularly high numbers on Texel, Vlieland, Terschelling, and mainland Friesland. Estimates of total numbers in May–June were less reliable due to poor geographical coverage, but a further 3000 eiders may have died.

Weakened common eiders congregated in small flocks along the coast, climbing ashore as often as possible (disturbance permitting). Long before such a terminal stage was reached, many nearshore eiders were incapable of flight. Weakened birds persistently stayed ashore. Shortly before death birds they be picked up and handled without any obvious reaction. Apart from eiders that died on the shore, many crawled inland, crossing roads and parking lots, to die in hidden corners in bushes and dune areas. Most of these were missed in beached bird surveys.

Oiled eiders found dead in winter amounted to 4.7% (n=7021), which was according to expectation (6%) based on the long-term trend (decline in logit-transformed fractions of oiled birds winter 1978/1979-1998/1999; *logit oil rate=* –0.04–0.12 *year*, $r^2=0.45$, DF=19, P<0.01). By contrast, non-oil-related mortality
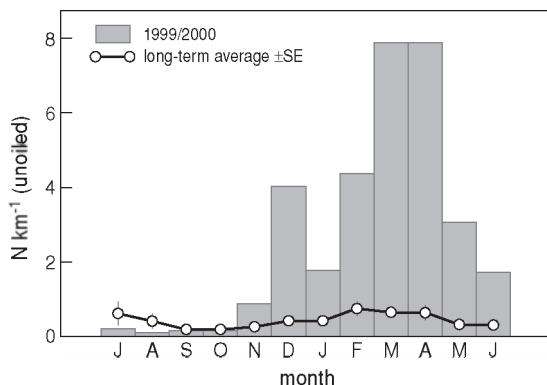
Figure 5.2 Seasonal pattern in common eider strandings in the Dutch Wadden Sea 1977–1999 (line; n km^{-1} ±S.E.) and densities observed in winter 1999/2000 (bars; n km^{-1}). Oiled birds were excluded.

Table 5.1 Extrapolated numbers of dead common eiders based on systematic beached bird surveys, November 1999–April 2000 (corrected for stretches of coast not visited, not corrected for eiders dying inland; see text).

	Subregions	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Total
1	Noord-Holland	9	10	28	115	285	54	71	30	600
2	Texel beach	19	73	35	90	561	482	220	115	1600
3	Vlieland beach	32	39	69	115	244	376	76	50	1000
4	Terschelling beach	4	42	4	22	48	48	16	7	190
5	Ameland beach	20	100	64	97	204	205	74	42	810
6	Schiermonnikoog beach	24	112	42	360	136	169	83	47	970
7	Rottum	9	46	29	44	93	94	33	19	370
8	Texel wadden sea side	53	66	158	259	839	591	197	165	2330
9	Vlieland wadden sea side	15	85	47	75	157	162	67	32	640
10	Griend	24	110	71	49	37	457	82	47	880
11	Terschelling wadden sea side	276	387	306	458	962	973	353	202	3920
12	Ameland wadden sea side	1	10	5	10	23	23	8	3	80
13	Schiermonnikoog wadden sea side	12	74	39	60	127	121	45	25	500
14	Balgzand	7	40	25	39	62	84	55	17	330
15	Afsluitdijk (barrier)	4	34	14	31	47	32	17	9	190
16	Friesland coast W	67	427	594	563	652	585	224	41	3150
17	Friesland coast E	73	825	261	130	426	535	254	146	2650
18	Groningen coast W	23	112	59	108	294	182	83	48	910
19	Groningen coast E	1	7	4	6	14	15	5	2	50
		673	2599	1854	2632	5211	5189	1962	1047	21,170
	% Adult male		3.2%	8.6%	15.8%	14.3%	31.6%	17.0%	13.7%	
	Sample aged		1202	538	656	1813	2186	259	226	

See Figure 5.1 for subregions. Proportion adult males only if n sexed and aged > 100. Totals are rounded to the nearest 10 birds.

in the Wadden Sea in winter 1999/2000 was unprecedented considering results of systematic beached bird surveys in the area over the previous 23 seasons (Figure 5.3).

In December 1999, the proportion of adult males was very low (3.2%) and most birds found dead were identified as juveniles or unaged birds in female plumage (probably also mainly juveniles). The proportion of adult males increased gradually from January through March, peaked in April, and declined again in
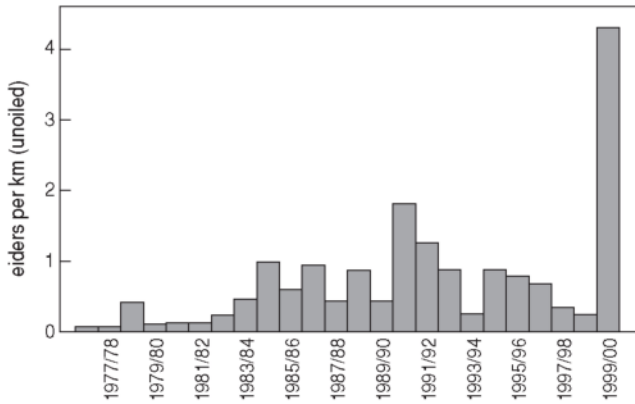
Figure 5.3 Winter mortality in common eiders in the Dutch Wadden Sea, November–April, 1977/1978–1999/2000. Oiled birds were excluded.

May and June (Table 5.1). Particularly high proportions of adult males (>30%) were found in the western Wadden Sea (sections 9–10) between 21 March and 20 April (47.1%, n=958 sexed and aged eiders), on the eastern Wadden Sea Islands early April (54.3%, n=70) and in the eastern Wadden Sea between 21 March and 10 April (33.9%, n=56). Using the extrapolations of Table 5.1, an estimated 5275 adult males may have been involved in the strandings between November and June. It is difficult to estimate total numbers of adult females due to identification problems, but a conservative estimate of 2500 individuals would lead to c. 7500 adult common eiders (one third of all birds found dead) involved in this mass mortality incident. Assuming a 1:1 sex ratio would lead to 10,500 dead adults.

Physical condition and parasites
The body mass of the eiders was 30–45% lower than published data for healthy birds of this subspecies (Table 5.2). Dissections proved that subcutaneous and deposited fat resources were completely depleted. Severe atrophy of the breast muscle indicated that few of the dissected casualties were capable of flight at the time of death. More detailed autopsies revealed severe atrophy of skeletal muscula-ture, serous atrophy of epicardial fat, a small, dark-tan liver with sharp edges, and a distended gall bladder. In all, 94.5% of the dissected eiders had a *Profilicollis botu-lus* (Acanthocephala) infection in the gastro-intestinal tract (Table 5.3). Total num-bers of acanthocephalans were counted in the Friesland material only, with 1790, 1811, 1825, and 1933 as maximum numbers. Infection levels in December 1999 (91.3%, n=23), February 2000 (92.5%, n=53), and March 2000 (100%, n=32) were similar. Infection levels in juveniles were significantly higher than those in adults (G_{adj}=9.393, DF=3, P<0.02; Table 5.3). *Profilicollis botulus* infections were associated with multifocal enteritis and in several heavily infected eiders, the acan-

Table 5.2 Body mass (g) of 157 common eiders found dead as fresh corpses, December 1999–March 2000.

Sex, age	Female	Juvenile female	Adult female	Juvenile male	Immature male	Adult male
Sample	8	61	7	57	4	20
Mean body mass	1384.4	1287.0	1420.7	1407.5	1462.5	1531.3
S.E.	39.2	23.1	42.6	19.3	61.3	28.0
Minimum	1160	895	1225	995	1280	1285
Maximum	1500	1800	1535	1820	1540	1795
Normal body mass (mean)[a]						
Denmark, winter		1770	2142	2080	2251	2315
W Baltic, drowned		2133	2588	2379	2541	2816

[a] 'Normal' mean body mass was taken from published sources: Denmark, mainly in winter (Cramp & Simmons 1977); wintering common eiders in good condition drowned in fishing nets in the western Baltic (Berndt *et al.* 1993).

Table 5.3 Presence and abundance of *Profilicollis botulus* in the intestine of 13 common eiders collected in Friesland (December 1999) and 98 eiders collected on Texel (December 1999–March 2000) and infection levels related to age (Texel sample).

Classification	Number of acanthocephalans	Sampling sites			Adults and immatures (%)	Juveniles (%)
		Friesland	Texel	%		
No infection	None	0	6	5.4	14.3	3.0
Light infection	Some to low tens	1	29	27.0	39.3	26.9
Moderate infection	Tens to low hundreds	3	23	23.4	28.6	22.4
Severe infection	Hundreds to thousands	9	40	44.1	17.9	47.8
Sample size		13	98		28	67

thocephalans had penetrated the intestinal wall, so that the heads could be seen hanging in the abdominal body, apparently without signs of severe peritonitis. Other helminths were the nematode *Amidostomum acutum* found in the gizzard (70% of all birds examined). Further parasites encountered in the intestines include the cestode *Microsomacanthus* sp. (38%) and the trematodes *Cryptocotyle* sp. (15%), Himasthla spp. (<5%), and *Microphallus* spp. (35%; Table 5.4). In some faecal samples of the dissected eiders also oocysts of the coccidia *Eimeria somateriae* (Protozoa; renal-coccidiosis) were found.

Table 5.4 Endoparasites encountered in 98 common eiders collected on Texel, December 1999–March 2000, including the location, the intermediate host (where known) and the frequency of occurrence (% infected).

		Location	Intermediate host	Infected (%)
Acanthocephala	*Profilicollis botulus*	Intestine	*Carcinus maenas*	94
Nematoda	*Amidostomum acutum*	Gizzard	–	70
	Streptocara californica	Gizzard	Gammarids	?
	Capillaria nyrocinarum	Intestine	–	?
Cestoda	*Microsomacanthus* spp.	Intestine	Insects/crustaceans	38
	Fimbriarioides intermedia	Intestine	Insects/crustaceans	<5
Trematoda	*Himasthla* spp.	Intestine	Snails	<5
	Cryptocotyle lingua	Intestine	Snails+fish	15
	Psilostomum brevicolle	Intestine	Snails	23
	Microphallus spp. (incl.: *Levinseniella/Spelotrema*)	Intestine	*Hydrobia ulvae/Littorina* spp.	35
	Gymnophallus somateriae	Intestine	Snails	<5
Protozoa	*Eimeria somateriae*	Kidneys	–	?
	Eimeria spp.	Intestine	–	?

?=encountered, but not systematically checked in all dissected individuals.

Wintering eiders

Between 1973 and 1999, complete mid-winter censuses always revealed at least 100,000 wintering common eiders (range 102,000–173,000, mean±S.D. 134,093±25,120, n=14). In January 2000, only 97,650 common eiders were found (Figure 5.4), of which 46,600 individuals (47.8%) occurred in North Sea coastal waters. That latter flock had largely disappeared by February (<10,000 remained). Prior to 1990, the North Sea coastal zone was of very limited importance (mean±S.D. 1.9±0.9% of the total wintering population, range 0.6–3.1%, n=6), but since 1990, a variable and sometimes very large proportion of common eiders wintered in the North Sea (1991–1999 28.5±16.7%, range 12.8–63.7%, n=8; Figure 5.4).

Prey abundance

Eulittoral cockle stocks (g AFDM m^{-2}) at Balgzand and Piet Scheveplaat were relatively high between 1993–1995 and in 1998–1999 (Figure 5.5). Cold winters in 1996 and in 1997 caused marked reductions in densities and total biomass. Winter biomass values were generally lower than in the preceding summer, as a result of mortality and continuing metabolic activity combined with low food sup-
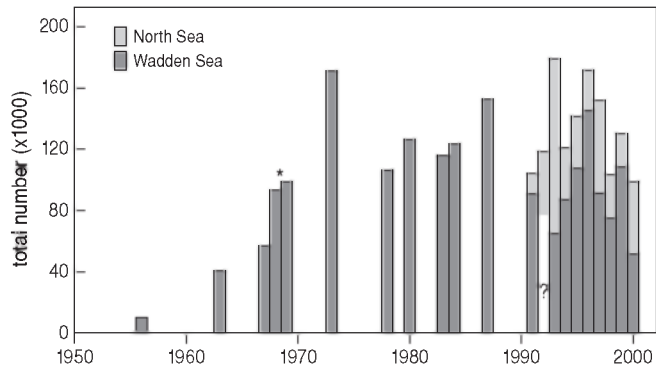
Figure 5.4 Total numbers of common eiders in mid-winter surveys in the Wadden Sea and adjoining North Sea; aerial and ship-based surveys combined. *, eastern half of the Dutch Wadden Sea not covered in 1968, numbers there have been intrapolated from 1967 (15,000) and 1969 (11,000) as 13,000. ?, no aerial survey of the Wadden Sea was available for 1992, only ship-based surveys of North Sea coastal waters.
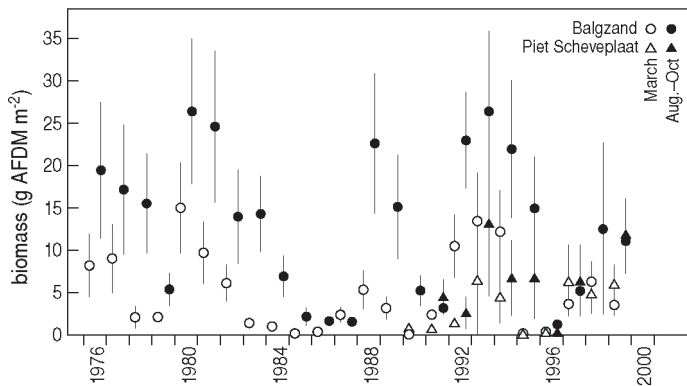
Figure 5.5 Biomass [g ash free dry mass (AFDM) m_2±S.E.] of cockles in the eulittoral at Balgzand (circles) and Piet Scheveplaat (triangles), August–October (black symbols) and March (white symbols), 1976–2000.

ply during autumn and winter. In mild to moderate seasons, winter biomass never dropped below a value of half that of the preceding summer. Eulittoral biomass values in 2000 were not exceptionally low compared with preceding years.

In sublittoral areas in the western Wadden Sea, all open for mechanical cockle fisheries, biomass reductions following cold winters were less pronounced (Figure 5.6). Fluctuations between summer and winter biomass values were considerably stronger than in the eulittoral. Total biomass variations did not follow the same
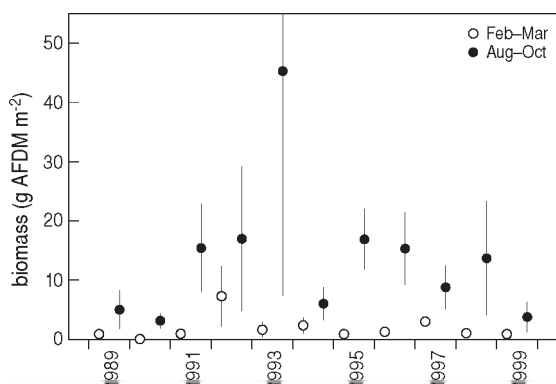
Figure 5.6 Biomass [g ash free dry mass (AFDM) m^{-2}±S.E.] of cockles in sublittoral areas in the western Wadden Sea (three samples), August–October (black symbols) and February–March (white symbols) 1989–2000.

winter-influenced pattern as found in the eulittoral and total cockle biomass in 1999/2000 was very low. Further data on cockle and mussel stocks were derived from national stock assessments (Smaal *et al.* 2001). Cockle stocks on 1 December 1999 were estimated at c. 60 million kg fresh flesh in eulittoral areas and a further 5 million kg in sublittoral areas. Sublittoral wild mussel stocks, assuming 27.5% flesh contents (Smaal *et al.* 2001) were estimated at c. 6.9 million kg fresh flesh mass, of which two-thirds were mussel seed and the remainder were at least 1-year old, eulittoral resources were estimated at 4.1 million kg fresh flesh mass. In comparison with five previous seasons, these figures were considered 'relatively high'. Estimates of blue mussel resources in culture plots indicate a stock of 38 million kg fresh mass (10.5 million kg fresh flesh mass); an 'average resource' for the 1990s, but considerably and consistently lower than published values for 1951–1989 (Figure 5.7).

Trough Shell (Spisula subtruncata) banks north of the Wadden Sea islands (off Texel) were extensively fished in late summer 1999 by c. 20 vessels, followed by small scale fisheries (two vessels) during most of the following winter (Leopold 1999). Inventories of shellfish stocks prior to and following the main fishery campaign indicated that in areas with >250 Spisula m^{-2}, 85% of the stock was removed, with only some 1-year-old molluscs remaining (Smaal *et al.* 2001).

Shellfish quality

The quality of cockles (BMI), showed a regular pattern of higher values in summer and lower scores in winter (Table 5.5). Cockle BMI in eulittoral areas was near average in summer 1999 and in winter 2000 at Balgzand, and only slightly below average at Piet Scheveplaat. In contrast, BMI values in sublittoral samples from
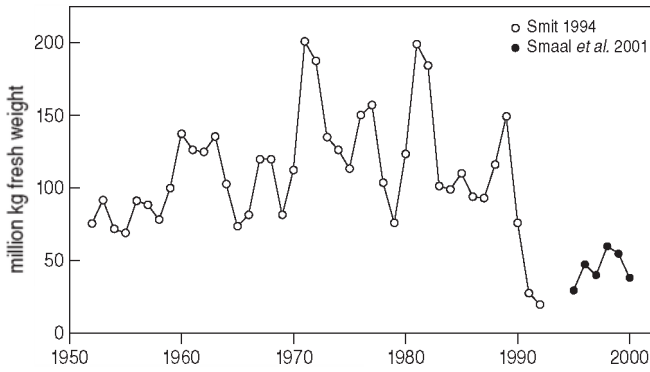
Figure 5.7 Estimates of mussel stocks in culture plots in the Wadden Sea (million kg fresh mass) from Smit (1994) and Smaal *et al*. (2001).

Table 5.5 Quality of cockles in summer and winter, expressed as body mass index (BMI in 106 g mm^{-3}), in eulittoral (Balgzand and Piet Scheveplaat) and sublittoral areas in the Wadden Sea (Figure 5.1) in the period 1989–2000.

Season	Balgzand		Piet Scheveplaat		Sublittoral areas	
	Summer	Winter	Summer	Winter	Summer	Winter
1989–1990	15.1	10.7			14.9	6.6
1990–1991	15.6	11.6		14.9	13.4	
1991–1992	11.3	8.7	13.4	11.8	13.1	8.3
1992–1993	15.3	8.5	13.7	10.0	14.8	7.9
1993–1994	11.5	8.0	15.4	10.9	15.4	9.3
1994–1995	13.0	8.3	15.4	9.8	12.3	6.8
1995–1996	14.6	8.1	16.2		13.6	7.2
1996–1997	12.8	7.3	13.3	8.7	14.6	7.5
1997–1998	17.3	10.0	19.7	10.2	14.9	8.5
1998–1999	17.1	9.1	11.8	6.7	15.4	8.4
1999–2000	15.4	9.1	13.4	8.0	12.1	6.3
Average 1989–1999	14.4	9.0	14.9	10.4	14.2	7.8
S.D.	2.1	1.3	2.4	2.4	1.1	0.9
Minimum	11.3	7.3	11.8	6.7	12.3	6.6
Maximum	17.3	11.6	19.7	14.9	15.4	9.3
Sample	10	10	8	8	10	9

1999/2000 values below the long-term minimum values (1989–1999) are indicated in italic.

the western Wadden Sea, both in summer (12.1) and winter (6.3), were the lowest on record over the last 10 years (Table 5.5). Annual average BMI-values (combining summer data with those of the following winter) in 1999/2000 equalled the long-term average in eulittoral areas at Balgzand (BMI 1999 12.2; 1989–1998 mean±S.D. 11.7±1.5) and Piet Scheveplaat (10.7 versus 11.7±2.1), but were the lowest on record in sublittoral areas (9.2 versus 11.1±0.8).

Annual average BMI-values of sublittoral adult mussels in 1999/2000 (4.4) were low compared with those in the previous 10 years (1989–1998 5.1±0.6), while both adult and 0-group mussels in eulittoral areas in 1999 were of average quality. Generally, sublittoral mussels, both adults and juveniles, show lower BMI values in the sublittoral than in eulittoral areas.

Shore crab abundance and parasite infections
Total numbers of adult green shore crabs during winter 1999/2000 at Balgzand and in the sublittoral parts of the western Wadden Sea were relatively high, but far from exceptional. The mean daily catch of green shore crabs, caught in the fish trap at the southern tip of Texel in autumn 1999 (147 day^{-1}), equalled average values observed during the preceding 10 years (148 day^{-1}, Figure 5.8). Of 119 green shore crabs collected February–March 2000, 5.9% were infected with cystacanths of *Profilicollis botulus*. A maximum of 20 cystacanths per crab were encountered. Smaal *et al.* (2000) reported crab densities as bycatch in demersal young fish surveys in September–October and indicated elevated densities, particularly in the western Wadden Sea (1994–1998 0.01–0.03 m^{-2}, 1999 0.04 m^{-2}).
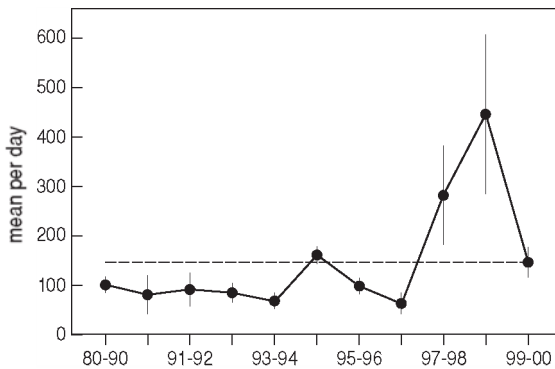
Figure 5.8 Mean (± S.E.) daily number of adult green shore crabs in standard fish trap catches at Texel, 1 September–15 November, 1989–1999 (NIOZ, unpublished data) and the average over 1989–1998 (dashed line).

Discussion

The Dutch Wadden Sea is used by millions of migratory, temporarily staging birds that utilise its resources of shellfish and other marine invertebrates. It is a wetland of international importance (RAMSAR Convention, EU Wild Birds Directive, EU Habitats and Species Directive) in which, however, shellfish resources are cultured and commercially harvested for human consumption.

It is clear that a major mortality incident occurred, but involving only the molluscivorous common eider. Wintering numbers of common eiders in winter 1999/2000 were perhaps slightly lower than normal, but more important was that 47% had abandoned the Wadden Sea to stay in North Sea coastal waters. This phenomenon has occurred repeatedly since 1990, but only twice on a similarly large scale (63% in 1993, 40% in 1997; Figure 5.4). Aerial survey design was modified in response to ship-based reports of increased use by eiders of North Sea coastal waters, so one could argue that eiders may have utilised the North Sea prior to the early 1990s. However, during coastal ship-based seabird surveys, substantial flocks (>1000) of common eiders were never encountered prior to 1991, which was confirmed by seawatching data that showed an increased use of North Sea coastal waters after the early 1990s (Camphuysen and Van Dijk 1983, Platteeuw *et al.* 1994, NZG/CvZ unpublished data). The sole exception was a southward movement of thousands of immature eiders in autumn 1975 along the mainland coast, followed by return movements in spring 1976. This exodus coincided with exceptionally low prey stocks (including cockles and mussels) and elevated mortality of common eiders and waders in the western Wadden Sea (Camphuysen 1997). In conclusion, wintering eiders have frequently utilised North Sea coastal waters in recent years, while that area was hardly used at all previously.

Poisoning, oil pollution and disease

Apart from the data presented earlier, a number of other factors that could have contributed to the death of the eiders can be ruled out. Changes in levels of heavy metals, polycyclic aromatic hydrocarbons, polychlorobifenyls (PCBs), hexachlorobenzene (HCB), tributyltin (TBT) and triphenyltins (TFT) between 1998 and 1999 were examined in water, sediment, suspended matter and mussels. No indications were found that any regularly monitored toxic substance may have caused the observed mortality (Werkman 2001). There was no evidence for 'red tide' poisoning from dinoflagellates or any other harmful algal blooms and shellfish were harvested for human consumption as usual. Proportions of oiled common eiders were in accordance with expectation during this mortality incident, compared with similar data collected over a 20-year period prior to this incident (Camphuysen 1998). Based on results of virologic, bacteriologic, and histopathologic examinations, there was no evidence of viral or bacterial disease as a cause of mortality in these eiders (Kuiken 2001).

Parasites

Acanthocephalans such as Profilicollis botulus are common and clearly visible parasites and therefore often the prime suspects for the cause of mortality (Grenquist 1970, Borgsteede 1997). Hario *et al.* (1995) reviewed acanthocephalan parasite outbreaks and found no evidence for direct parasite-induced mortality in common eiders, but reported combined occurrence of a weakened physical condition and heavy parasite burden. 'Healthy' eiders virtually always have some infection with acanthocephalans and 'natural' infection levels can be quite impressive (Table 5.6). Thompson (1985) showed that juvenile eiders (hatching early June) were free from P. botulus infection until 5–6 weeks post-hatching when they had been able to take crabs for food. In his experiments, infections (numbers of P. botulus per eider) rapidly increased in autumn and peaked in November, but subsequently declined through winter and by the following summer their abundance was similar to that in adult eiders. Under normal conditions juveniles would have been able to generate an appropriate immunological response towards gut parasites in the course of their first year (Thompson 1985), so that as in adults they should have been able to carry quite large loads of helminths without signs of sickness. We therefore believe that another factor must have contributed to their fate.

Table 5.6 Infection rates with *Profilicollis botulus* (% presence and abundance) in 'healthy' common eiders collected in the Ythan Estuary (east Scotland), in Newfoundland and Labrador (Canada) and along the west coast of Sweden.

Location	Sample	Presence (%)	Abundance	Source
Ythan Estuary, Scotland, 1955–1960	174 adult eiders	100	2–440	Garden *et al.* 1964
	375 juvenile eiders	100	3–2401	Garden *et al.* 1964
Newfoundland, Labrador, 1968–1969	110 eiders shot	92	1–654 (mean 80)	Bishop & Threlfall 1974
Sweden, west coast, 1968–1971	110 eiders shot	94.5	n.d.	Persson *et al.* 1974
Ythan Estuary, Scotland, 1970–1971	30 adult	76.7	Mean 29.8±9.4	Liat & Pike 1980[a]
	24 adult E	91.6	Mean 64.4±8.4	Liat & Pike 1980
	30 juvenile	96.6	Mean 272.3±64.5	Liat & Pike 1980
	32 juvenile E	93.8	Mean 270.9±59.4	Liat & Pike 1980
Ythan Estuary, Scotland, 1979–1982	38 adult	89	Mean 60±22, 0–753	Thompson 1985
	29 adult E	79	Mean 30±11, 0–297	Thompson 1985
	41 juveniles	n.d.	Mean 129±35, 0–1270	Thompson 1985

Range or mean number of acanthocephalans±S.E. per bird are given where known; n.d., no data, E = experimental data.
[a] No significant difference between sexes but mean number of worms significantly higher in juveniles than in adults (t=5.01, df=46, P<0.001).

Food

Diet and energetic requirements

Earlier studies indicated that 75% of the total consumption of carnivorous birds in the Wadden Sea was taken by only five species of birds, of which common eiders (28%) took by far the largest share (Smit 1981). Common eiders are principally subtidal predators and specialised feeders on common cockles and blue mussels (Swennen 1976a, Nehls 1989) that, unlike most other molluscivorous birds in the Wadden Sea, ingest shellfish prey whole and crush the shells in their muscular stomach. Green shore crabs, Baltic tellins (*Macoma balthica*), sand gapers (*Mya arenaria*), periwinkles (*Littorina littorea*) and common starfish (*Asterias rubens*) are frequently taken as secondary prey. Trough shells were not mentioned by these authors, but common eiders staging in North Sea coastal waters must have relied on this resource (Leopold *et al.* 2001a). Optimal diet theory predicts that food depletion should result in broader diets (Sih 1993). For common eiders, a shortage of preferred prey species could therefore have triggered a shift in feeding area: a partial exodus towards the North Sea where *Spisula* occurs.

From field observations and experiments, Nehls (1995) estimated the energy expenditure of wintering common eiders at 3000 kJ day^{-1} (4.3xbasal metabolic rate; BMR). Assuming an assimilation efficiency of 75% (Karasov 1986, Piersma 1994) and an average energy density of 22.5 kJ g^{-1} of cockles and mussels (Zwarts and Wanink 1993), the daily requirements of wintering eiders would amount to 177.8 g AFDM. With a wintering population of c. 97,000 individuals, a total of 3.12 million kg AFDM must have been required in winter 1999/2000; for average winter populations (1973–1999 134,450±25,700), c. 3.5–5.2 million kg AFDM. In comparison with shellfish stock assessments, assuming good quality prey and a water contents of c. 83% in shellfish-flesh (Kersten and Visser 1996, Zwarts *et al.* 1996b), common eiders would have required 18.3 million kg flesh mass in 1999/2000 (stock: common eider requirements=4.7:1). Earlier inventories of shellfish resources in the 1990s suggested that in most years the shellfish stocks exceeded the common eider requirements by a factor 7–10.

Prey stocks, prey quality, and prey availability

Our cockle data suggested that both quality (BMI) and stock were 'somewhat low' in winter 1999/2000. Our mussel BMI data also suggest a slightly lower value than in ten previous years. The observed fluctuations closely correspond with data from broad-scale inventories in the Wadden Sea by RIVO (Van Stralen and Kesteloo-Hendriks 1998) and match expectations that a series of mild winters has prevented spatfall and reduced individual cockle quality. Mild winters lead to comparatively low quality (lean) prey because cold-blooded animals maintain higher levels of metabolic activity during 'warmer' winters, while the food supply is low as usual (Honkoop and Beukema 1997). Shellfish inventories in the Wadden Sea indicated

a total resource of cockles and mussels of c. 87 million kg fresh flesh mass at 1 December 1999 (Smaal *et al.* 2001). None of these studies pointed to a very marked decline in shellfish quality or stock size, certainly not in comparison with the last 5–10 years.

Obviously, shellfish stocks are only partly available, because of size preferences of the birds and because of differences in prey quality, density, accessibility and profitability (Zwarts *et al.* 1996b). Ninety-two percent of the cockles occurred in eulittoral areas, which are not preferred feeding areas for common eiders (Smit 1981), and only (partly) accessible for them only during high tide. Of the mussel stocks, 49% occurred in culture plots, where common eiders are purposefully disturbed to scare them away (Smaal *et al.* 2001). Of the wild subtidal mussel stocks, 15% were >1 year old and 25% were mussel seed and therefore too small to be profitable prey (Nehls 1995). Hence, in total only 8.5% of the estimated total resource of c. 87 million kg fresh flesh mass in winter 1999/2000 (including cockles) was potentially suitable prey in favoured, constantly accessible feeding areas, 74% were partly accessible and under a strict tidal regime, and 12% were stocked in cultures. These figures, coupled with the fact that common eiders are only one of a number of molluscivorous birds in the Wadden Sea, suggest that the present stocks within the Wadden Sea may not be quite so large as the stock:requirement ratio would indicate.

The energetic and ecological consequences of mollusc consumption are considerable in birds that crush shells in their stomach (Nehls 1995). Estimates of the energetic requirements of common eiders (see above) have been made under the assumption of a 'normal' water content/AFDM ratio of mollusc flesh (83% water), while in fact recent winters were mild and molluscs therefore may have been lean. Much higher water fractions were measured in lean cockles (97.2% water; Visser *et al.* 2000). Assuming such water contents suggests that the entire shellfish stocks in winter 1999/2000 could have been insufficient for common eiders alone (111 million kg required, resource 87 million kg).

Earlier indications of food shortage
Substantial non-oil related mortality of molluscivorous waders and wildfowl in the Wadden Sea occurred during a series of three very mild winters (1989–1991) when there had been no spatfall of cockles and mussels, leading to very low resources in the Wadden Sea. These stocks were depleted by commercial fisheries in 1990 (Van Berkel and Revier 1991). In addition, virtually all mature musselbeds were removed from the eulittoral zone and these have shown little recovery ever since (Beukema and Cadeé 1996). Common eiders (Figure 5.3; Camphuysen 1997) and Eurasian oystercatchers (Camphuysen *et al.* 1996) experienced peak mortality levels following the depletion of shellfish stocks. Swennen (1991a) found that wintering eiders redistributed over previously unexploited parts of the Wadden Sea after the removal of mussel beds. Swennen *et al.* (1989) had indicated

that eiders obtained c. 20% of their prey from mussel culture plots, but since the early 1990s, the significance of mussel cultures for wintering eiders has increased markedly (Baptist *et al.* 1997, Berrevoets *et al.* 2000). Hence, for common eiders, this event marked the beginning of the distributional response to anomalies in food supplies in traditional wintering areas (Figure 5.4). The fisheries have responded to this range contraction over mussel cultures by (illegal) systematic chasing of eiders to scare them away. Yet, cultures seemed to have become a very important resource and there appeared to be a significant, negative relationship between mussel stocks in cultures and the proportion of eiders utilising North Sea coastal waters (R_S=–0.70, n=13, P<0.01). A reconstruction of mussel stocks in culture plots by Smit (1994) and Smaal *et al.* (2001) indicated a low level in most years since the early 1990s (Figure 5.7), explaining why common eiders increasingly utilised the North Sea in recent years.

Commercial fisheries
Between 1949 and 1989, cockle harvests steadily increased (from <2 million to 80 million kg fresh mass; Dijkema 1997), after which they became highly variable (Anonymous, 1999). The catch as a percentage of total cockle stocks (in densities of >50 m^{-2}) varied from 1–20% in the 1970s, to 4–96% in the 1980s and 8–25% in the 1990s (Van Stralen and Van Kesteloo-Hendrikse 1998). Between 55 and 96% were taken in years with particularly low stocks in the 1980s. The catch may seem rather insignificant in view of total cockle resources, but fishing effort is concentrated in high-density areas, i.e. in the most profitable areas for molluscivorous ducks (De Leeuw 1999), so that even a relatively minor catch has a great potential effect on prey availability. Pre- and post-fishing stock assessments showed how efficient cockle fisheries depleted subtidal cockle banks of the highest densities in 1998 when fisheries focused on subtidal areas (Van Stralen and Van Kesteloo-Hendrikse 1998).

Commercial fisheries for *Spisula subtruncata*, first developed in North Sea coastal waters in 1985, were extended from 1993 onwards to include the coastal zone off the Wadden Sea islands (Leopold 1993). In summer 1999, c. 85% of the fishable *Spisula* were removed within 1-month in an exceptionally extensive fishery campaign and with that the bulk of the available *Spisula* of suitable size north of the Wadden Sea islands (Leopold 1999).

Conclusions
To explain the excessive mortality of starved birds it was necessary that all available data were examined in a critical evaluation of the event, but also to look back in time. Combined fishery activities in the Wadden Sea in recent years, in particular the removal of permanent mussel banks and repeated, partial removals of high density cockle banks, have led to spatial shifts and contractions of the foraging range of wintering eiders not just in 1999, but since the early 1990s. Since that

time, offshore *Spisula* banks have been utilised by eiders as a refuge, notably in years with lower mussel stocks within the Wadden Sea. The utilisation of *Spisula* by common eiders should be seen as a clear sign that prey resources within the Wadden Sea were too low to sustain the wintering population of these birds. In autumn 1999, the *Spisula* banks became in turn severely overfished. We hypothesise that the population of common eiders collapsed as a result of a combination of factors: heavy fishing pressure on high density cockle banks and rather low stocks in mussel cultures over the past 10 years, some mild winters in a row with reduced spatfall and slightly reduced shellfish quality, plus stock depletion in the refuge area, i.e. the near-complete removal of *Spisula* off the Wadden Sea islands.

Chapter **6**

On the role of gastrointestinal helminths (*Amidostomum acutum* and *Profilicollis botulus*) in recent mass mortalities among Common Eider *Somateria mollissima* wintering in the Netherlands: a comparison between beached and shot birds

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Abstract

Common Eiders (*Somateria mollissima* L. 1758) wintering in the Netherlands showed mass mortalities in the winters of 1999/2000 and 2001/02 and three explanatory hypotheses have been advanced. The first proposes that the underlying cause of the mortality was food shortage, while the second proposes a parasite outbreak. The third combines both food shortage and parasites and states that food shortage caused high mortality among heavily parasitized individuals. To test the parasite outbreak hypothesis, we compared the parasite loads in beached (starved) and shot (healthy) Eiders, and studied if body condition was dependent on the parasite load of *Profilicollis botulus* in the intestine and/or *Amidostomum acutum* in the gizzard. These gastrointestinal helminths may occur in substantial numbers in the gastrointestinal tract and are potentially lethal. The prevalence (proportion of infected individuals in the population) and intensity of infection (number of parasites per bird) of *P. botulus* was respectively 92.2% and 287 ± 361 (1–1800) in 181 beached Eiders, and 83.8% and 109 ± 268 (1–2938) in 181 shot birds. The prevalence did not differ significantly between beached and shot Eiders, but was significantly higher in juveniles as compared to adults, probably as a result of differences in diet between the age groups. Compared to Eiders that were shot, the intensity of infection of *P. botulus* was 2–3 times higher in beached birds, with juveniles having 2-3 times more parasites than adults. The prevalence and intensity of infection of *A. acutum* was respectively 87.2% and 89 ± 113 (4–826) in 100 beached birds, and respectively 78.7% and 48 ± 98 (1–729) in 70 shot birds. The prevalence of *A. acutum* was significantly higher for beached birds. For this parasite, the intensity of infection in both beached and shot birds was 1–2 times higher in adults. Compared to shot birds, beached birds had a 30 % lower condition, 60 % lower liver mass and nearly no deposit of fat. Differences in body condition were explained by status (beached versus shot) and age, and were not explained by parasite loads. This is evidence against mass mortality being simply due to an outbreak of parasites. Elsewhere, we demonstrate that mass mortalities occurred in years with low food stocks. In combination with the somewhat higher prevalence and higher intensity of infection in beached birds, we propose that food shortage caused high mortality among parasitized individuals. The relative contribution of food shortage and high parasite loads to the level of mortality remains to be determined.

Introduction

In recent years, several episodes of mass mortality have been observed among Common Eiders wintering in the Netherlands (Camphuysen *et al.* 2002, Ens *et al.* 2002). Several hypotheses have been advanced to explain these mass mortalities. According to the food shortage hypothesis (Camphuysen *et al.* 2002), mass mortality is the result of starvation due to low stocks of harvestable food. Starvation was inferred from the low body mass of birds found dead and movements away from the traditional wintering area suggested a shortage of food in this area. Smaal *et al.* (2001) suggested an alternative 'parasite infection hypothesis' that the mass mortalities were primarily the result of parasite outbreaks. The importance of parasites was inferred from high parasite loads in many Eiders that were found dead, and from the fact that an intermediary host of one of the parasites, which is also prey to the Common Eider, was very common in the year with mass mortality. The third hypothesis states that mass-mortalities are the combined result of both food shortage and parasites (Grenquist 1970, Borgsteede 2001 and 2005). The idea is that individual birds can only sustain high parasite loads if they are able to acquire sufficient food.

For decades, diseases were considered to be an unlikely factor regulating the numbers of most wild birds, although empirical evidence was not available (Lack 1954), or were considered as a special form of predator (Ricklefs 1973). After combining population biology and parasitology, it was shown that parasites were able to regulate the host population, but there is a clear difference between the effect of microparasites and macroparasites (Anderson and May 1978, Anderson and May 1991). Microparasites (protozoans, viruses, bacteria) are characterised by a small size, a short generation time, the absence of a specialised, infective stage or intermediate hosts, the utilisation of vectors, reproduction within the host, and a strong immunological response or immunity after a rapid rise of parasites. Outbreaks of microparasites may lead to mass mortality of the host (see review in Newton 1998). In contrast, macroparasites (arthropods, helminths) have relatively complex life cycles and their infections are often chronic, leading to morbidity rather than (mass) mortality (Hudson and Dobson 1997). In many cases, parasite and host have co-evolved to a relationship where it is to the advantage of the parasite not to kill the host. The epidemiology and impact of macroparasites on the host are related to the parasite distribution within the host, age, intensity, density-dependent processes, time delays in development and the nutritional status of the host (Hudson and Dobson 1997). Most parasitic helminths live in the intestine, but also in other organs like gizzard, kidney or liver. For relatively few species of helminths, the life cycles are known (Janovy 1997). Helminths can either be transmitted directly or require an intermediate host (Rausch 1983). *Profilicollis botulus* that lives in the intestines of many birds, including Eiders, has infective stages in crustaceans (see below). Another common parasite in Eiders is *Amidostomum acutum*

that lives in the gizzard. Its cycle is direct (i.e. it has no intermediate hosts) and Eiders may become orally infected with the third stage larvae which is taken up directly from the water (Leiby and Olsen 1965). The two phyla we are dealing with here are respectively Acanthocephala or thorny-headed worms and Nematoda or roundworms (Rausch 1983).

The effects of infections with macroparasites are diverse, ranging from no (detectable) effects to death. Some species of helminths may have no (negative) effects (Dick and Burt 1971, Thomas 1986, Gray *et al.* 1989, Clinchy and Barker 1994). Other species affected host survival or fitness by increasing its risk of predation (Hudson *et al.* 1992a), changing its metabolism (Connors and Nickol 1991, Delahay *et al.* 1995, Hollmén *et al.* 1999), causing a decline in its body condition (Delahay *et al.* 1995, Millán *et al.* 2002), affecting the motivation to feed resulting in anorexia and loss of appetite (Hawkins 1993, Niezen *et al.* 1995, Coop and Holmes 1996, Kyriazakis *et al.* 1998). Host reproduction has been noted to decrease as a result of parasite infection, through reduced clutch sizes, hatching success, or chick survival (Hudson 1986, Saumier *et al.* 1986, Woodburn 1993, Hudson *et al.* 1992b). Finally, infections with macroparasites may reduce the attractiveness of the host for mates (Saumier *et al.* 1986, Read 1990, Folstad and Karter 1992) or reduce the ability of the host to compete for resources (Saumier *et al.* 1994) or mates (Rau 1983, Gray *et al.* 1989).

The pathogenicity of a helminth species can be dependent on host resistance (Watson *et al.* 1988), age and/or sex (Wallace and Pence 1986, Poulin 1996) and the intensity of infection (Lemly and Esch 1984). The intensity of infection may depend on prevalence (Bakke 1972) and density of the intermediate or definitive hosts (Holmes and Price 1986, Kennedy *et al.* 1986, Gray *et al.* 1989), and even the simultaneous occurrence of other parasites in the host (Bush and Holmes 1986, Sousa 1994). Testing the effects of helminths on the wild avian host or estimating mortality due to helminths can be achieved by experimentally manipulating the parasite load by reducing (Hudson 1986, Woodburn 1993) or increasing (Hollmén *et al.* 1999) the intensity of infection, or by comparing the parasite load of animals killed or found dead with an unbiased sample of wild animals (within population comparison). This latter approach has so far seldom been used (Hudson and Dobson 1997). Ideally, wild animals should be sampled at the same time and from the same region, but this approach depends on an existing long-term monitoring program of the parasitic fauna of wild and healthy birds.

The Common Eider *Somateria mollissima* is a large seaduck feeding primarily on Blue Mussels *Mytilus edulis*, but additionally also on other shellfish and crustaceans (Swennen 1976a, Beauchamp *et al.* 1992, Nehls 1995, Leopold *et al.* 2001a). A wide variety of helminths have been reported for Eiders (Swennen and Broek 1960, Persson *et al.* 1974, Borgsteede *et al.* 2005), but the species *Profilicollis botulus* Van Cleave 1916 (Acanthocephala) and *Amidostomum acutum* Lundahl 1848 (Nematoda) are by far the most commonly reported. *P. botulus* are attached

to the mucous membrane of the small intestine by a thorny proboscis (Persson *et al.* 1974) causing enteritis and perforation (Bishop and Threlfall 1974). The life cycle is indirect and Eiders, the final host, become infected with *P. botulus* after feeding upon the intermediate host, the Shore Crab *Carcinus maenas* (Swennen and Broek 1960, Rayski and Garden 1961, Ching 1989). Worms of the genus *Amidostomum* are found under the mucosal lining of the gizzard producing lesions (Leiby and Olsen 1965, Guglielmo and Burns 2001) causing symptoms like a loss of appetite, anaemia and emaciation (Herman and Wehr 1954). The life cycle is direct and birds associated with an aquatic life become orally infected with the third stage larvae (Leiby and Olsen 1965). Both species are reported to cause mortality among Eiders and also among other aquatic birds (Grenquist 1970, Thompson 1985, McLaughlin and McGurk 1987, Forrester *et al.* 1997, Kinsella and Forrester 1999). However, the problem with these reports is that they depend on nothing more than the observation of high parasite loads in birds found dead (Lampio 1946, Thom and Garden 1955, Clark *et al.* 1958, Swennen and Broek 1960, Rayski and Garden 1961, Bishop and Threlfall 1974, Wrånes 1988,). The birds found dead may have died for other reasons and the overall effect of these helminths on wild birds is therefore largely unknown.

To evaluate the role of these two helminths in the observed mortality events of Common Eiders in the Netherlands, we investigated the parasite loads of dead Eiders found during Beached Bird Surveys (BBS) in the Netherlands in winter, from November to April (Camphuysen *et al.* 2002, Ens *et al.* 2002). Ideally, we would have compared these data to the background parasitism in live Eiders from the same locality (Thieltges *et al.* 2006), but these data were not available. We therefore used data from Eiders shot in Denmark (Christensen *et al.* in prep) for comparison. We assume these birds to represent a random sample of healthy birds from the same population, because Eiders in the Netherlands and Denmark belong to the same Baltic-Wadden Sea flyway population (Swennen 1990, Desholm *et al.* 2002). On this basis, we compare the condition and parasite loads between starved birds (found dead in the Netherlands) and healthy birds (shot in Denmark), considering that the effects of high parasite loads on condition and mortality in Eiders should be primarily dependent on physiology of the birds and not on the geographic location. We will return to the validity of our approach in the discussion.

Predictions on prevalence and intensity of infection with *P. botulus* and *A. acutum*.

If parasites play no role in mass mortalities and they simply result from food short-ages, we predict that birds simply starve to death in such years. We expect no relationship between parasite load and condition and no difference in parasite load between starved birds (which all have a poor condition) and healthy birds (Figure 6.1A). Also, parasite load and prevalence should not be higher in years of mass
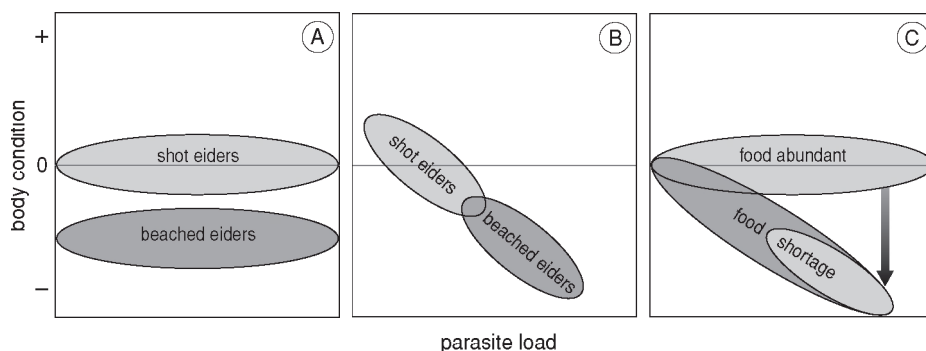
Figure 6.1 The relationship between parasite load and body condition (averaging zero in a population of healthy birds with an ample food supply) between shot and beached Eiders under three different hypotheses. (A) *The food shortage hypothesis* states that mass mortality is the result of food shortage only. Birds starve to death and parasite load does not affect condition, so that there is no difference in parasite load between starved birds (which all have a poor condition) and healthy birds. (B) *The parasite hypothesis* states that mass mortality is the result of parasites only. Condition decreases with increasing parasite load, so we expect and negative correlation between parasite load and condition for healthy birds (and probably also for the birds that died). We also predict substantially higher prevalences and parasite loads for the beached birds compared to the shot birds. (C) *The secondary cause hypothesis*, which states that the prime determinant of mass mortality is food shortage, but that when food is short, parasites increase mortality. When there is an ample supply of food, high parasite loads do not impact condition, so there is no relationship between parasite load and condition. However, when food is short, high parasite loads negatively impact condition and increase mortality.

mortality, unless starving birds switch to feeding on prey with a high risk of parasitism. Finally, bird mortality should be related to the primary food stocks and not to the stocks of prey transmitting a particular parasite.

In contrast, if mass mortality is the result of an outbreak of parasites, we expect a negative effect of parasite load on condition. Thus, for healthy birds (and probably also for the birds that died) we predict a negative correlation between parasite load and condition. We also predict substantially higher prevalences and parasite loads for the beached birds compared to the shot birds (Figure 6.1B). Furthermore, in years with mass mortality, parasite loads (and prevalence) should be higher, because under the parasite hypothesis, high parasite loads should be the primary cause of death in such years. Finally, we predict that conditions are such that birds run a high risk of becoming infected. For *P. botulus* this could be high densities of intermediate hosts for the parasite, that serve as prey for the Eider, like the Shore Crab *Carcinus maenas*. For *A. acutum*, which has a direct life cycle, this could be conditions that favour successful transmission of the parasite.

Finally, according to the third hypothesis, high levels of parasites are predicted to be observed in healthy birds in all years, but detrimental effects should only become clear at low food stocks. Only in years with low food stocks do we expect a

relationship as depicted in Figure 6.1B. In years with abundant food, we expect no relationship between parasite load and condition and no difference in parasite load between birds that were shot and birds found dead (Figure 6.1C).

We used our material to test these predictions and answer the following questions. First, what is the parasitological state of starved (beached) and healthy (shot) Eiders with respect to *P. botulus* and *A. acutum*? Did these differ, and if so, did age, sex, winter and status (beached or shot) explain these differences? Second, were body mass, liver mass and fat storage different for beached and shot Eiders? And if so, how are these differences related to age, sex, winter and status? Third, was the parasite load related to body condition? The results presented here on the prevalence and intensity are discussed and compared to data in the literature on the occurrence of both parasites in Common Eiders, and on the basis of these results, we address the fourth question: "What was the role of parasites in the observed mass mortality events among wintering Eiders in the Netherlands in recent years?".

Material and methods

Area and method of collection
Detailed information on body and liver mass, fat reserves and presence and number of two species of gastrointestinal parasites was collected from beached Common Eiders collected in winter 2001/02 in the Netherlands. Additional information (presence/absence data only) was available from beached birds collected in the Netherlands in winter1999/2000 (Camphuysen *et al.* 2002). Comparable, detailed data on body condition and parasite loads were obtained from a sample of Eiders shot in the Danish Wadden Sea and south-west Kattegat between 1 October and 28 February 2000/01 – 2002/03 (Christensen *et al.* in prep).

Regular beached bird surveys were used to calculate the average number of beached Eiders per km beach in winter (November–April) in the north-west Netherlands (Dutch Wadden Sea area and North Sea beaches from IJmuiden to Rottum; the main wintering range of the species in the Netherlands) (Camphuysen *et al.* 2002). These data were used to estimate the total number of Eiders that washed ashore in a given winter using statistical interpolation to correct for differences in the frequency with which different parts of the beach were searched (Ens *et al.* 2002). For the last two years, we used the strong relationship between the estimated total number of beached birds and the number of dead Eiders per km beach ($R^2 = 0.86$, n = 26, p < 0.0001) to estimate the total number of beached birds from the number of dead Eiders per km beach (total beached = 3796 * dead Eiders per km beach). The total number of beached birds divided by total population size yielded an estimate of the fraction beached during the winter, a minimum estimate of the overwinter mortality (Table 6.1).

Table 6.1 Size of the mid-winter population in January (Berrevoets and Arts 2003, De Jong *et al.* 2005), estimated total number of birds that beached from November until April (see text for details), dead Eiders per km coastline (Camphuysen 2005, Kats *et al.* 2007a), estimated winter mortality in wintering Eiders in the Netherlands (Kats *et al.* 2007a), and the stock of Shore Crab *Carcinus maenas* in the Wadden Sea (expressed as the average density N m^{-2} and sampled in autumn prior to winter) (De Boois & Bolle, pers. comm.). No data available is indicated with (–).

Winter	Midwinter population	Total beached	Dead Eiders per km coastline	Winter Mortality (fraction beached)	Density of Shore Crab
1992/93	164291	4184	0.87	0.025	–
1993/94	113638	1320	0.26	0.012	–
1994/95	136456	3643	0.87	0.027	0.0078
1995/96	166279	3347	0.77	0.020	0.0069
1996/97	140449	2878	0.66	0.020	0.0101
1997/98	98238	1420	0.34	0.014	0.0079
1998/99	128422	1095	0.25	0.009	0.0058
1999/00	97731	17399	4.83	0.174	0.0228
2000/01	112921	4185	1.38	0.037	0.0051
2001/02	104636	8339	2.69	0.078	0.0180
2002/03	86920	2555	0.60	0.029	0.0114
2003/04	113176	1518	0.40	0.013	0.0228
2004/05	116233	3417	0.90	0.029	0.0195

Dissection

The beached birds were all labelled (date and location of collection) and stored in plastic bags at –20°C. Only complete, clean and fresh carcasses were used, and for each corpse, sex and age (juvenile, immature, sub-adult, adult, both checked by plumage and gonad inspection), size (maximal wing length (mm), total length head to bill (to the nearest 0.1 mm), tarsus length (to the nearest 0.1 mm), body mass (to the nearest 5 g), subcutaneous fat (score from 0 to 5), and liver (wet mass in g) were recorded. Subcutaneous fat or fat content was defined as visible fat underneath the transparent skin in the furcula (F) and abdomen (A), which extended from the posterior end of the sternum to the cloaca (Rogers 1991). After removing the skin with feathers, fat became visible and was scored in 6 classes (Nolan and Ketterson 1983), but presented in 3 classes: no visible fat (or 0 = A and/or F with no fat); little fat or (1 = F < 33%, A < 50% covered); and a considerable amount of fat (or 2–6 = F > 33% and A > 50% covered).

Helminths in gizzard and intestine

The method of collection and quantification of both types of helminths is summarised and described in more detail elsewhere (Borgsteede 2005, Borgsteede *et al.*

2005). The entire gastrointestinal tract, including the gizzard and intestine, was removed for identification and quantification of two gastrointestinal parasites, i.e. *A. acutum* in the gizzard (Czaplinski 1962, Leiby and Olsen 1965) and *P. botulus* in the intestine (Khokhlova 1974, Ching 1989). For quantification of *A. acutum*, the gizzard was opened and rinsed and any worms that were visible at this point were collected. Next, the koilin layer was removed and worms were collected using a 6x stereo microscope. The stomach contents were sieved (mesh width 74 μm) and the number of worms present was microscopically (10x) counted. The koilin layer of the birds collected in the winter of 1999/2000 was not investigated, so prevalence and intensity of infection were probably underestimated (pers. obs. FB and Herman Cremers). *P. botulus* numbers were quantified after opening the intestine by counting worms present on the inner intestinal wall.

Estimating condition
An index of body condition was calculated from the difference between predicted and actual body mass, which was expressed as a percentage. As actual body mass is a combination of structural size and nutrient reserve mass (Piersma and Davidson 1991), the predicted body mass of beached Eiders was calculated from size and age corrected body masses of healthy Eiders. External size measurements were used to correct for structural size in multiple regression. We assumed that shot Eiders were in good condition and we regressed the masses of these presumably healthy birds against various measurements of their body size. A multiple regression approach was used to predict the body mass from age and structural size. We tested several regressions using bill length, wing length, age and sex and their interactions. The final model consisted of bill and wing length and age ($F_{3,40}$ = 17.64, p < 0.0001, R^2 = 0.57). The regression results indicated that bill and wing length can be used to predict the mass of an individual, but that adult birds were on average 221 gram heavier compared to juveniles (adult birds: estimated mass (g) = –1684.029 + 35.454*(bill) + 6.331*(wing); juvenile birds: estimated mass (g) = –1684.029 – 221.097 + 35.454*(bill) + 6.331*(wing). Body condition of the birds that starved and beached in the Netherlands was calculated as the difference between the actual and estimated mass and expressed as percentage of the estimated mass.

Statistical analyses
Data on parasites is presented as the prevalence, and intensity of infection. *Prevalence of infection* is expressed as the percentage of the infected hosts in a given sample (= (N_z/N) * 100 %, where Nz is the number of infected hosts, and N is the total number examined). *Intensity of infection* is expressed as the range and the mean number of parasites in infected hosts (= P/N_z, where P is the total number of helminths of a given species collected from the entire sample and Nz is the number of infected hosts). Birds were assigned to two age-groups, i.e. juveniles (incl. immatures) and adults (incl. sub-adults).

Data on prevalence and intensity of infection was analysed with Generalised Linear Models (GLM) using the statistical package Genstat (Lawes Agricultural Trust 2003). Differences in prevalence were analysed with four factors, i.e. status (beached, shot), age (juvenile, adult), sex (male, female) and infection (infected and parasite free), using log-linear models with a Poisson distribution. The quality of the fit of a model in GLM was approximately assessed by the scaled deviance (defined as minus twice the log-likelihood ratio between the model of interest and the full model that explains all variation), which has approximately a χ^2_d distribution (d is number of residual degrees of freedom). The approximation is best for large sample sizes, but is poor when sample size is small. The scaled deviance is a function of the dispersion parameter and the distribution depends on any estimate of that parameter. The estimate is obtained from the maximal model explaining all systematic variation. The importance of a term in GLM was assessed by (1) the difference between the scaled deviances of the model of interest and the model excluding the term, or (2) considering the ratios of mean scaled deviances between competing models, one of which is nested inside the other. The difference in scaled deviances has an approximate χ^2_t distribution (with t as the number of degrees of freedom of the term), which is a better approximation than the scaled deviance. The mean scaled deviance is the scaled deviance divided by the corresponding number degrees of freedom. The resulting ratios do not involve the dispersion parameter and have approximately an F distribution. Results are reported as deviance or log-likelihood ratio statistic of the data for each type of model, which is equivalent to the scaled deviance multiplied by the dispersion parameter. The fit of a sequence of nested models can be summarised by an analysis of deviance, which has the same interpretation as an analysis of variance, but the distribution only has an approximate χ^2 distribution. Misleading results are obtained with GLMs when sample sizes are small, which was shown for parasite prevalence (Gregory and Blackburn 1991) and intensity (Poiani 1992). Sample sizes were small for *A. acutum* and as a consequence differences in prevalence between groups were analysed in 2x2 contingency tables using the non-parametric χ^2. When sample size was less than five or at the extreme the Fisher Exact test with a two-tailed significance level was used.

Body condition was related to the abundance and intensity of infection of both parasites using multiple regression.

Results

Eider mortality and Shore Crab abundance
During the last decade, mass mortality of Common Eiders occurred in the winters of 2000 and 2002 when the density of Shore Crabs was high in the autumns prior to these winters (Table 6.1). However, in two other years with high densities of

Shore Crabs, no mass mortality was observed. As a result, when all data are analysed there is no longer a statistically significant relationship between the density of Shore Crabs (the intermediate host of *P. botulus*) and either the number of dead Eiders per km coastline (Spearman r = 0.26, P = 0.45, N = 11) or the fraction beached (Spearman r = 0.28, P = 0.40, N = 11).

Profilicollis botulus in beached and shot Common Eiders: prevalence and intensity

Total prevalence was high, amounting to 92.2% for beached (n = 268) and 83.8% for shot Eiders (n = 216) (Table 6.2). Within each status, using all three winters of data, prevalence was related to age, albeit not significantly in the case of shot birds (beached birds: $D_{11,1}$ = 6.34, p = 0.012; shot birds: $D_{11,1}$ = 3.47, p = 0.062) with higher prevalence among juveniles (Table 6.2). There was no evidence that prevalence differed between winters for beached birds ($D_{11,2}$ = 0.02, p = 0.984), but a tendency existed for shot birds ($D11,2$ = 2.89, p = 0.055). In a multiple comparison with status and the winters of 2001 and 2002, prevalence was only significantly related to age, but not to winter or status (Table 6.4A). Sex tended to have an effect on prevalence with a higher prevalence for females, but this did not reach statistical significance.

The intensity of infection averaged 287 (with a maximum of 1800) and 109 (with a maximum of 2938) for respectively beached and shot Eiders (Table 6.3). Table 6.3 and 6.4b show that (1) juveniles generally carried more parasites than adults, (2) beached birds often carried more parasites than shot birds and (3) even within a category a large variation in the intensity of infection was apparent. Furthermore, the intensity of infection in beached Eiders was dependent on the interaction between winter and age ($D_{7,1}$ = 6.00, p = 0.015), which was explained by differences among adults between years ($D3,1$ = 5.30, p = 0.024) with higher intensities among adults in 2001/02 compared to 2000/01 (Table 6.3). In shot Eiders, intensity of infection was dependent on the interaction between age and sex ($D_{11,1}$ = 23.57, p < 0.001), which was for both ages explained by winter (juvenile: $D_{5,2}$ = 4.88, p = 0.010; adult: $D_{5,2}$ = 5.59, p = 0.005) with low intensities in the winter of 2002/03 (Table 6.3). Sex was more important than winter for adults ($D_{5,1}$ = 35.50, p < 0.001) with 2.4 to 5.1 times higher intensities for adult females, and a tendency existed in juveniles ($D_{5,1}$ = 3.53, p = 0.064) with higher intensities in juvenile males in 2 out of 3 winters (Table 6.3).

In a multiple comparison with status and both winters of 2000/01 and 2001/02, intensity turned out to depend on the interaction between status, age and sex, but also between status, age and winter (Table 6.4b). Tables were broken down into sub-tables with respect to age, because juveniles, as in other studies, carried more parasites than adults. Within the juvenile age class, status and sex explained differences in intensity, with shot birds generally carrying fewer parasites than beached birds (Table 6.3).

Table 6.2 Inter-annual patterns in prevalence of infection (the percentage of birds infected) with *Profilicollis botulus* in the intestine and *Amidostomum acutum* in the gizzard, for beached and shot Common Eiders *Somateria mollissima* (J = juvenile, A = adult, M = male and F = female). No data available is indicated with (–).

| | | *Profilicollis botulus* | | | | *Amidostomum acutum* | | | |
| | | Beached | | Shot | | Beached | | Shot | |
Winter	Age/Sex	Prevalence (%)	n	Prevalence (%)	n	Prevalence (%)	n	Prevalence (%)	n
1999/00	JM	92.9	14	–	–	79.3	29	–	–
	JF	100	13	–	–	51.9	27	–	–
	AM	90.9	12	–	–	88.2	17	–	–
	AF	66.7	3	–	–	71.4	7	–	–
2000/01	JM	94.1	17	91.7	12	–	–	100	3
	JF	100	7	93.8	16	–	–	100	2
	AM	82.1	28	83.3	18	100	3	0.0	2
	AF	92.9	14	80.0	5	100	3	–	–
2001/02	JM	95.4	65	94.1	17	100	33	50.0	4
	JF	96.1	51	100	14	100	26	80.0	5
	AM	83.9	31	79.0	62	100	17	75.0	8
	AF	92.3	13	93.8	17	100	18	60.0	5
2002/03	JM	–	–	90.0	10	–	–	100	11
	JF	–	–	70.6	17	–	–	94.1	17
	AM	–	–	68.4	19	–	–	71.4	21
	AF	–	–	77.8	9	–	–	72.7	11
All data		92.2	268	83.8	216	87.2	180	78.7	89

Amidostomum acutum in beached and shot Common Eiders: prevalence and intensity

The prevalence of *Amidostomum* was high: 87.2% for beached birds and 78.7% for shot birds (Table 6.2). Years with no data in one of the four sex-age groups were excluded from the statistical analysis. For beached Eiders using data from 1999/2000 and 2001/02, variation in prevalence was explained by winter ($D_{7,1} = 40.40$, p = <0.001) and to a lesser extent by sex ($D_{7,1} = 5.70$, p = 0.017), because males in 1999/2000 had a higher prevalence compared to females and all beached birds were infected in 2001/02 (Table 6.2). Differences in prevalence in shot birds using only data from 2001/02 and 2002/03, tended to be related to age ($D_{7,1} = 3.83$, p = 0.050). The prevalence of *Amidostomum* in the winter of 2001/02 was only dependent on status with a significantly higher prevalence in beached birds (Table 6.2 and 6.4A).

Table 6.3 Inter-annual patterns (2000/01 – 2002/03) in the intensity of infection (mean number of parasites per infected host ± sd, range and sample size) of *Profilicollis botulus* in intestine and *Amidostomum acutum* in gizzard in beached and shot Common Eiders *Somateria mollissima* (J = juvenile, A = adult, M = male, F = female). No data available is indicated with (–).

| | | Profilicollis botulus | | | | | | Amidostomum acutum | | | | | |
| | | Beached | | | Shot | | | Beached | | | Shot | | |
Winter	Age/Sex	Mean ± sd	Range	n	Mean ± sd	Range	n	Mean ± sd	Range	n	Mean ± sd	Range	n
2000/01	JM	511±541	8 – 1800	16	186±146	7–473	11	–	–	–	15±13	3–29	3
	JF	363±406	40 – 1100	7	137±203	2–656	15	–	–	–	25±23	9–41	2
	AM	60±165	2 – 800	23	58±78	2–306	15	98±60	58–167	3	–	–	–
	AF	103±151	4 – 450	13	282±459	18–966	4	61±54	6–114	3	–	–	–
2001/02	JM	384±365	1 – 1600	62	374±720	4–2938	16	54±44	11–156	33	9±6	5–13	2
	JF	324±318	2–1600	49	153±239	10–926	14	40±31	4–141	28	22±23	5–55	4
	AM	181±386	4–1750	26	26±42	1–193	49	220±196	68–826	17	41±46	1–106	6
	AF	158±198	1–600	12	132±194	2–627	16	111±96	19–381	16	46±58	11–113	3
2002/03	JM	–	–	–	56±79	4–250	9	–	–	–	63±86	8–308	11
	JF	–	–	–	68±166	2–590	12	–	–	–	25±24	3–87	16
	AM	–	–	–	26±42	1–125	13	–	–	–	81±187	1–729	15
	AF	–	–	–	63±66	1–190	7	–	–	–	58±64	1–164	8
All data		287±361	1–1800	208	109±268	1–2938	181	89±113	4–826	100	48±98	1–729	70

Table 6.4 Analysis of the prevalence (multiple comparison using logistic regression (GLM)) and intensity of infection (multiple comparison using logistic regression (GLM) with Poisson distribution and over-dispersion) of two species of helminths (*Profilicollis botulus* and *Amidostomum acutum*) in beached and shot Common Eiders *Somateria mollissima* (Status: beached, shot; Age: juvenile, adult; Sex: male, female; winter): Only main effects and significant interactions are shown. Prevalence of *P. botulus* in 2000/01 and 2001/02 and *A. acutum* in 2001/02: no significant 2- and 3-way interactions. Intensity of infection of *P. botulus* in winters of 2000/01 and 2001/02 and *A. acutum* in all winters (1999/2000 – 2002/03): no significant 2- and 3-way interactions, and similar results in winter 2001/02 for *A. acutum* (not shown).

	Explanatory variables	(A) Prevalence			(B) Intensity of infection		
		d.f.	Deviance ratio (D)	p	d.f.	Deviance ratio (D)	p
P. botulus	Full model	15	1.45	0.115	15	9.06	< 0.001
	Status	1	0.43	0.510	1	15.34	< 0.001
	Age	1	9.74	0.002	1	60.60	< 0.001
	Sex	1	3.47	0.062	1	1.34	0.248
	Winter	1	0.07	0.792	1	0.04	0.844
	Age*Sex				1	7.98	0.005
	Status*Age*Sex				1	8.40	0.004
	Status*Age*Winter				1	8.29	0.004
A. acutum	Full model	7	3.80	< 0.001	7	10.58	< 0.001
	Status	1	24.61	< 0.001	1	19.60	< 0.001
	Sex	1	0.04	0.848	1	42.55	< 0.001
	Age	1	0.02	0.875	1	9.72	0.002

Among the 170 infected birds, the average intensity of infection for beached birds was 89 (maximum: 826), and for shot birds 48 (maximum: 729) (Table 6.3). Using all data, differences in the intensity of infection were primarily explained by age with higher intensity of infection in adults, but also by status and sex (Table 6.4B). These results were similar to the results using only data from the winter of 2001/02 (not shown).

Body and liver mass, and fat storage in beached and shot Eiders
Beached birds were extremely lean with 98% of the juveniles and 91% of the adults having no visible fat, whereas only 5% of the juvenile and 8% of the adult shot Eiders had no visible fat (Figure 6.2). The differences in body mass and liver mass were highly significant between shot and beached birds (Table 6.5). Body mass also differed significantly between sexes and ages (Table 6.5). The data indicate that adults are bigger and heavier than juveniles, and within an age class, males are bigger and heavier than females. A significant interaction between status and winter suggested that the two groups did not respond similarly in the two winters (Table 6.6A and 6.6B).

Figure 6.2 The fat content (expressed as the score of subcutaneous fat) in beached and shot Common Eiders *Somateria mollissima* separated for age (juv = juvenile, ad = adult). Fat score was divided into three categories: no visible fat (fat score = 0), little fat (fat score = 1) and a considerable amount of fat (fat score $\geq$ 2). Numbers above the bars indicate the sample size of each category

Table 6.5 Mean body and liver mass (expressed as wet mass (g.) $\pm$ sd and sample size) of Common Eiders Somateria mollissima with respect to status (beached, shot), age (J = juvenile, A = adult) and sex (M = male, F = female). No data available is indicated with (–).

| | | **Body mass** | | | | **Liver mass** | | | |
| | | Beached | | Shot | | Beached | | Shot | |
Winter	Age/Sex	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n
1999/00	JM	1408±136	27	–	–	–	–	–	–
	JF	1252±170	30	–	–	–	–	–	–
	AM	1536±112	14	–	–	–	–	–	–
	AF	1418±170	6	–	–	–	–	–	–
2000/01	JM	1460±169	20	2104±88	11	35±13	21	98±14	2
	JF	1344±224	8	1953±138	14	32±8	10	90±24	2
	AM	1602±194	25	2222±106	15	42±16	29	98±28	2
	AF	1487±104	10	2127±99	5	47±24	15	–	–
2001/02	JM	1400±139	78	2112±111	15	32±10	96	89±10	4
	JF	1337±141	62	2009±145	13	33±10	75	76±9	5
	AM	1573±171	40	2321±133	54	36± 13	43	93±14	8
	AF	1420± 219	22	2183±131	14	33±13	19	78±11	5
2002/03	JM	–	–	2021±198	6	–	–	92±14	10
	JF	–	–	1991±252	11	–	–	96±18	9
	AM	–	–	2543±268	8	–	–	98±19	14
	AF	–	–	2356±310	4	–	–	87±15	9
All data		1436	342	2162	170	36	306	90	70

Table 6.6 (A) Analysis of variance (ANOVA) of body mass (2000/01 – 2001/02), (B) ANOVA of liver mass, (log-transformed to obtain a normal distribution), and (C) analysis of covariance (ANCOVA) of body condition with three factors (Status: beached, shot; Age: juvenile, adult; Sex: male, female) and two covariates (infection with *Profilicollis botulus* (Pb) and *Amidostomum acutum* (Aa)), which were log transformed + 1. All main effects that were tested are shown, but interactions are only included if significant.

Explanatory variables	d.f.	F	p
(A) Body mass			
Full model	405	164.34	<0.001
Status	1	1821.11	< 0.001
Age	1	106.90	<0.001
Sex	1	48.33	<0.001
Winter	1	0.11	0.735
Status*Winter	1	8.28	0.004
(B) Liver mass			
Full model	335	21.52	<0.001
Status	1	261.85	<0.001
Winter	1	9.68	0.002
Age	1	7.18	0.008
Sex	1	0.44	0.507
Winter*Age	1	2.96	0.086
(C) Body condition			
Full model	91	9.83	<0.001
Sex	1	0.47	0.495
Age	1	8.40	0.005
Status	1	77.04	<0.001
Pb	1	3.25	0.075
Aa	1	0.05	0.831

Body condition and helminths in Common Eiders

Now that we have established that for both shot and beached Common Eiders juveniles generally carry more *Profilicollis* than adults and that adults generally carry more *Amidostomum* than juveniles, we would expect a negative correlation between the intensity of infection with the two species of parasite, when comparing individuals. Instead, we found no correlation at all (Figure 6.3), which can be explained by the extreme variation in parasite loads that occurs within each age-sex category. Consequently, we can treat the intensity of infection with *Profilicollis* as independent from the intensity of infection with *Amidostomum* in an analysis of the effect of these parasites on body condition. For both parasites we plotted body
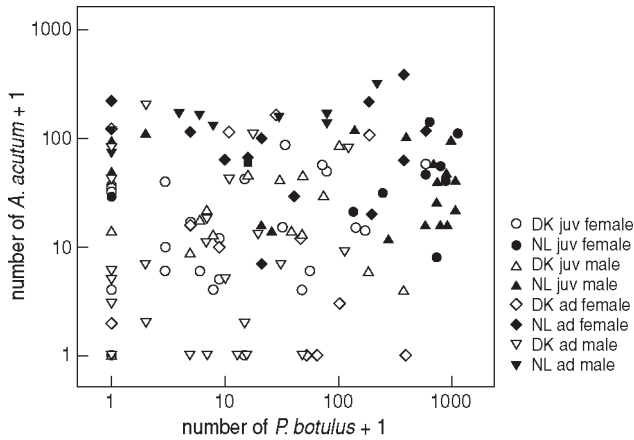
Figure 6.3 Log-log plot of Intensity of infection of *Profilicollis botulus* + 1 in intestine in relation to *Amidostomum* acutum + 1 in gizzard separated for beached (NL) and shot (DK) Common Eiders *Somateria mollissima* and different categories of age and sex.

condition (corrected for size and age) against parasite load, comparing beached and shot birds (Figure 6.4). There is a clear tendency for beached birds to have higher parasite loads than shot birds, in line with the results presented earlier. Body condition of beached birds, was approximately 30 % lower compared to shot birds, but did not show an obvious relationship with parasite load. Body condition was significantly explained by status, i.e. beached or shot, with a small contribution of age indicating that juveniles were even more emaciated than adults, but parasite load did not contribute significantly to body condition (Table 6.6c).

Discussion

Profilicollis botulus and Amidostomum acutum in Common Eiders and other waterfowl

The parasites *P. botulus* and *A. acutum* were abundantly present in both beached and shot Common Eiders (Table 6.2 and 6.3). In this study, differences in prevalence and intensity were mainly related to status and age (Table 6.2 and 6.3) for both parasites. Birds that were shot tended to have fewer parasites, which was true for both parasite species. The effect of age differed between the parasite species, with a higher prevalence and intensity observed among juveniles for *P. botulus* and among adults for *A. acutum*. A high prevalence and intensity of infection with *P. botulus* in juvenile Eiders compared to adults was also observed in many other studies (Garden *et al.* 1964, Kulachkova 1979, Liat and Pike 1980, Thieltges *et al.* 2006). In order to survive, juveniles feed more on amphipods (*Gammarus*
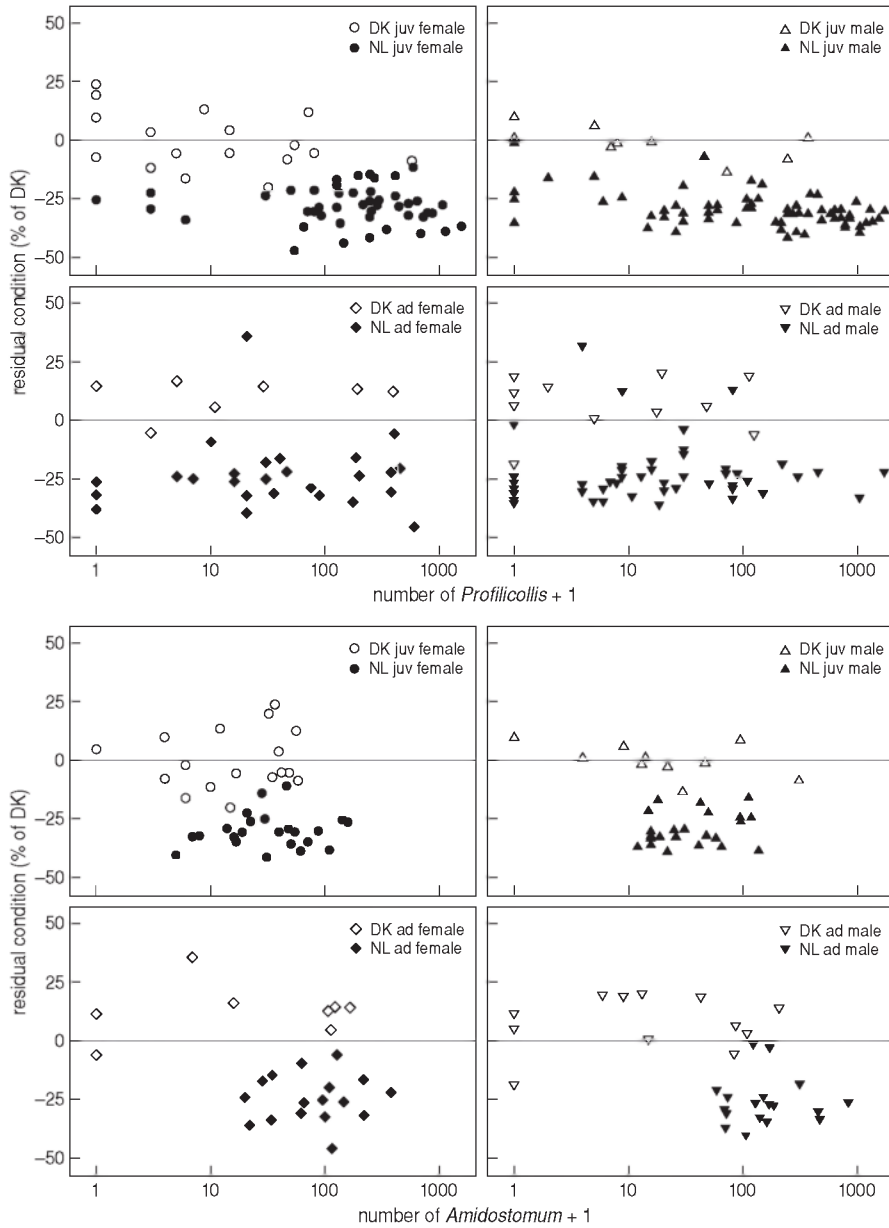
Figure 6.4 Condition (expressed as the % difference from the predicted mass of a shot bird, see methods) plotted against parasite load (on log scale). In each graph beached Eiders are compared to shot Eiders. The top graphs refer to *Profilicollis botulus* in the intestine and the bottom graphs to *Amidostomum acutum*. For each parasite, separate graphs are given for the different sex-age classes. Parasite loads were presented as the number of parasites +1, to allow inclusion of parasite-free birds in the graph (and in the statistical analysis, where we log-transformed the parasite load).

oceanicus) and crustaceans (*Carcinas maenas*), which are known inter-mediate hosts of two species of Profilicollis, and as a consequence juveniles have a higher risk of becoming infected with *Profilicollis* (Thompson 1985, Bustnes and Galaktionov 2004).

There are far fewer studies on prevalence and intensity of infection with *A. acutum*, but the results of some appear consistent with the results from this study (Kulachkova 1958, Persson *et al.* 1974, Thieltges *et al.* 2006). No differences in prevalence were found in this study within adults, but differences within adults (males: 83.3%; females: 49.2%) have been reported (Persson *et al.* 1974). Higher loads of *A. acutum* in adults compared to juveniles may simply relate to an effect of age (time susceptible to infection), and/or relate to differences in distribution and/or habitat selection or feeding behaviour, and within adults to different habitat use during breeding (Borgsteede 2005).

In beached birds, parasite loads are higher compared to shot birds, but intensity could have been even higher in beached birds, because parasites may have left the starving and dying host resulting in an underestimation of the actual number (Doster and Goater 1997).

Evidence for starvation
Differences in body mass were primarily explained by status, i.e. whether the birds were shot or beached. Shot and supposedly healthy birds were comparatively heavy compared to beached birds. The observed reduction of 28–35% in body mass of beached birds (Table 6.5) correspond with observations reported in the literature on starved and starving Eiders and other waterfowl. Reductions in body mass were 35-39 % for starved Common Eiders (Wrånes 1988) and 43–54 % in starved King Eiders *S. spectabilis* (Fournier and Hines 1994). Large reductions in body mass during starvation were also reported for several ducks (males and females) (Tufted Ducks *Aythya fuligula* (39–54%, 41–53%, Pochards *A. ferina* (33–48%, 29–49%), Scaup *A. marila* (53%, 54%), Goldeneyes *Bucephala clangula* (49%, 54%) (Suter and Van Eerden 1992)), and grebes (Little Grebes *Tachybaptus ruficollis* (56%) (Jenni-Eiermann and Schifferli 1989)). Reductions in body mass may be different between regions, because diving ducks from Switzerland starved at reductions in body mass of 29–41%, while similar species of diving ducks further North in the Dutch Wadden Sea starved at reductions of 48–54% (Suter and Van Eerden 1992). The probability of cold spells is higher and can last longer at higher latitudes in the more northern regions and as an adaptation to such cold spells, birds may store higher amounts of energy in colder areas or in areas with less predictable occurrence of cold spells.

Liver mass varied between 76 and 98 grams in shot and supposedly healthy Eiders (Table 6.5) and was higher than liver mass of females in spring (79 grams) prior to breeding (Guillemette and Ouellet 2005a). Differences in liver mass were

primarily explained by status with 57-64% lower mass for beached birds. Similar reductions in liver mass were reported for starved (41-51%) compared to healthy King Eiders *S. spectabilis* (Fournier and Hines 1994) and for breeding female Common Eiders during post-laying (63%) compared to pre-laying (Parker and Holm 1990). The size of the liver is flexible and responding rapidly to dietary changes (Tome 1984) or ovary growth (Guillemette and Ouellet 2005b) and provides protein during starvation (Fisher 1954), which explains the observed declines in liver mass.

In 5 to 8% of the Eiders shot during this study, no fat was found (Figure 6.2), a somewhat lower value than the 28 % reported for Eiders shot in Sweden (Persson *et al.* 1974). In contrast, subcutaneous fat was nearly absent in beached Eiders (Figure 6.2) and the breast muscles were atrophied in 93% of the examined beached birds (Ens *et al.* 2002), which was also reported for beached Eiders in Sweden (Persson *et al.* 1974). Absence of fat and depleted breast muscles were also reported for starved Pochards, Tufted ducks (Jenni-Eiermann and Schifferli 1989) and King Eiders (Fournier and Hines 1994).

Body mass in starving birds is reduced due to the depletion of fat reserves, muscles and organs in order to meet metabolic needs. The primary energy source is the adipose tissue (fat depot), followed by fat storage in liver and muscle (Whittow 1986). During the process of starvation, three distinct phases are recognised (Le Maho *et al.* 1981). In phase I, a change from proteolysis to fat mobilisation (Cherel *et al.* 1988, Robin *et al.* 1988), followed by fat becoming the main energy source and conservation of body proteins for vital structural and regulatory roles in phase II (Griminger and Scanes 1986, Owen 1989). During phase III, fat reserves are close to depletion and body proteins are extracted. Beached Eiders were characterised by strong reductions in body and liver mass (Table 6.5), almost complete absence of subcutaneous fat (Figure 6.2) and atrophied pectoral muscles (Ens *et al.* 2002), indicative of the final phase III. Summarizing, there is ample evidence that the beached Eiders starved to death.

The effect of helminths on body condition – empirical evidence

The joint effects of two types of helminths, i.e. an acanthocephalan *P. botulus* and nematode worm *A. acutum*, on the body condition of Common Eiders were investigated for the first time in this species. In addition, a within population comparison was also applied for the first time using beached and shot birds collected from the same Baltic-Wadden Sea flyway population, albeit at different localities (see later). We predicted a negative relationship between condition and parasite load under the parasite hypothesis. Body condition of beached birds was poor and was 30% reduced compared to apparently healthy birds (Figure 6.4). For a given sex and age class, beached birds generally had higher parasite loads than the birds that were

shot. However, rather surprisingly and despite large variation in parasite load, for birds of a given status (beached or shot), high parasite loads were not related with a poor body condition, although a trend seemed to exist for *P. botulus* (Table 6.6c). This was true when body condition was plotted against the intensity of infection with *P. botulus*, against infection with *A. acutum* or against both parasites. Christensen *et al.* (in prep) also failed to find evidence for a negative relationship between the load of *P. botulus* and condition in the Eider. In fact, for juveniles they found a significant positive relationship.

For birds, very few studies are available on the effects of helminths on body condition. Most studies consider the relationship between parasite load and body mass in birds of similar status (i.e. either all were shot or all were starved or oiled). A negative relationship between condition and the number of helminths is reported for Grey Partridge *Perdix perdix* (using breast muscle mass; (Tompkins *et al.* 2000)), female Willow Ptarmigan *Lagopus lagopus* L. (using ranked parasite intensities and body mass; (Holmstad and Skorping 1998)), Common Loons *Gavia immer* (lower body mass when infected: (Sidor *et al.* 2003)). Interestingly, body condition (body mass corrected for tarsus length) in Yellow-legged Gulls *Larus cachinnans* was negatively related to the number of some helminths species, particularly so if other species of helminths were also concurrently present (Bosch *et al.* 2000). However, negative relationships were not found in other birds, such as Rock Partridge *Alectoris graeca saxatilis* (Rizzoli *et al.* 1999), Ring-necked Pheasant *Phasianus colchicus* (Millán *et al.* 2002), Pied Flycatchers *Ficedula hypoleuca* (Potti and Merino 1995) and six species of Ardeidae (Navarro *et al.* 2005), and were also absent in mammals, such as Mountain Reedbuck *Redunca fulvorufula fulvorufula* and Gray Rhebok *Pelea capreolus* (Taylor *et al.* 2005).

Experiments are possible and may provide much insight. However, treating breeding female Common Eiders with an anti-helminth drug (fenbedazol) did not increase condition, decrease mass loss or return rate of successful females, but only return rate increased for unsuccessful females (Hanssen *et al.* 2003). The authors suggest that unsuccessful females are poor quality birds and that especially poor quality birds suffer from parasite infection. They argue that the benefit of reduced parasite loads for these low quality birds might be a down regulation of immune reactions, and not an increase in body condition as inferred from size-corrected body mass. However, the lack of effects on the host may have been caused by the administered drug, which according to one of us (FB) is inefficient in removing intestinal worms and therefore not appropriate. In addition, the actual reduction or removal of parasites was not assessed.

Mortality in the Netherlands: Food shortage and/or parasite infection?

Elsewhere, we have shown that there is good evidence that years of mass mortality coincided with shortage of sub-tidal mussels, which are the prime food resource in the western Dutch Wadden Sea (Ens and Kats 2004). To this we can now add the findings of this paper that there is no strong support for the alternative hypothesis that an outbreak of parasites was the primary cause of the mass mortalities as we will argue below. Before doing so, we must address the problem that from a statistical point of view, we cannot separate differences between birds that were shot or beached from differences between Eiders wintering in the Danish Wadden Sea and Eiders wintering in the Dutch Wadden Sea. While admitting this indisputable fact, we are inclined to believe that it does not invalidate our conclusions. First, Thieltges *et al.* (2006) recently collected Eiders from the nearby German Wadden Sea. These birds were killed by an oil spill in the winter of 1998/1999 when there was no elevated mortality of Common Eiders in the Wadden Sea. These birds were in good condition, yet carried high parasite loads. Values for the intensity of infection with *Amidostomum acutum* and *Profilicollis botulus* were in the same range that we reported for the shot and beached birds in this study. Second, the problem only applies when we compare groups, i.e. shot birds to beached birds, but does not apply to comparisons within groups dealing with the relationship between condition and parasite load, or differences between years. Our arguments against the parasite hypothesis rely on both types of comparisons.

Under the parasite hypothesis, we predicted a negative relationship between condition and parasite load, which was not supported by the data. The birds found dead in the Netherlands were in very poor body condition compared to the shot birds in Denmark, but within each category there was no evidence that high parasite loads were correlated with body condition.

Under the parasite hypothesis, we predicted a higher prevalence of parasites and higher intensities of infection in beached birds. In our study, the prevalence of both parasite species was very high in both shot and beached birds. In the case of *P. botulus*, prevalence only depended on age, with juveniles being more likely to carry the parasite. In the case of *A. acutum* shot and supposedly healthy birds were slightly less likely to carry the parasite. The most striking aspect of the intensity of infection with both parasites was the great variability between individuals, in either group of birds. Juveniles often had high loads of *P. botulus* and on average beached juveniles had more parasites than juveniles that were healthy, in line with other studies (Garden *et al.* 1964, Persson *et al.* 1974, Liat and Pike 1980, Thieltges *et al.* 2006). Beached adult males had higher intensities of infection of *P. botulus* in 2002. For *A. acutum*, adults tended to have higher intensities of infection than juveniles, and beached birds had more parasites than shot birds. These results on *A. acutum* could be taken as support of the parasite hypothesis. However, under

conditions of food shortage we expect the poor quality birds to die first and if poor quality birds have high parasite loads, which seems likely, we expect increased parasite loads in the starved birds (Hanssen *et al.* 2003). Alternatively, when feeding conditions deteriorate, feeding behaviour is predicted to change from risk-free feeding to more risky feeding on *P. botulus* infected crabs (Bustnes and Galaktionov 2004) in order to avoid starvation. Thus, the observation of higher parasite loads in beached birds compared to shot birds is also compatible with the hypothesis that food shortage is the prime cause of mass mortality, but that under conditions of food shortage poor quality birds (i.e. heavily parasitized individuals) suffer an increased mortality risk.

Under the parasite hypothesis, we expect high prevalence and intensity of infection in years of mass mortality. In the case of *P. botulus* there was no evidence for variation in prevalence between years within either beached or shot birds. In the case of *A. acutum* there was significant variation in prevalence between years within status, but in a direction contradicting the parasite hypothesis. Prevalence among beached birds was lowest in 1999/2000 (Table 6.2) when mortality was highest. Since we cannot rule out the possibility that we sometimes missed *A. acutum* due to initial imperfection in methodology in the first year of our study, not too much emphasis should be placed on this finding. It is quite possible that prevalence of *A. acutum* was 100% in beached birds in 1999/2000 as well. The intensity of infection with *P. botulus* in beached adults was higher in 2001/02 when mortality was highest. However, intensity of infection with this parasite was generally rather low in adults. Intensity of infection was much higher in juvenile beached Eiders and for this group there was no evidence of higher intensities of infection in 2001/02. We do not know if the intensity of infection with *A. acutum* varied between years, because we had only one year with a sufficient sample size of beached birds. Summarising, the data on variation between winters in prevalence and intensity of infection generally disagrees with the parasite hypothesis.

The parasite hypothesis was proposed by Smaal *et al.* (2001) because the mass mortality of 1999/2000 coincided with high autumn densities of Shore Crabs, which transmits *P. botulus*. However, the correlation between high autumn densities of Shore Crabs and mass mortality disappeared when data of recent years were added (Table 6.1).

Summarising, we conclude that the parasite hypothesis pur sang couldn't explain the recent mass mortalities in Common Eiders in the Dutch Wadden Sea. However, this by no means excludes the possibility that parasites played their part in the mortality, in combination with food shortage. Without parasites, the mortality that we observed might well have been less. According to Borgsteede (2005) possible costs for the host of a severe infection with *A. acutum* are (1) energy extraction for the parasite's maintenance, (2) the need to repair the damage to the muscular gizzard, (3) activated immune response, (4) possible disorder of function of the gizzard resulting in loss of appetite or anorexia, and (5) low input of nutri-

ents in intestine from gizzard and low absorption of nutrients in the intestine. When feeding conditions are good, the host may find it relatively easy to pay these costs and successfully fight the parasite. Careful experiments under controlled conditions are needed to measure these costs. When feeding conditions are poor, the host may not be able to pay the costs and succumb. This line of reasoning is in agreement with the idea "…that the diseases do not themselves form important mortality factors, but may lead to severe epidemics mainly as a result of other factors such as lack of food and exhaustion…" (Grenquist 1970).

Acknowledgements

The impact of man-induced and natural changes in shellfish stocks on population size, distribution and mortality of Common Eiders *Somateria mollissima* wintering in the Dutch Wadden Sea

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Abstract

We analyzed changes in mortality, population size and shifts in distribution of Common Eiders *Somateria mollissima* wintering in the Dutch Wadden Sea in relation to weather (winter severity) and stocks of shellfish prey (Blue Mussel *Mytilus edulis*, Edible Cockle *Cerastoderma edule*, Common Trough Shell *Spisula subtruncata* and American Razor Clam *Ensis directus*) using Generalized Linear Models (GLM).

We found no evidence that shifts in distribution or high mortality of Common Eider was related to stocks of Cockles. Instead, our analyses indicated a prominent role for the stock of subtidal Mussels, which are virtually restricted to the western Wadden Sea. When stocks of (medium-sized) subtidal Mussels were low, wintering Eiders shifted from the western Wadden Sea to the North Sea and mortality was increased. Mortality was especially high when, in addition to low stocks of subtidal Mussels, stocks of mature Common Trough Shells were low relative to the number of Eiders exploiting them. Thus, both the fishery on Common Trough Shells and mussel culture may impact the population of Common Eiders.

Mussel culture was introduced in the Wadden Sea in 1951 and this activity has the potential to increase as well as decrease the stock of subtidal Mussels in the Wadden Sea. Preliminary calculations for the 1990's by Bult *et al.* (2004b) suggest a slight positive effect of mussel cultures on the subtidal Mussel stock. However this calculation does not include cumulative effects and does not rule out the possibility that the activities of the fishermen actually decreased the stock of subtidal Mussels in the Wadden Sea during periods of scarcity. Whatever the cause, commercial landings of Mussels were at all-time lows in four seasons following the four winters with increased Eider mortality.

Determining the precise impact of mussel culture on the stocks of subtidal Mussels available to Common Eiders requires the development of a Mussel population model and the registration of all transports of Mussels.

Introduction

The Wadden Sea is a large tidal area in the northwestern part of Europe. To safeguard its internationally important natural values, the Dutch part of the Wadden Sea is a State Nature Monument and protected under the Ramsar convention and the European Union's Habitat and Bird Directives. In the Dutch Wadden Sea and the adjacent North Sea coastal zone, shellfish eating birds and the commercial shellfish fishery depend on the same natural resources. Conflicts may arise when shellfish stocks are low (Smit *et al.* 1998, Goss-Custard *et al.* 2004). Until 1990, there were no limitations imposed on the total commercial catch of shellfish, a condition which often leads to the "tragedy of the commons" (Hardin 1968), where the targeted stock is overexploited and, as a result, other fauna dependent on the overexploited stock is negatively impacted. In this respect, there is an interesting difference between the fishery on Cockles *Cerastoderma edule* and Cut Trough Shells *Spisula subtruncata*, which are both exploitative fisheries of the usual kind, and mussel culture, which is a combination of exploitative fishery on wild seed Mussels *Mytilus edulis*, and farming of the small Mussels to commercial size on strategically located culture plots (Dijkema 1997). Depending on the circumstances, mussel culture may either increase or decrease the total stock of Mussels in a given estuary (Bult *et al.* 2004b).

The Common Eider *Somateria mollissima* is the largest consumer of shellfish in the Wadden Sea (Smit & Wolf 1980) and dependent on shellfish stocks during winter (Swennen 1991a, Smit *et al.* 1998). In the Wadden Sea area the diet of Eiders consists mainly of Mussels supplemented with Cockles and a wide variety of alternatives, such as Cut Trough Shells, crabs, starfish and recently American Razor Clam *Ensis directus* (Leopold *et al.* 2001a, Leopold *et al.* 2005 or Chapter 4). Since the end of the 1980s, changes in distribution and increased mortality were repeatedly reported for wintering Eiders (Van der Kuip 1991, Baptist *et al.* 1997, Smit *et al.* 1998, Camphuysen *et al.* 2002). Analyzing these data, Camphuysen *et al.* (2002) hypothesized that "overfishing of Mussels and Cockles in the Wadden Sea in the early 1990s resulted in structurally reduced food resources, contractions of the foraging area of Common Eiders, and increased use of secondary prey in the North Sea". On the basis of beached bird surveys, pathological studies of dead birds and winter population censuses, it was concluded that mass mortalities of Common Eiders were most likely due to food shortages instead of pollution, oil spills or gastrointestinal parasitic infections (Camphuysen *et al.* 2002, Ens *et al.* 2002, Ens & Kats 2004, Kats *et al.* 2007b). Recently, quantitative estimates on the stocks of shellfish and total mortality of Eiders have become available as part of the EVA II research project, which aimed at assessing the impact of mechanized shellfish fisheries on the ecosystem of the Dutch Wadden Sea and Oosterschelde (Ens *et al.* 2004). This allowed us to perform a quantitative test of the hypothesis formulated by Camphuysen *et al.* (2002).

To this end, we related changes in population size, distribution, and mortality of Common Eiders to changes in the food supply. Two sets of data on the food stocks were available: a long-term and a short-term data set. Long data sets are to be preferred, but a long data set was only available for Mussels and Cockles, involving extrapolations from data on landings in the case of Mussels and from a local survey in the case of Cockles. The short-term data derived from quantitative surveys covering fewer years, but including all major species of shellfish prey and covering the entire feeding area of the Common Eider. The long-term and short-term data on shellfish stocks were collected independently of each other, and each data set had its own problems. We therefore decided to use both data sets in the analysis and investigate if the results were consistent.

None of the recent mass mortalities coincided with severe winters and we present data on winter severity to underline this. Since 1990, an estimated 70.000 dead Eiders have been recovered from Dutch beaches and the cumulative effect of these losses deserves scrutiny in view of the drastic fall of the Baltic/Wadden Sea flyway population over the same period documented by Desholm *et al.* (2002). To protect the populations of shellfish eating birds from additional mortality due to shellfish fishery in years with poor food stocks, a food reservation policy was introduced in 1993 as part of the new Sea and Coastal Fishery Policy (LNV 1993). We will discuss the effectiveness of this policy of food reservation in the light of our findings.

Methods

Study area
The Dutch Wadden Sea area consists of the Wadden Sea and the North Sea coastal zone in the northern part of the Netherlands between N 52° 25' – N 53° 35' and E 4° 25' – E 7° 00' (Figure 7.1). The Wadden Sea is separated from the adjacent North Sea by a chain of seven barrier islands and in the southern part by the coastline of the mainland. The Dutch Wadden Sea (2409 km^2) is a large tidal area characterized by tidal mud and sand flats with gullies, and natural beds of Mussels and Edible Cockles occurring in both the tidal and subtidal parts. In the analysis, the Wadden Sea is divided into the western (containing the islands of Texel, Vlieland, Terschelling and Griend: 1618 km^2) and the eastern Wadden Sea (containing the islands of Ameland, Schiermonnikoog, Rottum (including Rottumerplaat and Rottumeroog): 791 km^2) with large subtidal areas and commercial Mussel cultures present only in the western compartment and commercial Cockle fishery occurring in both compartments. The North Sea coastal zone ranges from IJmuiden to Rottum and during the study period its benthic fauna was dominated by beds of Cut Trough Shells *Spisula subtruncata* and recently invaded American Razor Clams *Ensis directus* (Smaal & Lucas 2000, Craeymeersch & Perdon 2006). Especially Cut Trough Shells were intensively fished.
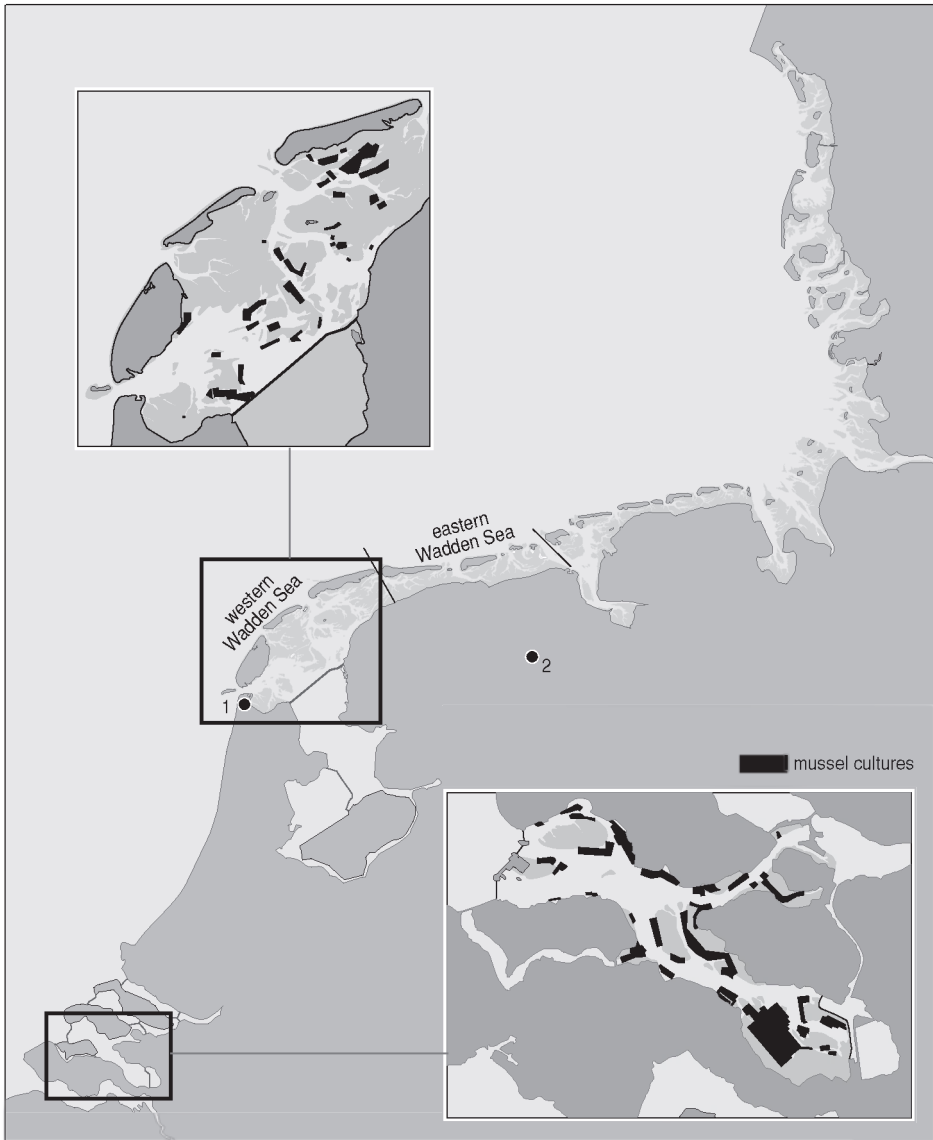
Figure 7.1 The international Wadden Sea area of Denmark, Germany and the Netherlands. The Dutch Wadden Sea area includes the Wadden Sea (low tide line) with the western Wadden Sea with mussel cultures (see detailed map) and weather station De Kooy (1) and the eastern Wadden Sea (weather station Eelde (2)) with the border between Terschelling and Ameland, and the coastal areas of the North Sea north of the Wadden Sea islands, along the west-coast of Noord-Holland and extending south to the Voordelta in the south-west Netherlands with mussel cultures in the Oosterschelde (see detailed map).

Shell-fishery and fishery regulations or acts

Mussel culture was introduced in Zeeland, which is located in the south-western part of the Neterlands, in 1856. Since the 18th century, fishery of wild Mussels (including many of the seed Mussels needed to stock the culture lots in Zeeland) and Cockles occurred in the intertidal and subtidal areas of both the Wadden Sea and Zeeland (Dijkema 1997). The annual landings of Mussels from the Dutch Wadden Sea were less than $5*10^6$ kg fresh wet mass (Bult *et al.* 2004b), but increased after the introduction of Mussel cultures in the western Wadden Sea in the beginning of the 1950's (Figure 7.2A). This introduction was stimulated by the outbreak of the Mussel-parasite *Mytilicola intestinalis* in Zeeland (Veer 1989, Stralen 2001). Areas for cultivating Mussels were appointed by the government and increased rapidly to a maximum of 70 km^2 in 1960 (Figure 7.2A) with some adjustments in location in later years (Bult *et al.* 2004b). The seed Mussels necessary for stocking the culture lots in the Wadden Sea and Oosterschelde were mainly fished in the Wadden Sea due to low spatfall in the Oosterschelde (Dijkema 1997). Some seed Mussels are transported directly to the Oosterschelde, other seed Mussels are first grown to medium-sized Mussels on culture lots in the Wadden Sea, before being transported to culture lots in the Oosterschelde (Dankers & Zuidema 1995). On average, seed Mussels reached commercial sizes in 2 or 3 years before being landed on the market in Zeeland (Bult *et al.* 2004b).

Traditionally, Cockles were collected by hand raking on the intertidal flats of the Wadden Sea at a low intensity (Dijkema 1997). The mechanized Cockle fishery was introduced in the 1960s and intensified from three ships in 1960 to 32 ships in 1981 (Dijkema 1997). This resulted in an increase in the annual landings (Figure 7.2C). In the early 1990s, when Cockle stocks were low, Cockle fishery switched to the North Sea to fish other shellfish, especially Common Trough Shells and recently American Razor Clam *Ensis directus* (Smaal & Lucas 2000, Dijkema 1997).

Before 1990, shellfish fishery was essentially open access, with no limits on total catches. In 1993, the Sea and Coastal Fisheries Policy (Structuurnota Zee- en Kustvisserij) came into effect. This policy aimed at stock conservation and taking nature protection into account, which included the implementation of permanently closed areas, covering 26% if the intertidal flats and the introduction of a policy of food reservation (LNV1993). The fishery for seed Mussels became effectively restricted to the subtidal parts of the (western) Wadden Sea. The policy of food reservation for shellfish eating birds (*i.e.* Common Eiders and Oystercatchers) was introduced to avoid additional mortality of birds due to mechanical shellfishery in years with low stocks of shellfish (Smit *et al.* 1998, Smaal & Lucas 2000a). The policy only included intertidal stocks of shellfish, which are of the utmost importance for Oystercatchers. Intertidal shellfishery was not allowed when estimated stocks were below a minimum predetermined level. The sub-tidal stocks of shellfish, which are important for Common Eiders, were not included in this policy initially.
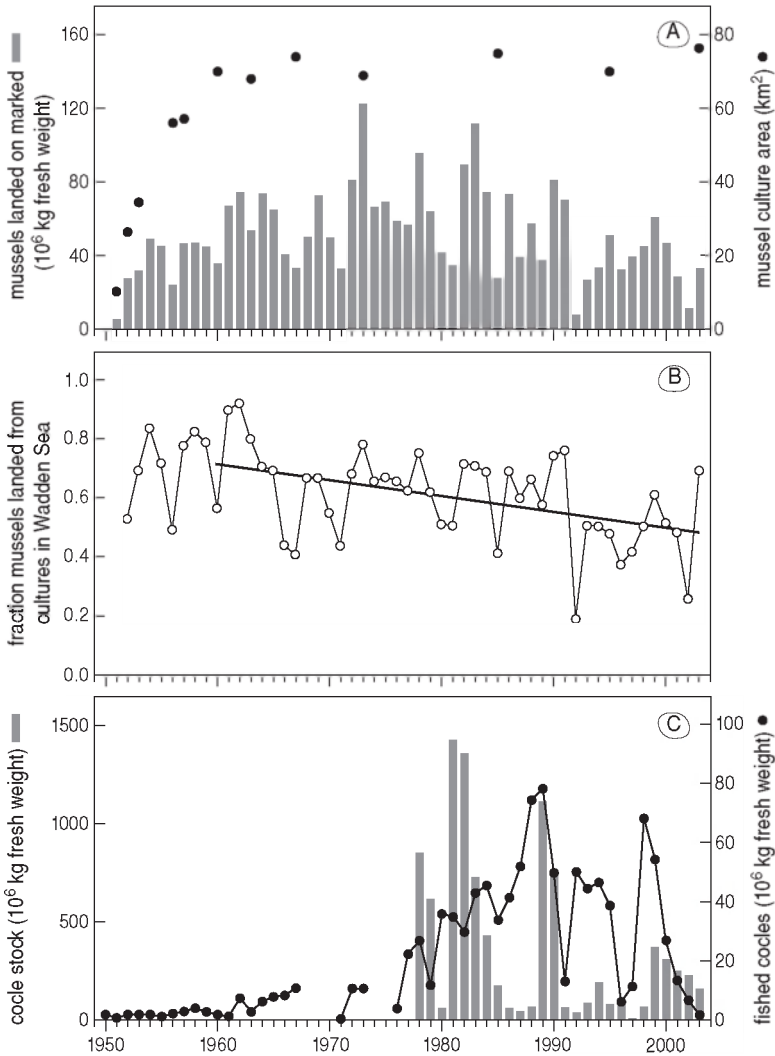
Figure 7.2 Long-term data on (A) the total stock (10^6 kg fresh wet mass) of consumption-sized Mussels *Mytilus edulis* landed on the market from Mussel cultures (filled bars: 1951-2003) in the western Wadden Sea and the area (km^2) of Mussel cultures (open circles: 1951-2003) in the western Wadden Sea (Veer 1989), (B) cultured Mussels in the Wadden Sea (1952-2003) landed on the market as a fraction of the total Dutch production of cultured Mussels with solid line representing data since stabilization in 1960 of the area of mussel cultures in the Wadden Sea (Fraction Wadden Sea cultured Mussels = -0.00532*Year + 11.14, d.f. = 43, R^2 = 0.19, p = 0.002), and (C) the total stock (10^6 kg fresh wet mass) of Cockles *Cerastoderma edulis* in the Wadden Sea and the stock of fished Cockles in the Wadden Sea.

Population size, distribution, and mortality of Common Eiders
Population estimates of wintering sea ducks can only effectively be determined during large scale aerial surveys (Komdeur *et al.* 1992) and the methods used in the Wadden Sea were described in detail elsewhere. The first aerial survey of the Wadden Sea was conducted in October of 1931 (Oordt 1932). Since then, 23 mid-winter surveys have been conducted between 1950 and 2003 with annual surveys since 1993 (Table 7.1). During aerial surveys before 1993 with sudden adverse weather conditions (*i.e.* thunderstorms, snowfall, icing and fog), some areas (less than 5-10 %) were missed and therefore the number of birds in these areas was estimated using other surveys (boat, land) or the average of surrounding years. Nautical charts replaced by GPS in 1993 were used for positioning during surveys, and the area was systematically and fully covered since 1993 using transects. Traditionally, Eiders wintered in the Wadden Sea with only very low numbers in the adjacent coastal area of the North Sea (up to the 10–15 m depth line), so little effort was invested in counting this area. The North Sea Coastal zone has been surveyed systematically since 1987, when Eiders became more common on the North Sea. The total number of wintering Eiders was designated in four areas (see Figure 7.1): western and eastern Wadden Sea, North Sea (along the Wadden Sea islands and the coast of Noord-Holland), and the south-western part of the North Sea (Dutch Voordelta and North Sea coast of Belgium). Wintering Eiders in the western and eastern Wadden Sea were corrected for the size of the area (resp. 1618 km^2 and 791 km^2) and expressed as density (Eiders/km^2). The Voordelta and North Sea of Belgium are considered as one wintering area for waterfowl and the numbers wintering in the Voordelta and Belgian North Sea (Waeyenberge *et al.* 2001, Waeyenberge & Stienen 2002) were highly correlated (1980-2003, excluding the outlying year of 1991): Voordelta = 4.5284*(Belgium North Sea) + 1297, R^2 = 0.65, n = 13, F = 22.9, P = 0.01. This correlation was used to estimate missing data.

The long-term data on mortality in winter of Common Eiders was based on the participation of numerous volunteers in the national Beached Bird Survey (BBS) and was performed along the coastlines of the whole Wadden Sea area and divided into transects (Camphuysen 1998, Camphuysen *et al.* 2002). Dead Eiders were counted and wings were clipped to avoid double counting. The method has been described elsewhere in more detail (Camphuysen 1998). Total mortality in winter was estimated using the most parsimonious model with transect, year and month as factors. This model included a smoothed function of month within each year, which assumes that the maximum number of beached Eiders is independent of year or month (see Appendix 7.1). Missing data in BBS were imputed using a log-linear model with a Poisson distribution, log-link, over-dispersion, and a correction for length of transect and effort, and the number of dead Eiders encountered during BBS was assumed to relate to the search effort (Ens & Kats 2004). Total mortality (expressed as the total estimated number of Eiders reported dead in the

Table 7.1 The size of the wintering population of Common Eiders Somateria mollissima in the Dutch Wadden Sea, the North Sea between IJmuiden and Rottum, the Voordelta (Berrevoets 2001), and the North Sea off the coast of Belgium based on large scale surveys conducted in January. When January counts were absent, surveys in December or February were used to estimate the wintering number. The numbers wintering in the Voordelta and Belgian North Sea (Waeyenberge *et al.* 2001, Waeyenberge & Stienen 2002) were highly correlated, and this was used to estimate missing data (see methods for details). Estimates are indicated in bold. No data available is indicated by (–), and incomplete data are placed between brackets. The year 1931 refers to the winter of 1930/1931.

| Year | Netherlands | | | | Belgium | References for Dutch Wadden and North Sea |
	western Wadden Sea	eastern Wadden Sea	North Sea	Voor-delta	North Sea	
1931	(0)	–	–	–	–	Oordt 1932
1956	(10000)	–	–	–	–	Verwey 1956
1963	(45000)	–	–	1976	150	Zweeres 1963
1967	41000	15000	–	1464	37	Swennen 1976a
1968	79000	13000	–	1315	4	Swennen 1976a
1969	86000	11000	–	2429	250	Swennen 1976a
1973	108000	60000	–	1523	50	Swennen 1976a
1978	98345	8477	(6)	929	71	Swennen 1978
1980	93658	18144	–	146	50	Swennen 1980a
1983	120136	3285	(114)	510	112	Van Buuren 1983)
1984	115217	4229	–	995	81	Swennen 1984
1987	131041	14359	(4994)	570	264	Swennen 1987
1988	–	–	121	1500	45	ESAS 2002
1989	–	–	107	6310	1107	ESAS 2002
1990	–	–	1855	3248	431	ESAS 2002
1991	86893	3137	12210	2485	4953	Swennen 1991c Baptist *et al.* 1997
1992	–	–	50620	5305	775	Baptist et al. 1997
1993	61397	11933	90961	6147	528	Berrevoets & Arts 2003
1994	82428	3692	27518	4560	58	Berrevoets & Arts 2003
1995	89411	17215	29830	1213	62	Berrevoets & Arts 2003
1996	117279	27650	21350	4880	412	Berrevoets & Arts 2003
1997	76367	14403	49619	8750	1821	Berrevoets & Arts 2003
1998	69394	4668	24176	3716	680	Berrevoets & Arts 2003
1999	93693	13593	21136	490	46	Berrevoets & Arts 2003
2000	35612	15451	46668	3027	200	Berrevoets & Arts 2003
2001	25314	6612	80995	425	45	Berrevoets & Arts 2003
2002	28856	19238	56542	2636	20	De Jong *et al.* 2002
2003	62163	23853	904	4318	577	Berrevoets & Arts 2003, De Jong *et al.* 2003

whole Wadden Sea area including the adjacent North Sea) in winter was calculated for three periods, *i.e.* early winter (November and December), mid-winter (January and February) and late winter (March and April). Survival in winter or fraction dead of the wintering population was calculated using total mortality divided by the sum of mortality in early winter (November and January) and size of the mid-winter population estimated in January. Whereas estimates of total winter mortality were available for all 26 years between 1978 and 2003, the fraction dead could only be estimated in 17 years, due to many missing counts in the 1980s. Obviously, errors in the counts will lead to extra errors in the estimate of the fraction dead. Thus, both the total mortality and the fraction dead are only partly satisfactory as measures of mortality rate of Common Eiders. For this reason, we used both measures and investigated if the results were consistent.

Food supply
The estimates of the stocks of shellfish in the intertidal and subtidal parts of the Dutch Wadden Sea were based on data collected by the Dutch Institute of Fishery Research (RIVO), fishermen, Research Center of the Green World (Alterra) and Fishery Inspectors. All participants were collaborating partners in the national research program for the evaluation of the shellfish fishery in the Netherlands (Ens *et al.* 2004), and methods were described in detail elsewhere (Bult *et al.* 2004b, Kamermans *et al.* 2003a, Rappoldt *et al.* 2004a). Estimates of the stocks of shellfish were available for Blue Mussels and Edible Cockles the Wadden Sea, and the Common Trough Shells and American Razor Clams in the adjacent coastal areas of the North Sea. Stock estimates were expressed as total fresh weight (including water, wet flesh mass and shell mass), except for American Razor Clams, which were expressed as the total number of individuals. Both the span of years for which data were available and the quality of the data varied, so we distinguish between long-term data and more precise short-term data.

The stock of intertidal Mussels in autumn was available since 1991 (Rappoldt *et al.* 2004a), and Mussels were divided in relation to size (seed: ≤ 30 mm; medium-sized: 30-50 mm; consumption ≥ 50 mm). For the long-term data since 1951, stocks of subtidal medium-sized Mussels in a given year were back calculated from the annual landings of Mussels reported by "Mosselkantoor" for the following year, assuming a fixed translation factor of 1.01, and the stock of seed Mussels in the previous year was calculated from the calculated stock of medium-sized Mussels assuming a factor 0.44. Thus, 0.44 kg seed mussels yield 1 kg medium-sized mussels the next year, which yield 1.01 kg consumption-size mussels the next year (Bult *et al.* 2004b). More precise estimates for December were available for wild subtidal Mussels (based on surveys in spring since 1991) and cultured subtidal Mussels (based on landings and relocation since 1992) since 1992 (Bult *et al.* 2004b).

The total stock of intertidal Cockles was available since 1978 and was based on surveys in spring since 1990 and extrapolation of data from the Balgzand area

before that year (Kamermans *et al.* 2003b, Ens & Kats 2004). More detailed information on size of intertidal Cockles was available since 1990 with Cockles divided into young (spat, 1st year, 2nd year) and older than 2 years. The stocks in September after fishing were calculated using data from the survey in spring, growth during summer (Kamermans *et al.* 2003a), and the direct (= catch) and indirect loss (= collateral damage) due to fishing (Rappoldt *et al.* 2004a). The stock of spat in September was estimated from the stock 1st year Cockles estimated in May of the following year multiplied by the inverse of the conversion factor of winter loss of 0.556 (pers. com. Rappoldt). The total stock of subtidal Cockles in September after fishery was calculated using the surveys in spring and estimates on growth and mortality during summer (Kamermans *et al.* 2003a, Ens & Kats 2004).

The stocks of Cut Trough Shells (divided into seed and mature), and American Razor Clam at the end of winter were based on surveys in May, available since 1995 (Smaal & Lucas 2000).

Weather

The severity of a winter between 1975 and 2003 was expressed as the Winter Severity Index *V* with the winter being defined as the period between November 1st and March 31st. The Winter Severity Index incorporates the length and the severity of cold periods during winter. The average *V* for the whole of the Wadden Sea was calculated using daily temperature measurements at De Kooy (near Den Helder: N 52° 55' E 4° 47') for the western Wadden Sea and at Eelde (N 53° 08' E 6° 30') for the eastern Wadden Sea (KNMI 2004). The Winter Severity Index *V* between 1975 and 2003 for both weather stations was calculated for every winter according to the following formula developed by IJnsen (1988):

$$V = 0.00275 \, v^2 + 0.667 \, y + 1.111 \, z$$

with v the number of frost days (days with $T_{min} < 0°C$), y the number of ice days (days with a $T_{max} < 0°C$) and z very cold days (days with $T_{min} < -10°C$). The scale of the Winter Severity Index *V* ranges between 0 and 100.

Statistics

The main objectives were to test whether differences in population size, winter mortality (or total number of beached birds) and shift in distribution of wintering Eiders could be related to variation in population size, food supply and winter severity, and to build predictive models. Winter mortality, population size, shift in distribution of wintering population and fraction dead of wintering were treated as the dependent variables and related to food variables and weather conditions in winter by Generalized Linear Models (GLM) with a log-link (log of the mean) and a Poisson distribution with over-dispersion (variance larger than the mean). Only

main effects were considered and interactions among variables were not examined. The most parsimonious model was selected on the basis of the Akaike information criterion (AIC) using all sub-sets regression and the significance of a variable was based upon the change in deviance. Mortality was corrected for the size of the adjusted wintering population (mid-winter population and total mortality between 1st November and 31st January) and expressed as fraction dead of the total wintering number. Angular transformation of fraction dead and log-transformation of Winter Severity and wintering population was necessary for analysis to meet the assumptions of normality and homoscedasticity. The effects of outliers on the fit were tested and identified using large standardized residuals.

Long-term (1978 – 2003) and a short-term (1990 – 2002) data was available for food stocks. For comparison of both time-series, the analysis of the long-term time-series was repeated using similar variables of the short-term time-series. Only for the short-term data set could the stock of a particular shellfish species be divided into stocks of particular size or age classes. The data was first analyzed using long-term (1978 – 2003) estimates of the total stock of subtidal seed and medium-sized Mussel data reconstructed from Mussel landings and total intertidal Cockles in the Wadden Sea. The analysis was repeated using the short-term (1991 – 2003) total stock estimates only. Subsequently, the analysis was repeated using the short-term data, but with more details with respect to size. Estimates of the stocks of shellfish in autumn or early winter were related to mortality, size and shift in distribution of the wintering population of Eiders in the following winter (*i.e.* autumn 1990 with winter 1990/91), except the estimated stocks of Cut Trough Shell, which were surveyed in spring (*i.e.* spring 1990 with winter 1989/90). For comparison of both time-series, the analysis of the long-term time-series was repeated using similar variables of the short-term time-series. Common Trough Shells Spisula subtruncata were not included in the analyses due to being aliased with the stock of medium-sized Mussels.

Results

Population size and distribution of wintering Common Eiders
When mussel culture was introduced in the Dutch Wadden Sea in 1950, the number of breeding Eiders already approximated 1500 pairs and was still rapidly increasing (Figure 7.3A). In contrast, the size of the total population of Common Eiders wintering in the Wadden Sea area was probably negligible at the time, compared to current numbers. The size of the wintering population increased from approximately 10.000 in 1956 to 150.000 in 1987 with exceptionally high numbers in 1973. Since 1993, when aerial counts have been performed in a standard fashion, the wintering population has declined from 165.000 to 87.000 in 2003 (r = –0.72, p = 0.012: Figure 7.3B). Variation in the size of the wintering popula-

tion in the total Wadden Sea area (1978-2003) was explained by the number of birds wintering in the western Wadden Sea (40.3 % explained deviance, p = 0.011) and North Sea (26.1 % explained deviance: p = 0.032), but not by the number in the eastern Wadden Sea (p = n.s.). Furthermore, the number of Eiders wintering on the North Sea was negatively related to those in the western Wadden Sea (r = –0.65, p = 0.016). In most years, wintering Eiders were concentrated in the western part of the Wadden Sea where the mussel culture plots and the wild subtidal mussel beds are located. Not only was the average of 81.000 Eiders 5.5 times higher than the number wintering in the eastern Wadden Sea, but also the average density of 50.1 birds/km^2 was 2.7 times higher compared to the eastern Wadden Sea (Table 7.1, Figure 7.3B and 7.3D).

Prior to 1991, low numbers of wintering Eiders occurred in the North Sea (less than 1.000), but numbers increased dramatically in the early 1990s, with exceptionally high numbers of 91.000 in 1993 and 81.000 in 2001 (Table 7.1 and Figure 7.3B). In those years, the majority of the birds occurred in the North Sea Coastal zone. The size of the wintering population in the southwestern part of the North Sea (Figure 7.3C) was low (average = 2855) with 89.4 % in the Dutch Voordelta.

Numbers wintering further south along the Belgian coast have always been low, except in 1991, *i.e.* around the time that food shortage in the Wadden Sea caused the Eiders to search for food elsewhere (Camphuysen *et al.* 2002).

Mortality of Common Eiders in winter (1978-2003)
During the period 1978-2003 more than 92.500 Common Eiders were estimated to have died in the Wadden Sea area in winter (November – April) with an annual average of 3562 dead birds, ranging from 740 in 1982 to 17.399 in 2000 (Figure 7.4 and 7.5). Mortality during early winter was positively related to mortality late in winter (n = 26, R^2 = 0.55, p < 0.001). Total mortality was not correlated with total population size (Figure 7.4) when all data was used. After excluding three significantly outlying years, which coincided with exceptionally high mortality (1990/91 and 1999/2000 – 2002/03), total mortality clearly increased with the size of the adjusted winter population. Henceforth, these three winters with exceptionally high mortality will be designated as 'kill'-winters.

The general pattern in mortality rate strongly resembled the pattern in total mortality (Figure 7.5). On average 3.5 % of the wintering population was reported dead each winter, but variation between winters was large and varied from 0.66 % in 1980 to 16.9 % in 2000 (Figure 7.5). During normal winters, only 1.6 % of the wintering population died, but this figure was 4.9 times higher (8.0 %) during 'kill'-winters (Figure 7.5). In the winter of 1992, we could not calculate a mortality rate since there was no count, but the high total mortality (app. 7.000 dead Eiders) and the strong resemblance between total mortality and mortality rate suggest this winter should also be classified as a "kill" winter.
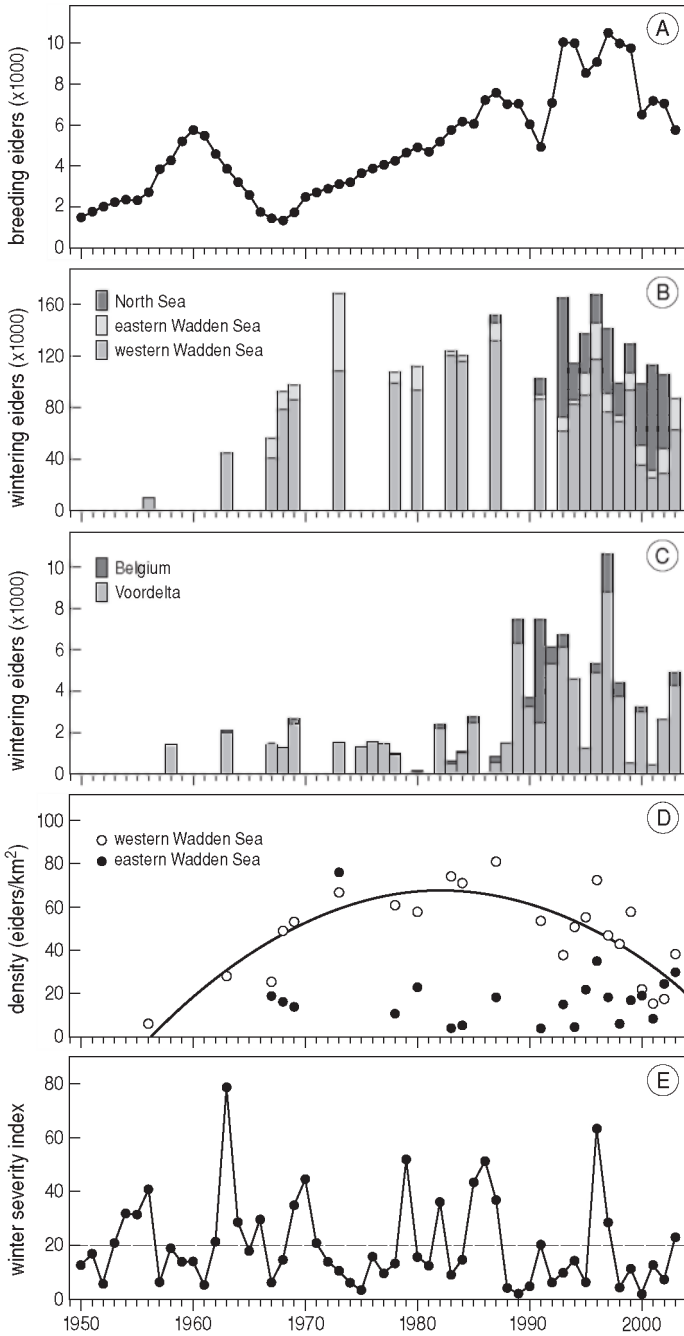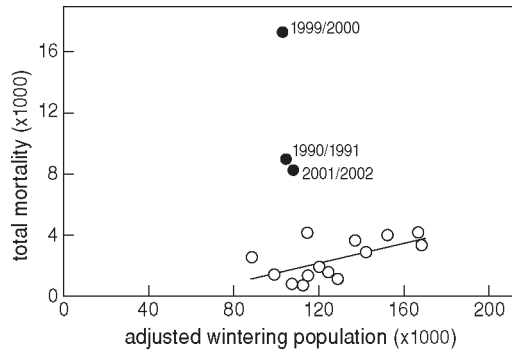
Figure 7.4 Total mortality (1977/78 – 2002/03) in winter (November – April) plotted against the size of the adjusted wintering population (size of mid-winter population in January plus mortality between November and January). Excluding outliers or known 'kill-winters' (black circles: 1990/91, 1999/2000 and 2001/02): Winter mortality = 0.0325*(Adjusted wintering population) - 1716, d.f. = 13, R^2 = 0.31, p = 0.023.

Long-term and short-term data on subtidal and intertidal food supply: Mussels, Cockles, Common Trough Shells and American Razor Clam.

Mussel cultures were traditionally found in the Oosterschelde, but were introduced in the western Wadden Sea in 1951. The area of culture plots and landings of cultured mussels increased respectively to $70 \, \text{km}^2$ and $35 \, 10^6 \, \text{kg}$ fresh weight Mussels in 1960 (Figure 7.2A). From 1960 onwards, the area with mussel cultures remained constant and the long-term data on the landings of cultured Mussels from the Wadden Sea (1960-2003) averaged $54.4 \, 10^6$ kg fresh weight. Mussel Landings from the Wadden Sea were considerably more variable (C.V.: 44.9 %) than landings from the Oosterschelde (C.V.: 31.8 %). Further, landings from the Wadden Sea represented 66 % of the landings from Dutch cultures until 1991 (Figure 7.2B), but declined to 46 % around 2003, indicating a 30 % reduction in the estimated stock of cultured mussels. Mussel landings from the Wadden Sea reached extremely low values in the winters of 1991/1992 and 2001/2002, *i.e.*

Figure 7.3 (left) Breeding and wintering population of Common Eiders *Somateria mollissima* in the Wadden Sea area and south-western North Sea, and wintering conditions (1950 – 2003): (A) size of the breeding population (expressed as the number of breeding females) in the Wadden Sea area (Kats *et al.* 2007c), (B) size of wintering population during mid-winter surveys in the Wadden Sea area, separated for western Wadden Sea, eastern Wadden Sea and adjacent North Sea coast of the Wadden Sea islands and Noord-Holland, (C) size wintering population in the south-western part of the North Sea (Dutch Voordelta and Belgium, see Table 7.1 for details), (D) the density (Eiders/km^2) in the western (Density Western Wadden Sea = -0.0999*Year^2 +396.2*Year – 392612, R^2 = 0.64, n = 23, p < 0.001) and eastern Wadden Sea, and (E) weather conditions during wintering (expressed as the average Winter Severity Index in the Wadden Sea area based on index of De Kooy for the western and Eelde for the eastern Wadden Sea). The year 1950 refers to the winter of 1949/1950.
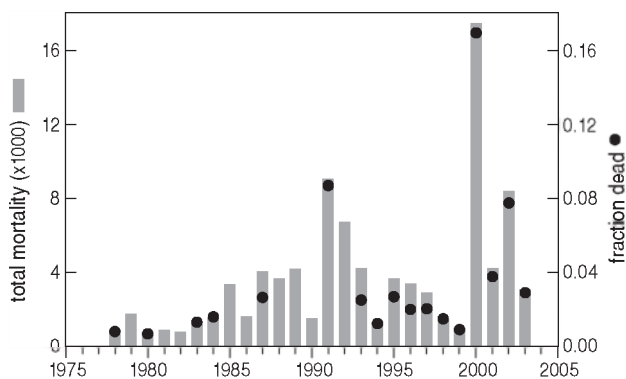
Figure 7.5 Total mortality of Common Eiders *Somateria mollissima* in the Wadden Sea area (1978 – 2003) in winter (November – April) expressed as the total estimated number of dead birds and the fraction dead of the adjusted wintering population (= total winter mortality /(mortality in November to January + mid-winter population. The year 1975 refers to the winter of 1974/1975.

around the time of the "kill" winters and the exceptionally high numbers of Common Eiders on the North Sea.

The short-term data on the total stock of subtidal Mussels in the western Wadden Sea showed that on average half of the total stock (52 %) was present on cultures: the fraction wild Mussels declined from 64 % of the total stock in 1993 to 40 % in 2003. On average 74 % of all medium-sized mussels was found on cultures (Table 7.2). The littoral Mussel beds virtually disappeared from the Wadden Sea in 1990 (Beukema & Cadée 1996), but the stock is recovering since then, albeit primarily in the eastern part of the Wadden Sea (Ens *et al.* 2004). Heavy spatfall (> 95 10^6 kg fresh wet mass) was observed in summers of 1994 and 2001, and smaller spatfalls occurred in the summers of 1996 and 1999 (Table 7.2).

Long-term estimates (1978-2003) of the total Cockle stock showed large fluctuations since 1978 with three peaks (> 600 10^6 kg fresh mass) observed in 1978-79, 1981–83, and 1989–1990. Since 1990, Cockle stocks were lower (< 400 10^6 kg fresh mass) with a small peak two years after the heavy spatfall of 1997 (Table 7.2). The amount of fished Cockles increased since the end of the 1970's and was high (> 50 10^6 kg fresh wet mass) in 1987-90, 1992 and 1998-99. The lowest catch of Cockles since 1980 was observed in 2003, which was comparable to the period before 1960. For the short-term data available, the total stock of subtidal Cockles (Table 7.2) was low compared to intertidal Cockles, averaging 8 % of the total Cockle stock.

The stock of Common Trough Shells in the adjacent North Sea varied considerably with heavy spatfall in 1995, 1996 and 2000 resulting in large mature stocks in 1997 and 2001 (Table 7.2). The stock of American Razor Clams was also quite variable with low stocks between 1999 and 2001 (Table 7.2).

Table 7.2 Stocks (10^6 kg fresh wet mass) of shellfish in the Wadden Sea and North Sea coastal zone. Stock in autumn (1990-2002) of intertidal Blue Mussels *Mytilus edulis* (seed, medium, large Mussels) and intertidal and subtidal Edible Cockles *Cerastoderma edule* (spat, 1 year, 2 year, ≥ 2 year) based on extrapolations from surveys in spring minus the stocks fished in autumn. Stock of subtidal Blue Mussels (seed, medium) in wild and cultured beds estimated for 31 December (1991-2003). Stocks of Common Trough Shells *Spisula subtruncata* (seed, mature) and American Razor Clam *Ensis directus* (total number of individuals in fixed sampling grid) in the coastal areas of the North Sea (1995-2002) within the 15 depth line based on surveys in May (Bult *et al.* 2004b, Ens & Kats 2004, Rappoldt *et al.* 2004a, Craeymeersch & Perdon 2006). No data available indicated by (–). The year 1991 refers to the winter of 1990/1991.

	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Wadden Sea intertidal food stocks													
Blue Mussels *Mytilus edulis*													
Seed	0.0	0.0	0.0	0.0	103.5	0.0	19.9	0.0	0.0	17.3	1.2	95.5	–
Medium	(10.4[a])	0.4	0.3	0.4	1.5	9.3	2.1	15.6	8.9	2.4	6.0	2.8	–
Large	(31.2[a])	1.3	1.0	1.1	0.0	1.9	3.1	9.5	7.2	8.0	9.7	14.2	–
Edible Cockles *Cerastoderma edule*													
Spat	1.8	33.3	31.9	9.1	20.6	0.7	12.2	136.2	9.0	9.5	15.7	3.1	–
1 years	10.7	13.8	96.9	128.5	22.5	46.2	3.3	35.1	389.5	32.7	35.8	60.7	–
2 years	0.0	0.0	11.0	41.7	21.2	11.4	1.7	1.6	28.7	265.4	22.9	33.0	–
≥ 3 years	59.5	16.3	7.3	35.6	32.8	47.6	2.2	0.4	1.5	11.3	230.6	136.4	–
Wadden Sea subtidal food stocks													
Blue Mussels *Mytilus edulis*													
Wild beds													
Seed	–	12	30	7	34	7	57	30	13	24	6	33	29
Medium	–	0	2	38	5	27	3	74	29	9	8	3	21
Cultured beds													
Seed	–	–	4	0	10	2	14	4	1	4	0	20	0
Medium	–	–	14	39	31	22	33	80	98	17	53	35	76
Edible Cockles *Cerastoderma edule*													
Total	2.7	0.0	54.7	26.7	10.0	18.0	2.0	8.0	22.7	9.3	8.7	16.0	29.3
North Sea													
Common Trough Shell *Spisula subtruncata*													
Seed	–	–	–	–	104.8	167.5	29.4	20.1	6.7	272.9	4.3	0.2	–
Mature	–	–	–	–	109.7	76.3	324.8	162.7	97.8	3.8	389.1	112.3	–
American Razor Clam *Ensis directus* (note: expressed as number)													
					5521	2426	3821	5782	528	303	533	12400	–

[a] No intertidal Mussels in 1990 due to fishery (Rappoldt *et al.* 2004a).

Relating population size, distribution and mortality of Common Eiders in winter to food and weather.

Variation in the size of the total wintering population in the Wadden Sea area was explained by the Winter Severity Index with an increase in population size when winters got colder, but not explained by food stocks (Table 7.3A). This was true for both the long-term and the short-term data set. In contrast, the numbers of wintering Eiders in the western Wadden Sea, as well as the number on the North Sea, were both related to the stock of medium-sized subtidal mussels in the western Wadden Sea (Table 7.3B and 7.3C). At low stocks of medium-sized subtidal mussels, the number of wintering Eiders in the western Wadden Sea was low, while numbers were high on the North Sea (Figure 7.6A and 7.6B). The statistical analy-
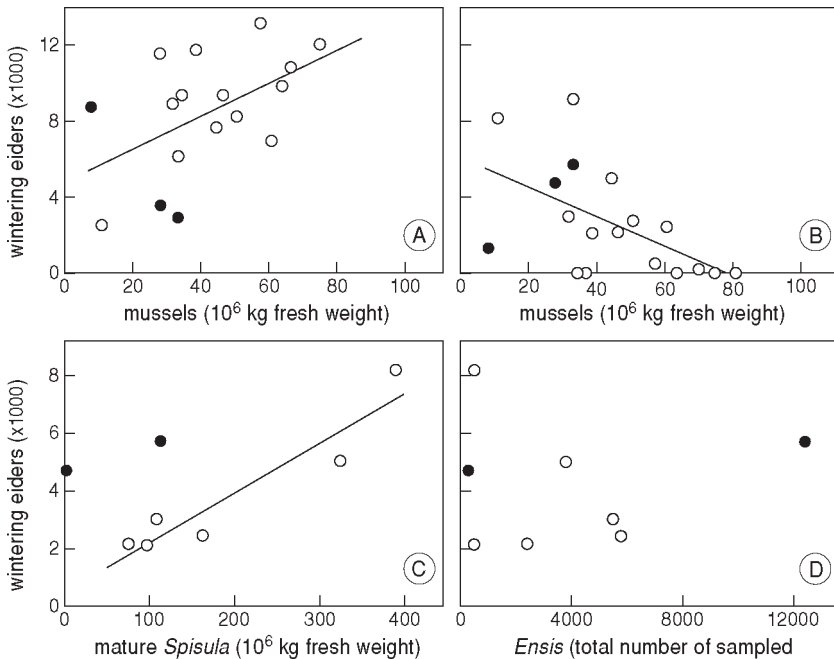
Figure 7.6 The size of the wintering population of Common Eiders *Somateria mollissima* in relation to food stocks. The number of wintering Eiders in (A) the western Wadden Sea (Wintering$_{WWS}$ = 8666.43 *(Medium-sized Mussels) + 47944, R^2 = 0.26, n = 16, p = 0.035) and (B) the North Sea (Wintering$_{NS}$ = -768 *(Medium Mussels) + 60494.6, R^2 = 0.31, n = 16, p = 0.017) in relation to the stocks of medium-sized Mussels *Mytilus edulis* (1970-2003), and (C) on the North Sea in relation to the total stock of Common Through Shells *Spisula subtruncata* between 1996 and 2002 (excluding 'kill'-winters of 1999/2000 and 2001/02: WinteringNS = 111 * (Mature *Spisula*) + 12095, R^2 = 0.87, n = 5, p = 0.020) and (d) American Razor Clams *Ensis directus* between 1995 and 2002: p = n.s.. Black symbols represent 'kill'-winters of 1990/91, 1999/00 and 2001/02.

Table 7.3 Analysis of the size of the population of Common Eiders *Somateria mollissima* wintering in the entire Dutch Wadden Sea area or subareas in relation to weather (expressed as winter severity index) and food stocks (expressed as 106 kg total fresh mass) of intertidal and subtidal Blue Mussels *Mytilus edulis* and Edible Cockles *Cerastoderma edule,* using both long-term and short-term data: (A) total Wadden Sea area, including the North Sea (expressed as the number of wintering birds), (B) western Wadden Sea and (C) North Sea. For more details see methods.

Model and variables	estimate	d.f.	AIC	D	P
(A) Total Wadden Sea area					
Long-term data					
Total		14		53847	
Lg(Wintering population)=			15219	17153	0.028
Intercept	11.426				
Lg(Winter severity)	0.282	1		171533	0.028
Short-term data					
Total		9		42535	
Lg(Wintering population)=			10948	19984	0.029
Intercept	11.418				
Lg(Winter severity)	0.00326	1		19984	0.029
(B) western Wadden Sea					
Long-term data					
Total		15		213997	
Lg(Wintering WWS)=			16463	107566	0.011
Intercept	10.133				
Subtidal Medium Mussels	0.01057	1		45399	0.035
Lg(Winter severity)	0.656	1		62914	0.020
Short-term and size-selective data					
Total		10		131971	
Lg(Wintering WWS)=	0.036		12883	74632	
Intercept	−10.22				
Subtidal Medium Mussels	0.00623	1		39080	0.048
Lg(Wintering population)	4.10	1		68550	0.015
(C) North Sea					
Long-term data					
Total		13		388416	
Lg(Wintering North Sea)=			16249	201045	0.055
Intercept	−22.5				
Subtidal medium Mussels	−0.0337	1		111959	0.035
Lg(Wintering population)	6.92	1		91689	0.051
Lg(Winter severity)	−1.182	1		60381	0.103
Short-term and size-selective data					
Total		8		116014	
Lg(Wintering North Sea)=			7319	41176	0.090
Intercept	11.159				
Subtidal medium Mussels	−0.00830	1		41176	0.090

sis of the short-term data indicated that the stocks of subtidal mussels were the driving force behind the shift in distribution. The stock of Cockles did neither affect the total number of Eiders wintering in the Wadden Sea area, nor the number wintering in the western part of the Wadden Sea or on the North Sea.

When kill winters were excluded, the number of wintering Eiders on the North Sea were positively related to the stock of mature Common Trough Shells (Figure 7.6C), but not to American Razor Clams (p = 0.46: Figure 7.6D).

In both the long-term data set and the more precise short-term data set, low stocks of medium-sized mussels were the best predictor of high mortality among Common Eiders (Figure 7.7A and Table 7.4). A problem with this analysis is that total mortality may be higher, not because mortality rate has increased, but because the size of the wintering population has increased (cf. Figure 7.4). We countered this problem in two ways. First, we included the size of the wintering population as an independent variable in the analysis (Table 7.4). Second, we calculated mortality rate by dividing the total mortality by the size of the wintering population and used mortality rate as the dependent variable (Table 7.5). In both cases, we again found a significant effect of the stock of medium-sized Mussels, even though sample sizes were reduced due to the fact that for several winters we lacked an estimate of the size of the wintering population of the Eiders. In the analysis using the long-term data set we also found a significant negative correlation between the stock of subtidal seed Mussels and mortality or mortality rate (Table 7.4 and 7.5), *i.e.* mortality rate was increased when stocks were low. Other patterns cropped up in the analyses, but not in a consistent fashion. Several analyses yielded a negative relation between mortality (or mortality rate) and the winter severity index. This could be a real effect, because shellfish lose more body mass in mild winters. In one case we observed a significant positive correlation between the stock of intertidal cockles and mortality (Table 7.4). Since it is hard to imagine a situation where high food stocks would increase mortality, and since the majority of analyses did not yield a significant effect of the stock of Cockles, we are inclined to believe that this result happened by chance.

Our data set on the stock of *Spisula* was short and so closely correlated to the stock of subtidal mussels that we could not include it as a separate independent variable in a multivariate analysis already including the stock of subtidal Mussels. However, the stock of mature *Spisula* was low in two years with mass mortality and simply plotting total mortality against the stock of mature *Spisula* yielded a significant negative correlation (Figure 7.7), which was absent for *Ensis* (p = 0.88). Additional evidence that *Spisula* was in short supply in years of mass mortality comes from Figure 7.6C, which suggests that in the years of mass mortality the number of Eiders wintering on the North Sea was too high given the stock of mature *Spisula* that the population depended on. The lack of such clear evidence for Ensis (Figure 7.6D) suggests that Ensis may not serve as a profitable alternative when other food stocks are low.
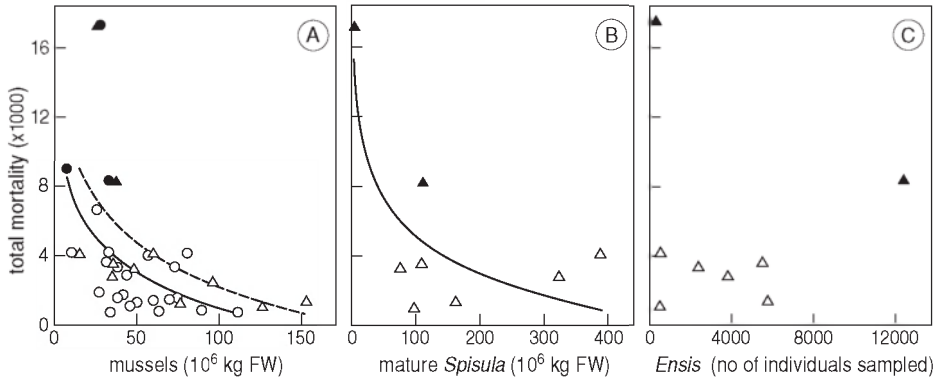
Figure 7.7 Total mortality in winter (expressed as the total estimated number of dead birds) in wintering Common Eiders *Somateria mollissima* in the Wadden Sea area in relation to the stocks (expressed as 10^6 kg fresh wet mass) of (A) long-term (1978-2002) subtidal medium Mussels Mytilus edulis (circles, solid line) on cultures (based on landings from the Wadden Sea area, see methods and Figure 2A for details): Lg(Total dead) = -0.02291*(Medium Mussels) + 9.169, d.f. = 24, p = 0.003); and short-term (1993-2003) subtidal mature Mussels (triangles, dashed line) on wild and cultured Musselbeds: Lg(Total dead) = -0.01753*(Mature Mussels) + 9.356, d.f. = 10, P = 0.022), (B) mature Cut Trough Shells *Spisula subtruncata* on the North Sea: Total dead = -3159*Lg(Mature *Spisula*) + 19706, d.f. = 7, p = 0.009) and (C) American Razor Clams *Ensis directus* on North Sea (p = n.s.). Black symbols represent 'kill'-winters of 1990/91, 1999/00 and 2001/02.

To summarize, the results indicate that the excessively high mortality in the winters of 1999/2000 and 2001/2002 was probably related to low stocks of subtidal Mussels in the western Wadden Sea coinciding with low stocks of Common Trough Shells on the North Sea.

Table 7.4 (next page) Analysis of the total mortality in winter (expressed as the estimated number of dead birds in the Wadden Sea area) in Common Eiders *Somateria mollissima* in relation to weather (expressed as winter severity index), adjusted wintering population (mid-winter population including mortality between 1st November and 31st January) and food stocks (expressed as 10^6 kg total fresh mass) of intertidal and subtidal Blue Mussels *Mytilus edulis* and Edible Cockles *Cerastoderma edule* in the Wadden Sea. Three analyses were performed: a long-term, short term and size-selective analysis. The long-term data analysis (1978-2001) used Winter Severity (Figure 7.3E), stocks of subtidal seed and medium Mussels (only cultured

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Mussels reconstructed from the annual landings from the Wadden Sea, Figure 7.2A), and intertidal Cockles (Figure 7.2C). The short-term data analysis (1991-2003) repeated the long-term analysis, but used more precise estimates of the different shellfish stocks: subtidal seed and medium Mussels (based on reconstruction – see methods) and intertidal Cockles (based on annual surveys). The size-selective analysis (1991-2003) repeated the short-term analysis, but included more details on size in Mussels (seed, medium) and Cockles ($\leq$ 2 years and $\geq$ 3 years old

Model and variables	estimate	d.f.	AIC	D	P
Long-term data					
Total (adjusted wintering population not included)		23		60979	
Lg(Winter mortality) =			27098	37576	< 0.001
Intercept	10.368				
Lg(Winter severity)	–0.798	1		7397	0.021
Subtidal seed Mussels	–0.0290	1		5812	0.037
Subtidal medium Mussels	–0.0197	1		14182	0.020
Total (adjusted wintering population not included)		14		48143	
Lg(Winter mortality) =			20266	37120	0.003
Intercept	–4.4				
Lg(Wintering population)	3.05	1		1474	0.274
Lg(Winter severity)	–0.651	1		2253	0.183
Subtidal seed Mussels	–0.0727	1		10332	0.002
Subtidal medium Mussels	–0.02677	1		12194	0.008
Short–term data					
Total (adjusted wintering population not included)		9		34636	
Lg(Winter mortality) =			13289	27867	0.003
Intercept	8.554				
Intertidal Cockles	0.00515	1		12530	0.009
Subtidal medium Mussels	–0.02431	1		24974	0.001
Total (adjusted wintering population not included)		9		34636	
Lg(Winter mortality) =			11582	30256	< 0.001
Intercept	47.38				
Lg(Wintering population)	–7.42	1		14920	0.002
Subtidal medium Mussels	–0.02305	1		24557	< 0.001
Size selective data					
Total (adjusted wintering population not included)		9		34636	
Lg(Winter mortality) =			11252	31422	0.002
Intercept	10.611				
Lg(Winter severity)	–1.427	1		14987	0.002
Intertidal large Mussels	0.1606	1		3994	0.034
Subtidal medium Mussels	–0.2923	1		11856	0.003
Total (adjusted wintering population not included)		9		34636	
Lg(Winter mortality) =			183	33254	< 0.001
Intercept	48.72				
Lg(Wintering population)	–7.678	1		16819	< 0.001
Intertidal medium Mussels	0.1297	1		2997	0.011
Subtidal medium Mussels	–0.03410	1		19250	< 0.001

Table 7.5 Analysis of the size of the population of Common Eiders *Somateria mollissima* wintering in the entire Dutch Wadden Sea area or subareas in relation to weather (expressed as winter severity index) and food stocks (expressed as 106 kg total fresh mass) of intertidal and subtidal Blue Mussels *Mytilus edulis* and Edible Cockles *Cerastoderma edule,* using both long-term and short-term data: (A) total Wadden Sea area, including the North Sea (expressed as the number of wintering birds), (B) western Wadden Sea and (C) North Sea. For more details see methods.

Model and variables	estimate	d.f.	AIC	D	P
(A) Total Wadden Sea area					
Long-term data					
Total		14		53847	
Lg(Wintering population)=			15219	17153	0.028
Intercept	11.426				
Lg(Winter severity)	0.282	1		171533	0.028
Short-term data					
Total		9		42535	
Lg(Wintering population)=			10948	19984	0.029
Intercept	11.418				
Lg(Winter severity)	0.00326	1		19984	0.029
(B) western Wadden Sea					
Long-term data					
Total		15		213997	
Lg(Wintering WWS)=			16463	107566	0.011
Intercept	10.133				
Subtidal Medium Mussels	0.01057	1		45399	0.035
Lg(Winter severity)	0.656	1		62914	0.020
Short-term and size-selective data					
Total		10		131971	
Lg(Wintering WWS)=	0.036		12883	74632	
Intercept	−10.22				
Subtidal Medium Mussels	0.00623	1		39080	0.048
Lg(Wintering population)	4.10	1		68550	0.015
(C) North Sea					
Long-term data					
Total		13		388416	
Lg(Wintering North Sea)=			16249	201045	0.055
Intercept	−22.5				
Subtidal medium Mussels	−0.0337	1		111959	0.035
Lg(Wintering population)	6.92	1		91689	0.051
Lg(Winter severity)	−1.182	1		60381	0.103
Short-term and size-selective data					
Total		8		116014	
Lg(Wintering North Sea)=			7319	41176	0.090
Intercept	11.159				
Subtidal medium Mussels	−0.00830	1		41176	0.090

Discussion

Fluctuations in the size and distribution of the population of Eiders wintering in the Dutch Wadden Sea

During the first half of the 20th century, only low numbers of Common Eiders (estimated at hundreds to a few thousand) were observed to winter in the Netherlands (Snouckaert van Schauburg 1908, Tinbergen 1930, Oordt 1932, Morzer Bruijns & Braaksma 1954, Tanis 1963). During the second half of the 20th century, the size of the wintering population increased to around 130.000, with a maximum of 165.000 in 1993. Although there are only a handful of Eider counts in the 1950s and the 1960s, and these counts were not executed according to the same strict methodology that we apply today, the data suggest that the increase in the population of wintering Eiders occurred well after mussel culture was introduced in the Dutch Wadden Sea in 1951. This could mean that the population of wintering Common Eiders increased in response to the introduction of the mussel culture, but alternative explanations, such as a strong increase of the populations breeding around the Baltic Sea, exist (Desholm *et al.* 2002). The Eiders wintering in the Wadden Sea originate from the Baltic Sea area (Swennen 1991a, Tiedemann *et al.* 2004), and the increase of that breeding population has been linked to the introduction of conservation laws and the regulation of hunting (Persson *et al.* 1974, Desholm *et al.* 2002).

Since 1993, the population wintering in the Netherlands declined in size from an average of 130.000 to fewer than 100.000 birds in 2000 (Table 7.1 and Figure 7.3b). A similar decline of 36 % from 1.2 million birds in 1990 to 0.76 million birds in 2000 was observed in the total Baltic/Wadden Sea flyway (Desholm *et al.* 2002).

Apart from changes in the size of the total flyway population, the size of the population wintering in the Dutch Wadden Sea area appeared to depend on the severity of winter. Population size was higher when winters were cold. Presumably, winters that were cold in the Dutch Wadden Sea, were also cold in the Baltic. Cold winters in the Baltic Sea resulted in an increase in ice-cover, which reduced open waters and access to food, and numbers of Eiders varied with the strength of winter (Nilsson 1984). As a consequence, Eiders are predicted to respond to these reductions in feeding conditions by wintering elsewhere in order to survive.

Camphuysen *et al.* (2002) already reported that Common Eiders shifted from the Wadden Sea to the North Sea coastal zone in response to a shortage of subtidal mussels. To this we can add that these were indeed birds from the western Wadden Sea, where large stocks of subtidal mussels traditionally occur, that moved. Numbers in the eastern Wadden Sea were always low, despite the presence of substantial stocks of littoral Cockles in many years. Although numbers on the North Sea increased when stocks of subtidal Mussels in the western Wadden Sea were low, we also found that numbers on the North Sea tended to be higher when

stocks of mature *Spisula* were high. Finally, the low food stocks in the Wadden Sea may have contributed to the sudden increase in the size of wintering population in the Voordelta and Belgium around 1990.

Mortality in relation to stocks of shellfish

Until the end of the 1980's, exceptional mortality among wintering and breeding Eiders in the Wadden Sea could always be explained by pollution of coastal waters with organochlorides (*i.e.* dieldrin and telodrin), oil and/or cleaning agents (Koeman *et al.* 1969, Camphuysen 1996). Since 1990, instances of mass mortality among Eiders seem to coincide with low stocks of shellfish. In the kill winters of 1999/2000 and 2001/2002, unusually large numbers of wintering Eiders were seen in apparently suboptimal habitat along the margins of the sea (salt marshes, harbors and dikes) adding to the impression that the birds were starving to death. In order to survive, Eiders were even observed digging out Cockles on muddy tidal flats at low tide instead of restricting their feeding to periods when the flats were covered with water (pers. obs. RK). We demonstrated that both the total mortality and the mortality rate of the wintering population in the Wadden Sea area were increased when the stock of subtidal medium-sized Mussels was reduced. In contrast, there was no evidence that mass mortality was related to or induced by pollution (Camphuysen *et al.* 2002), nor was there evidence that parasites were the prime determinant of mass mortality (Kats *et al.* 2007b, Chapter 6). This does not exclude the possibility that when all food stocks were low, Eiders shifted their diet towards Shore Crabs *Carcinas maenas* thus increasing their exposure to parasite infection (this crab is the intermediate host of the acanthocephalan *Profilicollis botulus*, known to infect Eiders, see Cleave & Rausch (1951) and Ching (1989)). The importance of medium-sized subtidal Mussels (30 – 55 mm) as a food source in winter is in agreement with field data from Germany (Nehls 1995) and Canada (Hamilton *et al.* 1999) and experiments on caged birds showing that subtidal Mussels are preferred over intertidal Mussels by feeding Eiders (Bustnes 1998). Our analysis also suggested that mortality was especially high when many more birds moved to the North Sea coastal zone than the stocks of mature *Spisula* could support (judging from the relationship between the number of Eiders wintering on the North Sea and the stock of mature *Spisula*). At present, we have no strong evidence that the American Razor Clam can serve as an alternative food source in periods when subtidal Mussels are scarce (Figure 7.7C). However, the estimates of the stock of the Razor Clam are very crude and do not distinguish between different age classes. Two lines of evidence show that Eiders can only profitably prey on some (small) age classes. First, some Eiders were found dead with large Ensis (> 100 mm) stuck in their throat (Swennen & Duiven 1989, Ens *et al.* 2002). Second, a fecal analysis showed the presence of only small (< 100 mm) Ensis (Leopold *et al.* 2007 or Chapter 4).

Common Eiders and shellfish fishery in the Netherlands

Camphuysen *et al.* (2002) hypothesized that "overfishing of mussels and cockles in the Wadden Sea in the early 1990s resulted in structurally reduced food resources, contractions of the foraging area of common eiders, and increased use of secondary prey in the North Sea". In this and in other studies (Ens *et al.* 2007), we have not been able to demonstrate that Cockles are an important food source for Common Eiders wintering in the Dutch Wadden Sea. As a result, our study does not support the idea that fishing of Cockles contributed to the mass mortality of Common Eiders. However, our studies clearly show that subtidal mussels play a very prominent role in determining the general distribution in the Wadden Sea (Ens *et al.* 2007) as well as in determining changes in distribution and mortality of wintering Common Eiders within and outside the Wadden Sea area. Our study also adds evidence to the conclusion of Camphuysen *et al.* (2002) that intensive fishing of *Spisula* banks in the autumn of 1999 contributed to the mass mortality in the winter of 1999/2000. The next winter, when stocks of subtidal Mussels were still low, there was a very high stock of mature *Spisula* and there was no mass mortality of Eiders.

Given the importance of subtidal Mussels to Eiders, it seems sensible to investigate in more detail the relationship between Common Eiders and the fishery and culture of Mussels. Since the introduction of mussel cultures in the western Wadden Sea in 1951, mussels were no longer restricted to wild littoral and subtidal beds, but also found in large numbers on subtidal cultured beds (Figure 7.1). Most mussel seed used to stock the mussel cultures in both the Wadden Sea and Oosterschelde is collected from natural beds in the subtidal parts of the Dutch Wadden Sea (Dijkema & Stralen 1989, Dijkema 1997, Smaal & Lucas 2000). After on average two years, seed mussels have reached commercial size and are fished for landing (Dankers & Zuidema 1995, Dijkema 1997, Smaal & Lucas 2000).

Mussel culture includes activities that may increase the stock of Mussels available to Common Eiders as well as activities that may decrease this stock. Activities that increase the stock are: (1) transport of Mussel seed from the littoral zone to the subtidal, (2) transport of Mussels to areas within the western Wadden Sea where growth is improved and mortality reduced, (3) active measures on culture plots against invertebrate predators of Mussels (mainly Starfish *Asteria rubens*) on culture plots. Activities that decrease the stock available to Common Eiders are: (1) transport of seed Mussels to culture plots outside the Wadden Sea (*i.e.* in the Oosterschelde), (2) transport of consumption sized Mussels to the auction in Yerseke, (3) chasing of Eiders from culture plots. In addition, it is possible that mussel seed fishery has a long-term effect on the probability of successful spatfall in later years. Thus, it is not immediately obvious whether mussel culture increases or decreases the stock of subtidal mussels available to Common Eiders in the western Wadden Sea.

Assuming that mussel fishery does not affect the probability of Mussel recruitment in future years and that scaring of Eiders from culture plots can be ignored, (Bult *et al.* 2004b) tentatively estimated for the 1990s that in an average year the net effect was positive and amounted to 15%. This does not exclude the possibility that mussel culture actually decreases the stock available to Eiders in periods of scarcity. The target production of the Mussel producers amounts to 100 million kg fresh weight per year, so annual landings considerably below this figure suggest a shortage of Mussels. Of course, only stock measurements can provide definitive proof of low sublittoral stocks, but we do know that when the landings reached an all time low in the early 1990s, the littoral wild beds were completely depleted (Ens *et al.* 2004). Furthermore, the mussel farmers are well aware of the fact that, even though Mussels may be sold at a high price in years of scarcity, high variability is a drawback for the industry that depends on a dependable supply of Mussels over the long term.

It turns out that in years when total landings are low, landings from the Wadden Sea are particularly low (Figure 7.8). A possible explanation is that in periods of scarcity more seed and medium-sized Mussels are shipped from the Wadden Sea to culture plots in the Oosterschelde, thereby exacerbating the shortage of Mussels in the Wadden Sea. According to the mussel farmers, exactly the opposite happens. They preferentially stock the culture plots in the Wadden Sea because Mussels grow better than on the plots in the Oosterschelde. In years of scarcity, a greater percentage can be stored on the plots in the Wadden Sea, whereas a large amount of seed Mussels forces them to transport relatively more of these seed Mussels to the Oosterschelde. No direct data on transports of Mussels are available. On the basis of reconstructed data, Bult *et al.* (2004b) find no evidence for increased transports in years of scarcity. However, their reconstruction is based on the assumption that of each age class a constant fraction is transported to the Oosterschelde. By assuming that a constant fraction is transported each year, it is impossible to find evidence for increased transports in years of scarcity. In addition, it may be asked if we should investigate this issue simply on a yearly basis, ignoring cumulative effects. Following a good spatfall, the stock-increasing activities of mussel farmers, like the transport to areas where growth is good, probably outweigh the stock-decreasing activities, like the transports to the Oosterschelde. However, the more years it takes before a new good spatfall occurs, the more likely it is that the cumulative impact of stock-decreasing influences will start to outweigh the stock-increasing influences. It is even possible that at the end of such a period, there are fewer Mussels in the Wadden Sea than would have been present had there been no mussel culture. Under the hypothesis of cumulative effects, scarcity of Mussels results from a run of years with poor spatfall. Each year, Mussels are transported from the Wadden Sea to the Oosterschelde and to the market, so that fewer and fewer Mussels remain in the Wadden Sea. A "long" run of years with poor spatfall will lead to a high scarcity of Mussels and a small pro-
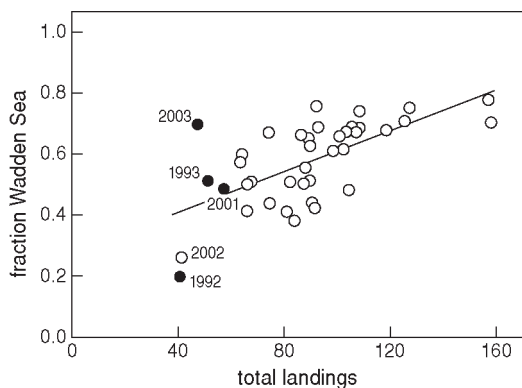
Figure 7.8 The fraction of Mussels *Mytilus edulis* landed from the Wadden Sea cultures in relation to the total landings (expressed as million kg fresh wet mass) of Mussels from Dutch coastal waters (= Wadden Sea and Oosterschelde) in the period since 1965 when the production area in the Wadden Sea stabilized at around 70 km^2. Years following a kill winter (1992, 2001 and 2003) or following a presumed kill winter (1993) are marked with filled symbols.

portion of Mussels that can be landed from the Wadden Sea, explaining the relationship in Figure 7.8. From the viewpoint of the fishery this is a form of recruitment overfishing, *i.e.* the stock of wild mussels available for transport to the culture beds in the Wadden Sea is not always sufficient.

Policies to safeguard shellfish-eating birds from the negative impacts of shellfish fishery

Following the shortage of shellfish and the increased mortality of shellfish-eating birds in the early 1990s, the Dutch government has sought to implement policies that would prevent shellfish fisheries from having a negative impact on the shellfish-eating birds. We will discuss the effectiveness of these policies in the light of our findings. The first policy was introduced in 1993 as part of the new Sea and Coastal Fisheries Policy (LNV1993). It was a policy of food reservation that amounted to a ban on shellfish fishery when shellfish stocks were below a threshold value. Initially, the policy only applied to littoral shellfish stocks, whereas Common Eiders primarily depend on sublittoral shellfish stocks. Following the mass mortality of Common Eiders in the winter of 1999/2000 and a critical evaluation of the policy of food reservation (Ens 2000), the policy was changed in 2000. Since that time, a total of 8.6 million kg shellfish flesh had to be reserved for the Common Eiders in the sublittoral areas. However, the new policy did not take into account differences in profitability and availability of the different shellfish species, *i.e.* Cockles, Mussels and *Spisula* were treated as equally profitable, which is not valid as this and other studies show, e.g. (Bustnes 1998). The policy also assumed that all shellfish left for the birds could be harvested by them, which

ignores the fact that birds can only harvest a fraction of the available biomass (Goss-Custard *et al.* 2004). A more general criticism is that a policy of food reservation only looks at a single year and thereby ignores cumulative impacts of shellfish extraction (Ens *et al.* 2004). Finally, the food reservation policy assumes that extraction of shellfish is the only way by which the fishery impacts the birds. This assumption appears to be wrong for suction dredging of cockles, which was shown to have long-term negative impacts on the sediment and recruitment of shellfish (Piersma *et al.* 2001), as well as the quality of the Cockles that serve as food for the Knot *Calidris canutus* (Gils *et al.* 2006a). Thus, a policy of food reservation can only work if (1) the fishery only impacts the stock of shellfish, (2) cumulative effects of shellfish extraction are taken into account, (3) differences in availability and profitability of prey are properly taken account of. The fact that mass mortality of Eiders occurred in the winter of 2001/2002, despite the changes to the policy of food reservation in 2000, seems at least partly due to the fact that these conditions were not met in the revised policy.

In 2004, the Dutch government decided on a new policy document that will remain in effect until 2020 (LNV 2004). Mechanical cockle fishery will no longer be allowed in the Dutch Wadden Sea and the policy of food reservation is abandoned for that area. For the fishery on *Spisula* no specific policies are formulated other than that the number of permits will remain limited and that the fishermen must come up with a fishing plan that will be tested against the requirements of the EU Wild Birds and the EU Habitats Directives. The new policy on mussel seed fishery and mussel culture in the sublittoral zone consists of restrictions on the areas where fishery can take place and restrictions on transport of mussel seed. Some areas will be permanently closed for studying the impact of mussel fishery on natural values. In autumn, mussel seed fishery is only allowed in areas thought to be unstable, *i.e.* the chance that the Mussels will survive there is thought to be low. There are no restrictions on transport of the Mussels. In spring, there are no restrictions on the locations of the fishery, but 85% of the fished Mussels must remain at least one winter in the Dutch Wadden Sea. Several implicit and explicit assumptions underlie this new policy. First, it is assumed that mussel fishery does not have a negative impact on the spatfall of Mussels, *i.e.* other causes than the mussel fishery are thought responsible for the declining productivity of Mussels (Figure 7.2). Second, it is assumed that areas can be defined where Mussels are likely to settle, yet have a high chance of disappearing during the winter; this disappearance not being due to predation by birds. Third, it is assumed that restricting the transport for one year of 85% of the Mussels fished during spring provides sufficient guarantees that for each single year, the positive effects of mussel fishery on the stock of Mussels in the Dutch Wadden Sea will exceed the negative effects. To date, the only scientific evidence to support these assumptions are the tentative calculations of Bult *et al.* (2004b) that, on average, mussel cultures had a small positive effect (15%) on the stock of sublittoral Mussels in the Dutch Wadden Sea

during the 1990s. As we have seen, this is not an independent assessment as it also takes as point of departure the assumption that the fishery does not affect the recruitment of Mussels.

Conclusion

Our study makes clear that both exploitative fishery of *Spisula* and mussel culture may affect the numbers, the distribution and the mortality of Common Eiders. Whether the new shellfish policy provides sufficient guarantees against negative impacts of these fisheries on Eiders is not proven and requires further study. First, it must be investigated if mussel seed fishery has an impact, either positively or negatively, on spatfall of Mussels in future years. Second, a Mussel population model must be developed and tested, that allows us to assess the impact on the Mussel stock of transport of Mussels between culture plots in the Wadden Sea and transports of Mussels from the Wadden Sea to the Oosterschelde. Third, all transports of Mussels should be registered, so that these data can serve as input for the Mussel population model.

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

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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 mollissima*) 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 m^2 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 m^2 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% shorecrab *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

Table 8.1 The correlation between the area in a grid cell covered by littoral cockle *Cerasto-derma 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).

Grid size (m)	Winters kept separate		Winters averaged per grid cell	
	Pearson r	N	Pearson r	N
750	0.23	54792	0.45	4566
1500	0.34	14688	0.56	1224
3000	0.45	4116	0.62	343
5000	0.53	1692	0.66	141
10000	0.62	516	0.71	43

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 8.2 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).

Grid size (m)	Winters kept separate		Winters averaged per grid cell	
	Pearson r	N	Pearson r	N
750	0.70	54792	0.91	4566
1500	0.72	14688	0.91	1224
3000	0.78	4116	0.93	343
5000	0.81	1692	0.94	141
10000	0.85	516	0.97	43

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

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:

$$Eiders = e^{(a+b*MSw+c*MSp+d*ML+e*CS+f*CL)} \tag{1}$$

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)
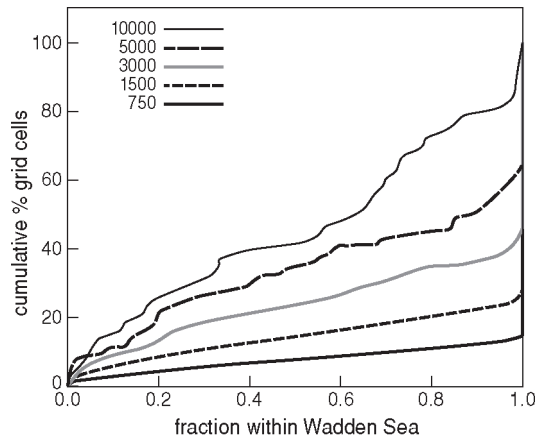
Figure 8.1 Cumulative frequency distribution of the area of a grid cell within the Dutch Wadden Sea (i.e. consisting of littoral or sublittoral areas) for different grid cell sizes.

- 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 (m^2)
- 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)
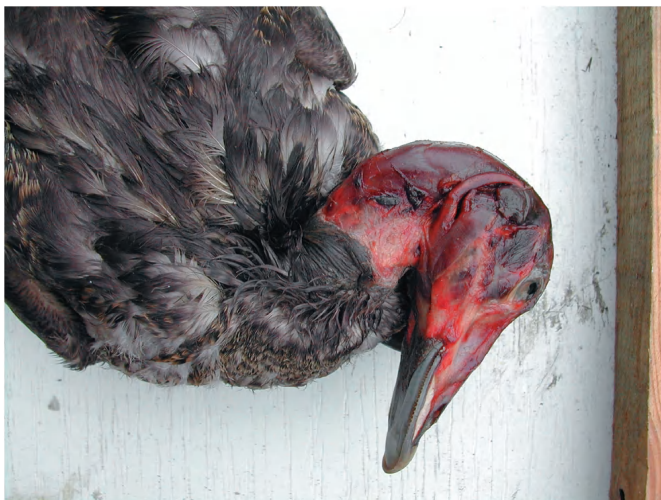
Horror in the Wadden Sea. Scalped Eiders were frequently reported (alive and dead) since the end of the 1990's, but sightings and recoveries were restricted to in the western part of the Wadden Sea. (Photo: Alterra)

Profilicollis botulus (orange/yellow worms) in the intestine of a dissected Common Eider collected during mass-mortality. (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
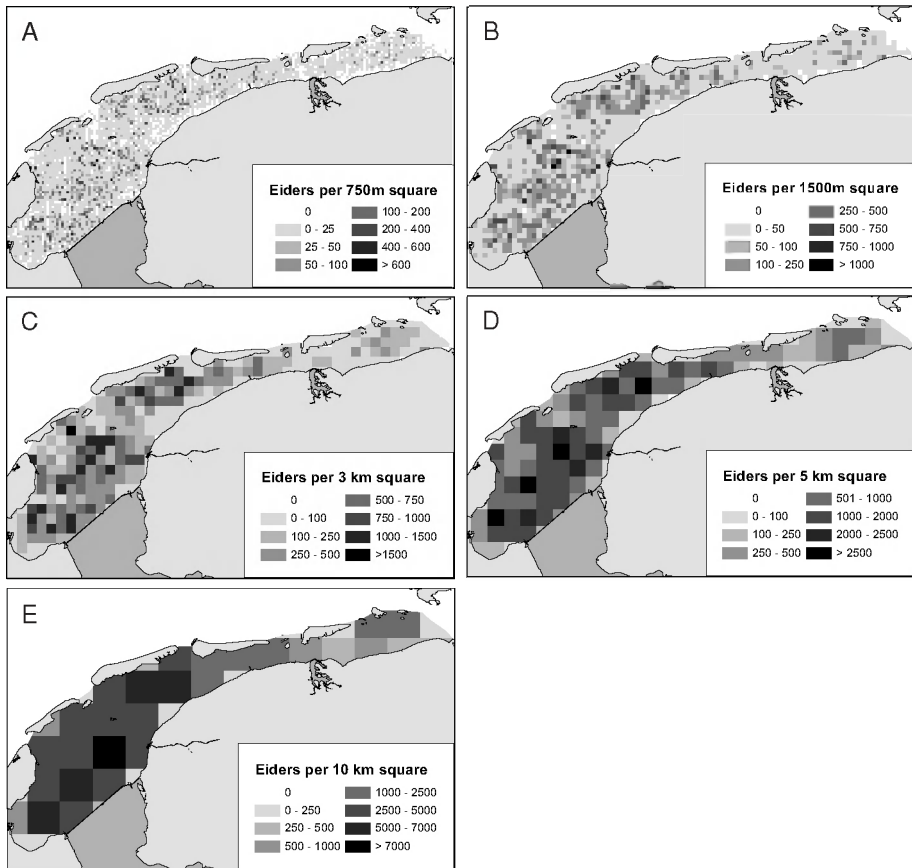
Figure 8.2 Average distribution of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea for the winters 1994-2004 at different spatial scales, i.e. grid cells of different size: (A) 750 m, (B) 1500 m, (C) 3000 m, (D) 5000 m, (E) 10000 m.

The remainings of Shore Crabs *Carcinas 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)
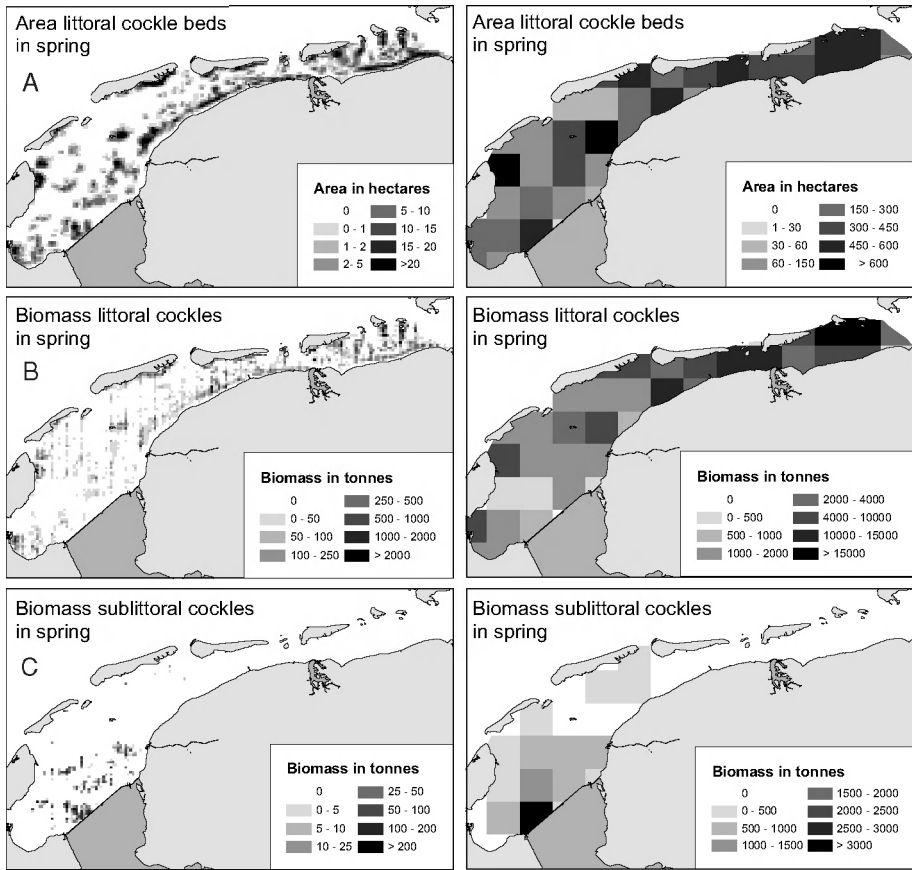
Figure 8.3 Average distribution in the Dutch Wadden Sea over the winters 1994-2004 of (A) area littoral cockle *Cerastoderma edule* beds in spring, (B) biomass littoral cockle beds in spring, and (C) biomass sublittoral cockle stocks in spring,. Graphs on the left indicate the average distribution using 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.

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
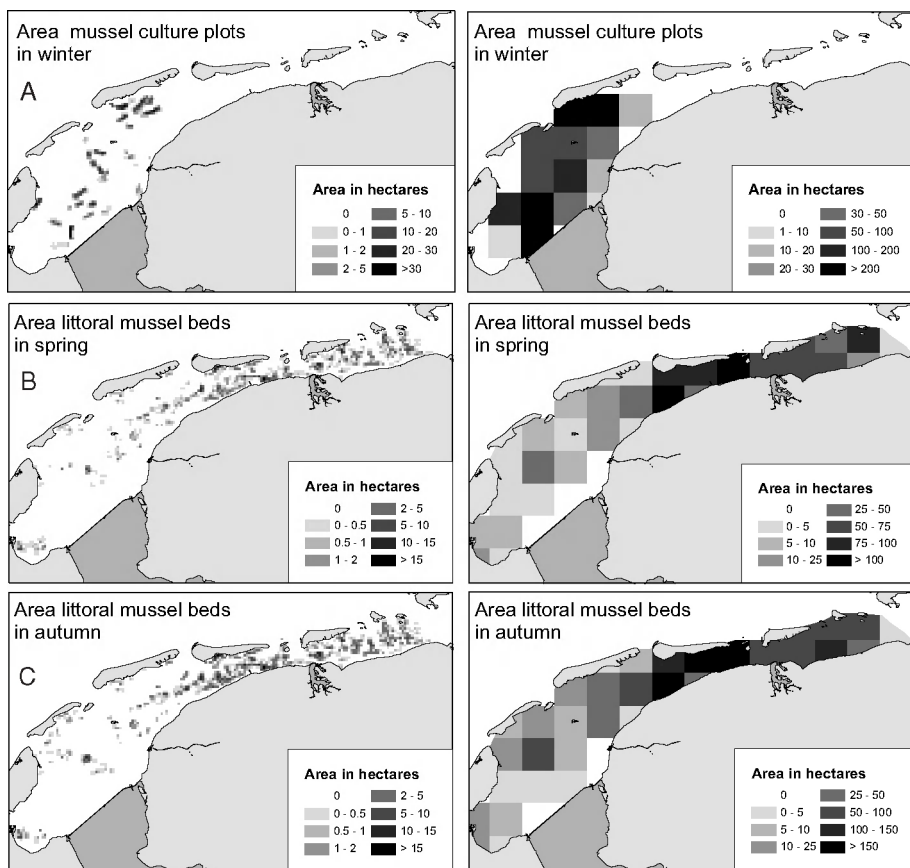
Figure 8.4 Average distribution in the Dutch Wadden Sea over the winters 1994-2004 of (A) area covered with mussels *Mytilus edulis* on sublittoral culture plots, (B) area of littoral mussel beds in spring, and (C) area littoral mussel beds in autumn. Graphs on the left indicate the average distribution 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.

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).
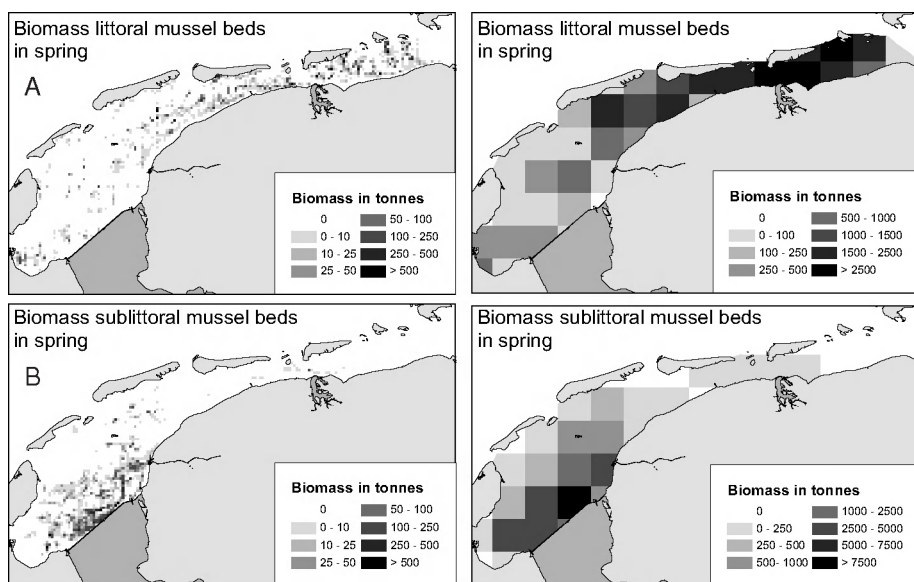
Figure 8.5 Average distribution in the Dutch Wadden Sea over the winters 1994-2004 of (A) biomass littoral mussel *Mytilus edulis* beds in spring and (B) biomass wild sublittoral mussel stocks in spring. Graphs on the left indicate the average distribution using a grid cell size of 750 m by 750 m and the graphs on the right indicate the average distribution using a grid cell size of 10 km by 10 km. See text for details.

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 ($P<0.01$).

Grid size (m)	N	Pearson r untransformed counts	Pearson r transformed counts
750	13698	0.02	0.05
1500	3672	0.09	0.19
3000	1029	0.31	0.45
5000	423	0.44	0.68
10000	129	0.59	0.79
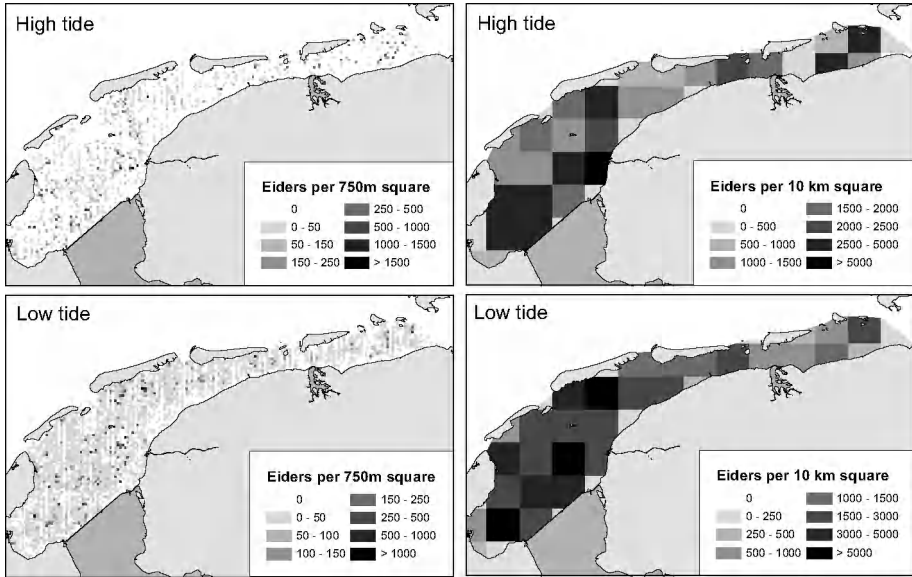
Figure 8.6 Comparison of the distribution of Common Eiders *Somateria mollissima* counted during high tide and during low tide in the Dutch Wadden Sea, averaged for the winters of 2000, 2001 and 2003, for two spatial scales: grid cell size of 750 m by 750 m on the left and a grid cell size of 10 km by 10 km on the right. Top graphs are during high tide and bottom graphs are during low tide.

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.7 (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:

$$Eiders = e^{(a+b*MSw)} \tag{2}$$

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

191
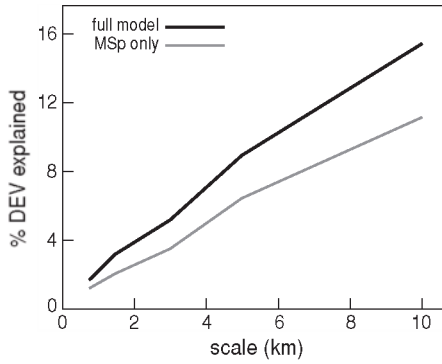
Figure 8.7 Common Eider *Somateria mollissima* distributions from shellfish information at various spatial scales (0.75, 1.5, 3, 5, 10 km) in the Dutch Wadden Sea. % deviance explained by the models "Full:" *Eiders* $= e^{(a+b*MSw+c*MSp+d*ML+e*CS+f*CL)}$and "MSp only (= culture plots only)": *Eiders* $= e^{(a+b*MSp)}$; winters of 1994-2004.
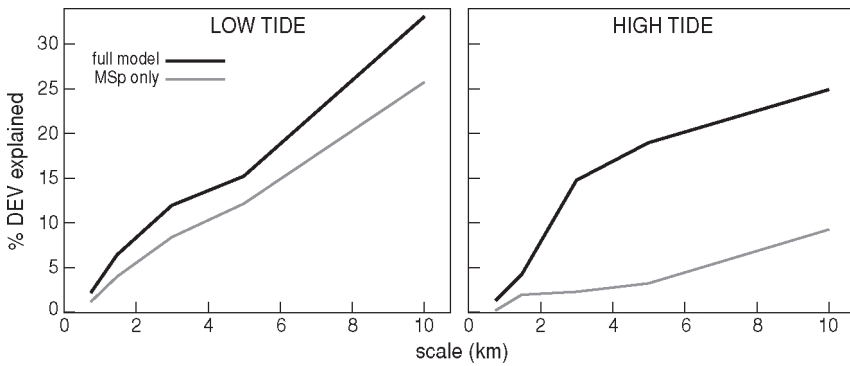
Figure 8.8 Common Eider *Somateria mollissima* distributions from shellfish information at various spatial scales (0.75, 1.5, 3, 5, 10 km) in the Dutch Wadden Sea. % deviance explained by the models "Full:" *Eiders* $= e^{(a+b*MSw+c*MSp+d*ML+e*CS+f*CL)}$and "MSp only (= culture plots only)": *Eiders* $= e^{(a+b*MSp)}$; winters of 2000, 2001, 2003 during low tide and high tide.
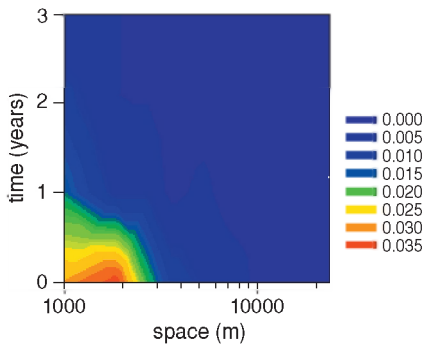
Figure 8.9 Non-ergodic correlogram of Common Eider *Somateria mollissima* distributions in the Dutch Wadden Sea at multiple space-time scales. Period 1994-2004.

increased with spatial scale and that roughly $^3/_4$ 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 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

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.

winter	all	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	n
df - empty	472	42	42	42	42	42	42	42	42	42	42	42	
df - full	470	40	39	40	40	39	42	41	41	41	40	40	
ML		–	0.00			0.00							2
MSw	0.00	0.04	0.00	0.00						0.01	0.00		5
MSp	0.00	0.01	0.00	0.01		0.01		0.04	0.00	0.03	0.00	0.02	9
CL					0.00								1
CS					0.00	0.00							2
empty	1860971	223336	116846	262535	184376	160137	220824	53292	46469	57214	166912	261017	
full	1589648	186739	55646	183278	131635	86356	220824	49047	36203	52507	109036	177441	
% DEV expl.	15	16	52	30	29	46	0	8	22	8	35	32	

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-

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.

winter	all	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	n
df - empty	50225	4565	4565	4565	4565	4565	4565	4565	4565	4565	4565	4565	
df - full	50221	4563	4560	4563	4563	4562	4563	4561	4562	4563	4561	4562	
ML	0.00	-	0.00		0.01	0.00	0.03		0.00	0.00	0.00		7
MSw	0.00		0.00	0.00				0.00		0.00	0.00		5
MSp	0.00	0.01	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	10
CL	0.00	0.03	0.02		0.01	0.02		0.00			0.04		6
CS			0.00					0.01	0.01			0.00	4
empty	6870187	849037	547008	859532	785252	625954	799407	298745	167579	212784	605271	1011604	
full	6748894	843355	520651	832908	777000	570974	795060	293011	163764	199098	591777	884716	
% DEV expl.	2	1	5	3	1	9	1	2	2	6	2	13	

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.

Distribution of Eiders and shellfish at the scale of 750 m
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.
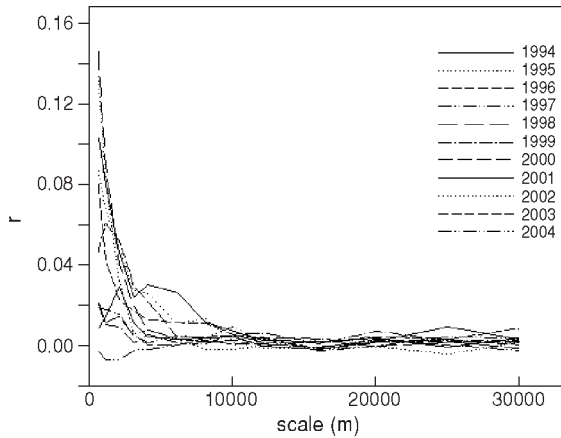
Figure 8.10 Non-ergodic cross-correlogram between the number of Common Eiders *Somateria mollissima* and the surface area of mussel culture plots with mussels (MSp) in the Dutch Wadden Sea. Years separate for the period 1994-2004.

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 focussing 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 lager 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 structure 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 distributions and their prey. For instance Schneider & Piatt (1986) observed that the pattern 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 resolutions 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 prevent 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 & Schneider 1997, Robinson *et al.* 2002, Robinson *et al.* 2004).

On a more general note, animal distributions are generally the result of processes 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 logistical 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 lager 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 con-
clusion 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), sub-
littoral 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 com-
pared 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 attrac-
tiveness 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 pri-
marily 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 cock-
les (Ens & Kats 2004). However, a much more thorough investigation of the actu-
al 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 differ-
ences 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.

Rise and fall of the nesting population of the Common Eider *Somateria mollissima* in the Netherlands since 1906: a demographic reconstruction distinguishing between catastrophic mortality events and non-breeding

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Abstract

In the Netherlands, Common Eiders *Somateria mollissima* successfully established a breeding colony in 1906 on the coastal barrier Wadden Sea Island of Vlieland. The size of the colony increased rapidly from 350 breeding females in 1940 to 4000 in 1960, but declined to 800 breeding females in 1968 due to a large-scale pollution peak in coastal waters with organochlorides and recovered slowly. By 1980, the colony had regained stability but at a lower level with a long-term average (1980-2003) of 2150 (1050 – 2700) breeding females. Declines in the number of breeding females were observed anew between 1988 and 1993 and since 2000, and it is the purpose of this paper to examine the causes in demographic terms (making use of the results of a ringing programme at this colony).

The number of fledglings produced has been highly variable (0-3000) with two periods with low productivity (resp. 70 and 29 fledglings^{-year} in 1966-1977 and 1989-1994) coinciding with the first two declines in breeding numbers. Since 1994 production of fledglings has been comparable to the 1980s.

Beach surveys of carcasses (systematic data since 1978) substantiate increased mortality of adult eiders in the Dutch Wadden Sea during the periods of colony decline (1988-93 and since 2000) but these figures include migrants from other populations and non-breeders.

Estimates of annual survival in females from the Vlieland colony were calculated using MARK based on females caught and ringed as fledgling or as breeding adult at the nest. For females caught as fledgling (1975-1985), long-term average survival was 0.926 ± 0.028 for juveniles, 0.971 ± 0.010 for immatures and 0.921 ± 0.002 for adults. Long-term (1974-2003) survival of breeding females was on average 0.927 (± 0.008 S.E.) with a constant reporting rate of 0.241 (± 0.019 S.E.). Survival was reduced during the 10 'kill-years' (1984, 1988-92, 2000-03) identified by the beach carcass surveys and averaged 0.872 (± 0.006 S.E.), in contrast to 0.955 (± 0.006 S.E.) in normal years.

Survival of breeding females, juveniles and immatures derived from the ringing programme at Vlieland were negatively and highly significantly related to total mortality assessed by the survey of beached carcasses along the Dutch coast.. Adult females caught at the nest were primarily reported dead during the breeding season (April-June, in the 'kill-years' especially May). The beached surveys of dead eiders (which include losses from the abundant wintering population) revealed extensive pre-breeding mortality in late winter and spring.

Annual estimates of survival were extrapolated since 1985 for the population trajectory using total annual mortality as a predictor of juvenile, immature and adult female survival. Adult females caught at the nest were primarily reported dead during the breeding season (normal years: April – June; 'kill-years': May), while total annual mortality peaked prior to breeding in March. The propensity of breeding (probability of an individual in the age group to breed) for immatures

(2nd and 3rd year old birds) was estimated at respectively 0.188 (± 0.072) and 0.696 (± 0.138).

Population trajectories were calculated for the colony on Vlieland in order to predict the total pool of breeding females and calculate the expected annual fraction of non-breeding in the population. This model exercise relied on actual data on the number of breeding females and fledglings (assuming equal sex ratio at fledging) and estimations data for the probability of breeding in 2nd and 3rd year old females and the annual survival of juvenile, immature, all adult and only breeding adult females. Comparison of the empirical census data revealed the existence of widespread non-breeding in adult females of the Vlieland population (up to 60%) during two periods which coincided with mass-mortality in the beach surveys and colony declines (1988-1992, 2000-2003).

The rapid recovery of the Vlieland colony between 1991 and 1994 can be accounted for by re-entry from the extensive pool of non-breeding adult females originating in 1988-1990 as revealed by the population modelling. The current decline (starting 2000) has not yet been reversed.

This study shows that long-lived breeding bird species such as the Common Eider can qualify as a quality indicator of an entire ecosystem, i.e. Wadden Sea, providing they are the subject of long-term ecological investigations. A simple enumeration of the total number of breeding females is an inadequate measure of the underlying processes, and study must include total mortality estimated from ringed individuals, estimates on the annual production of young, and the annual rate of non-breeding.

Introduction

Non-breeding (or intermittent breeding) is one of the major determinants of fitness at the individual level (Newton 1989). Non-breeding has been frequently reported in many species especially for long-living species, such as raptors (Newton 1985), gulls (Bradley *et al.* 2000, Hatch 1987), geese (Rockwell *et al.* 1985), cormorants (Boekelheide & Ainley 1989), auks (Jones & Montgomerie 1992), flamingos (Cezilly *et al.* 1996) and sea ducks (Coulson 1984). In order to survive individuals may decide to skip current reproductive effort if insufficiently recovered from the previous breeding attempt and/or when the current circumstances were not sufficient to allow sustainable reproduction. Intermittent or skipping reproduction can be interpreted as an adaptive strategy to avoid the potential costs

of breeding and to increase the Residual Reproductive Value and maximize Lifetime Reproductive Success (Aebischer & Wanless 1992, Wooler *et al.* 1989).

At the population level, non-breeding affects the growth rate of a population and is potentially an important regulatory mechanism (Hémery *et al.* 1986). The importance of non-breeding has been undervalued in population biology and evolutionary ecology (Cam *et al.* 1998). Extensive non-breeding has been reported for a breeding population of Common Eiders *Somateria mollissima* in England with non-breeding varying up to 65 % in some years (Coulson 1984). Coulson studied an individual colony over a twenty-five year period and relied on an ongoing ringing programme to elucidate the demographic factors that might explain the changes in numbers of breeding eiders he observed (increasing trend 1958–82). Common Eiders are capital breeders and females use body condition relative to a fixed threshold as a cue for breeding (Drent & Daan 1980). Females rely completely on stored reserves for breeding (Thomas 1988), which are stored prior to breeding in the vicinity of the breeding colony (Christensen 2000, Parker & Holm 1990). In the Dutch breeding colony on Vlieland, female eiders are non-migratory and extremely philopatric to the natal and breeding colony throughout their annual cycle (Swennen 1991a), and are dependent on food availability near the breeding colony for survival and reproduction.

In this paper we investigated the temporal decline (1988–1993) in the number of breeding females, and the subsequent recovery up to 2000 which was observed in the total Dutch breeding population and individual colonies. Detailed information on breeding reproduction and survival of the breeding colony on Vlieland (1974–2003) was used to calculate a reconstruction of the population trajectory of the potential breeders in order to distinguish whether the observed declines in breeding numbers relate to reduced survival and/or non-breeding.

First, how did the size of the breeding population on Vlieland develop since the re-establishment in 1906? And, how did the colony develop with respect to total number of fledglings produced? Long-term data on the number of breeding females was based on an historic reconstruction until 1962 (c.f. Swennen 1976a, 1991a). Since then, the number of breeding females and fledglings produced were estimated annually.

Second, did total annual mortality vary between years and within years? Did patterns in total mortality differ in years with mass-mortality? Mortality was estimated for each month using beach surveys of carcasses (1977/78 – 2002/03) in order to calculate annual (November to October) and seasonal (winter: November – April) estimates.

Third, how did annual survival of females vary in time? Did survival vary with age and breeding? Estimates of annual female survival were calculated using MARK. Annual survival of juvenile, immature and all adult females was estimated using the females caught and banded with steel rings as fledgling (1975–1985), while survival of adult breeding females (representing a sub-sample of the total

pool of adult females) was estimated using breeding females caught at the nest (1974–2003). This independent data set allowed comparison with the mortality estimated from the beach carcass survey 1978–2003.

Fourth, what was the probability of first breeding in 2nd and 3rd year old females? The probability of first breeding in 2nd and 3rd year old females was based on females ringed as fledgling and subsequently reported as breeding in the colony in the following years using all data females ringed as fledglings (aluminium: 1962–1973; steel: 1974–85).

Finally, population trajectories for the breeding colony on Vlieland were calculated in order to explain whether the observed declines in the observed number of breeding females (1988–94 and since 2000) were related to reduced survival and/or increased non-breeding?

Methods

Study area
The Dutch section of the Wadden Sea (N 52° 45' – N 53° 33' and E 6° 43' – E 6° 56') is a large tidal area (2409 km^2) in the northern part of the Netherlands and is characterised by tidal mud- and sand flats with gullies, and natural beds of Atlantic Blue Mussels Mytilus edulis and Edible Cockles Cerastoderma edule occurring in the tidal and sub-tidal parts of the Wadden Sea. Vlieland is one of the six coastal barrier islands and is located in the western part of the Wadden Sea (1618 km^2).

Data collection

Breeding biology of the colony on Vlieland
BREEDING FEMALES AND FLEDGLINGS
The development of the size of the breeding colony (expressed as the number of breeding females) on Vlieland since the beginning of the 20th century was based on previous reviews (Swennen 1976a, Camphuysen 1996) and extended up to the breeding season of 2003. Since 1962, annual surveys on the number of breeding females are indirect and derived from counts of birds on the water around the colony (Duiven & Zuidewind 2001) conducted prior to the hatching of the first nest, which was in general observed in the second week of May. This count is based on a complete survey of males (where juvenile and adult can be distinguished) and female eiders taken all together due to difficulties in aging females in the field. The number of breeding females was calculated as follows on the assumption that the breeding females are all on the nest and that the ratio of breeding females to adult males is 1:1:

Breeding females = Adult males – (all females – juvenile males)   (1)

Missing data (1992, 1996 – 1999) was imputed using monitoring data of a fixed plot in the Vlieland colony (Vallei van het Veen, unpublished data Peter de Boer) using those years when data of both types of survey were available (breeding females = 1752*Log(Vallei van het Veen) – 825, n = 7, R^2 = 0.76, p = 0.011).

The number of successful fledglings of 5 – 7 weeks old was assessed in the first week of July during surveys at high tide, because mortality among ducklings peaked during the first weeks after hatching and crèches of fledglings rested near the natal island at high tide (Swennen 1991b). For Vlieland, fledgling data was available for 1947 and since 1962 with no data during two periods (1989-93, 1998-99). Swennen (1989) carried out experiments on the role of food and predation on the survival of fledglings and increased the number of successful fledglings at the Vlieland colony with in total 1895 fledglings in 1975 (93), 1976, (826) and 1978 (976). These experimentally raised birds were ringed so their fate can be traced.

SURVIVAL, FIRST BREEDING AND TOTAL MORTALITY OF THE VLIELAND CONTINGENT
Estimating time and age dependent female survival and reporting rates of a local population followed standard procedures as applied to ringed individuals. Survival (Φ) and recovery rates (ρ or probability of a marked bird being reported dead) were estimated for live capture and dead reporting data using MARK (White & Burnham 1999). The NIOZ (1963–1996) and Alterra/RuG teams (2001–2003) caught Eiders in the Wadden Sea during a long-term banding program with dead birds being reported to the Dutch Bird Banding Scheme (Vogeltrekstation Heteren). The analysis was restricted to females due to their extreme philopatric nature of breeding, i.e. life-time dependence on the colony of hatching and breeding (Coulson 1984, Swennen 1991a). In the Netherlands, Eiders were caught since 1963 and ringed with steel rings starting in 1974, which were used in this analysis. Ringing data was available for breeding adult females caught at the nest (1974–2003: between the end of April and the end of May) and for females caught as 6 to 8 week old fledglings near the colony (1975–1985: the beginning of July). Fledglings were caught around the age of 6–8 weeks, because mortality among juveniles was predominantly observed during the first 4 weeks since hatching (Swennen 1989). Time-dependent survival was analysed with a year running from 1 November until 31 October.

Time dependent-survival of females in the breeding pool was estimated for adult breeding females (caught at nest: n = 2109), and for juvenile, immature and adult females (caught as fledgling: n = 2238). The inclusion of time and age-dependent survival and reporting rates in the models was determined by the lowest value of the Akaike Information Criterion (AIC), which selects the most parsi-

monious model explaining the data best with the smallest number of parameters. In MARK, the fit of the model to the data (H0: model not different from data) was tested by means of a bootstrap Goodness of Fit (running 100 simulations). Significant individual model hypothesis, only if nested, were tested by likelihood ratio test (LRT) and were considered significant at p < 0.05 (White & Burnham 1999). The degree of over-dispersion was given by the variation inflation factor $\hat{c}$. Models were corrected for over-dispersion at values of $\hat{c} \geq 2$ using the adjusted over-dispersion factor $\hat{c}$, which was calculated as the ratio between the models deviance and the average boot-strapped deviance, and the most parsimonious corrected model was subsequently selected by the lowest value of Q_{AIC}.

Age of first breeding

The probability of first breeding in relation to age was calculated using the following model:

$$E[x_{ij}] = n_j * p_{ij} = n_j * \{(m_i * b(j\text{-}i)*s(j\text{-}i)\}/\{(\textstyle\sum_{k<j}) m_k*b(j\text{-}k)*s(j\text{-}k)\},$$

with x_{ij} the number of female birds, recovered in year j, which were ringed in year i, n_j the number of female birds, recovered as breeding in year j, p_{ij} the probability that a bird recovered in year j was ringed in year i, m_i the number of females ringed as fledgling m in year i, $b(j\text{-}i)$ the breeding fraction of birds of age $j\text{-}i$, $s(j\text{-}i)$ the probability of annual survival of birds of age $j\text{-}i$. Hence, x_{ij} followed a multivariate hypergeometric probability distribution, but since $m>>n$ this can be approximated by a multinomial distribution. So the log-likelihood ($L = -\sum x_{ij} \log p_{ij}$) was minimised in order to obtain parameter estimates. It was assumed that $b(j\text{-}i)$ equals 0 when $(j\text{-}i) \leq 1$; $b(j\text{-}i)$ equals b_2*b when $(j\text{-}i)=2$; $b(j\text{-}i)$ equals b_3*b when $(j\text{-}i)=3$; and $b(j\text{-}i)$ equals b when $(j\text{-}i)>3$. Furthermore for $(j\text{-}i)>1$, the survival rate $s(j\text{-}i)=s_0s_1{}^{j\text{-}i}$ when I < 1974 (aluminium rings) and $s(j\text{-}i)=s_0s_2{}^{j\text{-}i}$ when i $\geq$ 1974 (steel rings). Hence s_1 includes the rate of ring loss.

Total mortality derived from beach surveys of the Dutch coast-line

Total annual mortality of Common Eiders (or the total estimated number dead birds) in the Wadden Sea area was assessed by numerous volunteers (participating in the long-term national Beached Bird Survey or BBS along both North Sea and Wadden Sea shorelines) as reported by Camphuysen *et al.* (2002). BBS were conducted by walking along the high-tide line while counting and describing all encountered dead corpses with respect to age, sex, oil and freshness of the corpse, and double counts were avoided by clipping the primaries of both wings. The total estimated number of dead Eiders was calculated using log-linear models with a Poisson distribution, a log-link and over-dispersion. Data was corrected for effort and length of the transect, and the number of dead Eiders encountered during BBS was assumed to be equal to the effort (Ens & Kats 2004, Kats *et al.* 2007a).

The data was best explained by a model with transect, year and month as factors and the month by year interaction. One has to realise that the current estimates of the total annual mortality are an underestimation representing the minimum total mortality, because corpses were transported by currents outside the Wadden Sea area, and sometimes Eiders have been removed from coastal areas prior to our surveys to avoid complaints from tourists, which was observed on Texel (pers. obs. RK). For the temporal patterns in mortality, total mortality was separated for winter (1 November – 30 April) and summer (1May – 31 October).

Modelling the expected size of the breeding colony on Vlieland
The variation in the size of the breeding population was modelled for the colony of Vlieland (1978–2002) in order to determine whether the low numbers of breeding females (1988–94 and since 2000) related to increased mortality and/or due to periodic non-breeding. Population trajectory of the total pool of breeding females (PBF) was calculated from estimated breeding and survival parameters using the following equations:

$$PBF_{t+1} = NBF_t * S_{ad(t)} + R_{(t+1)} \tag{2}$$

$$
\begin{aligned}
R_{(t+1)} \quad = \quad & + (NF_{(t)} * SRF * S_{juv(t)} * AB_{juv}) \tag{3} \\
& + (NF_{(t-1)} * SRF * S_{juv(t-1)} * S_{imm(t)} * AB_{imm1}) \\
& + (NF_{(t-2)} * SRF * S_{juv(t-2)} * S_{imm(t-1)} * S_{imm(t)} * AB_{imm2}) \\
& + (NF_{(t-3)} * SRF * S_{juv(t-3)} * S_{imm(t-2)} * S_{imm(t-1)} * S_{ad(t)} * AB_{ad})
\end{aligned}
$$

where t = time, PBF = total pool of breeding females, R = the number of new recruited females, NBF = actual number of breeding females (Figure 9.2), NF = total number of fledglings or at age of 6–8 weeks old (Figure 9.2), SRF = sex ratio of 1 at fledging (Swennen 1991a), S = survival, ad = adult, juv = juvenile or 1st year old, imm = immature or 2nd and 3rd year old, AB = probability of age dependent breeding, imm1 = 1st year immature or 2nd year old, imm2 = 2nd year immature or 3rd year old. Trajectories were calculated using annual survival estimates of juvenile, immature and adult breeding females, the probability of breeding in 2nd and 3rd year old females, the total number fledglings produced, and the sex ratio at fledgling, and were compared with the observed number of breeding females. The total pool of breeding females in the first year of the population trajectory, i.e. 1974, was varied by increasing the proportion of the non-breeding for this year from 0% to 50%. Trajectories were calculated using the observed number of fledglings, constant and time-dependent survival of juveniles, immatures and (1) all adult females, (2) only adult breeding females. Calculations were done separately with (3) the actual number of experimentally increased number of fledglings (1976–1978) or alternatively the number of "natural" fledglings estimated for those three years (without the experimental supplement).

Recruitment of the colony on Vlieland was assumed to depend solely on local reproduction (i.e. the number fledglings produced in previous years in the same colony), because only a small fraction (9 out of 641) of the breeding females were recaptured at the neighbouring island indicating negligible exchange (Swennen 1991a). No data was available for the number of fledglings produced in 1989, 1998 and 1999, but fledgling estimates were calculated using the number of breeding females as predictor since 1983 (Fledglings = 0.4626*(Breeding females) – 575, R^2 = 0.393, F = 10.4, d.f. = 17, p = 0.005) and were estimated at respectively 456, 783 and 881. Two population trajectories were calculated with a constant or long-term average survival and a time-dependent survival of juveniles, immatures (2nd and 3rd year old birds) and adults (older than 3 years and breeding females.

Results

Settlement, colony size and fledglings

The first breeding female on Vlieland was found in 1906 and the colony increased from 21 nests in 1928 to 350 nests in 1940, which was also the size of the total Dutch breeding population. The colony grew rapidly to 4000 in 1960 representing 70% of the total breeding population. A steep decline to 800 nests in 1968 was observed, but the size of the breeding colony recovered slowly to approximately 2200 around 1980 (representing 45 % of total breeding population). Since then, the colony approached stability around an average colony size of 2135 fluctuating between 1035 in 1991 and 2716 in 1999, but declined steeply thereafter (Fig. 9.1).

The long-term data on number of fledglings produced in the breeding colony of Vlieland extends with some gaps from 1962 to 2003 and averages 533 fledglings^{-year} but inter-annual fluctuations were large (0 – 3230) (Figure 9.1). The number of fledglings was low between 1966 and 1977 (70 fledglings^{-year}), but recovered in the period 1978-1988 (mean 753 fledglings-year). Between 1990 and 1993 the annual output was less than 10 fledglings with respectively 6, 3, 0 and 0 fledglings.

Total mortality

The total mortality from the beach carcass survey fluctuated widely (Figure 9.2: estimated annual total 922 – 22527) and was predominantly observed in winter (22 out of 26 years) between November and April. Over all years winter mortality (November through April) accounted for 65% of the annual carcass finds. Mortality predominating in summer (May through October) was only observed twice (1996: 49.6%; 1998: 48.7%) in years with low overall losses, but in three consecutive years clustering around a major mortality event (1989: 49.3%; 1990: 22.4%; 1991: 44.1%). For further analysis we have classified ten years as "kill-years" of heightened mortality (1985, 1989–1993, 1995, 1996, 2000–2002) and display the monthly totals in Figure 9.3 as contrasted to the "non-kill years". The
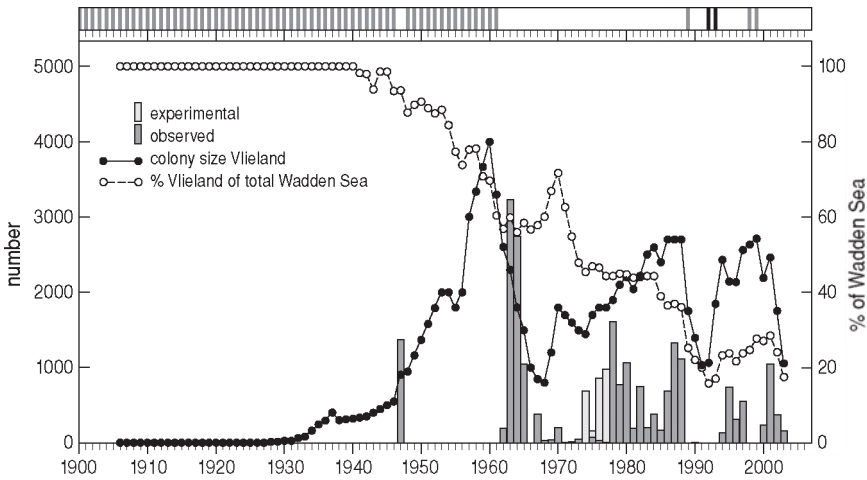
Figure 9.1 Long-term (1900-2003) data on the total number of breeding females (filled circles and line) and 6-8 weeks old fledglings of both sexes (dark grey bar) of Common Eiders *Somateria mollissima* in the breeding colony on Vlieland in the western Wadden Sea. Data on fledglings was not available for 1900-46, 1948-61, 1989 and 1998-99, but the number of fledglings was experimentally increased with 93 to 165 in 1975, 827 to 860 in 1976 and 975 to 982 in 1977 (light grey bar). Low number of fledglings were observed in 1990 (6) and 1991 (2), and no fledglings in 1992 and 1993. Location of the breeding colony on Vlieland in the Wadden Sea is indicated in the inserted map. Years with no observations (grey bars) and no fledglings (black bars) are indicated in the upper panel.

total number of Eiders reported dead per month in the beach surveys was on average 2.9 times higher in kill years (peaking in spring and early summer, Figure 9.3). These seasonal trends can be compared with the number of adult female breeders ringed at the nest (Vlieland) subsequently reported dead, sorted according to the same classification of years. Mortality of the local resident breeding females peaked in spring and early summer, with a pronounced May peak in the "kill-years"

Female survival

Female survival of three age classes (juveniles, immatures, adults) using females caught at fledglings (1975–1985) and of adult breeding females (age unknown) caught at the nest (1974–2003) were based upon estimates of the most parsimonious model, which included time-dependent survival and constant reporting rates for both datasets. Long-term average female survival increased from 0.926 ± 0.028 in juveniles (Figure 9.4A) to 0.971 ± 0.010 in immatures (Figure 9.4B) and to 0.981 ± 0.002 in adults (Figure 9.4C) for females caught as fledgling. Variation was large between years within each age-class, but decreased with age-class (Figure 9.4A-C). Long-term annual survival of breeding females caught as breeding females at the nest averaged 0.927 ± 0.008, but averaged 0.872 during 10 'kill'-years
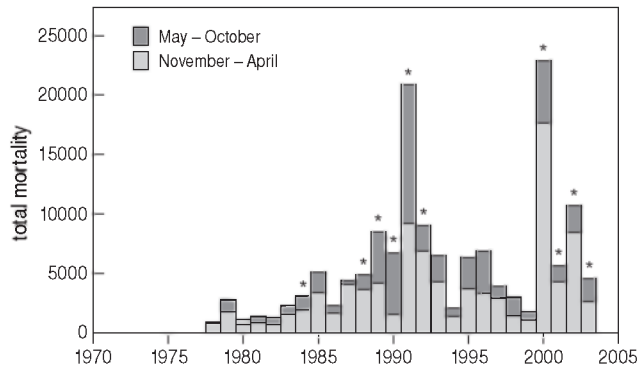
Figure 9.2 Beach survey of total mortality of Common Eiders *Somateria mollissima* in the Wadden Sea area (1977/78 – 2002/03) during winter (November – April: white bars) and summer (May – October: black bars). Years commence in November, and winter 77/78 is booked as 1978. Years with increased mortality of nesting female eiders (see Figure 9.4D) marked with asterisks (*).
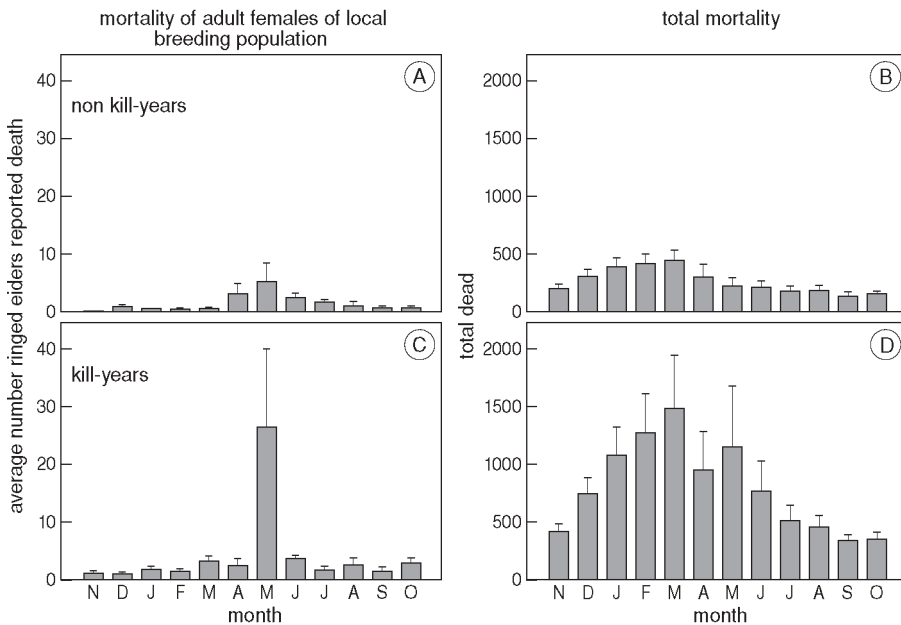
Figure 9.3 Seasonal patterns of mortality (expressed as the monthly average number of birds reported dead with ± s.e.) in adult breeding female Common Eiders *Somateria mollissima* ringed at the nest (1974–2003) in the colony of Vlieland in (A) non-kill years and (B) kill-years (1984, 1988–1992, 2000–2003), and the total estimated number of Eiders reported dead in the Wadden Sea area in (C) non-kill years and (D) kill-years (1984, 1988–1992, 2000-2003). Years run from November through October and were defined as kill-years when survival in adult breeding females was reduced (< 0.90) and total mortality was above average (>5000). Females ringed as juveniles were not included.

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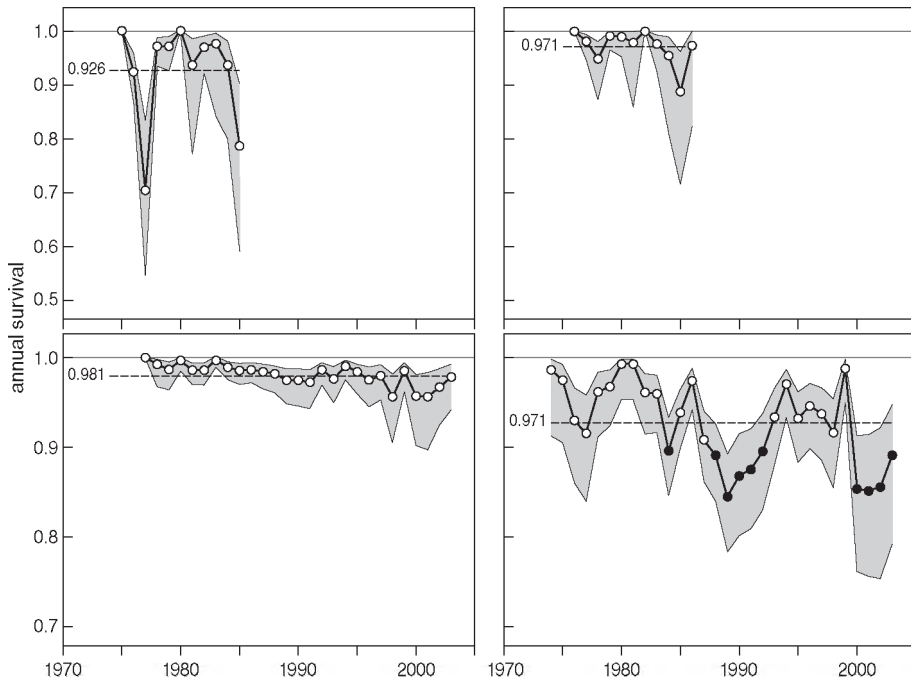
Figure 9.4 Long-term (1974–2003) patterns in annual survival (± 95% confidence intervals) of female Common Eiders *Somateria mollissima* in the colony of Vlieland (Wadden Sea area). Estimates of annual female survival were calculated for (A) juveniles, (B) immatures, (C) all adults using only female ringed as fledglings (1975–1985) and (D) breeding adults using only females ringed at the nest (1974–2003): Survival breeding adult females = 2.59*(Survival all adult females) – 1.62, R^2 = 0.42, n = 27, p = 0.0003. Annual survival was estimated using a model with time-dependent survival and constant reporting rate of respectively 0.623 and 0.478. Long-term average survival shown by dashed line (values in figure). Years run from November through October. Years of heightened mortality of breeding females indicated by black dots in panel D.

(< 0.900: 1984, 1988–92, 2000–03) and 0.955 in normal winters (Figure 9.4D). Annual survival estimates of adult females of both datasets were positively correlated (see text Figure 9.4 and Tables 9.1A, 9.1B and 9.2).

Female survival for adults ringed at the nest was best explained by total mortality in winter (F=32.51, P<0.001), but was not improved by including mortality in summer (F=2.19, P=0.15). Female survival was negatively related to total annual mortality as determined from the beach surveys, both for individuals originally ringed as fledgling and recovered as juvenile, immature, or adult as well as those ringed as adult on the nest (Figure 9.5). The tight relationship between the data for nesting females from Vlieland with the general beach surveys dominated by eiders from other populations argues for accepting a common and local cause behind variation in mortality in these disparate groupings.

Table 9.1A Results of annual or time-dependent survival models based on recoveries of dead breeding female Eiders caught at the nest and banded in the breeding colony on Vlieland, The Netherlands. (t = time, S = survival rate, r = reporting rate, c = constant).

Model	AIC	AIC Weight	Number of Parameters	Deviance
Sc rt	4100.4	0.99993	31	437.6
St rc	4120.6	0.00004	31	457.8
St rt	4121.5	0.00003	53	412.9
Sc rc	4209.5	0.00000	2	605.6

Table 9.1B Results of the Common Eider survival and recovery models based on recoveries of dead eiders ringed as female fledgling of 6 – 8 weeks old in the colony of Vlieland, the Netherlands: testing age dependence in annual survival and reporting rates with the models listed ranked by the Akaike Information Criterion (AIC) with the most parsimonious model at the top.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	#Par	Deviance
1 {S(age 1=1, 2=2, 3=3 4-10=4, 11-20=5, +20= 6)r(t)}	6492.5	0.0	0.63574	1	35	326.7
2 {S(age 1=1, 2=2, 3-10=3, 11-20=4, +20=5)r(t)}	6493.9	1.5	0.30322	0.477	34	330.2
3 {S(17 age)r(t)}	6499.4	6.9	0.01987	0.0313	46	310.8
4 {S(18 age)r(t)}	6499.6	7.2	0.01762	0.0277	47	309.0
5 {S(16 age)r(t)}	6500.6	8.1	0.01106	0.0174	45	314.1
6 {S(15 age)r(t)}	6501.7	9.2	0.00642	0.0101	44	317.2
7 {S(20 age)r(t)}	6502.9	10.4	0.00349	0.0055	49	308.0
8 {S(10 age)r(t)}	6504.0	11.6	0.00196	0.0031	39	330.0

Model notation:
S = Φ = survival,
r = ρ = reporting rate,
t = time or annual dependent parameter,
c = constant parameter,
JUV = juvenile or 1st year,
IMM = immature or 2nd year,
AD = adult,
XX age = number of age classes

Table 9.2 Results of the Common Eider survival and recovery models based on recoveries of dead eiders ringed as female fledgling of 6 – 8 weeks old in the colony of Vlieland, the Netherlands: testing age dependence in annual survival and reporting rates with the models listed ranked by the Akaike Information Criterion (AIC) with the most parsimonious model at the top.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	#Par	Deviance
1 {S(juvt immt adt)r(juvc immc adc)}	6473.0	0.0	0.59184	1	54	267.6
2 {S(juvt immt adc)r(t)}	6475.1	2.2	0.19947	0.337	53	271.9
3 {S(juvt immt adt)r(juvt immt adt)}	6478.3	5.3	0.04121	0.0696	62	256.1
4 {S(juvt immt adt)r(juvt immt adc)}	6478.3	5.3	0.04121	0.0696	62	256.1
5 {S(juvt immt adt)r(juvt immc adc)}	6478.3	5.3	0.04121	0.0696	62	256.1
6 {S(juvt immt adt)r(juvt immt adc)}	6478.3	5.3	0.04121	0.0696	62	256.1
7 {S(juvt immt adt)r(juvimmt adt)}	6480.4	7.5	0.01424	0.0241	63	256.1
8 {S(juvt imm1t imm2t adt)r (juvc imm1c imm2c adc)}	6480.5	7.5	0.01389	0.0235	65	251.9
9 {S(juvt immt adt)r(juvimmt adc)}	6481.5	8.5	0.0083	0.014	63	257.2

Model notation:
S = Φ = survival,
r = ρ = reporting rate,
t = time or annual dependent parameter,
c = constant parameter,
JUV = juvenile or 1st year,
IMM = immature or 2nd year,
AD = adult,
XX age = number of age classes

Age of first breeding

The first model was considered to be the best model (Table 9.3A) and resulted in the estimated probability of breeding in the second year at 0.188 (± 0.072 S.E.) and in the third year at 0.696 (± 0.138 S.E.)(Table 9.3B). Breeding was expected to be absent during the first year with the probability set at 0, but females of 4 years and older are able to breed with a probability of 1.

Modelling the breeding population on Vlieland: separating mortality from non-breeding

Several population trajectories were calculated to estimate the total pool of breeding females in order to investigate the observed declines or suppressions in the number of breeding females and finally to distinguish mortality from non-breeding. Therefore, the total pool of breeding females in the colony of Vlieland was estimated using the number of breeding females, number of female fledglings, and the probability of breeding in 2nd and 3rd year old females, survival of juveniles,
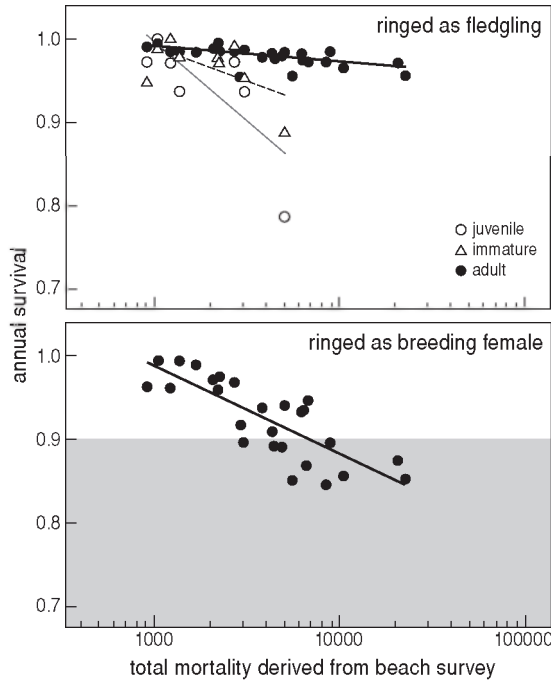
Figure 9.5 Total annual mortality in the Wadden Sea area and female survival in the colony of Vlieland. Survival of females (A) ringed as fledgling (1975-1985): juvenile ($S_{juv\ fem}$ = -0.000041*Mortality + 1.03, R^2 = 0.73, d.f. = 7, p = 0.007; black squares, thin solid line), immature ($S_{imm\ fem}$ = -0.00002*Mortality + 1.01, R^2 = 0.56, d.f. = 8, p = 0.020; open circles, dashed line) and adult females ($S_{ad\ fem}$ = –0.0000012*Mortality + 0.9867, R^2 = 0.34, d.f. = 25, p = 0.0019; grey triangles, solid line), and (b) ringed as breeding female (1974-2003): breeding female ($S_{breeding\ female}$ = –0.0000059*Mortality + 0.957, F = 46.0, R^2 = 0.42, d.f. = 25, p = 0.0002; grey squares, bold solid line). Years of heightened mortality (arbitrary boundary of survival of breeding females less than 0.900) highlighted in lower panel.

Table 9.3 Model results for estimating the probability of breeding for females only in the second and third year after fledgling: A) log-likelihood (L) of the models, and B) parameter estimates for the first model.

A)	Model	L	Parameters	B)	Parameter	Estimate	S.E.
	Full	803	86		b_2	0.188	0.072
	First	870	4		b_3	0.696	0.138
	b(1)=0	883	2		s_1	0.860	0.013
	null	1046	0		s_2	0.956	0.034
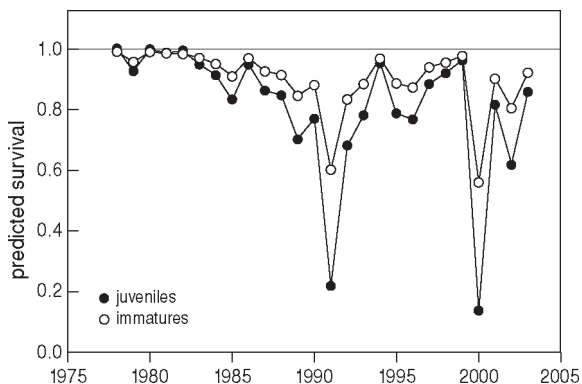
Figure 9.6 Predicted annual survival of juvenile and immature females using significant relationships in Figure 9.5. Years run from November through October.

immatures and adult breeding females. Two types of trajectories were calculated using long-term averages or annual estimates of survival. Annual survival estimates of juvenile and immature females were predicted using the significant dependence on total annual mortality (Figure 9.6).

The breeding and survival estimates used for the calculation of the population trajectory of the breeding colony on Vlieland were based on the number of breeding females (Figure 9.1), the total number of fledglings (Figure 9.1), the equal sex ratio at fledging (Swennen 1991a), propensity to breed depending on age (Table 9.3), survival of adult breeding females (Figure 9.4d), and survival of juvenile and immature females caught as fledgling (Figure 9.6). Although the model was run with constant survival to begin with, a second version with time-dependent survival is considered an improvement and the outcome is displayed in Figure 9.7.

The breeding population on Vlieland recovered until the middle of the 1980's, underwent a large decrease between 1988 and 1991 followed by a rapid upsurge and then since 1999 the number of breeding females again declined (Figure 9.1 and 9.7). When the model outputs predicting the number of breeding females available in the population are compared to the observed colony counts (Figure 9.7) discrepancies emerge concerning both phases of rapid change. In the period 1988–1992 far fewer females nested than were alive in the population according to the model outputs (both with and without accounting for the extra input of fledglings in 1975–77) The models with fixed propensity to breed depending on age and time-dependent survival point to the existence of a considerable pool of non-breeding females during periods of lowered survival or mass-mortality (1988-1992, 2002–2003). The overall pattern did not change drastically within both models when the fraction of non-breeding arbitrarily set in the first year (1974) was increased from 0% to 50% non-breeding. The size of the total pool of breeding
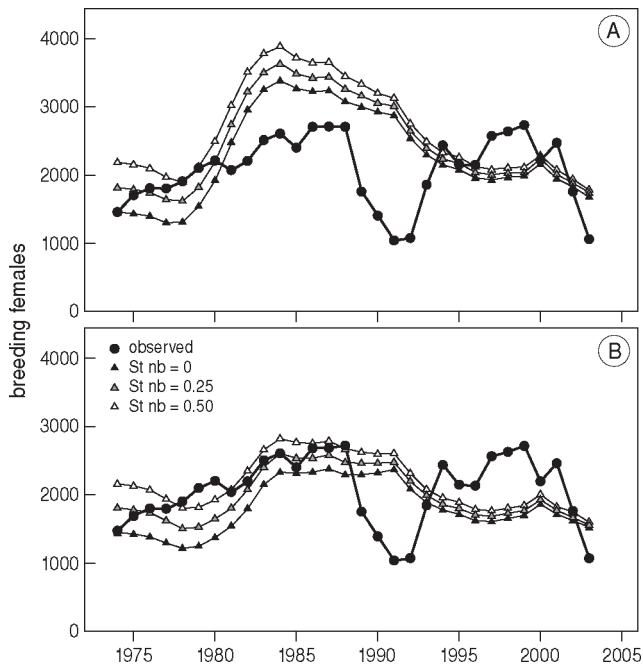
Figure 9.7 Population trajectory of the *predicted* pool of potential breeding female Common Eiders *Somateria mollissima* on Vlieland with the *observed* number of breeding females shown for comparison. The predicted pool of breeding females is derived from the population model (see text) using fixed propensity of breeding females in 2nd, 3rd and $\geq 4^{th}$ year (Table 9.3) and time-dependent estimates of survival (St) of juveniles and immatures (Figure 9.6) and adult survival of breeding females (Figure 9.4D). For the starting year of 1974, the effect of non-breeding (nb) was varied and calculated for 0.00, 0.25 and 0.50 non-breeding. Panel (A) includes the fledglings released experimentally (1975-77, see text) and panel (B) excludes them.

females averaged 9 (25% non-breeding in initial year) and 18 % (50% non-breeding in initial year) higher compared to the model without non-breeding in 1974. The maximum proportion of non-breeding was predicted to be observed in 1991 and estimated between 0.64 and 0.67 for the time-dependent survival model, which was 10% lower for the constant survival model with non-breeding between 0.58 and 0.62 (Figure 9.7). These values are well within the range reported by Coulson (1984) for an eider colony in England. Further, the models predicted non-breeding in 1989 to vary between 17–26% for the constant survival models and 41–47 % for time-dependent survival models, which was in agreement with the estimate of 35 % non-breeding in 1989 reported for this population by Swennen (1991a). We conclude that the observed recovery of the Vlieland population following the decline in the late 1980s could be explained by birds from the non-

breeding pool returning to nest, and does not require the postulation of an extraordinary input of fledglings from former years, or the influx of adult breeders from elsewhere. If and when the Vlieland population will recover from the decline that set in after 2001 is still unknown at present. According to the modelling a considerable proportion of the females alive in 2003 refrained from breeding so there is potential for rapid recovery.

To determine which parameters have the greatest impact on the model predictions, a sensitivity analysis was applied on both models and each parameter was lowered with 10 % and subsequently the new population trajectory was calculated. For the constant survival model, long-term (1974–2003) survival reductions of 10 % within each pre-adult ($1^{st} - 3^{rd}$ year) class resulted in a total decline of 9 % of the total pool of breeding females between 1974 and 2003, but 10 % reductions in the long-term *survival* of *breeding adult females* resulted in dramatic reductions of 54 % as expected in a long-lived species.

Discussion

Explaining abrupt changes in size of the breeding colony on Vlieland

In 1906, a breeding colony of Common Eiders was established on Vlieland and after a slow start, the colony grew rapidly between 1940 and 1960 (Figure 9.1). The colony nearly crashed during the 1960s due to the pollution of coastal waters with chlorinated hydrocarbons (Swennen 1972). The colony recovered during the 1970s and entered a new plateau period in the late 1980s when the size of the colony approached 2700 breeding females. A catastrophic depression in breeding numbers was observed in 1988 with a low of only 1000 nesting females in 1990-1991 and recovery setting in from 1992 on (Figure 9.1). The collapse in breeding numbers has been related to severe reductions in the stocks of shellfish on which the eiders feed (Camphuysen 1996). The unanswered question in this scenario was to elucidate the role of non-breeding in driving these numerical changes as distinct from mortality of the nesting females. The rapid recovery from 1992 onwards could hardly be explained by entry of new recruits and hinted that non-breeding was involved in this population as had earlier been established for a nesting colony in England (Coulson 1984). Recently (2002) a sudden fall in nesting numbers at Vlieland has again been observed but the course of recovery is still unknown.

Fortunately vital parameters (breeding propensity dependent on age, mortality) can be derived from recoveries of female eiders ringed in the breeding colony on Vlieland (either as fledgling or caught on the nest). Survival of female eiders increases with age from juvenile to adults (Table 9.4), which was also reported for female eiders in Scotland (Bailie & Milne 1982). Mortality of female eiders was predominantly reported around the breeding season (Figure 9.3) and survival of adult breeding females was lower compared to all adult females (Figure 9.4C+D).

Both of these findings point to a suvival cost of breeding. Survival of all age groups in the Vlieland material was negatively related to total mortality for the eider population as a whole along the Dutch coast assessed from beach carcass surveys (Figure 9.5). The Vlieland data are thus representative for more than simply a local event. The survival of all adult female eiders (0.981: Figure 9.4C) and adult *breeding* females (0.927: Figure 9.4D) in the Netherlands was high compared to the values of 0.80 (Paludan 1962) and 0.90 (Noer & Hansen 1990) in Denmark, 0.895 in England (Coulson 1984), but closely similar to the value of 0.96 for Scotland (Baillie & Milne 1982).

Evidence and causes of non-breeding among Eiders in the Netherlands

Life history aims to unravel the lifetime management and timing of reproduction based on the assumption that trade-offs exist between various components of fitness (Drent & Daan 1980, McNamara & Houston 1996, Stearns 1992). Managing energy between functions within the individual becomes important when the amount of energy is limited resulting in a physiological trade-off between those functions. Reproduction and survival compete for the same resources and the costs of reproduction are described by a trade-off between current and future reproduction (Reznick 1985, Stearns 1989).

The decision to breed or not to breed is controlled by the physiological or conditional state of the parent (i.e. amount of stored energy) and local environmental conditions (Drent & Daan 1980). Condition of the parent relate to territory quality (Daan *et al.* 1990, Lunn & Boyd 1993), fat (Witter & Cuthill 1993) and protein reserves (Houston *et al.* 1995), foraging skills (Heinsohn 1991), parasite load (Norris *et al.* 1994, Møller 1993) and immune function (Gustafsson *et al.* 1994). Differences in individual (Curio 1983) and/or phenotypic quality (Harris & Wanless 1995) are also involved.

Non-breeding is a widespread phenomenon and may relate to age (Forslund & Pärt 1995), body condition and individual quality (Caladine & Harris 1997), weather (Quakenbush & Suydam 1999, Rönkä *et al.* 2005), predators (Bertram *et al.* 1934, Bird & Bird 1940), dispersal (Danchin & Cam 2002), pair bond (Mougin *et al.* 1997, Orell *et al.* 2004), and food, population density and/or previous activities (Danchin & Cam 2002). Non-breeding has been reported among long-living seabirds including several species of eiders, such as Common Eider (Coulson 1984), Steller's Eider *Polysticta stelleri* (Quakenbush & Suydam 1999) and King Eider *Somateria spectablis* (Bertram *et al.* 1934, Bird & Bird 1940).

In the previous study on the breeding population of Common Eiders on Vlieland, non-breeding was assumed to be negligible, but some evidence suggested that non-breeding did occur to some extent (Swennen 1991a). Non-breeding was suspected for 1968 and estimated to involve 35% of the breeding female stock in 1989 compared to 1988. Drawing on an additional fifteen years of ring recoveries the present study using a population trajectory with time dependent estimates of

female survival confirmed that non-breeding did indeed occur and was extremely prominent around 1990 (Figure 9.7). This result was also found employing constant female survival (graph not shown). Coulson (1984) suggested that density dependent processes play an important role in the occurrence of non-breeding. This can be clarified by considering non-breeding during the phase of population growth and at population stability at our colony.

First, the population trajectory showed that non-breeding was low during population growth (1974–1980) and the size of the predicted pool of breeding females was similar to the number of breeding females (Figure 9.7). In a British breeding population of Common Eiders on Coquet Island (1968–1981), non-breeding during population growth was on average less than 10% (average: 6.3%) accompanied by larger clutches and higher survival and recruitment (Coulson 1984).

Second, the incidence of non-breeding can be considered in a breeding population approaching stability in the late 1980s (Figure 9.2). The breeding colony on Vlieland reached stability, when the colony size entered the range of 2700 breeding females coinciding with the observed long-term decline in clutch size and fecundity (expressed as the average number fledglings produced per breeding female) (Kats *et al.* 2007c). Similar patterns were also observed in the English breeding population, which was close to reaching stability (Coulson 1984).

Now the question remains: What demographic factors account for the observed decline in the number of breeding females on Vlieland between 1988 and 1992? Although survival of the breeding females was reduced in the years of the dip in nesting numbers, the decline set in prior to the observed declines in breeding and a recovery in survival was already observed during the years of massive non-breeding (Figure 9.4). Second, the estimated fall in survival of the breeding females is quantitatively insufficient to account for the fall in nesting numbers (compare Figure 1 with Figure 9.4D). We conclude from the population model (Figure 9.7) that a large pool of adult breeding females was in existence which adequately explains the strong and quick recovery in the number of breeding females in the following years (Figure 1). The pool of adult females was large due in part to the presence of large number of fledgling eiders released after experimental feeding trials (1975–77: Swennen 1991a, 1991b) which can be seen by comparing Figure 9.7A with 9.7B. That these experimental releases contributed to these patterns in recovery since 1992, is likely because some of those experimental females were later reported breeding (1994–96: n = 20, unpublished data Kats) and some were recovered dead as late as 2002 (unpublished data Kats). Local production during the years of the population low (1990-1993) could not affect the pool of breeding females, because the production of fledglings was nearly absent (Figure 9.1). We exclude the possibility of immigration since breeding females show a high degree of natal philopatry (Swennen 1991a). These considerations are set out in the overview (Table 9.4)

We conclude that non-breeding was the main cause of the observed decline in the breeding population between 1988 and 1992, and as argued elsewhere was

Table 9.4 Overview of demographic parameters implicated in collapse and recovery of the breeding population on Vlieland 1988-1993.

Parameters		Conclusions
(a)	mortality of nesting females	increased but losses insufficient to explain decline (Figure 9.4d)
(b)	recruitment failure	fledging output through 1988 adequate (Figure 9.1) despite increased mortality of juveniles and immatures (Figure 9.6) pool of potential breeders does not fall until 1991 (model, Figure 9.7)
(c)	"non-breeding" or skipping breeding	modelling pool of potential breeding females (Figure 9.7) reveals massive non-breeding during decline (up to $2/3$ of pool) and re-entry during colony recovery; degree of non-breeding is negatively related to the local food supply (Figure 9.8)

caused by a reduction in the food supply available to the eiders in the Wadden Sea (see Chapter 10). The size of the breeding colonies in the Netherlands is limited by the area mudflat near the colony and year-to-year variations in breeding were related to variation in local food supply (Kats *et al.* 2007c). The observed declines in breeding with increased non-breeding coincided with years when food stocks were in general low in the whole Wadden Sea (Beukema 1993, Beukema & Cadée 1996). The number of breeding females was positively related to local stock of mussels and the presence of small cockles (Kats *et al.* 2007c). We assume that in seasons of low food stocks, a large proportion of breeding females was not able to store locally sufficient energy in order to breed successfully. As a consequence, breeding females skipped breeding on the short term in order to survive in the long run. In the colony on Vlieland, the incidence of non-breeding is related to the density of profitable food in the vicinity of the colony, which consisted of mussels and small cockles (Figure 9.8).

However, the recent decline in the size of the breeding colony on Vlieland population since 2000 has not yet been reversed and deserves attention. The available evidence assembled in our population model suggests that the total pool of adult breeding females has declined steadily since the mid 1980s (Figure 9.7A) or at least since 1992 (Figure 9.7B). The pool at our latest estimate (2003) had fallen to the level of the mid 1970s (Figure 9.7, holds true for both models). This is an indication that the Vlieland eiders are currently faced with the accumulated impact of lower fledgling production (Figure 9.1) with lowered survival of the nesting females (Figure 9.4d). It should be noted that at the most recent survey (2003) the food stocks around Vlieland were again as low as in the year 1990 and almost as depleted as in 1991 (the all-time low in the 14-year data set, see Figure 9.8). It is a matter of great urgency to continue the study at this critical juncture.
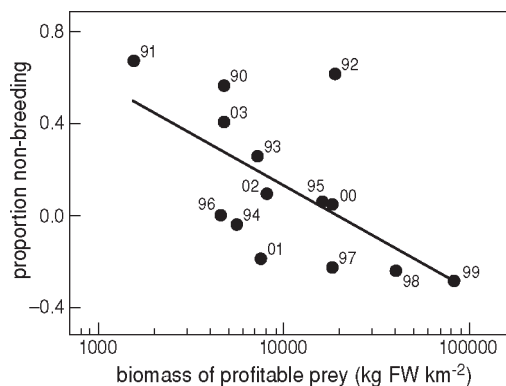
Figure 9.8 The proportion non-breeding female Common Eiders *Somateria mollissima* in the breeding colony on Vlieland (1990-2003) in relation to the food stocks (expressed as the density of fresh weight/km^2) of profitable prey (mussels Mytilus edulis and small cockles Cerastoderma edule) sampled on the mudflats near the breeding colony. The regression is shown, Non-breeding = -0.46*Log(Total profitable density) + 1.95, n = 14, R^2 = 0.37, p = 0.020 (taken from Kats *et al.* 2007c).

Implications for monitoring programs

In long-lived birds, such as Common Eiders, periodic non-breeding has been observed before and in our study coincided with unfavourable conditions for breeding. Non-breeding could be interpreted as a prudent-parent-strategy (Drent & Daan 1980) in order to survive and invest in future breeding attempts, and to increase lifetime reproductive success. As shown in this study, the occurrence and the large variation in non-breeding can have serious consequences for monitoring programs when populations of long-living birds are concerned. Monitoring specific target bird species as indicators of an entire ecosystem has its drawbacks, because monitoring programs usually rely only upon the annual count of the number of breeding females. This is not sufficient for science-based decision making, especially in long-lived species. Therefore, we strongly encourage future monitoring programs of long-lived species, such as the eider, to include the assessment of non-breeding (in addition to the assessment of the total number of breeding females) and the number of fledglings produced. It is essential to include a long-term ringing program to generate annual input of survival estimates for population modelling, which has been demonstrated in this study to be a fruitful tool for science-based decision making. In addition, further knowledge on the spatial and temporal use of the local mudflats and the extent of its dependence on these tidal food stocks near the breeding colony is needed in order to predict the effects on food shortage on breeding performance of a monitoring species.

Acknowledgements

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Can breeding numbers of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea be explained by local feeding conditions?

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Abstract

Breeding Common Eiders *Somateria mollissima* were discovered on the Dutch Wadden Sea islands Vlieland and Terschelling in 1906 and became established on the remaining islands within 40 years. We here provide an overview of the census of breeding numbers on the Dutch islands through 2003.

The breeding colonies increased in size and the total breeding population appeared to reach saturation in the late 1990's (11 000 breeding females) with similar numbers in the western and eastern part of the Wadden Sea. Since then the Dutch breeding population has declined by 40% with severe losses in the western segment which has fallen below the levels of the late 1960's.

The size of individual colonies at saturation (maximum number of breeding females) is related to the size of tidal area near the colony, and there is convincing evidence for density dependent factors in reproduction (clutch size and fledgling production).The limited data from other colonies match the fifty-year data set for Vlieland relating fecundity to density of breeding females (related to the feeding area near the colony).

Declines in the number of breeding females were observed in the 1960's, 1988-1992 and since 1997. The first episode relates to pollution of coastal waters with chlorinated hydrocarbons causing a 75% reduction in population size with a declining impact from west to east. After closure of the pollution source the colonies recovered during 1970's.

A 30% decline in breeding numbers set in around 1990, coinciding with major reductions in the stocks of shellfish around the breeding islands due to the commercial shellfish fishery. Information from surveys of the food stocks throughout the Wadden Sea is inadequate to pinpoint this as data are lacking from spring before the eider breeding season. Recovery was rapid after 1992 but a fresh decline in breeding numbers has been observed since about 1999, with a forty percent loss up to 2003.

For the colony of Rottum in the eastern Wadden Sea a statistically significant relationship of densities of breeding females with local stocks of tidal mussels was established in a five-year data set following the first sizeable and successful settlement of tidal mussels in 2000. For this colony recent counts (2000-2004) conform to this trend since mussel recovery and the data for Vlieland are qualitatively in agreement. On Vlieland, non-breeding was negatively related to the total density of profitable food.

This study indicated that local feeding conditions are important for the breeding population in the Netherlands. Maximum colony size increased with the tidal area near the breeding colony and non-breeding was negatively related to the total density of profitable in the tidal area when the breeding colony has reached stability. The introduction of Marine Protected Areas (MPA) near the breeding colonies is a successful management tool for the protection of breeding birds with a

dependence on local food supply and evidence suggested that size of the MPA is of crucial importance. Since 2000, breeding increased only in the colony with complete protection of tidal flats since the early 1990's and subsequent re-establishment of tidal mussels beds (i.e. Rottum), but declined in all other colonies with only a part of the tidal flats protected. There is an urgent need to refine the measurement of breeding and food supply to reflect the resources the eiders rely on for breeding, and this will entail the inclusion of non-breeding and a new sampling programme on potential food sources in spring.

Introduction

The Wadden Sea is an area of international importance for many bird species during various stages of their annual cycle, which depend on the local food supply for wintering and breeding. Shellfish eating birds rely heavily on the *harvestable* fraction of the specific shellfish, which has been demonstrated in the Wadden Sea for wintering Knots *Calidris canutus* (Zwarts & Wanink 1993, Piersma *et al.* 1993), Oystercatchers *Haematopus ostralegus* (Zwarts *et al.* 1996b), and Common Eiders *Somateria mollissima* (Nehls 1995). Common Eiders depend in winter predominantly on the subtidal areas of the Wadden Sea (Swennen 1989, Ens *et al.* 2006), and are the most important consumers of shellfish in the Wadden Sea representing >65 % of the total biomass consumed (Swennen 1991, Smit & Wolff 1980). However, the breeding population of Common Eiders in the Netherlands, is predicted to be dependent on the stocks of tidal shellfish near the breeding colonies (Swennen 1991a). In this species, females are highly philopatric to the colony of breeding irrespective of season (Swennen 1991a) and eiders are capital breeders indicating that energy needed for breeding is accumulated locally prior to breeding.

In this paper we document long-term breeding numbers of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea (1906–2003). Recently, the breeding population and the individual colonies reached saturation and we investigated the predicted dependence of local feeding conditions for breeding (Swennen 1991a) and evaluated the role of Marine Protected Tidal Areas. We update previous reviews on the number of breeding females in each colony (Swennen 1976a, Camphuysen 1996) with recent data up to 2003. As a first step in understanding the limitation of colony size the maximum number of breeding females in the colonies was related to local feeding conditions expressed as the area mudflat near each colony. Further evidence of colony saturation was supplied by clutch size and fecundity (or the average number of fledglings produced per breeding female) data collected through the years. Fecundity was related to the number of breeding

females corrected for the area mudflats near the breeding colony in order to reduce the effects of differences in size between colonies. We finally explore whether breeding numbers responded to changes in the total supply of profitable food near the colony and if tidal mussels were important for breeding as predicted. The number of breeding females (1990–2003) was related to the total density of profitable prey (i.e. mussels and small cockles) near the breeding colony using large scale surveys in spring (cockles) or reconstructed for spring (mussels). Tidal musselbeds were re-established in some areas in 2000 after being nearly absent for 10 years in the Dutch Wadden Sea. The importance of tidal musselbeds for breeding Common Eiders was illustrated by comparing the density of breeding females in the colonies on Vlieland and Rottum (2000–2004) when stocks of secondary prey (i.e. small cockles) were low, but with large differences in the protection status of the tidal feeding area near the colony. The importance of protecting local food stocks for breeding eiders is discussed in relation to the introduction of Marine Protected areas near breeding colonies.

Methods

Study area
The Wadden Sea (N 52° 45' – N 53° 33' and E 6° 43' – E 6° 56') is a large tidal area (2409 km^2) in the northern part of the Netherlands and separated from the North Sea by a chain of seven coastal barrier islands (Texel, Vlieland, Terschelling, Ameland, Schiermonnikoog, Rottumerplaat, Rottumeroog) and contains one central island (Griend). Rottumerplaat and Rottumeroog form together the complex Rottum and are here treated as one. The coastlines of Fryslân, Groningen and Noord-Holland (Figure 10.1) border the southern part. The Wadden Sea is characterised by tidal flats with gullies, and natural beds of Atlantic Blue Mussels *Mytilus edulis* and Edible Cockles *Cerastoderma edule* occurring in the tidal and sub-tidal parts of the Wadden Sea. The western Wadden Sea (1618 km^2) is defined as the tidal areas between Texel and Terschelling (including Griend) and the eastern Wadden Sea (791 km^2) extends from Ameland to Rottum.

Breeding population, clutch size, and fledglings
The time course of development of the breeding population (expressed as the number of breeding females) since the beginning of the 20th century was reconstructed for each breeding colony (or island) using previous reviews (Swennen 1976a), extended up to the breeding season of 2003. More than 95 % of the Dutch breeding population is found on islands in the Wadden Sea, the subject of this paper. Marginal areas, i.e. salt marshes in the Wadden Sea of Noord-Holland (Balgzand, Boer *et al.*) Fryslân and Groningen (Weide 2004), and Zeeland in the south-west of the Netherlands ((Sluijter 1988) were not included.
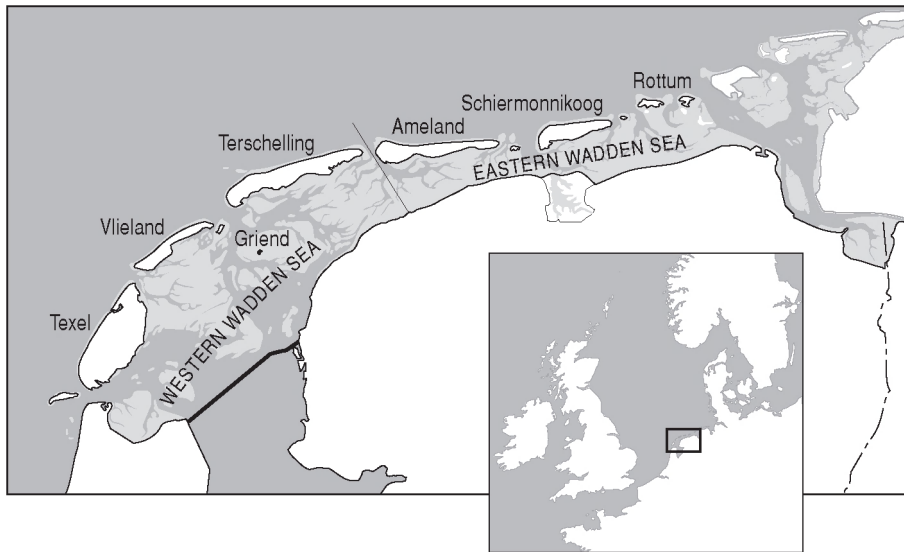
Figure 10.1 Geographic location of the breeding colonies of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea (Texel, Vlieland, Terschelling and Griend in the western Wadden Sea and Ameland, Schiermonnikoog and Rottum in the eastern Wadden Sea).

The size of the breeding colonies was assessed by numerous volunteers, researchers of the Dutch Centre for Field Ornithology (SOVON) and wardens of islands in the Wadden Sea for the Dutch State Forestry (SBB), Natuurmonumenten and Fryske Gea. In general, three methods were used to assess the number of breeding females (Camphuysen 1996): (1) total counts of nests in small colonies (Texel, Griend), (2) nest counts in representative fixed plots with an extrapolation to total area (Terschelling, Ameland, both islands of Rottum), and (3) the 'differential-method' (Vlieland, Schiermonnikoog). For nest counts (method 1 and 2), breeding colonies were visited at or after hatching in the first week of May, because all breeding females were at the nest and visitation of the nest as late as possible in the in incubation period reduced disturbance to a minimum (Bolduc & Guillemette 2003), although others reported no effects of visitation on daily survival rates of the nests (Grand & Flint 1997). The number of breeding females was equated to the number of nests encountered, which included nests with only down, down with eggs, remains of eggs after predation or hatching, hatchlings or an incubating female. The 'differential-method' (method 3) estimated the total number of breeding females derived from a high tide count of eiders around the whole island in the first week of May (Hoogerheide & Hoogerheide 1958, Duiven & Zuidewind 2001, Hoogerheide 1950, Swennen 1976a) when sex-ratio is at parity near the colony (Swennen *et al.* 1979). Adult males, juvenile

males and females were counted separately, and all age groups of females were lumped due to difficulties in determining age in the field. The number of breeding females was calculated as follows on the assumption that the breeding females are all on the nest and that the ratio of breeding females to adult males is 1:1:

Breeding females = Adult males – (all females – juvenile males)   (1)

Clutch-size data was only available for Vlieland (1947–2003) and long-term data on fledglings (of 5 to7 weeks old) was available for Vlieland (1947–2003) and Rottum (1979–2003), with short-term data (1975–1983) available for Texel, Terschelling, Ameland and Schiermonnikoog. The number of fledglings of 5–7 weeks old was assessed in the first week of July during surveys at high tide. This moment was chosen because mortality among ducklings peaks during the first weeks after hatching and crèches of fledglings resting near the natal island at high tide are readily counted (Swennen 1991b). For Vlieland, fledgling data was available since 1962 with gaps during two periods (1989-93, 1998-99). For Rottum, surveys of ducklings in June (4 weeks old) and of fledglings in July (8 weeks old) were available since 1979. The number of fledglings in July was related to the number of ducklings in June (Fledgling$_{July}$ = 0.94 * (Duckling$_{June}$) – 61; n = 13, R^2 = 0.52, p = 0.003) and within both islands of the Rottum complex, the number of fledglings on Rottumerplaat was related to the number of fledglings on Rottumeroog (Fledgling$_{Rottumeroog}$ = 0.74 * (Fledgling$_{Rottumerplaat}$) + 46; n = 9, R^2 = 0.39, p = 0.04).

Area tidal flats and stocks of shellfish

The stock estimates of shellfish in the tidal and sub-tidal parts of the Dutch Wadden Sea (1990–2004) were obtained from joint surveys by the Dutch Institute of Fishery Research (RIVO), fishermen, Research Centre of the Green World (Alterra) and Fishery Inspectors of the Department of Agriculture, Nature and Food quality (LNV). All participants were collaborating partners in the national research program for the evaluation of the shellfish fishery in the Netherlands (EVA II). The estimates of the shellfish stocks at the beginning of winter were based on large-scale shellfish surveys, the fished stocks, the mussel stocks on cultures and historical data (Bult *et al.* 2004b, Kamermans *et al.* 2004b, Rappoldt *et al.* 2004a, Rappoldt *et al.* 2004b). The area with cockles in the tidal part of the Wadden Sea was assessed during surveys in May (Zwarts 2003). A long-term data series on the area covered with cockles was available since 1976, although no data was available for 1977, 1978, 1979, 1983 and 1992. Relative changes in time of the area with cockles within the western and eastern Wadden Sea, were expressed as an index calculated with the area of cockles in 1976 set at 100 and the other years expressed relative to 1976. The area with cockles in 1976

was considered to reflect a relatively unaffected situation, because cockles were fished at very low intensity until the end of the 1970's. The cockle fishery intensified and mechanised only during the early 1980's (Ens & Kats 2004). The area of tidal flats near the colonies of the barrier islands was calculated using a Geographic Information System (GIS) linked to recent hydrographical surveys.

Statistics

Long-term data on the number of breeding females was available for all breeding colonies, but was rather scarce for Schiermonnikoog and missing data was imputed using TRIM (Pannekoek & Strien 2001). A log-linear Poisson model with year effects using long-term data of both or one of the neighbouring islands, i.e. Rottum and/or Ameland, was run and revealed that deviations were smallest for the model with only Rottum and largest for the models with Ameland.

The analysis of the number of breeding females in relation to the density of profitable food supply, i.e. mussels and small cockles, was analysed using an ordinary generalised least squares regression with fit by maximum likelihood, autocorrelation due to repeated measurements of years (Durban & Watson correction with a time lag up to a maximum of 5 years), area as factor (i.e. western and eastern Wadden Sea), and transformation of breeding (square root), food density and winter severity (both logarithmic) in order to meet the assumptions of normality. One outlying year, i.e. 1991, was excluded from the analysis due to its high standardised residual.

Results

Breeding, clutch size and fledgling production

The first breeding female in the Netherlands was found in 1906 on the coastal barrier island of Vlieland in the western part of the Dutch Wadden Sea (Appendix 1 and Figure 10.2A) and the size of this colony increased from 21 nests in 1928 to 350 nests in 1940. During the 1940's, breeding colonies were established almost simultaneously on the adjacent islands (Terschelling in 1941 and Texel in 1942), and Schiermonnikoog (1941), followed by Ameland (1945) and Rottum (1947) (Appendix 10.1 and Figure 10.2A). The breeding population in the Wadden Sea area increased from 21 in 1928 to 5745 in 1960 breeding females with 97.5 % breeding in the western Wadden Sea, primarily on Vlieland, but declined to 1337 breeding females in 1968 in the aftermath of a pollution incident (Koeman *et al.* 1969). The breeding population as a whole, but also the individual colonies, subsequently recovered and increased further in size. Individual colonies in the western Wadden Sea first reached plateau values around 1960, while the eastern colonies levelled off at the end of the 1980's. The small colony on Griend in the central Wadden Sea stabilized since 1997.
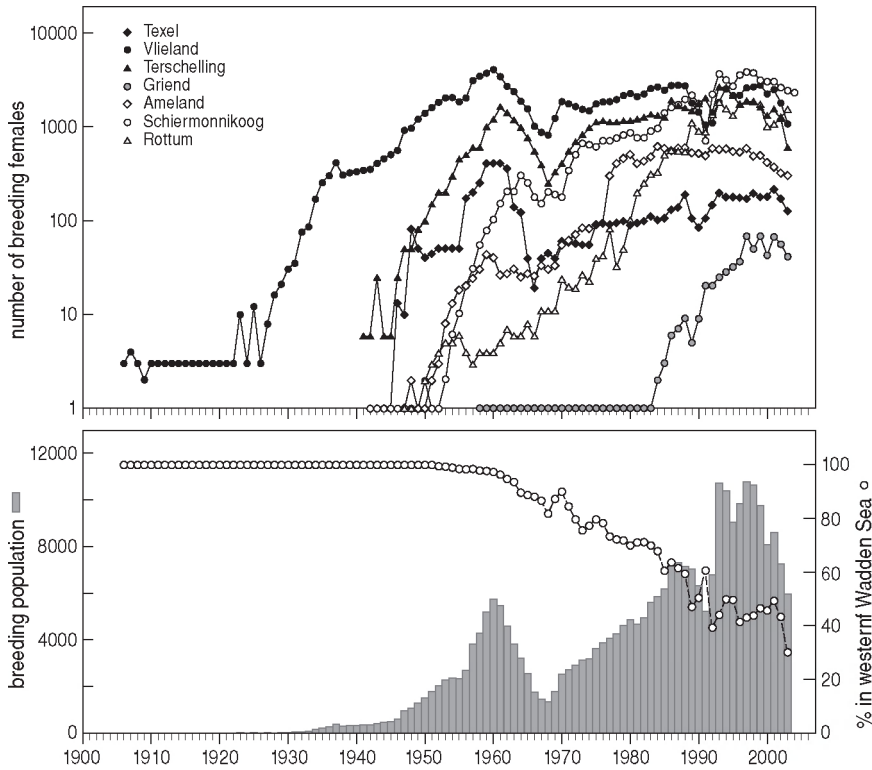
Figure 10.2 Long-term (1900–2003) patterns in the breeding population of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea area: (A) settlement and development of individual colonies (expressed as the number of breeding females) on coastal barrier islands in the western and eastern Wadden Sea, and on a central island (Griend) in the central Wadden Sea (see Appendix 1 for data), (B) distribution within the Wadden Sea (expressed as number of breeding females and fraction of the total breeding population in the western Wadden Sea). See Appendix 10.1 for data and details).

The Dutch breeding population as a whole reached saturation from 1989 onwards with on average 8500 (5200–10800) and a plateau of approximately 11000 breeding females in the late 1990's. At this point, the number of breeding females in both the western and eastern Wadden Sea sector was similar (Figure 10.3). The figure demonstrates that numbers in the western and eastern Wadden Sea changed in parallel in the period 1970–1990. The strong growth of the Rottum colony in the late 1980's coinciding with a decline at Vlieland brought the eastern segment to prominence, and the majority of the Dutch breeding population has been found in the latter area ever since. Recent counts show that numbers declined markedly in the western Wadden Sea since 2000–2001. As of 2003, 70% of the Dutch breeding population is now found in the eastern Wadden Sea (Figure
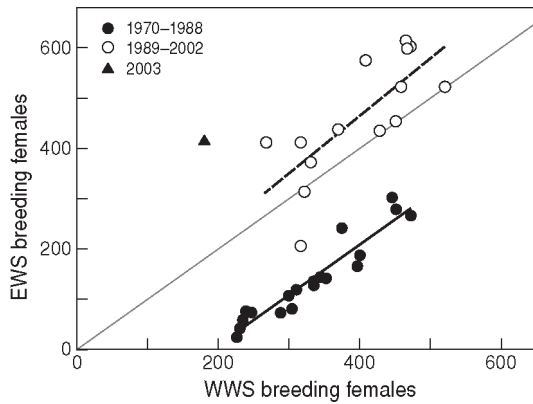
Figure 10.3 Differences in development of the breeding population of Common Eiders *Somateria mollissima* (1970–2003) between the western (WWS) and eastern (EWS) Wadden sea in the periods 1970–1988 (EWS = 1.004*WWS – 1923, R^2 = 0.90, p < 0.001) and 1989-2002 (EWS = 1.150*WWS – 29.9, R^2 = 0.57, p = 0.002, and in 2003. Breeding numbers in both parts of the Wadden Sea are equal along the grey line.

10.2B). The Dutch breeding population suffered a 40% drop over the past six years, with declines at Vlieland, Terschelling and discerned as far eastwards as Ameland.

On Vlieland, a long-term decline in clutch size of 0.0146 eggs*year^{-1} was observed from 4.854 in 1964 to 4.315 in 2003 (Figure 10.4). The number of fledglings increased with 0.93 fledglings*breeding female^{-1} (n = 40, R^2 = 0.55, p < 0.001) considering all islands during colony growth, but declined by 87% to 392 on Vlieland and 71% to 282 on Rottum after saturation.

Does the area of mudflat limit colony size, fledgling output and fecundity?
The maximum size of the breeding colonies (Figure 10.5A) as well as the fledgling production (Figure 10.5B) appears to be limited by the area of tidal flats in the vicinity of the colony. These relations suggest that the appropriate spatial scale for studying the relation between food stock and breeding is the individual colony (island).

Fecundity or the average number of fledglings produced per breeding female was negatively related to the density of breeding females on the potential feeding grounds (Figure 10.6). Breeding output thus declined with the density of breeding females indicating the involvement of density dependent processes of interference and/or competition during the period of feeding prior to breeding by breeding females and later when raising ducklings.
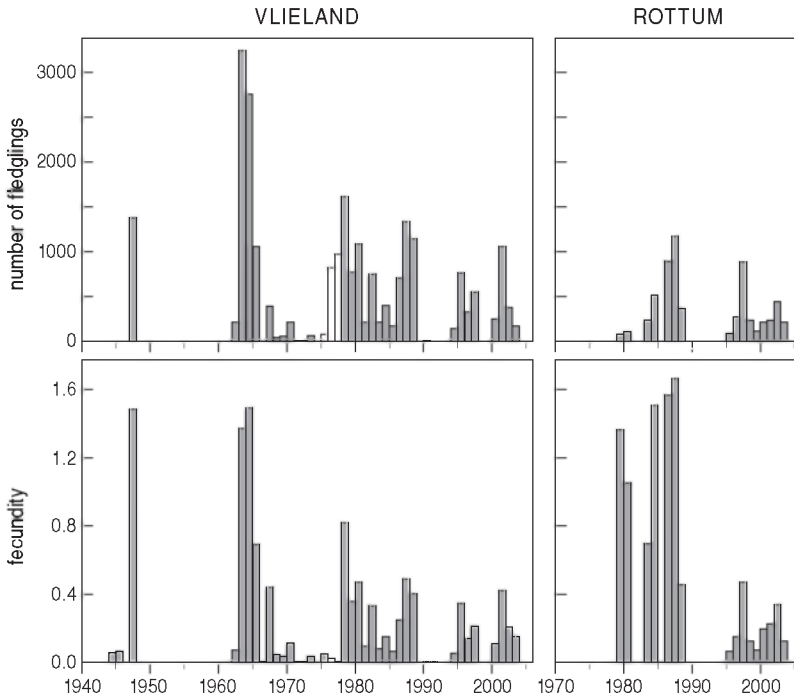
Figure 10.4 Comparison of long-term data (1940–2003) on the number of 5 - 7 weeks old fledglings and fecundity (expressed as the average number fledglings per breeding female) in two breeding colonies of Common Eiders *Somateria mollissima* within the Dutch Wadden Sea. Data (Vlieland in the western Wadden Sea in 1947, 1962–1988, 1990–1997 and 2000–2003 with additional release of fledglings from feeding experiments conducted in 1975–1977 (white bars), and Rottum in the eastern Wadden Sea in 1979, 1980, 1983–1984, 1986–1988 and 1995–2003). The fecundity on Vlieland was calculated excluding the experimental manipulations (see Swennen (1991a) for details).

Local food supply and (non-)breeding

Given the relationship detected between colony size at saturation and the area of mudflats adjoining each island, we expected to find relationships between breeding, i.e. total number of breeding females and proportion non-breeding, and changes in the food stocks as determined by the large-scale surveys. To our dismay we were unable to confirm the first expectation using all colonies (Table 10.1). When colony numbers were related to local food stocks (mussels and small (less than 2 years old) cockles) over 14 years and corrected for autocorrelation no convincing pattern emerged. Among the larger colonies only Vlieland (Table 10.2) showed a statistically significant correlation between breeding numbers and food stocks, and calculations for the entire data set or sector (western and eastern Wadden Sea) failed to provide consistent results. Introducing a weather variable (winter severity, IJnsen 1988) did not improve matters (Table 10.1). We are forced

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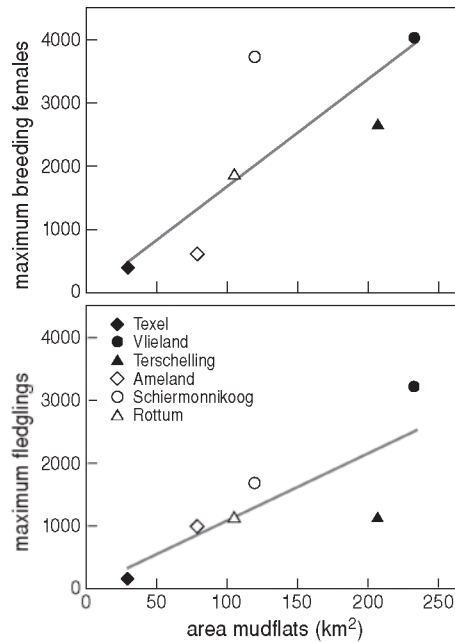
Figure 10.5 The area mudflat (km^2) near breeding colonies of Common Eiders *Somateria mollissima* on coastal barrier islands in the Wadden Sea and the long-term maximum colony size on Texel, Vlieland, Terschelling, Ameland, Schiermonnikoog and Rottum: (A) colony size (expressed as the number of breeding females: $Colony_{max} = 16.79*Area$, $F = 9.11$, $R^2 = 0.65$, $P = 0.039$ and (B) colonial productivity (expressed as the maximum number of 5–7 weeks old fledglings: $Fledglings_{max} = 10.79*Area$, $F = 9.08$, $R^2 = 0.64$, $P = 0.039$.
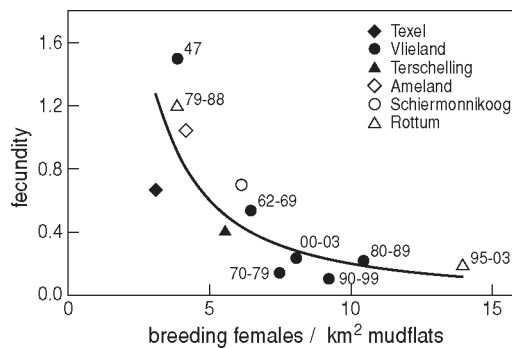
Figure 10.6 The fecundity (expressed as the average number of fledglings produced per breeding female) and the density of breeding female Common Eiders *Somateria mollissima* with long-term data for the breeding colonies on Vlieland (1947, 1962–69, 1970–79, 1980–1989, 1990–99, 2000–03) and Rottum (1979–88, 1995–2003), and short-term data for Texel (1975–1982), Terschelling (1975–1982), Ameland (1975–1982) and Schiermonnikoog (1975–1981): Fecundity = $7.84*$Female density $^{-1.61}$, $R^2 = 0.675$.)

Table 10.1 An ordinary least square (OLS) regression of breeding population of Common Eiders *Somateria mollissima* on the density of small cockles ($\leq$ 2 years old) and tidal mussels, winter severity and area as factor (western and eastern Wadden Sea): (A) Total Wadden Sea: Residual standard error = 7.501 on 21 degrees of freedom, Multiple R^2 = 0.3166, Adjusted R^2 = 0.1864, $F_{4,21}$ = 2.432, p = 0.07942. Correction autocorrelation with time lag of 1 year: autocorrelation = 0.222, D-W Statistic = 1.1499, p = 0.006, Residual standard error = 8.276, Degrees of freedom: 26 total; 21 residual, AIC = 181.8170. (B) Western Wadden Sea: Residual standard error = 8.837 on 9 degrees of freedom, Multiple R^2 = 0.1726, Adjusted R^2 =: -0.1032, $F_{3,9}$ = 0.6257, p = 0.6162. Correction autocorrelation with time lag of 1 year: autocorrelation = 0.129, D-W Statistic = 1.2762, p = 0.096, Residual standard error = 12.920, Degrees of freedom: 13 total; 9 residual, AIC = 88.12177. (C) Eastern Wadden Sea: Residual standard error = 5.843 on 9 degrees of freedom, Multiple R^2 = 0.4418, Adjusted R^2 = 0.2557, $F_{3,9}$ = 2.374, p = 0.1380. Correction autocorrelation with time lag of 2 years: autocorrelation = 0.232, D-W Statistic = 1.134, p = 0.112, Residual standard error = 5.083, Degrees of freedom: 13 total; 9 residual, AIC = 90.16146.

Model variables	Estimate	S.E.	p	Corrected for autocorrelation		
				Estimate	S.E.	p
(A) Breeding Wadden Sea = small cockles + tidal mussels + Winter severity + area						
intercept	37.49	14.83	0.0196	58.59	9.65	< 0.001
Small cockles	1.97	1.22	0.1207	–0.12	0.87	0.8937
Tidal mussels	–0.49	0.61	0.4329	0.33	0.55	0.5627
Winter severity	3.27	2.00	0.1172	1.20	1.05	0.2638
Area as factor	8.59	3.48	**0.0223**	4.91	4.68	0.3060
(B) Breeding western Wadden Sea = small cockles + tidal mussels + Winter severity						
Intercept	23.55	28.83	0.435	49.02	20.77	0.0426
Small cockles	3.52	2.61	0.211	0.32	1.84	0.8660
Tidal mussels	–0.31	0.97	0.759	0.79	0.78	0.3372
Winter severity	2.01	3.21	0.547	0.53	2.10,	0.8082
(C) Breeding eastern Wadden Sea = small cockles + tidal mussels + Winter severity						
Intercept	48.72	15.77	0.0116	38.32	14.66	0.0281
Small cockles	1.93	1.19	0.1404	2.67	1.01	**0.0269**
Tidal mussels	–1.24	0.75	0.1327	–1.55	0.64	**0.0390**
Winter severity	5.30	2.33	**0.0487**	7.42	2.25	**0.0094**

to conclude that our measure of food stocks fails to capture the essence of the food resource for the total number of breeding female eiders.

However, our expectation concerning the incidence of non-breeding in relation to the food stocks was confirmed. For the colony on Vlieland a fourteen-year run of data (1990–2003) on the proportion of non-breeding in adult females is available from an exercise on population modelling (Kats *et al.* 2007d). Plotted against the total food stock of profitable prey (mussels and small cockles) sampled on the mudflats designated as feeding area of this colony in these years, a statistically significant negative relationship emerges (Figure 10.7).

Table 10.2 Estimates of slopes and intercepts of colony size expressed as the number of breeding female Common Eiders Somateria mollissima in relation to the log of the profitable food density of mussels and small cockles of ≤ 2 years old on the tidal flats near the breeding colony.

Island	Slope ± se	Intercept ± se	R^2	n	p
Texel	34 ± 9	211 ± 14	0.56	14	**0.002**
Vlieland	835 ± 316	3621 ± 643	0.37	14	**0.021**
Terschelling	-34 ± 181	1664 ± 386	0.00	14	0.855
Griend	14 ± 9	66 ± 17	0.18	14	0.136
Ameland	-90 ± 48	364 ± 67	0.22	14	0.087
Schiermonnikoog	572 ± 417	3365 ± 526	0.15	13	0.197
Rottum	-22 ± 98	1379 ± 187	0.00	14	0.829
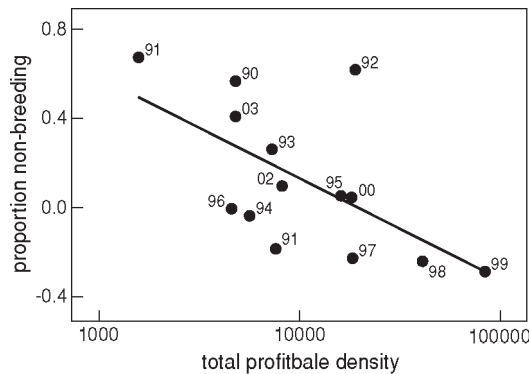
Figure 10.7 The proportion non-breeding female Common Eiders *Somateria mollissima* in the breeding colony on Vlieland (see Kats *et al.* 2007d for details) and the total density of profitable prey (kg fresh weight/km^2), i.e. mussels and (small) cockles, on the mudflats near the breeding colony (1990-2003, figures identify years): Non-breeding = -0.46*Log(Total profitable density) + 1.95, n = 14, R^2 = 0.37, p = 0.020.

The importance of tidal mussels and Tidal Marine Protected Areas

The importance of tidal mussels for females preparing for breeding was shown by a comparison between the breeding densities on Rottum and Vlieland in relation to the density of tidal mussels between 2000 and 2003 (Figure 10.8) when the stock of secondary prey (i.e. small cockles) was very low. Breeding on Rottum increased (50 %) after the settlement in 2000 and subsequent increase in tidal mussels during the following years, but declined (52 %) on Vlieland where settlement of tidal musselbeds was absent (Figure 10.8). The density of breeding females on Rottum increased significantly with the density of tidal mussels (p = 0.018). Further, these
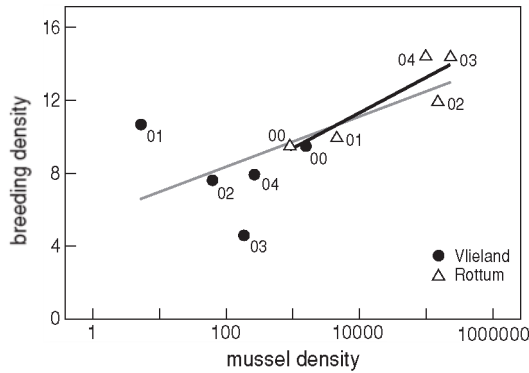
Figure 10.8 The density of tidal mussels (kg total fresh weight/km^2 tidal area) and breeding (number of breeding females/km^2 tidal area) of the breeding colonies on Vlieland (2000 –2004,n = 5, p = 0.663) and Rottum (Breeding density = 1.92*Log(Mussel density) + 3.49; n = 5, R2 = 0.77, p = 0.051: solid line), and both colonies together (Breeding density = 1.37*Log(Mussel density) + 5.52; n = 10, R^2 = 0.49, p = 0.024; grey line).

differences suggest a positive contribution of Marine Protected Areas near the breeding colonies of Common Eiders, because the tidal area near the breeding colony on Rottum has been completely protected and remained undisturbed since the early 1990's. However on Vlieland, only a minor fraction (<20 %) of the tidal area was protected and as a consequence disturbed due to mechanical dredging of cockles from the tidal feeding areas near the breeding colony.

Discussion

Settlement and saturation of the breeding population

After the discovery of a breeding female on Vlieland in 1906 (Thijsse 1907), a permanent breeding population in the Netherlands became a fact. Breeding numbers started to increase on Vlieland since 1930 and colonies settled on other islands during the 1940's from west to east (Figure 10.2A). Why the most westerly islands were settled first remains enigmatic but is possibly related to local differences in habitat and dune access for the inhabitants. Until 1960, the majority of the Dutch breeding population (97.5%) was found in the western Wadden Sea (Figure 10.2B). In the first half of 1960's, breeding females especially in the western Wadden Sea were severely decimated by pollution of coastal waters with chlorinated hydrocarbons (Koeman *et al.* 1969), but recovered slowly (Figure 10.2A and 10.2B). Since 1970, breeding colonies in the eastern Wadden Sea increased and size was similar to the western Wadden Sea by the end of the 1980's (Figure 10.2B and 10.3).

The total breeding population in the Wadden Sea stabilised by the end of the 1980's fluctuating around an average of 7500 (5200 – 10800) breeding females (Figure 10.2B), and the number of breeding females in both parts of the Wadden Sea was similar around 1990 (Figure 10.3). However, the timing of stabilisation was different for individual colonies, because the colonies in the western Wadden Sea (Texel to Terschelling) stabilised around 1960, while those in the eastern part (Ameland to Rottum) stabilised 30 years later around 1990 (Figure 10.2A). Saturation of the breeding colonies was accompanied by a long-term decline in clutch size on Vlieland (Figure 10.4), a strong reduction in the number of fledglings produced on Vlieland and Rottum since colonies stopped growing (Figure 10.4), and a decline in fecundity (or the number of fledglings*breeding female^{-1}) with colony size (or density of breeding females: Figure 10.6).

Factors affecting the size of a breeding colony
The factors affecting the size of a breeding colony, which was expressed as the number of breeding females or the proportion non-breeding, are pollution (chemicals, oil), disease, management of breeding areas and local feeding conditions.

First, Dutch coastal waters of the North Sea and Wadden Sea were polluted with chlorinated hydrocarbons in the 1960's (Koeman *et al.* 1969) causing mortality and non-breeding among breeding females (Swennen 1991a). A temporary decline in the size of the breeding population was observed (Figure 10.2B) and the impact and duration declined from west to east reflecting the dilution of the pollutants which entered the Wadden Sea at the western inlet (Figure 10.2A). An oiling accident near Texel and Vlieland in the winter of 1969/70 caused mortality among Eiders (Swennen & Spaans 1970) with a temporary decline in colony size on Texel and Vlieland (Figure 10.2A).

Second, avian cholera caused mortality among breeding females within parts of the colony on Vlieland in 1981 (Swennen & Smit 1991, and see graph) and the number of breeding females were temporarily reduced in those areas in the following years. There was no evidence of widespread cholera outbreaks during recent years of intensive fieldwork in the colonies (1994–2003).

Third, the management of the breeding areas can have a serious impact on breeding females. Breeding females are easily disturbed in areas with public access with long-term effects in small parts within two high density breeding areas on Vlieland (Kroon's Polder's dike and Bomenland), which were completely abandoned by breeding females when opened to the public during the breeding season. In areas with cattle, females are found breeding in inaccessible areas (permanent enclosures on the salt marshes of Schiermonnikoog: Otto Overdijk personal observation) and are easily disturbed by free-running horses as well (Posthuiskwelder on Vlieland: Piet Duiven personal observation). Breeding was also found to be affected by a rise in groundwater level, which was observed on Vlieland in 2002 when nests containing eggs were abandoned after a sudden rise in water level in the

Kroon's Polders (RK personal observation). Recent evidence from Ameland showed that breeding was negatively correlated with a relative rise in groundwater level due to local gas extraction (Meesters *et al.* 2005), which possibly affected the long-term use of the same nest by breeding females, but long-term involvement of local extraction of shellfish should also not be ignored and deserves attention (see Table 10.2).

Fourth, the size of the breeding colonies was apparently limited by local feeding conditions. The observed maximum number of breeding females in the history of the colony is related to the size of the area mudflat near the breeding colony (supporting an average maximum density of 16.8 breeding females/km^2 mudflats, Figure 10.5A). The maximum number of fledglings produced also reflects the mudflat area locally available (with an average maximum density of 10.8 fledglings/km^2 mudflats). Furthermore, fecundity declined with the density of breeding females (Figure 10.6) indicating that density dependent processes are involved, such as competition for food and interference between feeding females prior to breeding and/or between females feeding with their offspring.

At stability, the breeding population and individual colonies are predicted to be dependent on the local food supply of profitable prey species for breeding near the colony, and the number of breeding females is predicted to increase or non-breeding to decrease with the density of profitable mussels and/or small cockles. First, a decline in the total breeding population (30%, Figure 10.2b) and individual colonies (up to 62% in the colony on Vlieland, Figure 10.2a) was observed between 1986 and 1991 when food density was extremely low (Beukema 1993). Second, breeding since 1990 tended to increase with small cockles in both parts of the Wadden Sea (Table 10.1 and 10.3), which was confirmed for the western colonies on Texel and Vlieland (Table 10.2), but not for one of the eastern colonies. In the eastern Wadden Sea, breeding numbers also responded to winter severity as expected (increasing after cold winters, see Table 10.1) but this effect was not detected for the western compartment nor for the entire material (Table 10.1). A positive effect of small cockles on breeding numbers emerged for the eastern compartment, and an inexplicable negative effect of tidal mussel stocks. Neither of these effects was substantiated in the western compartment, nor were they found in the total data set (Table 10.1) so the explanatory power of these relationships is weak. Third, non-breeding (or the proportion of breeding females of the total pool of available females) in the breeding colony on Vlieland (1990–2003) was negatively related to the density of local food supply (Figure 10.7).

Tidal mussels are important for breeding, because (1) breeding numbers in the eastern Wadden Sea remained high after the establishment of musselbeds following the spatfall of mussels in 2001 (Figure 10.2A), (2) breeding declined in the western Wadden Sea in the absence of successful spatfall in 2001 (Figure 10.2A), and (3) breeding on Rottum increased recently since the settlement of musselbeds

(Figure 10.2A). Further west on Ameland and Schiermonnik-oog mussel stocks were apparently not sufficient in combination with small cockles to support an increase in breeding. The data indicated that local feeding conditions and supply of profitable shellfish were important for breeding, but failed to show strong significant overall patterns for the number of breeding females. The absence of these strong patterns could be related to the short time period, the focus of shellfish monitoring program on harvestable densities for mechanical shellfishery, the absence of annual estimates and the role of possible alternative prey species for breeding eiders (such as Soft Shell Clam *Mya arenaria*, American Razor Clam *Ensis americanus*, Shore Crab *Carcinas maenas*, Starfish *Asterias vulgaris*), the impact of tidal shellfishery on local food supply prior to breeding in autumn, inter-annual differences in prey quality, and difficulties with monitoring the number of breeding eiders accurately throughout the breeding season. The correlation between non-breeding and profitable food on Vlieland (Figure 10.7) suggests that non-breeding is a more appropriate and promising variable than the total number of breeding females in a given year to investigate variation in a stable breeding population with a dependence on local food supply.

Factors reducing local food supply for breeding
Food supply on the tidal flats near the breeding colonies is important for breeding and breeding is predicted to increase with food supply. Therefore, factors reducing local food supply accessible to breeding females are important for understanding variation in breeding at population stability. Many natural and human-induced processes may contribute to reductions in the supply of shellfish and are summarised below.

Natural processes contributing to reductions in the supply of shellfish relate to temperature, wind and predation. Severe winters are known to reduce food supply (Beukema 1979, Beukema 1985, Strasser *et al.* 2001a), because some shellfish (i.e. cockles) are cold-sensitive causing large scale mortality (Beukema 1990), which was observed for cockles after the severe winters of 1995/96 and 1996/97 (Table 10.3). Cold-resistant species (i.e. mussels) can be reduced by ice scouring in severe winters (Strasser *et al.* 2001a). Strong winds (>9 Bft) have been reported to reduce the stocks of shellfish (Nehls & Thiel 1993), but it remains unclear whether the shellfish were completely destroyed or partly transported to other more sheltered areas within the system. Predation by birds contributed to reductions in the supply of shellfish, but can be highly variable, ranging from 10 to 80% of the total stock removed by Oystercatchers (Meire 1993, Goss-Custard *et al.* 1996b). In culture plots, starfish have been reported to destroy complete stocks.

Human-induced processes are also involved in reducing the supply of shellfish and are related to climate change, introduction of exotic species and the extraction by mechanical shellfishery. Climate change has caused a gradual increase in temperature during the last 40 years and cold winters have become less frequent in

Table 10.3 Non-breeding of Common Eiders *Somateria mollissima* in the colony of Vlieland in the Dutch Wadden Sea using model predictions (until 2003) with time-dependent survival and age-dependent breeding (see Kats *et al.* 2007d or Chapter 9 for details) and two spring counts (1996, 2003–05) of females near the breeding colony .

| Year | Differential count | Model predictions | | Spring counts | | |
	number of breeding females	total pool of breeding females	fraction non-breeding	April	May	fraction non-breeding
1985	2400	3712	0.35			
1986	2700	3638	0.26			
1987	2700	3660	0.26			
1988	2700	3456	0.22			
1989	1755	3334	0.47			(>0.35 ad1)
1990	1395	3199	0.56			
1991	1035	3134	0.67			
1992	1066	2774	0.62			
1993	1849	2502	0.26			
1994	2432	2338	-0.04			
1995	2147	2270	0.05			
1996	2135	2128	0.00	2240	823	0.37
1997	2564	2087	-0.23			
1998	2632	2113	-0.25			
1999	2716	2111	-0.29			
2000	2196	2297	0.04			
2001	2464	2078	-0.19			
2002	1754	1942	0.10			
2003	1055	1778	0.41	1337	762	0.57
2004	1825			1329	286	0.22
2005	1226			1513	800	0.53

ad1 According to Swennen (1991a): 'In 1989, the number of pairs along the coast was about the same as in the foregoing years in the beginning of the breeding season. However, the number of nests was only 65 % of that in 1988. The number of non-breeding females remained high during the whole season.'

temperate regions, such as the Wadden Sea. Successful spatfall of shellfish and settlement is associated with cold winters, because predation of 0-class shellfish by crabs and starfish is low after severe winters (Strasser *et al.* 2001b). Therefore, a gradual rise in temperature reduces the frequency of spatfall and increases predation by crabs and starfish. Furthermore, analyses showed that flesh content of shellfish declines at the end of the winter when temperature during winter increases (Honkoop & Beukema 1997) and as a consequence the profitability of shellfish is expected to decline for feeding females prior to breeding after warm winters.

The introduction of exotic species by humans is threatening to alter the species composition of shellfish in the Wadden Sea (Lotze *et al.* 2005). Recently, the

Japanese Oyster *Crassostrea gigas* is currently invading the Wadden Sea and threatens the re-establishment and persistence of musselbeds in the Wadden Sea (Nehls *et al.* 2006, Dankers *et al.* 2006). Not all introductions are deleterious however. *Ensis americanus* is a recent invader of the Wadden Sea but has been discovered by wintering Eiders and might become an important alternative prey species in the future. The extraction of tidal shellfish reduces the stocks of shellfish (Beukema 1993), but will only affect food supply for breeding in years when food stocks are low, especially in the direct vicinity of the breeding colonies, which may have contributed to the long-term decline in the size of the breeding colony on Ameland.

Evaluation of the Marine Protected Areas in the Wadden Sea
Unrestricted fishery for tidal mussels and cockles in combination with failure of recruitment and settlement in subsequent years (Smit *et al.* 1998) caused an extremely low food supply in the early 1990's and a heated public debate between fishermen and nature conservationists. As a consequence, shellfisheries were banned from some tidal flats in the Wadden Sea creating Marine Protected Areas (MPA), which covered the total tidal area near Rottum and parts near Texel and Terschelling since 1993 (LNV 1993), but also parts of the tidal flats near Vlieland, Griend, Ameland and Schiermonnikoog since 1998 (LNV 1998). Detracting from these measures cockles were fished near Vlieland in these closed areas during the autumn and winter of 2002/03. Since 2000, breeding colonies with only a small part of the tidal area near the colony assigned as a MPA declined in size, while the colony with a completely protected tidal area (i.e. Rottum) increased in size due to re-establishment of tidal musselbeds near the breeding colonies after more than 10 years of absence. These are the first results suggesting that MPA's could have a high potential to be a successful management tool for the protection of birds (i.e. eiders) depending on local food for breeding, and their food supply in the Wadden Sea (re-establishment of tidal musselbeds).

In the future, a monitoring program of Common Eiders as the indicator species of the quality status of the Wadden Sea should include the annual assessment of non-breeding survival, and spatial use of tidal areas by females preparing for breeding, and a more detailed food sampling program of the food stocks near breeding colonies in late winter or early spring.

Appendix 10.1 Historic data and size reconstruction (1900-2003) of the breeding colonies of the Dutch breeding population of Common Eiders *Somateria mollissima* in the (A) western and (B) eastern Wadden Sea. Numbers given in normal display are based on counts, values in bold were imputed using surveys of plots (see Kats *et al.* 2007e in prep. for details), underlined values were calculated with surveys of adjacent years using linear filling, italic values are an average of a given minimum and maximum count, italic and underlined values only a minimum value was available, + breeding but no count available.

(A) Breeding colonies in the western Wadden Sea

Year	Texel		Vlieland		Terschelling		Griend	
	n	Reference	n	Reference	n	Reference	n	Reference
1900								
1901								
1902								
1903								
1904								
1905								
1906			3	Thijsse 1925	2	Tanis 1963		
1907			4	Thijsse 1907				
1908			3	Wilcke 1956				
1909			2	Thijsse 1909				
1910			3	Wilcke 1956				
1911			3	Wilcke 1956				
1912			3	Wilcke 1956				
1913			3	Wilcke 1956				
1914			3	Wilcke 1956				
1915			3	Wilcke 1956				
1916			3	Wilcke 1956				
1917			3	Wilcke 1956				
1918			3	Wilcke 1956				
1919			3	Wilcke 1956				
1920			3	Wilcke 1956				
1921			3	Wilcke 1956				
1922			3	Wilcke 1956				
1923	+	Drijver 1923	10	Brouwer 1924				
1924			3	Wilcke 1956				
1925			12	Oordt 1925				
1926			3	Brouwer & Haverschmidt 1928				
1927			8	Brouwer & Haverschmidt 1928				
1928			16	Wilcke 1956				
1929			21	Wilcke 1956				
1930			30	Thijsse 1930b Thijsse 1930a				
1931			35	Thijsse 1931				
1932			75	Wilcke 1956				
1933			85	Brouwer & Haverschmidt 1935				
1934			168	Brouwer & Haverschmidt 1935				
1935			250	Brouwer 1936				
1936			300	Brouwer 1937				
1937			400	Wilcke 1956				
1938			300	Wilcke 1956				
1939			313					
1940			325					
1941			338		6	Brouwer 1942		
1942	1	Brouwer 1943	350	Makkink 1942	6	Tanis 1963		
1943	1		400		25	Jongens 1943		
1944	1		450		6	Tanis 1963		
1945	1	Brouwer 1945	500		6	Tanis 1963		
1946	13	Brouwer 1950	550	Wilcke 1956	25	Tanis 1963		
1947	10	Junge 1952	900	Swennen 1991	50	Tanis 1963		
1948	80	Junge 1952	950	Hoogerheide 1950	50	Junge 1952		
1949	50	Junge 1952	1160		80	Junge 1952		
1950	40	Junge 1952	1370	Junge 1952	100	Tanis 1963		

Year	Texel		Vlieland		Terschelling		Griend	
	n	Reference	n	Reference	n	Reference	n	Reference
1951	44	Junge 1952	1580		150	Junge 1952		
1952	50	Dijksen & Dijksen 1977	1790		200	Mörzer Bruijns & Braaksma 1954		
1953	50	Dijksen & Dijksen 1977	2000	Wilcke 1956	200	Mörzer Bruijns & Braaksma 1954		
1954	50	Dijksen & Dijksen 1977	2000	Rooth 1960	300	Junge 1955		
1955	50	Dijksen & Dijksen 1977	1800	Wilcke 1956	450	Tanis 1963		
1956	170	Dijksen & Dijksen 1977	2000	Rooth 1960	500	Tanis 1963		
1957	200	Dijksen & Dijksen 1977	3000	Hoogerheide & Hoogerheide 1958	600	Tanis 1963		
1958	250	Dijksen & Dijksen 1977	3333		600	Tanis 1963	1	Oosterhuis & Dijk 2002
1959	400	Dijksen & Dijksen 1977	3667		1000	Tanis 1963	1	
1960	400	Zomerdijk 1990	4000	Jong 1976	1200	Tanis 1963	1	
1961	400	Dijksen & Dijksen 1977	3300		1600	Tanis 1963	1	
1962	350	Anonymous 1965	2600	Swennen 1991	1388	Brouwer 1942	1	
1963	138	Dijksen & Dijksen 1977	2300	Spaans & Swennen 1968	1176		1	
1964	120	Dijksen & Dijksen 1977	1800	Swennen 1991	964		1	
1965	39	Dijksen & Dijksen 1977	1500	Swennen 1991	752		1	Oosterhuis & Dijk 2002
1966	19	Dijksen & Dijksen 1977	1000	Spaans & Swennen 1968	540	Swennen 1976	1	
1967	39	Dijksen & Dijksen 1977	850	Swennen 1991	395		1	
1968	45	Dijksen & Dijksen 1977	800	Swennen 1976	250	Zwart 1985	1	
1969	40	Dijksen & Dijksen 1977	1200	Swennen 1991	325		1	
1970	60	Dijksen & Dijksen 1977	1800	Swennen 1976	400	Swennen 1976	1	
1971	59		1700	Swennen 1991	540		1	
1972	57		1600	Swennen 1991	680		1	
1973	56		1500	Swennen 1991	820		1	
1974	54	Dijksen & Dijksen 1977	1450	Swennen 1991	960		1	
1975	90	Swennen 1983	1700	Swennen 1983	1100	Swennen 1983	1	
1976	92	Swennen 1976	1800	Swennen 1976	1150	Swennen 1976	1	Oosterhuis & Dijk 2002
1977	90	Swennen 1983	1800	Swennen 1983	1100	Swennen 1983	1	
1978	94	Swennen 1983	1900	Swennen 1983	1100	Swennen 1983	1	
1979	98	Swennen 1983	2100	Swennen 1983	1150	Swennen 1983	1	
1980	88	SOVON	2200	Swennen 1983	1150	Swennen 1983	1	Oosterhuis & Dijk 2002
1981	93	SOVON	2050	Swennen 1983	1200	Swennen 1983	1	
1982	97	Kats *et al.* 2007e in prep	2200	Swennen 1983	1250	Zwart 1985	1	Oosterhuis & Dijk 2002
1983	110	Kats *et al.* 2007e in prep	2500	Swennen 1991	1350	Zwart 1985	1	Oosterhuis & Dijk 2002
1984	100	SOVON	2600	Swennen 1991	1297		2	Oosterhuis & Dijk 2002
1985	106	SOVON	2400	Swennen 1991	1243	SOVON	3	Oosterhuis & Dijk 2002
1986	129	SOVON	2700	Swennen 1991	1900	SOVON	6	Oosterhuis & Dijk 2002
1987	137	SOVON	2700	Swennen 1991	1680	SOVON	7	Oosterhuis & Dijk 2002
1988	188	Kats *et al.* 2007e in prep	2700	Swennen 1991	1565		9	Oosterhuis & Dijk 2002
1989	105	SOVON	1755	Swennen 1991	1450	SOVON	5	Oosterhuis & Dijk 2002
1990	83	Kats *et al.* 2007e in prep	1395		1730		9	Oosterhuis & Dijk 2002
1991	104	SOVON	1035	Dijksen & Klemann 1992	2009	Kats *et al.* 2007e in prep	20	Oosterhuis & Dijk 2002
1992	145	SOVON	1066	Kats *et al.* 2007e in prep	1443	Kats *et al.* 2007e in prep	20	Oosterhuis & Dijk 2002
1993	194	Kats *et al.* 2007e in prep	1849	Koks 1994	2650	SOVON	25	Oosterhuis & Dijk 2002
1994	180	Kats *et al.* 2007e in prep	2432	Duiven & Zuidewind 2001	2579	SOVON	28	Oosterhuis & Dijk 2002
1995	179	SOVON	2147	Duiven & Zuidewind 2001	2154	SOVON	32	Oosterhuis & Dijk 2002
1996	175	SOVON	2135	SOVON	1756	SOVON	36	Oosterhuis & Dijk 2002
1997	168	SOVON	2564	Kats *et al.* 2007e in prep	1865	SOVON	67	Oosterhuis & Dijk 2002
1998	194	SOVON	2632	Kats *et al.* 2007e in prep	1805	SOVON	49	Oosterhuis & Dijk 2002
1999	176	SOVON	2716	Kats *et al.* 2007e in prep	1625	SOVON	68	Oosterhuis & Dijk 2002
2000	178	Kats *et al.* 2007e in prep	2196	SOVON	1292	SOVON	42	Oosterhuis & Dijk 2002
2001	214	Kats *et al.* 2007e in prep	2464	SOVON	1536	SOVON	66	SOVON
2002	170	Kats *et al.* 2007e in prep	1754	SOVON	1190	SOVON	55	SOVON
2003	126	Kats *et al.* 2007e in prep	1055	SOVON	590	Kats *et al.* 2007e in prep	41	SOVON
2004								
2005								
2006								

(B) Breeding colonies in the eastern Wadden Sea

Year	Ameland		Schiermonnikoog		Rottumerplaat		Rottumeroog	
	n	Reference	n	Reference	n	Reference	n	Reference
1900								
1901								
1902								
1903								
1904								
1905								
1906								
1907								
1908								
1909								
1910								
1911								
1912								
1913								
1914								
1915								
1916								
1917								
1918								
1919								
1920								
1921								
1922								
1923								
1924								
1925								
1926								
1927								
1928								
1929								
1930								
1931								
1932								
1933								
1934								
1935								
1936								
1937								
1938								
1939								
1940								
1941			1	Mooser 1973				
1942			1					
1943			1					
1944			1					
1945	1	Valk 1976	1	Mooser 1973				
1946	1	Hoogerheide 1950	1					
1947	1	Hoogerheide 1950	1				1	Braaksma 1973
1948	2	Junge 1952	1				1	Braaksma 1973
1949	1	Valk 1976	1	Junge 1952			1	
1950	1		2	Mooser 1973	1	Braaksma 1973	1	Junge 1952
1951	2		1		1		2	
1952	3	Valk 1976	1	Junge 1955	1		3	
1953	8		2	Junge 1955	1		4	
1954	13	Valk 1976	6		1		4	
1955	18	Valk 1976	10	Mooser 1973	1		5	Braaksma 1973
1956	20	Valk 1976	20		1		3	Braaksma 1973
1957	24	Valk 1976	30	Zweeres 1958	1		2	Braaksma 1973
1958	30	Valk 1976	53		1	Braaksma 1973	3	Braaksma 1973
1959	43	Valk 1976	77		1	Braaksma 1973	3	Braaksma 1973
1960	40	Valk 1976	100	Swennen 1976	1	Braaksma 1973	3	Braaksma 1973

Year	Ameland		Schiermonnikoog		Rottumerplaat		Rottumeroog	
	n	Reference	n	Reference	n	Reference	n	Reference
1961	26	Valk 1976	150		1		4	Braaksma 1973
1962	27	Valk 1976	200	Mooser 1973	1		6	Braaksma 1973
1963	30	Valk 1976	200	Mooser 1973	1	Braaksma 1973	5	Braaksma 1973
1964	25	Valk 1976	300	Mooser 1973	1		5	Braaksma 1973
1965	27	Valk 1976	250	Mooser 1973	1		7	Braaksma 1973
1966	25	Valk 1976	175	Swennen 1976	1		5	Braaksma 1973
1967	33	Valk 1976	150	Mooser 1973	1		10	Braaksma 1973
1968	30	Valk 1976	200	Swennen 1976	1		10	
1969	33	Valk 1976	188		1	Braaksma 1973	10	Braaksma 1973
1970	55	Valk 1976	175	Swennen 1976	9	Braaksma 1973	15	Braaksma 1973
1971	60	Valk 1976	336		4	Braaksma 1973	16	Braaksma 1973
1972	70	Valk 1976	497		1	Braaksma 1973	18	Braaksma 1973
1973	82	Valk 1976	658	Tekke 1975	5	Nolet 1988	22	Nolet 1988
1974	81	Valk 1976	629		5	Nolet 1988	18	Nolet 1988
1975	90	Swennen 1983	600	Swennen 1983	10	Nolet 1988	30	Nolet 1988
1976	90	Swennen 1976	700	Swennen 1983	2	Nolet 1988	40	Nolet 1988
1977	300	Swennen 1983	700	Swennen 1983	40	Nolet 1988	40	Nolet 1988
1978	400	Swennen 1983	750	Swennen 1983	7	Weijman 1979	25	Weijman 1979
1979	450	Swennen 1983	800	Swennen 1983	20	Weijman 1979	29	Weijman 1979
1980	500	Swennen 1983	850	Swennen 1983	50	Weijman 1980	50	Weijman 1980
1981	400	Swennen 1983	750	Swennen 1983	85	Bouman *et al.* 1981	110	Bouman *et al.* 1981
1982	425	Swennen 1983	746	Kats *et al.* 2007v	125	Bouman *et al.* 1982	125	Bouman *et al.* 1982
1983	471	Kats *et al.* 2007e in prep	889	Kats *et al.* 2007e in prep	110	Bouman *et al.* 1983	200	Bouman *et al.* 1983
1984	609	Kats *et al.* 2007e in prep	932	Kats *et al.* 2007e in prep	130	Haaf *et al.* 1984	200	Haaf *et al.* 1984
1985	577	Kats *et al.* 2007e in prep	1362	Kats *et al.* 2007e in prep	250	Haaf *et al.* 1985	250	Haaf *et al.* 1985
1986	558	Kats *et al.* 2007e in prep	1553	Bakker 1987	210	Bruyn *et al.* 1986	350	Bruyn *et al.* 1986
1987	589	Kats *et al.* 2007e in prep	1667	Kats *et al.* 2007v	246	Kats *et al.* 2007e in prep	304	Kats *et al.* 2007e in prep
1988	582	Kats *et al.* 2007e in prep	1917	Kats *et al.* 2007e in prep	281	Kasemir & Lutterop 1988	257	Kats *et al.* 2007e in prep
1989	523	Kats *et al.* 2007e in prep	2105	Kats *et al.* 2007e in prep	624	Kasemir & Lutterop 1989	481	Valkenburg & Koopman 1989
1990	514	Kats *et al.* 2007e in prep	1718	Kats *et al.* 2007e in prep	516	Lutterop & Kasemir 1990	383	Koopman & Keijl 1990
1991	479	Kats *et al.* 2007e in prep	699	Dijksen & Klemann 1992	644	Lutterop & Kasemir 1991	227	Dijken & Steenge 1991
1992	582	Kats *et al.* 2007e in prep	2188	Bakker 1987	769	Lutterop & Kasemir 1992	581	Dijken & Steenge 1992
1993	568	Kats *et al.* 2007e in prep	3617	Kats *et al.* 2007e in prep	1245	Kasemir & Lutterop 1993	580	Dijken & Steenge 1993
1994	574	Kats *et al.* 2007e in prep	3102	Kats *et al.* 2007e in prep	744	Lutterop & Kasemir 1994	806	Bruin & Dijken 1994
1995	538	Kats *et al.* 2007e in prep	2678	Kats *et al.* 2007e in prep	767	Kasemir & Lutterop 1995	570	Dijken & Koopman 1995
1996	534	Kats *et al.* 2007e in prep	3490	Kats *et al.* 2007e in prep	932	Lutterop & Kasemir 1996	810	Dijken & Koopman 1996
1997	579	Kats *et al.* 2007e in prep	3710	Kats *et al.* 2007e in prep	1212	Kasemir & Lutterop 1997	641	Dijken & Koopmans 1997
1998	478	Kats *et al.* 2007e in prep	3670	Kats *et al.* 2007e in prep	1061	Lutterop & Kasemir 1996	783	Ubels & Edelenbos 1998
1999	490	Kats *et al.* 2007e in prep	2444	Overdijk 2004	959	Lutterop & Kasemir 1999	735	Edelenbos & Ubels 2000
2000	412	Kats *et al.* 2007e in prep	2480	Overdijk 2004	589	Lutterop & Kasemir 2001	419	Bouman & Olsthoorn 2000
2001	372	Kats *et al.* 2007e in prep	2943	Overdijk 2004	635	Kasemir & Lutterop 2001	412	Bouman & Olsthoorn 2002
2002	318	Kats *et al.* 2007e in prep	2553	Overdijk 2004	739	Hovinga & Zoer 2002	516	Bouman & Olsthoorn 2003
2003	299	Kats *et al.* 2007e in prep	2377	Overdijk 2004	1043	Hovinga & Zoer 2003	482	Brederode & Roersma 2004
2004			2288	Overdijk 2004				
2005								
2006								

Appendix 10.2: "Historical review of range changes in the Common Eider in relation to life history"

The history of settlement and range expansion breeding Common Eiders
The distribution of breeding colonies of Common Eiders was historically restricted to the Arctic, but a southward extension of the breeding range towards the temperate regions was observed in the 19th and first half of the 20th century (Cramp & Simmons 1977). In temperate regions, literature on the presence of breeding colonies was scarce, but observations were available for the Farne Islands in the 7th century with Cuthbert, the bishop of Lindisfarne, protecting breeding Eiders (Swennen 1976a). In the 17th and 18th century, colonies were present on a few islands in the Danish part of the Baltic (Joensen 1973) and along the Scottish coast (Parslow 1973). The number and size of colonies were small in the 19th century and in some areas even until 1950, because Eiders were exploited for eggs, down and/or meat (Bauer & Glutz Von Blotzheim 1969, Conover 1926, Cramp & Simmons 1977, Norton 1907).

The expansion of the breeding range of Common Eiders was separated into five distinct phases: *breeding attempts* by a single or few females, *settlement of the primary colony* with continuous breeding in low numbers, settlement of secondary colonies in surrounding area, *growth* with a strong increase in the size of the primary colony, and finally *stabilisation* of all the surrounding colonies fluctuating between lower and upper limits. The patterns in the expansion of the breeding range in the coastal areas of the southern North Sea, including the Wadden Sea, and as far south as southern Brittany in France (Collingwood 1912) were also observed for the British Isles (Baxter & Rintoul 1953, Kennedy *et al.* 1954, Parslow 1973) and for American Eiders *Somateria mollissima dresseri* along the east coast of North America (Cannell & Maddox 1983, Gross 1944, Hebard 1960, Paynter 1951). Further, the process of colony settlement was not continuous and a colony was settled at a certain distance from the nearest colony and the areas in between become occupied in the following decades.

In the international Wadden Sea, the first breeding attempts (1800-1920) were reported for Sylt (1795-1805) in Denmark (Ringleben 1955), Amrum (1877-79) in Germany (Kumerloeve 1956) and Vlieland (1906) in the Netherlands (Thijsse 1907). After the primary colonies were permanently established, all colonies subsequently increased in size. These colonies may have acted in the following years as the core islands for the settlement of secondary colonies, such as Rømø in 1870, Fanø in 1903, Mandø in 1920 in Denmark (Swennen 1976a) and Föhr (between 1910 and 1915) in Germany (Kumerloeve 1956). In the Netherlands, secondary colonies were established first on the surrounding islands (Terschelling and Texel) in the early 1940's and by the end of the decade colonies were established on the remaining islands. Similar patterns in growth and settlement of secondary colonies were observed in Scotland with settlement on the mainland around 1850 (Baillie

& Milne 1989, Parslow 1973), and in Maine and southern New Brunswick (Gross 1944, Paynter 1951). In the Dutch part of the Wadden Sea, the development in size of the colonies was different in the western and eastern part with stabilisation around respectively 1960 and 1990 (Figure 10.2), although inter annual differences in size can be large.

Settlement

The driving forces, which enable a successful settlement of a new breeding colony, are reviewed using literature on the factors affecting successful breeding in eiders of the genus Somateria, and the successful settlement of the breeding colony in the Netherlands on Vlieland will be discussed in relation to the reviewed factors.

In order to establish a successful breeding colony, the local conditions need to cover and fulfil the basic needs for successful breeding by Eiders. The breeding cycle of Eiders can be divided into three breeding periods: (1) pre-breeding with storage of energy prior to breeding for breeding, (2) breeding with nest selection and incubation, (3) post-breeding with recovery of breeding females and the survival of fledglings.

First, Common Eiders are capital breeders (Meijer & Drent 1999) and females need to store large amounts of energy up to 20 % (hyperphagia) prior to breeding to cover the costs of egg formation and laying, and fasting during incubation (Criscuolo *et al.* 2000, Gabrielsen *et al.* 1991, Korschgen 1977, Parker & Holm 1990). In the Netherlands ringing has shown that breeding females do not migrate, as all recoveries derive from the colony of origin or the immediate vicinity (Swennen 1976). Indeed, the breeding females return to the natal island (and often to the previous nest site (Swennen 1976a)) as has been shown elsewhere (Bustnes & Erikstad 1993, Cooch 1965, Coulson 1984, Grenquist 1965, Paludan 1962, Reed 1975, Swennen 1990). Non-migrating females in Denmark and southern Finland stored energy for breeding locally (Christensen 2000, Hario & Öst 2002). While migrating females, which breed in northern Finland, stored energy for breeding at the wintering grounds and locally (Hario & Öst 2002). Therefore, the food stocks near the breeding colony are of the utmost importance for successful breeding. The absence of ground predators favours the increase in the female's survival (Götmark & Åhlund 1988), because females prior to breeding undergo hyperphagia and as a consequence face temporary flightlessness (Guillemette & Ouellet 2005a,b).

Second, the selection of the nesting site is an important factor for increasing the success of breeding and relate to increased vegetation cover and height (Bregnballe *et al.* 2002, Choate 1967, Gorman 1974, Kilpi & Lindström 1997, Laurila 1989, Schmutz *et al.* 1983), predators (Åhlund & Gotmark 1989, Laurila 1989, Mehlum 1991, Schamel 1977), low level of human induced disturbance, such as boating, public access or cattle (Choate 1967, Laurila 1989), short distance to the shore (Laurila 1989, Schmutz *et al.* 1983). The vegetation provided

camouflage during breeding, for example the disappearance of lyme grass *Elymus arenarius* due to the breeding cormorants *Phalacrocorax carbo sinensis* are believed to have contributed to decline in the size of some colonies in Denmark (Bregnballe *et al.* 2002). The presence of predators at the breeding grounds may have two opposite effects on the success of breeding with reduced survival of incubating females and/or clutch by mammalian ground, such as rats *Rattus* spp., American Mink *Mustela vison*, Red Fox *Vulpes vulpes*, Arctic Fox *Alopex lagopus*, feral cats (Ahlèn & Anderson 1970, Bregnballe *et al.* 2002, Desholm *et al.* 2002, Flint & Grand 1997), and aerial predators (gulls Laridae: Herring Gulls *Larus argentatus*, Lesser Black-backed Gulls *Larus fuscus*, Great Black-backed Gulls *Larus marinus*, Glaucous Gull *Larus hyperboreus* and Mew Gull *Larus canus* (Ahlèn & Anderson 1970, Coulson 1984, Grand & Flint 1997, Mendenhall & Milne 1985, Milne 1972), crows Corvidae: Carrion crows *Corvus corone* (Coulson 1984, Gorman 1974, Mendenhall & Milne 1985, Milne 1972) and Magpies *Pica pica* (Ahlèn & Anderson 1970), Arctic Skua *Stercorarius parasiticus* (Ahlèn & Anderson 1970) and white-tailed eagles *Haliaeetus albicilla* (Sulkava *et al.* 1997, Kauhala & Auniola 2001). Females may also benefit by increased nesting success from nesting in the vicinity of birds with successful deterrence of other aerial and ground predators, such as Short-eared owls *Asio flammeus* (Brenninkmeijer *et al.* 1998), Snow Owl *Bubo scandiacus*, Pomarin Jaegers *Stercorarius pomarinus*, colonies of gulls Laridae sp. (Schamel 1977) and terns *Sterna* spp. (Bourget 1973, Coulson 1984, Swennen 1989), and Lesser Snow Geese Anser *caerulescens caerulescens* (Robertson 1995).

Third, in the post-hatching period females need to recover after incubation (Bolduc & Guillemette 2003) to ensure survival of both herself and her offspring. This post-breeding recovery must depend on the stock of sufficient and profitable prey near the breeding colony due to the high degree of philopatry throughout the annual cycle. Just prior to laying, females have impaired flight ability or under windstill conditions even temporarily flightless (Guillemette & Ouellet 2005a,b) increasing their vulnerability to predators (Götmark & Åhlund 1988). Survival in the colony depends strongly on the absence of ground predators (Götmark & Åhlund 1988). For long, the survival of hatchlings, ducklings and fledglings have been negatively associated with the presence of breeding Laridae (Ahlèn & Anderson 1970, Götmark 1989, Götmark & Åhlund 1988, Hillstrom *et al.* 1994, Mawhinney *et al.* 1999, Mawhinney & Diamond 1999, Munro & Bédard 1977), but the predation upon ducklings in the first 10 days after hatching was the elimination of the unfit (Swennen 1989). The reduced fitness of the ducklings causing high mortality rates between 4–7 days after hatching among ducklings were primarily related to low stocks of sufficient and suitable sized prey (i.e. various species of small or young invertebrates: Corophium volutator, *Nereis diversicolor, Arenicola marina, Crangon crangon, Carcinas maenas* and *Jassa falcata*) abundantly found on seaweed along dikes and tidal mussel beds and stress again the importance of local food stock for breeding Eiders (Swennen 1989). Under certain conditions, disease

may also play an important role, such as Goose Virus Hepatitis causing additional mortality among 2–3 weeks old ducklings (Swennen 1991b, Swennen *et al.* 1979), infectious bursal disease virus (Hollmén *et al.* 2000), reovirus (Hollmén *et al.* 2002), adenovirus (Hollmén *et al.* 2003), but it remains unclear where and how these diseases are obtained and whether they were associated with high densities of animals during breeding near the colonies Therefore, diseases mentioned above are not expected to play a role of importance during the settlement of a new colony, but may become important when populations have become stable and/or are under stress.

What favoured the first breeding attempts and subsequent settlement of a breeding colony in the Wadden Sea and more specifically the isle of Vlieland? First, feeding conditions were favourable to support the annual cycle in the western part of the Wadden Sea, because the mudflats in the western Wadden Sea were characterised by the presence of mussel beds in the first half of the 20th century (Kuenen 1942, Maas-Geesteranus 1942, Straaten 1965, Tesch & Veen 1933, Verwey 1952). Second, ground predators were absent and the first breeding females may have also benefited from the presence of gull colonies. Third, Vlieland was a sand plain without dunes and vegetation during the 19th century, but the plains became completely vegetated within 10 years after the introduction of the non-native Beach grass *Ammophila arenaria* in 1900 (Vries 1950). Additional vegetation cover for breeding females increased on Vlieland starting in 1902 with the establishment of plantations of pines, mainly *Pinus nigra* (Westhoff & Van Oosten 1991) for logging resulting in Bomenland. Fourth, human disturbance was low in terms of visitation and the collection of down, eggs and meat was prohibited since 1930. Further, breeding Eiders enjoyed the effects of conservation, because the area was protected by law since 1925 and was one of the first nature conservation areas in the Netherlands (Wilcke 1956). And finally, the small ponds and channels in Bomenland and the Kroon's Polders (constructed from 1905 to 1922 for agricultural purposes) provided both quick and easy access to fresh water for incubating females during recess and 0–3 days old hatchlings (Swennen 1989).

Synthesis

The rise and fall of Common Eiders in the Netherlands

Common Eiders in the Baltic/Wadden Sea flyway

The focus of this thesis is on Common Eiders *Somateria mollissima mollissima* in the Dutch part of the international Wadden Sea, which are part of the Baltic/Wadden Sea flyway (Chapter 2). The population of Common Eiders in the Baltic/Wadden Sea flyway comprises breeding populations along the coast of the Baltic Sea (Finland, Sweden, Estonia, southern Norway (i.e. Skagerrak), Denmark and Germany) and in the international Wadden Sea (Denmark, Germany and the Netherlands) (Chapter 2). The subspecies mollissima includes breeding populations in Britain and Ireland (Ogilvie 2005), but these are not further considered here. Large differences in the distribution throughout the annual cycle exist between populations within the flyway. The geographic location of the breeding population in the flyway determines whether the population is (a) completely migratory or (b) sedentary or partly migratory. In partly migratory populations, the migratory behaviour also depends on age and/or sex. Ringing data indicated that the majority of the Common Eiders from the Baltic and Wadden Sea (> 95 %) were reported within the flyway extending south along the North Sea coast of Belgium and Atlantic coast of France (Swennen 1991a, Fransson & Petterson 2001, Bakken *et al.* 2003). Migration outside the flyway was reported for some Common Eiders from Norway (to Svalbard and Iceland: Bakken *et al.* 2003), and the Netherlands (to United Kingdom and Ireland: Swennen 1991a, Kats unpublished data). There is indirect evidence that the flyway of the Baltic population includes the east coast of Great Britain although not many individuals are involved. A few Common Eiders from Great Britain ringed as ducklings or breeding adults were later recovered in the Baltic as far as Finland (Wernham *et al.* 2002). Almost all were males and these movements presumably reflect pair bonds formed during winter, the males following their mates back the next season ('abmigration').

The breeding populations in the eastern part of the Baltic Sea (eastern Sweden, Finland and the Baltic countries) are considered completely migratory (Cramp & Simmons 1977) and mix on the wintering grounds in the western Baltic Sea, Kattegat, inner Danish waters and in the Wadden Sea from Denmark to the Netherlands (Noer 1991, Swennen 1991a, Fransson & Petterson 2001). The migratory status of the eastern breeding populations is probably related to difficulties in accessing food in winter near the breeding areas due to ice.

The breeding populations in the western part of the Baltic Sea (Denmark, southern Norway, western Sweden) and the Wadden Sea (Denmark, Germany, and the Netherlands) are qualified as resident or partly migratory (Cramp & Simmons 1977). For the breeding population in the Netherlands, differences in migration are age and sex dependent (Swennen 1991a). A small degree of dispersal of 13.7 % (38 out of 278 birds reported dead outside the Wadden Sea area) was reported for 1st and 2nd calendar year of both sexes. Differences in site-faithfulness are extreme between the sexes as deduced from the Dutch ringing material, in line

with the findings in Britain alluded to above. Swennen (1991a) reported that males originating from the Dutch Wadden Sea were reported at an average distance of 1270 km from the natal area, whereas females were highly site faithful to the breeding colony throughout the annual cycle. Adult females were always recaptured in the same breeding colony (April to June) and reported dead in the vicinity of the natal island outside the breeding season (July to March).

The total size of the Baltic/Wadden Sea flyway: a mismatch between breeding and wintering numbers

The total flyway estimate of the wintering population has decreased by 36 % from 1.18 million birds in 1991 to 0.76 million birds in 2000 (Table 2.1), but most of the national breeding trends show no equivalent decrease since the mid-1990's (Figure 2.1, 2.2, 2.6, 2.7, 2.10). Due to a lack of national breeding estimates between 1991 and 2000, no overall assessment of the changes in the total flyway breeding population could be made. No national breeding population estimates are available for Sweden since the middle of the 1980's (Sveriges Fåglar, SOF 2002), while this country has been known to host approximately one-third of the total Baltic breeding population (Almkvist *et al.* 1974). Furthermore, trends in breeding numbers at a few local areas may not be representative of those in the population as a whole. However, the 36 % decline in the total wintering population in the flyway offers the best assessment of the population change and gives some cause for concern. The apparent mismatch between the reductions in wintering numbers and the apparent stability in local breeding numbers was explained by the presence of a considerable pool of non-breeding birds (Chapter 2 and 9). The non-breeding pool acts as a buffer during periods of reduced competition for pre-breeding feeding habitat or breeding habitat resulting from reduced adult female survival. The non-breeding pool may also become visible during periods with an excess of suitable food (Chapter 9).

To summarise, the 36 % decline in winter numbers between 1991 and 2000 reflects a significant population decrease throughout the flyway, not distinguishable at present in the trends of national breeding numbers due to the buffering effects of the non-breeding element of the population. Once the pool of non-breeders is also exhausted, declines in the breeding populations will be detected.

Wintering population of Common Eiders in the international Wadden Sea since 1987

The long-term (1987-2002) average size of the mid-wintering population in the whole of the international Wadden Sea area was approximately 270000 birds, but a decline was observed in recent years (1999 to 2002) from 285000 to 162500 birds (Figure 11.1). The majority of the wintering population was found in the Netherlands (110000) and Schleswig-Holstein (80000) with remaining birds wintering in Niedersachsen (60000) and Denmark (30000). The size of the wintering
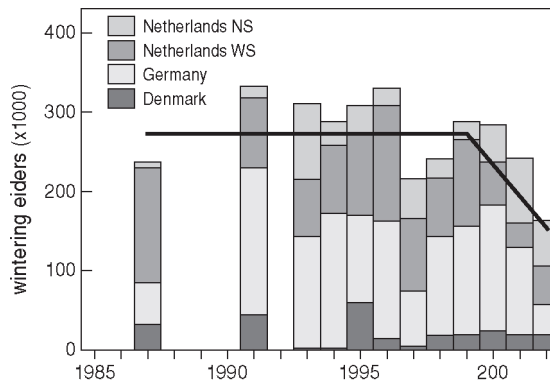
Figure 11.1 The size of the wintering population of Common Eiders *Somateria mollissima* in the international Wadden Sea assessed by aerial surveys: the Wadden Sea (area between the islands and the mainland coast) and North Sea in the Netherlands (area north of the islands and along the mainland coast of Noord-Holland), Germany, and Denmark. In years with missing bars no counting data was available and the year of 2000 is the winter of 1999/2000. (After Scheiffarth & Frank 2005 and Swennen *et al*. 1989).

population within all regions declined since 1995. The wintering population in the Netherlands varied in parallel with the numbers in Schleswig-Holstein (r_s = 0.673, p< 0.05, n = 11: Scheiffarth & Frank 2005) suggesting that similar processes may control the size of the wintering population in both regions. In Germany, the wintering numbers in Dithmarschen (southern part of Schleswig-Holstein) are negatively correlated to the numbers in Niedersachsen (r_s = -0.571, p< 0.05, n = 15: Scheiffarth & Frank 2005) indicating a shift between both regions.

Phenology of Common Eiders in the international Wadden Sea
The phenologies or seasonal patterns of Common Eiders in four parts of the Wadden Sea show that differences in numbers were large in the course of the year between and within those parts (Swennen *et al*. 1989, Scheiffarth & Frank 2005, Figure 11.2). The seasonal differences are explained by differences in utilisation of those parts by eiders in their annual cycle, i.e. breeding, moulting and wintering. The local breeding populations are reflected by low numbers observed in all parts in spring (April - May). Common Eiders from both the local and Baltic breeding population utilise the Wadden Sea for moulting (June – October) and for wintering (November – March). In general, the central parts of the Wadden Sea (Schleswig-Holstein, Niedersachsen and the eastern part of the Dutch Wadden Sea) are used as moulting area, while the periphery (Denmark and the western part of the Dutch Wadden Sea) are used as wintering area (Figure 11.2).

Scheiffarth and Frank (2005) found that the seasonal patterns were constant in
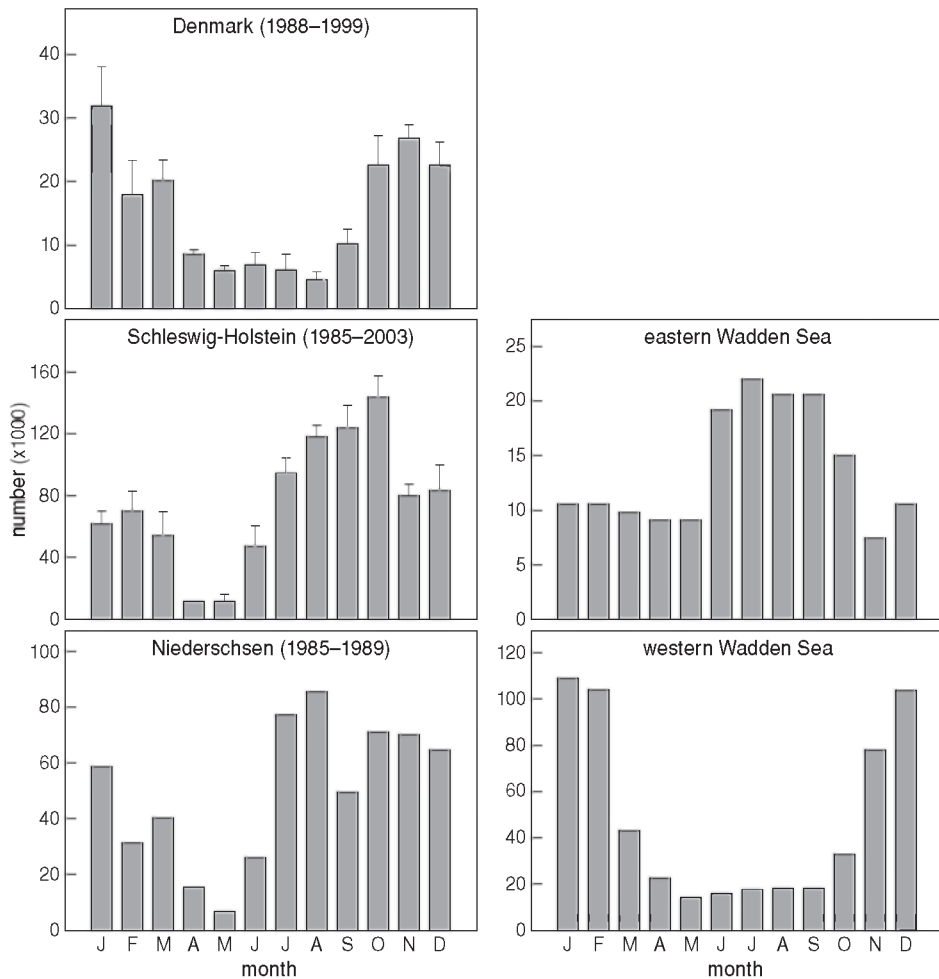
Figure 11.2 Phenologies of Common Eiders in the international Wadden Sea: Netherlands (eastern and western Wadden Sea), Germany (Niedersachsen and Schleswig Holstein), Denmark (For details see Scheiffarth & Frank 2005 and Swennen *et al.* 1989).

time and that only the patterns in distribution changed during the 1990's, but evidence from the Netherlands suggests that seasonal patterns in winter were not constant and did change. In general, the size of the wintering population increases in the course of winter to a maximum and declines towards the end of winter in March and April, when the Baltic wintering population migrates to their breeding areas (Petersen 1974, Swennen 1980b, Camphuysen & Van Dijk 1983). The within-wintering numbers of Common Eiders in the Dutch Wadden Sea show that the timing of the maximum number of wintering Common Eiders during winter has
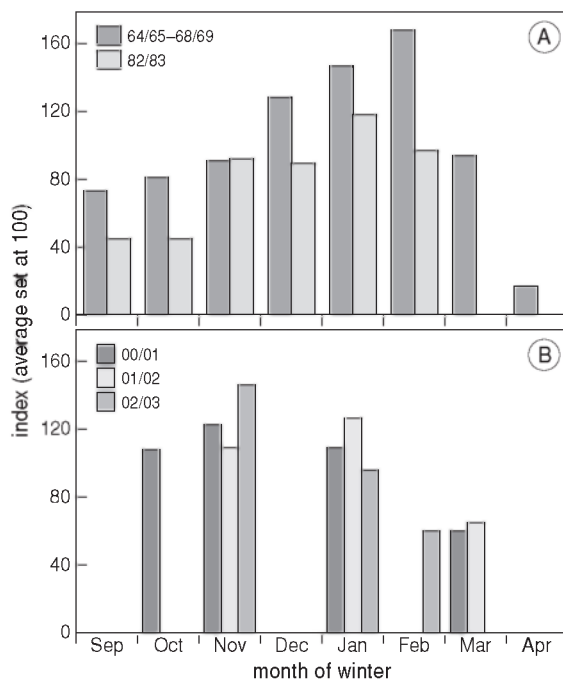
Figure 11.3 Seasonal pattern of wintering eiders (expressed as an index with the average set at 100) (A) before 1990 (between 1964/65 and 1968/69 (Swennen 1976a) and in 1982/93 (Swennen 1983, Van Buuren 1983)), and (B) after 1990 (between 2000/01 and 2002/03 (De Jong *et al.* 2002 and 2003).

changed from an observed maximum in February in the 1960's, January in the 1980's to a maximum in November between 2001 and 2003 (Figure 11.3). During a 40 year period, Common Eiders have been leaving the Wadden Sea earlier in winter suggesting that the Dutch Wadden Sea has become less attractive for wintering possibly due to a long-term decline in suitable food stocks and/or food quality.

Two populations of Common Eiders in the Netherlands: wintering and breeding
Nowadays, two populations of Common Eiders are present in the Netherlands, i.e. the wintering population and the breeding population. The wintering population is a mixture of the migrating population from the Baltic Sea area and the resident local Dutch breeding population. These two populations will be discussed separately.
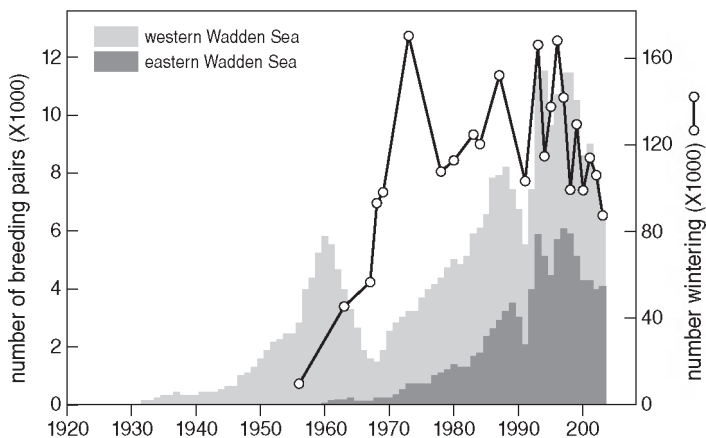
Wintering Common Eiders

Size and distribution of wintering Common Eiders in the Netherlands since 1987

The first Wadden Sea wide aerial census was performed in January 1987 and the Dutch wintering population was estimated at 147300 birds. The size of the wintering population declined significantly from 165000 in 1993 to 87000 in 2003 (Figure 7.2b and 11.4). Variation in the distribution of the total wintering population (1978-2003) was explained by the number of birds wintering in the western part of the Wadden Sea and the North Sea (Chapter 7). The numbers in the eastern Wadden Sea have been stable since the 1960's at an average of 16400 birds (Figure 7.2b) at a lower density compared to the western compartment (Figure 7.2d). In general, wintering eiders were concentrated in the western Wadden Sea averaging 81000 birds, but things changed at the end of the 1980's when there was a major exodus from the Wadden Sea. The number of wintering eiders on the North Sea increased dramatically due to food shortage in the Wadden Sea, with exceptionally high numbers of 91000 in 1993 and 81000 in 2001 representing the majority of the Dutch wintering population (Table 7.1, Figure 7.2b).

Long-term patterns in mortality of wintering Common Eiders in the Netherlands

Since 1978, approximately 100000 Common Eiders have died in the Wadden Sea area during winter (November – April) with a maximum of 17500 birds in the winter of 1999/2000 (Figure 7.3 and 7.4). On average 3.25 % of the wintering

Figure 11.4 The number of breeding Common Eiders in de western and the eastern part of the Dutch Wadden Sea and the total number of Common Eiders wintering in the Wadden Sea and the North Sea coastal zone (after Ens *et al.* 2006).

population was reported dead each winter, but mortality rate varied considerably between winters from 0.66 % in 1980 to 16.9 % in 2000 (Figure 7.4). The winters of 1990/91, 1991/92, 1999/2000 and 2001/02 are classified as so-called 'kill-winters', because mortality rate was much higher than the long-term average.

Testing hypotheses concerning mortality of wintering eiders
in the Netherlands: parasites and/or food shortage
Common Eiders (*Somateria mollissima* L. 1758) wintering in the Netherlands showed mass mortalities in the winters of 1999/2000 and 2001/02 (Chapter 7) and three hypotheses are proposed to explain these mass mortalities (Chapter 6):

1. Food shortage hypothesis (Camphuysen *et al.* 2002):
   Mass mortality is the result of starvation due to of low stocks of harvestable food. Starvation was inferred from the low body mass of birds found dead and movements away from the traditional wintering area suggested a shortage of food in that traditional wintering area.
2. Parasite infection hypothesis (Smaal *et al.* 2001):
   Mass mortalities were considered primarily the result of parasite outbreaks. The importance of parasites was inferred from high parasite loads in many Eiders that were found dead and the fact that an intermediary host (Shore Crab *Carcinas maenas*) of one of the parasites, which is also prey to the Common Eider, was very common in the year with mass mortality.
3. Food shortage induced parasite infection hypothesis (Grenquist 1970, Borgsteede *et al.* 2005, Borgsteede 2001 & 2005):
   Mass mortalities are here considered to result from individual birds not being able to sustain high parasite loads caused by an increase of (parasitized) crabs in the diet due to the inability to acquire sufficient food. Food shortage caused high mortality among heavily parasitized individuals.

The role of parasites during mass-mortality was investigated to test whether the observed mass mortalities were explained by an outbreak of parasites (Hypothesis 2) or food shortage of suitable prey (Hypothesis 1 and 3). Ideally, one would like to compare the parasitological status (and body condition) of dead and live birds within the same area, but the collection of healthy specimens for this purpose proved to be practically impossible due to the conservational status of the Wadden Sea. Therefore, a within flyway comparison was employed using a sample of beached eiders from the Netherlands and healthy eiders from Denmark, which were collected during legal hunting on wintering eiders. The comparison of birds from different wintering grounds within the Baltic/Wadden Sea flyway was considered valid, because Eiders in the Netherlands and Denmark belong to the same Baltic-Wadden Sea flyway population (Desholm *et al.* 2002, Swennen 1990), and parasitological effects on condition and mortality are expected to depend on physiology of the birds and not on geographic location. This conclusion was recently

supported by a study of the parasitological status of eiders that died in an oiling incident (i.e. wreckage of the vessel Pallas) southwest of the island of Amrum in the German sector of the Wadden Sea, i.e. These specimens were otherwise healthy, and Thieltges *et al.* (2006) reported that: *"A comparison with the parasite loads of eiders from the mass mortality in the winter of 1999/2000 [in the Netherlands] shows that parasite numbers were by no means exceptional for birds from the area. Hence, parasites alone are unlikely to have caused this mortality".*

The majority (> 75%) of all the beached and shot eiders were infected with *P. botulus* and *A. acutum* (Table 6.2). The prevalence differed with respect to age (higher in juveniles) for *P. botulus* and status (higher for beached birds) for *A. acutum* (Table 6.4). Compared to Eiders that were shot, the intensity of infection of *P. botulus* was 2-3 times higher in beached birds, with juveniles having 2-3 times more parasites than adults (Table 6.3 and 6.4). The intensity of infection of *A. acutum* in both beached and shot birds was 1-2 times higher in adults (Table 6.3 and 6.4). In general, the observed differences in prevalence and intensity of *P. botulus* between age groups result from differences in diet with juveniles having a higher proportion of crabs in their diet (see Bustnes & Galaktionov 2004 and Thompson 1985). To explain the observed differences for *A. acutum* between beached and shot birds is a difficult task due to the absence of basic knowledge on transmission of *A. acutum* in wildlife. However, the observed differences between beached and shot birds may be associated with differences in distribution and/or feeding, which have been reported for differences within adults. Further, the condition of beached birds was much worse compared to shot birds with for beached birds a 30% lower condition, 60% lower liver mass and nearly no deposit of fat (Table 6.5 and Figure 6.2), which was similar to starvation patterns in several species of wildfowl and waders (see Discussion Chapter 6). Differences in body condition were explained by status (beached versus shot) and age, but not by parasite loads (Table 6.6). This is telling evidence against the parasite infection hypothesis. Mass mortality was not the result of an outbreak of parasites, but occurred in years with low food stocks.

Feeding behaviour of Common Eiders

Common Eiders are large sea ducks, which feed by diving (intertidal and sub-tidal) and dabbling (intertidal) on a large variety of prey species and sizes. In the Wadden Sea area, important species of shellfish for wintering and breeding Common Eiders are mussels, cockles and *Spisula* (Chapter 3), and recently also *Ensis* is included in the diet (Chapter 4 and 5). The mussels and cockles are found in both the intertidal and sub-tidal areas of the Wadden Sea, while *Spisula* is restricted to the North Sea. *Ensis* occurs in the lower intertidal and sub-tidal areas of the Wadden Sea, as well as the North Sea.

In general, prey is collected by diving to the bottom of the sea up to 40 meters deep. The collected shellfish are swallowed whole and as a consequence the maximum size of a given prey taken by feeding eiders is physically limited, which is observed for mussels (maximum 7cm) and *Ensis* (maximum 10 cm). The shellfish are crushed in the stomach for the absorption of the nutrients in the digestive tract. A modelling exercise by Brinkman *et al.* 2003 on the energy budget of wintering eiders covering only the daily existence energy (DEE) has shown that the most important costs are related to crushing of shellfish in the stomach, the basal metabolism rate (BMR) and digestion. The energetic cost of crushing represented a large part of the eiders energy budget and is related to the shell mass, which varies between and within species of shellfish. A between and within species comparison with respect to profitability using the flesh/shell ratio and modelling exercise of prey choice showed that profitability declined from sub-tidal mussels, intertidal mussels, intertidal cockles, sub-tidal cockles to *Spisula*. Seed mussels are less profitable than medium-sized and consumption mussels, although this difference was related to the assumption of the model that eiders were allowed to take only one mussel during each diving cycle. The simplification in this approach (the assumption of a single-mussel intake pattern) is not in agreement with my dissections, as I often observed clumps of small mussels in the oesophagus.

Wintering Common Eiders in relation to shellfish in the Dutch Wadden and North Sea

CONSEQUENCES FOR NUMBERS AND DISTRIBUTION

The analysis of the long-term (1994-2004) distribution of the Common Eiders in the Dutch Wadden Sea (Figure 8.4) in relation to the distribution of intertidal and sub-tidal cockles and mussels (Figure 8.5) using log-linear models revealed that subtidal mussels were the most important factor in determining the distribution of Eiders in the Dutch Wadden Sea, irrespective of scale (Figure 8.7). However, more deviance was explained with increasing scale (Figure 8.7) which is probably 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. In the eastern part of the Wadden Sea, the distribution of Eiders seemed to be largely driven by intertidal mussels. Cockles were not found to be of importance relative to the intertidal and subtidal mussel stocks as very few analyses showed any significant contribution of either subtidal or intertidal cockle stocks to the distribution of Eiders (Table 8.4).

Subtidal mussels (wild and cultured) are virtually restricted to the western part of the Dutch Wadden Sea (Figure 8.5) where traditionally most Eiders were present in winter (Figure 8.4). Further, the majority of the sub-tidal mussels are nowadays found on mussel cultures (Table 7.5) explaining the importance of those cultured stocks compared to the wild sub-tidal stocks during the 1990's (Table 8.4) The sub-tidal mussels, including those on cultures, have been of crucial importance

during the 1990's for the survival of the wintering population of Common Eiders in the Dutch Wadden Sea. These findings should not be taken as evidence that mussel culture benefits Common Eiders. First, eiders may simply follow the mussels: had these been left on the wild sublittoral beds, than wild sublittoral beds would have been the most important feeding area. Second, stocking behaviour of mussel cultures in the Wadden Sea may depend on the total mussel stock. It is possible that in years of mussel scarcity the majority of the mussels on cultures is grown on cultures outside the Wadden Sea (Fig 7.8) making these mussels inaccessible for the wintering population resulting in food shortage causing mass mortality (Figure 7.7). The depletion of sub-tidal mussels in the Wadden Sea during the early 1990's resulted in a shift of wintering eiders to the North Sea (Camphuysen *et al.* 2002).

On the North Sea, the distribution of Common Eiders is related to the distribution of *Spisula subtruncata* (Leopold 1993, 1996, Leopold *et al.* 1995, Figure 7.6)). *Spisula* was the only abundant shellfish in the area during the 1990's (Craeyneersch & Perdon 2004). Large numbers of Eiders were found feeding over banks of *Spisula* and *Spisula* was observed in the faeces of feeding Common Eiders collected along the Dutch mainland coast (Leopold 1996) and in stomach analysis (Ens & Kats 2004) after the die-off of Common Eiders in 1999/2000 (Camphuysen *et al.* 2002) and 2001/02 (Ens *et al.* 2002). Recently, the abundant stocks of *Spisula* have declined rapidly to the point of virtual extinction, but have been replaced by American Razor Clam *Ensis americanus*, which increased dramatically in abundance (Bult *et al.* 2004b, Craeymeersch & Perdon 2004). Nowadays, flocks of Eiders have been found feeding on *Ensis* in the Wadden Sea and to a lesser degree on the North Sea (observations by Jan van Dijk and Bram Fey). Whether *Ensis* stocks represent a long-term alternative to mussels and *Spisula* in the future remains to be seen.

CONSEQUENCES FOR MORTALITY

Low stocks of medium-sized mussels were the best predictor of high mortality among Common Eiders (Figure 11.5A, Table 7.3). Despite fluctuations in the total wintering population, analysis confirmed that mortality was significantly affected by the stock of medium-size mussels. Although fewer years are available for analysis, the same conclusion holds for mortality *rate*, which is the more logical variable.

The data set on the stock of *Spisula* was short and so closely correlated to the stock of subtidal mussels that *Spisula* could not be included as a separate independent variable in a multivariate analysis already including the stock of subtidal mussels. However, the stock of mature *Spisula* was low in two years with mass mortality and simply plotting total mortality against the stock of mature *Spisula* yielded a significant negative correlation (Figure 11.5B), which was absent for *Ensis* ($p = 0.88$). Additional evidence that *Spisula* was in short supply in years of
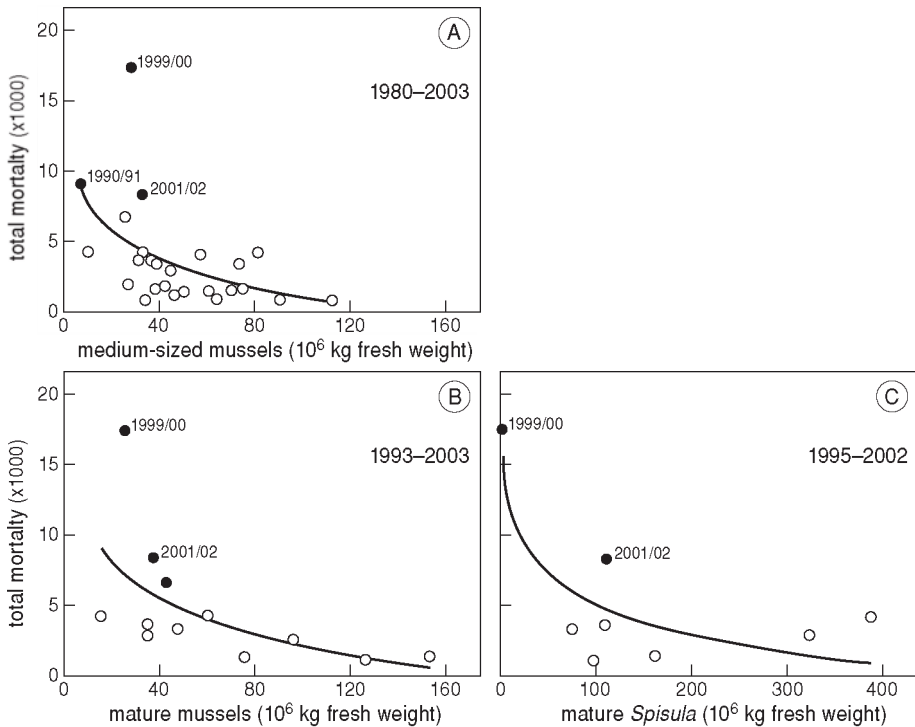
Figure 11.5 Total mortality in winter (expressed as the total estimated number of dead birds) in wintering Common Eiders *Somateria mollissima* in the Wadden Sea area in relation to the stocks (expressed as 10^6 kg fresh wet mass) of A) subtidal medium-sized Mussels *Mytilus edulis* on cultures (1980-2003): Lg(Total dead) = -0.02291*(Medium Mussels) + 9.169, d.f. = 24, p = 0.003), (B) subtidal mature wild and cultured Mussels (1993-2003): Lg(Total dead) = -0.01753*(Mature Mussels) + 9.356, d.f. = 10, P = 0.022), and (C) mature Cut Through Shells *Spisula subtruncata* on the North Sea (1995-2002): Total dead = -3159*Lg(Mature *Spisula*) + 19706, d.f. = 7, p = 0.009). Black symbols represent 'kill'-winters of 1990/91, 1999/00 and 2001/02. For more details see Figure 7.7.

mass mortality comes from Figure 7.6C, which suggests that in the years of mass mortality the number of Eiders wintering on the North Sea was too high given the stock of mature *Spisula*. The lack of such clear evidence for the role of *Ensis* as an alternative food (Figure 7.6D) may simply reflect the shortcomings of our knowledge of how this food source is exploited by Eiders.

To summarize, the excessively high mortality in the winters of 1999/2000 and 2001/2002 was caused by low stocks of subtidal mussels in the western Wadden Sea coinciding with low stocks of *Spisula* on the North Sea.

Breeding Common Eiders

Developments in the size of the Dutch breeding population (1900-present)

The breeding attempt on Vlieland in 1906 (Thijsse 1907) resulted in successful settlement of a breeding colony and subsequent settlement of secondary colonies in the Wadden Sea. The size of the Dutch breeding population in 1960 was estimated at 5750 breeding females in 1960 with only 2.5 % of the total in the eastern Wadden Sea (Figure 11.4).

The breeding population crashed in the 1960's causing a 75 % reduction in population size from 5750 in 1960 to 1350 breeding females in 1969 (Appendix 10.1) due the pollution of coastal waters with chlorinated hydrocarbons (Koeman *et al.* 1969, Swennen 1972). The impact of this pollution declined from the west to the east in terms of numbers and duration (Figure 10.2). After closure of the pollution source the colonies recovered and increased in size during 1970's and stabilised in the 1980's. However, a fresh decline in the number of breeding females was observed between 1988 and 1992 (Figure 11.4), which was explained by non-breeding as a response to low food supply near the breeding colonies (Chapter 9 and 10). The total breeding population recovered quickly during the following years due to the presence of large numbers of these non-breeding females. At the end of the 1990's, the total population was estimated at 11000 breeding females with similar numbers in both the western and eastern part of the Wadden Sea (Figure 11.4). Since then the Dutch breeding population has declined by 40% with severe losses in the western segment which has fallen below the levels of the late 1960's. In the eastern Wadden Sea, a decline was observed at the end of the 1990's similar to the western part, but breeding numbers recovered since then and an increase was observed (Figure 11.4). The differences in the two segments within the Dutch Wadden Sea were tested by comparing the breeding colonies on Vlieland (western) and Rottum (eastern) in relation to intertidal food stocks (Chapter 10).

General requirements for breeding Eiders

Breeding in Common Eiders is explained by the ability of breeding females to fulfil the needs for successful breeding which are related to the local conditions near and/or in the breeding colony. The basic breeding biology of Common Eiders is presented in detail in Appendix 10.2 and is summarised below.

First, Common Eiders are capital breeders with breeding females storing large amounts of energy (hyperphagia) prior to breeding resulting in an increase in body mass up to 20 %, which cover all the costs of breeding (i.e. egg formation, egg laying, non-stop incubation). The food stocks near the breeding colony are of the utmost importance to ensure the build up of energy reserves and post-incubation recovery of females in the Dutch breeding population.

Second, nest site selection contributes to successful breeding and relates to vegetation characteristics of the nesting site (reducing costs of incubation and detection by aerial predators), degree of human induced disturbance in the colony (public access, cattle) and distance to the shore.

Third, survival of offspring is dependent on the stocks of sufficient and profitable prey abundantly found in intertidal mussel beds near the breeding colony (Swennen 1991a).

**Evidence of colony saturation**
The breeding colonies increased in size (Chapter 9 and 10, Appendix 10.1, Figure 10.2), but stabilisation was reached at different periods for the western and eastern Wadden Sea with stabilisation in respectively the early 1960's and late 1980's (Chapter 10, Figure 10.3 and 11.4). Since that time large fluctuations have occurred. Although, the breeding colonies increased in size, the total breeding population appeared to reach saturation in the late 1990's with a maximum of 11000 breeding females. At that time the numbers were similar in the western and eastern part of the Wadden Sea, but since then the Dutch breeding population has declined by 40% with severe losses in the western segment which has fallen below the levels of the late 1960's. What determined the saturation of the breeding colonies? How was reproduction affected by saturation of the colonies?

First, the size of individual colonies at saturation, which is expressed as the maximum number of breeding females in the history of the colony, is related to the size of tidal area near the colony (Chapter 10 and Figure 10.5A). The maximum number of breeding females in a colony increases with the size of the tidal area near the breeding colony indicating that the tidal areas near the breeding colonies are important feeding areas for breeding females.

Second, there is convincing evidence that reproduction (clutch size, fledglings and fecundity) is density dependent as has been documented elsewhere (Hario & Rintala 2006). A long-term decline in the average clutch size was observed for the breeding colony on Vlieland (Chapter 10). The maximum number of fledglings (5 – 7 weeks old) is dependent on the size of the tidal area near the colony (Chapter 10 and Figure 10.5B). Therefore, the tidal areas near the breeding colonies are also important feeding areas for fledglings, as was suggested by Swennen (1991a). Long-term data on fecundity in the colony of Vlieland showed that the average number of fledglings produced per breeding female decreased with the density of breeding females (Figure 10.6). The limited data from other colonies in the Dutch Wadden Sea match the fifty-year data set for Vlieland relating fecundity to density of breeding females (Figure 10.6).

The dependence on intertidal food stocks near the colony for breeding
A 30% decline in breeding numbers around 1990 coincided with major reductions in the intertidal stocks of shellfish, i.e. mussels and cockles, around the breeding islands
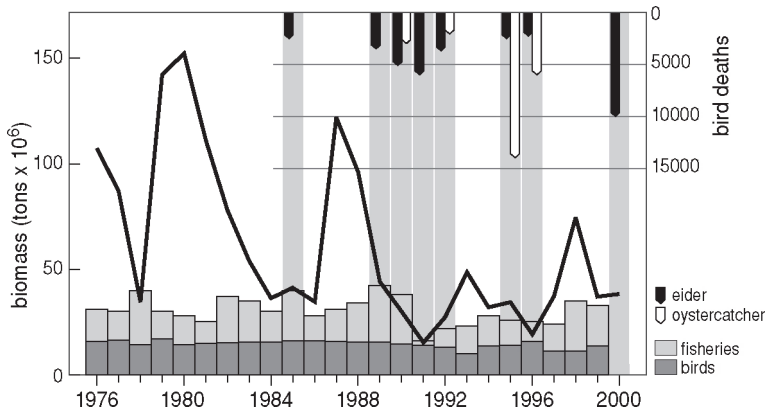
Figure 11.6 The carrying capacity of the western part of the Dutch Wadden Sea (1985-2003) with the maximum predicted annual total stocks of shellfish (i.e. mussels and cockles), total annual consumption (Common Eiders + Oystercatchers) and extraction (mechanical shellfishery on mussels and cockles). Shown also are the mortality statestror for eiders and oystercatchers, scale at the right. After Brinkman and Kats (2005).

due to the commercial shellfish fishery. However, recovery of the number of breeding females was rapid after 1992 and decline in breeding numbers was explained by an increase of non-breeding. This was shown by a modelling exercise for the breeding population on Vlieland using long-term predicted estimates on juvenile, immature and adult survival of females, and the number of breeding females (Figure 11.6). The intertidal stocks of shellfish were not sufficient to meet the requirements needed for successful breeding and as a consequence females were forced to skip breeding during this period in order to survive for future reproduction.

Recently, a fresh decline in breeding numbers has been observed since about 1999, with a 40% loss up to 2003 (Figure 10.2, 10.3 and 11.4). Information from surveys of the food stocks throughout the Wadden Sea is inadequate to pinpoint this as data on quality (flesh/shell ratio) and alternative prey (such as *Ensis*) are lacking from early spring before the eider breeding season. However, for the colony of Rottum in the eastern Wadden Sea a statistically significant relationship of densities of breeding females with local stocks of intertidal mussels was established in a five-year data set following the first sizeable and successful settlement of intertidal mussels in 2000 (Figure 10.8). For this colony recent counts (2000–2004) conform to this trend since mussel recovery. The data for Vlieland are qualitatively in agreement. On Vlieland, non-breeding was negatively related to the total density of profitable food after the commercial shellfishery took place, i.e. mussels and cockles, near the colony. That the local food supply near this colony has declined drastically in recent years is evidenced indirectly by the disappearance of Common Eiders from the zone of tidal flats, with a withdrawal to the deeper waters according to aerial census (Arts & Berrevoets 2006).

Concluding remarks for breeding population

To summarise, several lines of evidence show that tidal areas and the feeding conditions near the breeding colonies of Common Eiders are of huge importance for the breeding population in the Netherlands: (1) maximum colony size and breeding output increased with the tidal area (Figure 10.5), (2) non-breeding was negatively related to the total density of profitable food in the tidal area (Figure 9.8) and (3) breeding density is related to the local stock of mussels in intertidal mussel beds since 2000 (Figure 10.8).

The intertidal flats of the Dutch Wadden Sea are a State Nature Monument and protected under the Ramsar convention and the European Union's Habitat and Birds Directives. As a consequence, Marine Protected Areas (MPA) have been introduced in the Dutch Wadden Sea to safeguard the protection of intertidal habitats and its inhabitants (i.e. birds depending on intertidal food stocks throughout their annual cycle). However, evidence suggests that MPA's fail to provide adequate protection, which is related to size of the MPA and policy making trying to make the best of worlds (win-win) for both conservation and economical exploitation.

First, the success of MPA's for breeding Common Eiders is dependent on the size of the MPA. Since 2000, breeding numbers increased only in the colony with a MPA covering the complete intertidal flats (Rottum), while a decline in breeding was observed in a breeding colony (Vlieland) where only a part of the tidal flats were considered as MPA.

Second, some areas in the Wadden Sea were only afforded MPA status for a restricted number of years, so that fishery on shellfish (i.e. mechanical dredging of cockles and mussels) did take place, when the areas did not have the MPA status (Ens *et al.* 2004). Long-term effects of cockle dredging have been shown for two other populations of shellfish eating birds, i.e. the Knot and the Oystercatcher, in both cases contributing to the observed declines (Rappoldt *et al.* 2004a, Verhulst *et al.* 2004, Van Roomen *et al.* 2005, Van Gils *et al.* 2006a). In short, cockle dredging makes the sediment coarser causing reductions in settlement of cockles (Piersma *et al.* 2001), worsened feeding conditions of newly settled cockles (Drent *et al.* 2004), reduced prey quality for Knots (Van Gils *et al.* 2006b) and finally reducing survival with a 25 % decline in Knot population size (Van Gils *et al.* 2006a). For Oystercatchers, it could be proven that mechanical cockle dredging reduced the stocks of cockles, causing severe reductions in condition and survival of the birds, and contributing to a 40 % decline in population size despite the creation of large MPAs (Verhulst *et al.* 2004). It took 15 years after the introduction of MPA of the whole tidal area near Rottum for intertidal mussel beds to become fully re-established. This illustrates the long-lasting impact of dredging of intertidal shellfish and subsequent slow recovery of the intertidal ecosystem (Versteegh *et al.* 2004). The local breeding population of Common Eiders responded immediately after the settlement of intertidal mussel beds with an increase in breeding numbers (Chapter 10).

Future perspectives for Common Eiders in the Dutch Wadden Sea

In order to make predictions on the future of both breeding and wintering Common Eiders in the Dutch coastal waters, one needs to have enough detailed knowledge on the total functioning of the ecosystem as a whole in a long-term perspective. Reliable predictions depend on the availability of annual and long-term monitoring data on stock estimates and distribution of the primary (sub-tidal mussels) and secondary food species (intertidal mussels, *Spisula*, *Ensis*, cockles) in the diet of Common Eiders, food selection criteria of Eiders, and annual monitoring data on population size, distribution and mortality of the wintering and breeding population.

The future for Common Eiders in the Dutch Wadden Sea area is uncertain, because several large scale processes in the flyway pose a threat and are discussed below. The processes interacting with Common Eiders in de Wadden Sea relate to processes in the Baltic Sea and the variations in the stocks of intertidal and subtidal shellfish in the Wadden Sea.

Processes in Baltic Sea

The observed declines in the size of the Dutch (Chapter 7, Figure 11.4), German and Danish (Table 2.1, Figure 11.1) wintering populations in the Wadden Sea are in agreement with the 36 % decline in the total size of the Baltic/Wadden Sea flyway population since the beginning of the 1990's (Chapter 2). Further, a mismatch exists between the size of the total wintering population and the total breeding population, which indicates that the decline is related to a possible change in breeding conditions. Globally, all eider populations of the genera Somateria and Polysticta are in decline and currently considered to be of conservation concern throughout their entire circumpolar range (CAFF 1997, Ogilvie 2005). Therefore, it is obviously of crucial concern to continue and intensify the frequency of the coordinated aerial surveys to monitor the fate of the total flyway population. Several factors, mainly human-induced, are involved in the observed decline in the size of the Baltic breeding population and relate to hunting, predation, disease and feeding conditions in the Baltic Sea area.

First, a long tradition of hunting on sea ducks, including Common Eiders, exists in the Baltic region. The hunting pressure was high during the 1970's, regularly exceeding 140000 birds shot, but declined during the last decades (Chapter 2). During recent years, on average 90000 Common Eiders are shot annually in the Baltic, which is still three to four times higher than the numbers of Eiders known dying in the mass mortalities and it is still unknown whether the current level of hunting is sustainable.

Second, predation by the American Mink *Mustela vison* has caused significant reductions in breeding densities of waterfowl (Nordström *et al.* 2002). The mink has spread to most parts of the Common Eiders breeding range and is considered

to be a potential threat for the breeding population. However, the recovery of the White-tailed Eagle *Haliaeetus albicilla* population (and subsequent increase of predation) can also be an important factor (Kilpi & Öst 2002).

Third, viruses (such as Avian Cholera) reduce adult and duckling survival and recruitment (Christensen *et al.* 1997, Hollmén 2002), while parasites (acanthocephalan) are associated with other factors (see Chapter 6).

Fourth, mortality resulting from by-catch in gill nets has increased and numbers can be substantial as shown in Greenland waters (Merkel 2004).

Fifth, the stocks of macrozoobenthos in the Baltic Sea area changed during the last 30 years due to changes in eutrophication (Perus & Bonsdorff 2004). These stocks increased during the 1970's (Cederwall & Elmgren 1980), peaked by the end of the 1980's after which a general decrease has taken place (Perus & Bonsdorff 2004). As a consequence feeding conditions for Common Eiders probably deteriorated resulting in a decline in breeding numbers, because females were unable to store sufficient energy reserves for breeding. However, actual measurements on sea duck feeding conditions at this stage still need to be done (Rönkä *et al.* 2005)

Factors causing variations in the stocks of intertidal and sub-tidal shellfish in the Wadden Sea

Several lines of evidence show the importance of the stocks of shellfish in tidal areas for the Dutch breeding population and the sub-tidal areas for the wintering population of Common Eiders in the Netherlands. Therefore, any decline in the stocks of shellfish, whatever the cause, has the potential to negatively affect the feeding conditions for the breeding and wintering population. The variations in the stocks of shellfish relate to climatic (winter temperature and storms or climate change) and anthropogenic factors (eutrophication, invasion of exotic species and extraction by mechanical shellfishing industry), and/or resulting in a combination of both climatic and anthropogenic factors. Each factor is discussed with respect to the effect on the stocks of shellfish and whether the factor has contributed to reductions in the stocks of shellfish. Finally, the combined effects of all factors is discussed.

Climatic factors: winter temperature and storms
WINTER TEMPERATURE

Low temperatures in cold and severe winters affect macrofaunal communities dramatically causing declines in the number of species, abundance and biomass (Beukema 1989, Armonies *et al.* 2001, Reiss *et al.* 2006). Low winter temperatures in cold to severe winters contribute to mortality among shellfish (Beukema *et al.* 1993, Armonies *et al.* 2001, Strasser *et al.* 2001a). The extent of this mortality is dependent on the cold sensitivity of the various species of tidal and subtidal shellfish, and the presence of ice during these winters.

First, a third of the macrobenthic species on the tidal flats of the Wadden Sea is sensitive to low winter temperatures (Beukema 1989, 1990) and mass mortality in cold periods has been reported for cockles, Soft-shell Clam *Mya arenaria* and Cut Trough Shells *Spisula subtruncata* (Beukema *et al.* 1993, Leopold *et al.* 1998, Armonies *et al.* 2001, Strasser *et al.* 2001a). Cockles are most sensitive to low temperatures and complete or almost complete local extinctions have been reported for several winters during the 20th century (see Strasser *et al.* 2001a for references). In the Dutch Wadden Sea, low temperatures in the cold winters of 1995/96 and 1996/97 severely reduced the short-term and long-term intertidal stocks of cockles based on the abundance and the landing of cockles, although stocks of sub-tidal cockles were not affected (Chapter 5 and 7, and Figure 7.5). The stocks of subtidal *Spisula subtruncata* in the Dutch and German coastal North Sea were completely destroyed during the cold winter of 1995/96 (Leopold *et al.* 1998, Armonies *et al.* 2001).

Second, severe winters with ice result in an increase in mortality among tidal shellfish, because shellfish may be crushed due to scraping by drifting ice floes and additionally, complete ice coverage may suffocate shellfish (Beukema 1989, Dankers & Koelemaij 1989, Strasser *et al.* 2001a). Tidal mussel beds are known to suffer from severe winters with ice floes and ice scouring, and the large variation in mortality depends on the geographic distribution and winter severity (see Strasser *et al.* 2001a). In the Dutch Wadden Sea, the mussel is considered as a hard-winter species (Beukema 1990) due its high freezing resistance compared to cockles (Bourget 1983). Nonetheless, during the severe winter of 1995/96, nearly half of the area with tidal mussel beds in the Dutch Wadden Sea disappeared due to ice (Dankers *et al.* 2004)

Although the low temperatures do result in short-term or within-winter reduction in the stocks of shellfish, in the long-term, stocks of shellfish increase due to a generally better recruitment after cold winters (Beukema 1992b, Beukema *et al.* 1998 and 2001a, Strasser *et al.* 2001a, 2003 and references therein in Beukema and Dekker 2005). The increase in recruitment after cold winters is explained by the improved settlement of shellfish after these cold winters, because abundance of various predators (Starfish *Asterias vulgaris*, Shore Crabs *Carcinas maenas*, Shrimps *Crangon crangon*) of 0-group of various species of shellfish, including mussels and cockles have been strongly reduced (Beukema *et al.* 1993, Beukema & Dekker 2005, Beukema 1991, 1992a, Strasser & Gunther 2001). The opposite is observed during mild and warm winters with high temperatures in winter and spring. The high winter and spring temperatures have been implicated in the failure of successful recruitment of several species of shellfish, such as cockles, *Macoma balthica* and *Mya arenaria*, due to increased predation by Shrimps *Crangon crangon* (see Beukema & Dekker 2005 and references therein). Other epibenthic predators, such as Shore Crabs *Carcinas maenas* and Starfish *Asterias rubens*, are also known to arrive earlier and are more abundant on the tidal flats after mild winters compared

to cold winters (Reise 1985, Beukema 1991, 1992b) and these increments in the consumers will increase predation on larvae and first year shellfish. Therefore, a long-term decline in the stocks of shellfish is predicted when climate warming is an ongoing process.

STORMS

The vulnerability of tidal mussel beds in relation to storms may relate to variation in shelter, age and temporal patterns in tenacity.

First, Nehls and Thiel (1993) showed that mussel beds that remained after severe storms were primarily found in sheltered areas near islands. Consequently, these mussel beds persisted over long periods, but the 'highly dynamic' mussel beds in exposed areas disappeared. However, the direction of the storms determines which areas should be interpreted as sheltered.

Second, Dankers *et al.* (2004) suggest the age of tidal mussel beds as a prominent factor explaining the vulnerability to storms, because young mussel beds are qualified as dynamic, especially in exposed areas, due to the weak attachment to the sediment, which contributes to the vulnerability of mussel beds to storms. However, it has not been shown yet whether storms really have caused mass-mortality among (a part of) the mussels in a tidal mussel bed or whether the disappearance of all or part of a tidal mussel bed on a given location is simply the result of a redistribution of mussels into sub-tidal areas in the vicinity. Unfortunately, a detailed monitoring program of sub-tidal mussel beds at the appropriate scale is currently still in development and not available yet.

Third, temporal variation in tenacity (or byssal attachment strength) of mussels on rocky shores is large with tenacity being two times higher in winter compared to summer (Carrington 2002a). The seasonal differences are explained by physiological constraints between bysall thread production and gonad development (Carrington 2002b). Therefore, not only the magnitude of storms should be considered, but also the timing of storms in relation to seasonal or temporal patterns in tenacity is important to interpret the effects of storms. The survival of mussels is dependent on the attachment of mussels to the sediment, and changes in the optimal sediment structure for attachment and settlement of tidal mussel beds may increase the vulnerability of tidal musselbeds to storms.

In the international Wadden Sea, average annual reductions of tidal mussel beds (up to app. 30 %) are generally observed between autumn and winter, which is a part of the natural system, and these losses during winter are compensated in spring and summer after successful recruitment of mussels (Dankers *et al.* 2004). Storms contribute an additional 20 % to the average loss of mussel beds in autumn and winter, and total winter loss with severe storms was estimated at a maximum of app. 50 % (Nehls & Thiel 1993, Dankers *et al.* 2004).

To summarize, the observed increase in winter temperature and the frequency of severe storms are strongly related to climate warming, which started at the beginning of the 20th century, also known as the 'hockey stick' (Van Dorland & Jansen 2006). The winter and spring temperature contributes to considerable variability in annual recruitment and as a consequence the year-to-year variability in the stocks of shellfish (Beukema *et al.* 1998, 2001a, Strasser *et al.* 2001a+b, 2003, Van der Meer *et al.* 2001, Philippart *et al.* 2003, Beukema and Dekker 2005). Winter temperatures and the frequency of severe storms are predicted to increase due to the ongoing process of climate warming and are predicted to cause long-term declines in the stocks of shellfish due to less frequent renewal of the stocks of shellfish, which is observed after cold and severe winters, in combination with increased predation of larvae and 0-group of shellfish, which is observed after mild and warm winters. Therefore, the predicted long-term decline in the stocks of shellfish will also have long-term consequences for their consumers, i.e. shellfish eating birds and the shell fishing industry. Food shortage for both shellfish eating birds and the shell fishing industry is unavoidable when their total consumption is kept constant. To make matters even worse for the Common Eider, another consequence of climate warming is a decline in quality or body condition of shellfish (Honkoop & Beukema 1997). The quality of shellfish expressed as the flesh/shell ratio (Ens & Kats 2004) determines the profitable fraction of shellfish for shellfish eating birds swallowing whole shellfish, like the Common Eider (Nehls 1995, 2001, Scheiffarth & Frank 2006).

Anthropogenic factors: eutrophication, invading exotics and shellfishery
EUTROPHICATION
The decrease in eutrophication of the Wadden Sea has been caused by a decline of nutrient input (N and P) from rivers (Essink *et al.* 2005) resulting from policies, introduced since the 1970's, aiming to reduce the pollution of open waters. The observed decline in nutrients resulted in changes in composition and density of algae, shellfish and worms, and birds (Philippart *et al.* 2007). An ecosystem model by Brinkman and Smaal (2004) showed that the decline in nutrients since the 1980's reduced the productivity resulting in a 50 % reduction of the predicted maximum capacity of stocks of shellfish in the western Wadden Sea.

INVADING EXOTICS
The Pacific Oyster *Crassostrea gigas* has recently invaded the Wadden Sea from the south-western parts of the Netherlands, where Oyster reefs make swimming a dangerous day-out. Intertidal mussel beds are threatened due to the settlement of the exotic reef-building Pacific Oyster, which rapidly colonizes the Dutch coastal waters (Kater & Baars 2003, Dankers *et al.* 2004) and the German part of the international Wadden Sea (Nehls *et al.* 2006). The Pacific Oyster is predicted to increase and colonize large parts of the Wadden Sea, which has already been

observed in the Oosterschelde (Kater & Baars 2003). According to Essink *et al.* (2005), it is clear that the Oysters are replacing mussels at an increasing rate over the long run, but Nehls *et al.* (2006) point out that evidence of direct competition between mussels and the Pacific Oysters is hard to obtain. However, Kater and Baars (2003) showed a strong overlap in habitat between mussels and Pacific Oysters in the Oosterschelde, where mussels were ecologically replaced by these oysters, but not between cockles and oysters. At present, the overlap in habitat between cockles and oysters is small with Pacific Oysters being 'most common in habitats that are unsuitable for cockles' suggesting the absence of competition in unsuitable cockle habitats (Kater *et al.* 2006). The future is uncertain for cockles when Oysters expand their distribution towards more suitable cockle habitats possibly resulting in an increase in competition between cockles and oysters. So far the invasive Pacific Oyster is not subject to predation by the local fauna (including the Common Eider), and this absence of consumers helps to explain its rapid increase.

SHELLFISHERY

In the Wadden Sea, cockles and mussels in both the tidal and subtidal areas are extracted mechanically and by hand raking, although the latter will not be discussed here. The mechanical extraction of shellfish has raised a great deal of concern, especially among conservationists of the Wadden Sea since the end of the 1980's. The concern relates to the international status of the Wadden Sea and the fixed economical targets of mechanical shellfishery, i.e. mussel fishery, in an ecosystem with declining stocks of shellfish.

First, the Wadden Sea is an area of huge ecological importance for a wide variety of animals and is proposed as a candidate for the UNESCO list of world treasures. Therefore, it is more important to know whether and to what extend the commercial extraction of shellfish has affected or is going to affect the profitable and harvestable stocks of shellfish available to breeding and wintering Common Eiders throughout their annual cycle.

Second, the shellfish fishery will be affected by (1) a reduction in productivity (Brinkman and Smaal 2004) resulting from reductions in nutrient loads or eutrophication (Essink *et al.* 2005), and (2) a reduction in successful recruitment of shellfish due to climate warming (Beukema & Dekker 2005). A great deal of concern has been raised, because the stocks of shellfish are predicted to decline in future, but the annual target is kept constant by the mussel fishery. The current annual target is based on the high mussel production in the past (1960's to 1980's) and is not adjusted to the current lower level of productivity. As a consequence, the risks of over-fishing in the years to come increase when the annual targets set by the mussel fishery remain unchanged.

In general, a sizable fraction of the shellfish stock is extracted by mechanical shellfishery, but this fraction shows large annual variations ranging from 3 % up to

38 % for intertidal cockles, more than 95 % of intertidal mussels and up to 85 % for subtidal mussels (Smit *et al.* 1998, Dankers *et al.* 2004, Ens *et al.* 2004, Ens *et al.* 2006). The extraction of shellfish by mechanical shellfish fishery is discussed separately for the intertidal and sub-tidal.

INTERTIDAL SHELLFISHERY

Around 1990, intertidal mussels and cockles were almost completely removed from the Dutch Wadden Sea by intensive shellfish fishery (Beukema 1993, Beukema & Cadee 1996, Ens *in prep.*). Since then, the recovery of intertidal cockle and mussel beds was slow due to a combination of high levels of predation on juvenile shellfish and/or difficulties in the settlement of larvae on the sediment. The delay in recovery of the intertidal stocks of shellfish may indicate that the mechanical fishery of shellfish has long-term effects on the ecosystem. Several studies investigated whether the sediment properties were changed by the mechanical dredging of cockles from the tidal flats causing the delay in recovery of both cockle and mussel beds (Piersma *et al.* 2001, Zwarts *et al.* 2004). The stocks of intertidal cockles showed the first signs of recovery since the middle of the 1990's, while intertidal mussel beds started to recover since the beginning of the new millennium. It has been suggested that the recovery of intertidal mussel beds was promoted by cockles, because a part of mussel seed settled on cockles in the eastern part of the Wadden Sea since 2000 (Dankers pers. com., Brinkman *et al.* 2004). The re-settlement and subsequent recovery of intertidal mussel beds since 2000 was restricted to the eastern part of the Wadden Sea (> 95 %) and was estimated at 2693 ha in spring of 2006 (Goudswaard *et al.* 2006). It is intriguing to speculate why re-settlement of intertidal mussel beds was absent in the western part of the Wadden Sea, except for the sheltered Balgzand, which was completely closed to fishery since the beginning of the 1990's. The crucial question is: Why have intertidal mussel beds not recovered yet in the western part of the Wadden Sea? The delay in recovery of intertidal mussel beds is hypothesized to result from the long-term high fishing intensity which changed the sediment properties affecting settlement of shellfish, in combination with reductions in settlement success due to (increased) predation by marine organisms, such as Shrimps *Crangon crangon*, and/or the higher level of wind-exposure compared to the eastern Wadden Sea.

SUB-TIDAL SHELLFISHERY

Since 1992, the average proportion sub-tidal mussels on mussel cultures compared to 'wild' sub-tidal mussels increased from 40 to 70 % (Chapter 7 and Figure 11.7) and additional evidence indicated that sub-tidal mussels are subjected to over-exploitation (Ens *et al.* 2006). Mussel fishery was unrestricted until the introduction of a policy for the shellfishery in 1993 and an all-time low in the stocks of intertidal and sub-tidal mussels was observed around 1990 (Chapter 7) due to over-exploitation (Ens *in press*). Since 1993, fishing on tidal mussels was more or
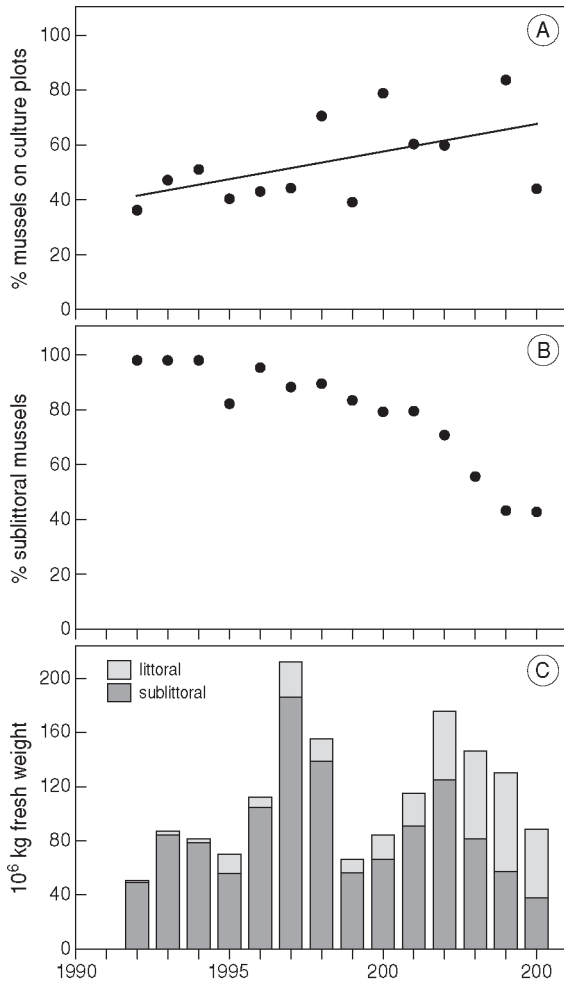
Figure 11.7 Stocks of mussels in the Dutch Wadden Sea since the early 1990's. (A) The fraction of sublittoral Mussels that occurs on culture plots, (B) the stock of sub-tidal mussels expressed as a fraction of the total stock of mussels, and (C) the total mussel stock, separated into littoral and sublittoral mussel stocks expressed as million kg fresh weight in winter. All data based on Bult *et al*. (2004b), Craeymeersch *et al*. (2005), Kamermans *et al*. (2005) and Van Stralen *et al*. (2006) (After Ens *et al.* 2006).

less prohibited (LNV 1993) and as a consequence tidal stocks of mussels recovered and increased (Chapter 7 and 10, Figure 11.7), which was not the case for subtidal mussels (Figure 11.7). The majority of the mussels are nowadays found on tidal flats (Figure 11.7) in contrast to the past when the majority of the mussels in the Wadden Sea were sub-tidal. Long-term effects of overexploitation of sub-tidal mussels and subsequent slow recovery of mussel stocks are not affected by a short-

age of reproducing mussels, because the production of larvae is gigantic. The most likely explanation for a lack of recovery is a shortage of substrate suitable for the settlement of these larvae. Dare *et al.* (2004) similarly reasoned that a shortage of suitable substrate explained why mussel beds have not recovered yet in the Wash on the east coast of England after over-exploitation in the early 1990's. Sub-tidal mussels are of crucial importance for wintering Common Eiders with respect to their population size, distribution and mortality (Chapter 7 and 8). Analysis of the rate of change of the Dutch wintering population shows that the size of the wintering population decreases with the available stock of sub-tidal mussels per wintering eider (Figure 11.8) indicating that a carrying capacity model is needed.
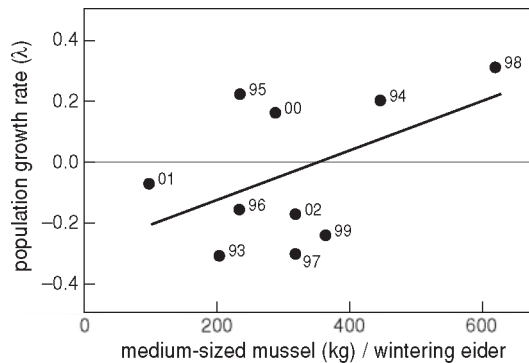
Figure 11.8 Population growth rate (PGR or $\lambda = (Nt+1/Nt)-1$, where Nt refers to population size at time *t* with carrying capacity at $\lambda = 0$ (horizontal line), modified after Sibly *et al.* (2003)) of Common Eiders wintering in the Netherlands (1993-2003) and stocks of sub-tidal medium-sized mussels on mussel cultures for each wintering eider: $\lambda = 7.9 \cdot 10^{-4}$ (Food per wintering eider) $- 0.28$, d.f. $= 9$, $r^2 = 0.23$, $p = 0.16$. See figure 7.7 for details.

THE COMBINED EFFECTS OF CLIMATIC AND ANTHROPOGENIC FACTORS

The mechanized fishery on shellfish put the Wadden Sea system under increasing pressure, because the fixed annual (economic) targets set by the fishery were not adjusted to the declining stocks of shellfish. As a consequence, the risk of over-exploitation of shellfish increased and caused the strong decline in intertidal mussel stocks in the late 1980's (Ens, *in press*). Brinkman and Kats (2005) combined the outcomes of the carrying capacity model of the western Wadden Sea by Brinkman and Smaal (2004), which predicted the maximum stocks of shellfish (i.e. mussels and cockles) with total estimates on consumption of shellfish-eating birds (Common Eiders, Oystercatchers) and extraction by the mechanical fishery

on mussels and cockles (Figure 11.9). Consumption by birds and extraction by fishery were relatively constant, but the extraction by fishery was not adjusted to the declining predicted stock and as a consequence resulting in mortality among Common Eiders and also Oystercatchers. Mortality was elevated in years when the difference was small between the total predicted stock and the consumed and extracted stock (Figure 11.9).
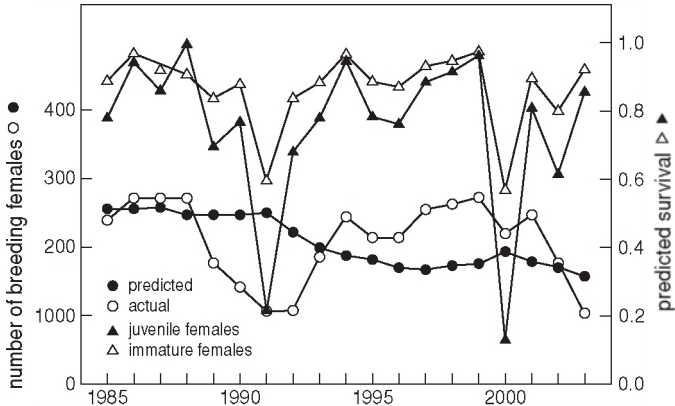

Figure 11.9 Population trajectory of the breeding colony on Vlieland (1985-2003) with the actual (white circles) and predicted (black circles) number of breeding females, and the predicted survival of juvenile (1st year) females (black triangles) and immatures (2nd and 3rd year) females (white triangles). See Chapter 9 and Figure 9.6 and 9.7 for details on calculations)

The Dutch *breeding* population of Common Eiders is dependent on the stocks of intertidal shellfish (especially mussel beds) to breed and raise offspring successfully (Swennen 1991a, Chapter 10). The ongoing invasion of the Pacific Oyster taking over the intertidal mussel beds in the Wadden Sea results in a decline of intertidal mussels. This in turn, will result in a decline in the size of the breeding population of Common Eiders in the Netherlands, unless the stocks of other species of shellfish (such as *Ensis* and *Mya*) are sufficient (quantity) and/or profitable (quality) enough to allow successful breeding. At the logical end point of this reasoning, one should seriously consider the possibility that Common Eiders might entirely disappear from the Wadden Sea as a breeding bird.

Similar concerns can be raised for the *wintering* population of Common Eiders that also depend on shellfish in the Dutch Wadden Sea. On the one hand, stocks of shellfish are predicted to decline due to an interacting process during the coming decades resulting from a warming climate (Van Doorland & Jansen 2006), declining productivity (i.e. declining nutrient input, Philippart *et al.* 2007) and/or an
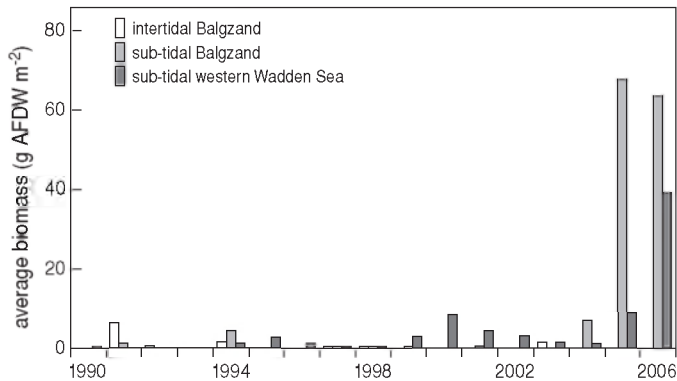
Figure 11.10 Long-term data (1990-2006) on the average stock (g AFDW m^{-2}) of American Razor Clam *Ensis directus* (< 10cm) in the intertidal Balgzand (> -90 cm NAP: n = 13), sub-tidal Balgzand (< -90 cm NAP: n = 2) and sub-tidal areas (n = 3) in the western part of the Dutch Wadden Sea (i.e. Aflsuitdijk-Scheurrak-Harlingen). Data was collected at the end of summer and see Dekker (2007) for more details

increase of highly competing invading Pacific Oysters (Nehls *et al.* 2006), while on the other hand, the annual target of the shellfishing industry, i.e. musselfishery, is set at a fixed level, based on highly productive periods before 1990. A constant fishing pressure in a system where the long-term stocks of shellfish are predicted to decline, can only be interpreted as a worse case scenario for Common Eiders in the Netherlands. The relative increase in fishing pressure may lead to food shortage resulting in additional mortality among wintering Common Eiders. However, *Ensis* has recently invaded the sub-tidal parts of the Wadden Sea and may serve as an alternative food source in the future (Figure 11.10). Preliminary results show that Eiders are able to feed on *Ensis* (< 10 cm)(Chapter 4).

Ideas for future research
Globally, all eider populations of the genera Somateria, including the Common Eider *Somateria mollissima*, and Polysticta are in decline and currently considered to be of conservation concern throughout their entire circumpolar range (CAFF 1997, Ogilvie 2005). Therefore, it is obviously of crucial concern to continue the coordinated aerial survey of wintering, but also moulting, and ground-based surveys of breeding Common Eiders to monitor the fate of the flyway population. Annually 115000 Common Eiders are shot in the Baltic, which far exceeds the numbers in mass-mortalities that we have experienced in the Wadden Sea. At this stage, it is unknown whether the current level of hunting is sustainable. Therefore, the current hunting practises in the Baltic should be analysed using a modelling approach with hunting statistics and survival analysis using many thousands of ringed Common Eiders within the flyway.

The Dutch Wadden Sea area is being used by Common Eiders for breeding and wintering, but also for moulting. Although moulting is not discussed in this thesis research, available evidence shows that especially the eastern part of the Dutch Wadden Sea is being used by large numbers of moulting eiders (>20000) in summer and early autumn (Swennen 1976a, 1991a, pers. com. Klaas Kruijer, Figure 11.2). Moulting Eiders are very sensitive to human disturbance, such as boating (Thiel *et al.* 1992), due to being flightless and moulting areas of Common Eiders should therefore be included in monitoring and conservation programs.

For the Dutch breeding population of Common Eiders depending on intertidal stocks of shellfish, there is an urgent need to refine and extend the current annual measurements of breeding. At present, only the number of breeding females is monitored using various methods in different colonies. One uniform method should be used in all breeding colonies and should include size estimates of the pool of non-breeding females (Chapter 2 and 9), because declines in the breeding population may not become visible for long in the breeding numbers due to the presence of non-breeding females. To understand long-term population dynamics, annual measurements should also include estimates on breeding success, fledgling production and survival of males and females, which can easily be obtained by a ringing program of fledglings and adults. Further, the intertidal food supply is important for successful breeding, but a long-term monitoring program of quantity and quality of the harvestable fraction for breeding Common Eiders timed in relation to the breeding cycle is not available. Monitoring the intertidal food supply should reflect the resources for breeding and therefore also a new sampling programme on potential tidal food sources in spring is necessary (Chapter 2, 9, 10).

The monitoring of the wintering population in the Netherlands should be adjusted to and be part of a large-scale international monitoring program of Eiders in the international Wadden Sea and Baltic Sea. To understand the patterns in distribution and mortality, a food sampling program should include mussels, cockles, *Spisula*, *Ensis* and possibly *Mya*, because the latter two may become important alternatives in the future for wintering eiders. The continuation of beached bird surveys is of great importance, because they provide long-term and reliable annual estimates of mortality for this species and many others. The spatial and temporal use and depletion of various resources in winter is important to understand in order to explain the distributional and mortality patterns in wintering Common Eiders. The predictive modelling undertaken by Rappoldt *et al.* (2004a&b&c +Rappolt & Ens 2006) relating mortality rates in the wintering population of the Oystercatcher to their food stocks is a promising line to follow. These workers were able to translate food stocks as obtained from large-scale sampling programmes in both the Dutch Wadden Sea, Oosterschelde estuary and Westerschelde estuary to potential intake rates of Oystercatchers under the prevailing tidal regimes (Rappoldt & Ens 2006). A shortfall in potential intake (in their model reflected in the daily time budget) matched years of increased mortality in the Wadden Sea,

and the model was able to predict the carrying capacity of the Westerschelde for Oystercatchers with great realism (Rappoldt & Ens 2006). A similarly sophisticated model for the Common Eider is worth striving for, and needs details on the spatial and temporal use of food resources by Common Eiders. Data on the resource use of individual Eiders can be achieved with the aid of the telemetric techniques now available.

Further, our study makes clear that both exploitative fishery of *Spisula* and mussel culture may affect the numbers, the distribution and the mortality of Common Eiders. Whether the new shellfish policy introduced in 2004 provides sufficient guarantees against negative impacts of these fisheries on Eiders is not proven and requires further study. First, it must be investigated if mussel seed fishery has an impact, either positively or negatively, on spatfall of Mussels in future years. Second, a Mussel population model must be developed and tested, that allows us to assess the impact on the Mussel stock of transport of Mussels between culture plots in the Wadden Sea and transports of Mussels from the Wadden Sea to the Oosterschelde. Third, all transports of Mussels should be registered, so that these data can serve as input for the Mussel population model.

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Summarizing the rise and fall of Common Eiders

Common Eiders in North-western Europe and the Netherlands

Many species of Eiders worldwide are currently threatened. During the past decade the Common Eider has joined the ranks of concern. The total wintering population in North-western Europe, i.e. the Baltic Sea and Wadden Sea area, decreased by 36 % from 1.18 million birds in 1991 to 0.76 million birds in 2000.

Common Eiders are large sea ducks, which feed by diving (in the intertidal and sub-tidal) or dabbling (intertidal) utilizing a large variety of prey species with a strong preference for specific size-classes. In the Wadden Sea area, important species of shellfish for wintering and breeding Common Eiders are Mussels *Mytilus edulis*, Cockles *Cerastoderma edule* and Cut-trough Shells *Spisula subtruncata*, and recently also American Razor Clam *Ensis americanus* is included in the diet. The Mussels, Cockles and Ensis are found in both the intertidal and sub-tidal areas of the Wadden Sea, while *Spisula* is restricted to the North Sea.

Wintering Common Eiders in the Netherlands dependent on sub-tidal Mussels

In the international Wadden Sea area, the long-term (1987-2002) size of the wintering population averaged 270000 birds with a decline in recent years. Wintering Eiders were most numerous (110000 birds) in the Netherlands, where numbers also declined from 165000 in 1993 to 87000 in 2003. Here, wintering Eiders were traditionally concentrated in the western Wadden Sea. A major exodus of Common Eiders from the Dutch Wadden Sea to the North Sea in combination with mass-mortality was observed during the winters of 1990/91 and 1991/92, but also in recent years (1999/2000 and 2001/02). The exodus in combination with mass-mortality was best explained by starvation, due to low stocks of suitable

shellfish. An alternative hypothesis, that mass mortality was caused by the outbreak of parasites, was examined in detail but rejected.

The distribution of wintering Common Eiders in the Dutch Wadden Sea was driven by the stocks of (wild and cultured) sub-tidal Mussels. Cockles were only found to be important in winters with massive spatfall in the preceding years (1996/97, 1997/98). Sub-tidal Mussels are restricted to the western part of the Dutch Wadden Sea where traditionally most Eiders were present in winter. Since the 1990's, a substantial part of the sub-tidal Mussels are found on Mussel cultures, accounting for the importance of these cultured stocks compared to the wild sub-tidal stocks for wintering Eiders. The patterns in stocking of Mussel cultures by Mussel fishermen indicated that in years of Mussel scarcity the majority of the Mussels on cultures is grown on cultures outside the Wadden Sea making these Mussels inaccessible for the wintering population causing food shortage and mass mortality.

On the North Sea, Common Eiders were distributed in relation to *Spisula*, but the abundant stocks of *Spisula* have recently been replaced by American Razor Clam *Ensis* which is now common in the Wadden Sea as well. Whether *Ensis* could serve as a long-term alternative to Mussels and *Spisula* for the Eider in the future remains to be seen.

Low stocks of medium-sized Mussels were the best predictor of high mortality among Common Eiders in winter. The excessively high mortality in the winters of 1999/2000 and 2001/2002 was caused by low stocks of subtidal Mussels in the western Wadden Sea coinciding with low stocks of *Spisula* on the North Sea.

Dutch breeding population of Common Eiders dependent on tidal Mussel beds

The first breeding attempt in the Netherlands was reported on Vlieland in 1906 and was the basis of the successful settlement of the Dutch breeding population. Breeding colonies were established on the remaining islands and increased in size during the first half of the 20th century. From 1950 onwards, colonies saturated and reached stability, but at different periods for the western (early 1960's) and eastern Wadden Sea (late 1980's). The size of the breeding population was estimated at 6000 breeding females in 1960.

In general, successful breeding in Common Eiders is dependent on the food stocks near the breeding colony needed for building up energy reserves prior to breeding and post-incubation recovery of females. In addition, favourable nesting conditions (vegetation cover, freedom from human disturbance, and short distance to the shore) are crucial. Survival of offspring is dependent on the stocks of sufficient and profitable prey abundantly found in intertidal Mussel beds near the breeding colony.

The pollution of coastal waters with chlorinated hydrocarbons in the 1960's caused a 75% reduction to 1350 breeding females in 1969. After the closure of the pollution source, the colonies recovered and increased in size during 1970's and stabilised in the 1980's. In the Netherlands, the maximum size (number of breeding females) and reproductive output (clutch size, fledglings and fecundity) of breeding colonies is related to the tidal area near the breeding colony, thus confirming that the tidal areas near the breeding colonies are important feeding areas for both breeding females and their fledglings.

A dramatic 30% decline in breeding numbers was observed around 1990, coinciding with major reductions in the intertidal stocks of shellfish, i.e. Mussels and Cockles, around the breeding islands due to the commercial shellfish fishery. However, recovery of the number of breeding females was rapid after 1992 and the dip in breeding numbers was explained by the incidence of non-breeding. This conclusion is based on a modelling exercise for the breeding population on Vlieland using estimates on juvenile, immature and adult survival of females (derived from a long-term ringing program, i.e. 25 years) to reconstruct the potential breeding population, in relation to the number of breeding females actually observed. The intertidal stocks of shellfish around 1990 were apparently not sufficient to meet the requirements needed for successful breeding and as a consequence females were forced to skip breeding in order to survive for future reproduction.

Since 1999, a fresh decline in breeding numbers (with a 40% loss up to 2003) has been observed in the western part of the Wadden Sea, but information from surveys of the food stocks throughout the Wadden Sea is inadequate to pinpoint the underlying cause for this as data on quality (flesh/shell ratio) and alternative prey (such as *Ensis*) are lacking from early spring before the Eider breeding season. However, for the colony of Rottum in the eastern Wadden Sea a statistically significant relationship of densities of breeding females with local stocks of intertidal Mussels was established in a five-year data set following the first sizeable and successful settlement of intertidal Mussels in 2000, which was immediately followed by an increase in Eider breeding numbers. The data for Vlieland are qualitatively in agreement, where non-breeding was negatively related to the total density of profitable food, i.e. Mussels and Cockles, after the commercial shellfishery took place near the colony.

Populatie veranderingen bij Eidereenden: Wel en wee van *Somateria mollissima* in Nederland

Eidereenden in noordwest Europa

Bijna alle soorten eidereenden worden wereldwijd bedreigd en dit is ook het geval voor de Eidereenden in noordwest Europa. De grootte van de totale winter populatie Eidereenden in de Oostzee en Waddenzee is met 36 % afgenomen van 1.18 miljoen vogels in 1991 tot 0.76 miljoen vogels in 2000.

Eidereenden zijn grote zeeeenden en zoeken al duikend (diep water) of grondelend (droogvallend) naar voedsel. Het dieet van de eidereend bestaat uit een grote variatie aan prooidieren, waarbij op grootte en kwaliteit wordt geselecteerd. In Nederland zijn Mossels, Kokkels, Halfgeknotte Strandschelpen, en recentelijk ook Mesheften van belang voor de broedende en overwinterende Eidereenden. De Mossels, Kokkels en Mesheften worden gevonden in zowel de droogvallende en diepe delen van de Waddenzee gevonden, terwijl de Halfgeknotte Strandschelpen alleen in de Noordzee worden aangetroffen.

Overwinterende Eidereenden in Nederland afhankelijk van onderwater mosselen

In het internationale Wadden zee gebied overwinterden tussen 1987 en 2002 gemiddeld 270000 eidereenden met een afname gedurende de laatste jaren. De grootste aantallen (gemiddeld 110000 vogels) werden waargenomen in Nederland, waarbij de aantallen ook afnamen van 165000 in 1993 tot 87000 in 2003. In Nederland zijn de eidereenden traditioneel geconcentreerd in het westelijke deel van de Wadden Zee. Gedurende de winters van 1990/91 en 1991/92, maar ook recentelijk nog in 1999/2000 en 2001/02, is een grote exodus van het traditionele overwinteringsgebied, nl. westelijke Waddenzee, naar de Noordzee opgetreden.

Deze exodus in combinatie met massa sterfte wordt verklaard door verhongering vanwege een laag aanbod van geschikte schelpdieren en niet door een uitbraak van parasieten.

De verdeling van overwinterende Eidereenden in het Wadden Zee gebied wordt gestuurd door diepwater mosselen, zowel wild als gekweekt. Kokkels, en dan vooral de kleine, zijn alleen van belang voor overwinterende Eidereenden in jaren volgend op een grootschalige zaadval (bijv. 1996/97, 1997/98). Diepwater mosselen komen hoofdzakelijk voor in het westelijke deel van de Wadden Zee, waar traditioneel gezien de meeste Eidereenden overwinteren. Een aanzienlijk deel van de diepwater mosselen sinds het begin van de jaren '90 wordt gevonden op mosselpercelen en geeft het grote belang aan van de gekweekte bestanden ten opzichte van de wilde mosselen voor overwinterende Eidereenden. De patronen in de bevoorrading van de mossel percelen in de Wadden Zee door mosselkwekers laten zien dat in jaren met een tekort aan mossels het overgrote deel van de mossels gekweekt worden op mossel percelen buiten de Wadden Zee. Dit heeft er toe geleid dat deze mossels onbereikbaar zijn geworden voor over winterende Eidereenden met massa sterfte als gevolg. Eidereenden op de Noordzee verspreiden zich in relatie tot de Halfgeknotte Strandschelp, maar deze eens zo talrijke alternatieve voedselbron is recentelijk verdwenen en vervangen door Mesheften. Het is de vraag of Mesheften kunnen dienen als een alternatief, zoals de Halfgeknotte Strandschelpen op de Noordzee, voor Mossels is niet bekend al hoewel er wel aanwijzingen voor zijn. Lage bestanden aan halfwas-mosselen zijn de beste voorspeller van verhoogde sterfte onder Eidereenden. De massa sterfte in de winters van 1999/2000 en 2001/02 is veroorzaakt door een tekort aan diepwater mosselen in de westelijke Wadden Zee, welke ook nog eens samenviel met de lage bestanden van de Halfgeknotte Strandschelp op de Noordzee.

Broedende Eidereenden in Nederland afhankelijk van droogvallende mossels

De eerste broedende eidereend in Nederland is gerapporteerd in 1906 op Vlieland en heeft de basis gevormd voor de zeer succesvolle vestiging als broedvogel. Tot halverwege de 20ste eeuw zijn kolonies gevestigd op de overige eilanden, en namen toe in grote met een Nederlandse broedvogel populatie van 6000 broedende vrouwen in 1960. Stabilisatie van kolonies was verschillend in de wadden zee, waarbij de westelijke kolonies stabiliseerden in de vroege jaren '60 en de oostelijke in de late jaren '80.

Vanwege de vervuiling van de kustwateren met gechloreerde koolwaterstoffen in de jaren '60 nam de broedpopulatie met 75 % af tot ongeveer 1350 broedende vrouwen in 1969. Nadat de lozing was gestopt, vond herstel plaats van de kolonies in de jaren '70 en stabiliseerden pas in jaren '80, bijna 20 jaar later. Vanaf het

einde van de jaren ´80 trad wederom een verandering op voor de overwinterende en broedende Eidereenden in Nederland. Tijdens de jaren '90 hebben grote fluctuaties plaats gevonden (5200–11000 broedende vrouwen), maar de aantallen waren vergelijkbaar in zowel de westelijke als de oostelijke Wadden Zee. Daarna is de Nederlandse broedvogel populatie met 40% afgenomen, waarbij de aantallen in de westelijke Wadden Zee zo sterk zijn afgenomen dat de huidige aantallen lager zijn de aantallen in het einde van de jaren '60.

Om succesvol te kunnen broeden zijn Eidereenden afhankelijk van het voedsel aanbod en broedomstandigheden in de directe omgeving van de kolonie, want vrouwen zijn extreem plaatstrouw aan de kolonie gedurende het gehele jaar. Voordat aan broeden kan worden begonnen is het nodig een dusdanige energievoorraad aan te leggen, die de kosten dekt van het leggen van de eieren en het onafgebroken uitbroeden van de eieren door het vrouwtje. Lukt het vrouwtje niet om deze energievoorraad aan te leggen dan wordt broeden overgeslagen. Tijdens het broeden (ongeveer 28 dagen) verlaat het vrouwtje incidenteel het nest om te drinken, maar niet om te eten. Het locale voedsel is verder van groot belang voor de overleving en het herstel van het broedende vrouwtje na broeden, want deze is dan sterk vermagerd door het langdurige broeden. Het locale voedsel is verder ook van groot belang voor de overleving van de kuikens en de aanwezigheid van in droogvallende mosselbanken voorziet de kuikens, maar ook de herstellende vrouwtjes, van geschikt en voldoende voedsel. Verder zijn de locale broedomstandigheden ook van groot belang voor succesvol broeden, zoals voldoende vegetatie bedekking van het nest vanwege de aanwezige predatoren, menselijke verstoring (toerisme, vee) en afstand tot de kust en drinkwater.

In Nederland wordt de maximale grootte (aantal broedende vrouwen) en reproductie (legsel grootte, kuiken productie en fecunditeit) van de kolonie bepaald door het wadoppervlak bij de kolonie. Dit benadrukt het grote belang van het droogvallende wad in de directe omgeving van de kolonie als forageer gebied voor zowel de broedende vrouwen als de kuikens.

Rond 1990 nam de broed populatie in Nederland af met 30%. Deze afname viel samen met de grootschalige onttrekking van droogvallende schelpdier bestanden, zoals de mossel en de kokkel, door de schelpdiervisserij, waarbij ook de droogvallende platen in de nabijheid van de kolonies niet werden ontzien. Desondanks was het herstel van het aantal broedende vrouwen snel sinds 1992. Dit herstel wordt verklaard aan de hand van een populatie model voor de kolonie op Vlieland. Dit model maakt gebruik van een unieke lange termijn serie (25 jaar) van ring terugmeldingen, het aantal broedende vrouwen en de totale kuiken productie. De overlevingsanalyse (MARK) gebruikmakend van de ring terugmeldingen leverde schattingen van de jaarlijkse overleving van eerste jaar, onvolwassen (twee en derde jaar), en volwassen vrouwtjes. Dit model laat duidelijk zien dat de tijdelijke afname in de jaren rond 1990 met een laag voedsel aanbod verklaard wordt door een toename van het aantal niet-broedende vrouwen. Droogvallende schelpdier bestan-

den waren onvoldoende voor vrouwen om tot broeden te kunnen komen en om te overleven werd broeden in deze jaren overgeslagen.

Sinds 1999 is er wederom een afname van 40 % tot 2003 waargenomen in het aantal broedende vrouwen in vooral het westelijke deel van de Wadden Zee, maar het is onduidelijk of dit nu komt door een toename van niet-broedende vrouwen of door een echte afname van het aantal beschikbare vrouwen. Daarnaast kan door de gebrekkige informatie over de schelpdier bestanden in de gehele Waddenzee geen uitspraak gedaan worden of deze afname te maken heeft met de kwaliteit van de schelpdieren en of alternatieve voedselbronnen zoals Ensis een rol hierbij spelen. Opvallend is dat voor de kolonie van Rottum in de oostelijke Wadden Zee een significante relatie is gevonden waarbij de dichtheid van broedende vrouwen toeneemt met de locale bestanden aan droogvallende mossels. Deze relatie is gebaseerd op een vijfjarige data set na de eerste substantiële en succesvolle hervestiging van droogvallende mosselbanken in 2000 en broedende Eidereenden reageerden meteen met een toename in het aantal broedende vrouwen. De gegevens van Vlieland zijn kwalitatief hiermee in overeenstemming. Verder is voor de kolonie op Vlieland niet-broeden negatief gerelateerd aan de totale dichtheid van profijtelijke schelpdieren, nadat visserij heeft plaats gevonden in de nabijheid van de kolonie. In recente jaren is het locale droogvallende voedselaanbod op Vlieland drastisch afgenomen en dit heeft er volgens de recente vliegtuigtelling toe geleid dat de overwinterende Eidereenden zich hebben verplaatst van de wadplaten naar de diepere delen van de westelijke Waddenzee.
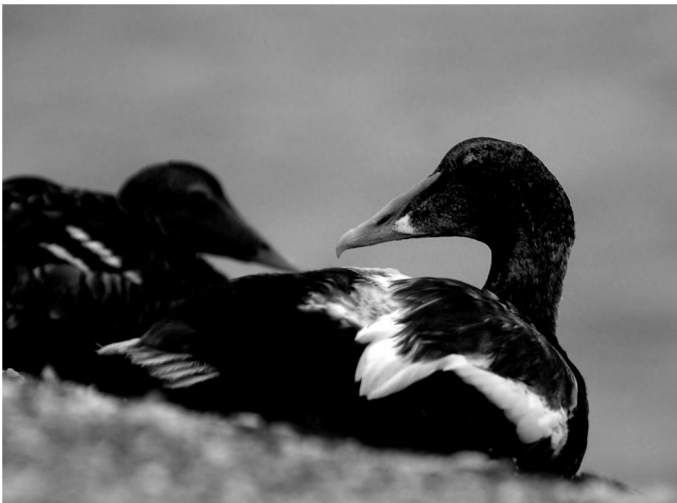
Dankwoord

De totstandkoming en de afronding van mijn proefschrift is alleen mogelijk geweest dankzij de samenwerking met veel mensen, die op een geheel eigen wijze en/of op een of meerdere manieren een bijdrage in welke vorm dan ook hebben geleverd. Ik ben dan ook iedereen erg dankbaar voor haar of zijn bijdrage, steun, inspiratie en vertrouwen in zowel het heden als het verleden.

Laat ik beginnen met het verleden. Wonend in Friesland in de buurt van de Waddendijk en spelend bij 'Us Mearke' op Vlieland, ben ik gefascineerd geraakt door de Waddenzee. Het plezier van planten werd me al vroeg bijgebracht door Piet Lagas op en rond de Woldberg. Mijn interesse voor vogels werd gewekt door de excursies op Vlieland onder leiding van Rein Rollingswier en Bake Mulder in de Kroon's Polders. Dit heeft er toe geleid dat ik op de lagere school een spreekbeurt heb gehouden over ...... de eidereend. Later werd mijn interesse voor vogels wetenschappelijk aangewakkerd door Joop Jukema, die mij verder het algemene nut en de waarde van ringonderzoek heeft doen inzien bij het wilsterflappen. Via de FFF ben ik door Albert Ferwerda meegenomen om wadvogels te tellen bij Zwarte Haan. Al deze invloeden hebben mij er toe bewogen om biologie te gaan studeren. Door het vertrouwen en enthousiasme van Jan Komdeur ben ik gestimuleerd om met dit promotie onderzoek.

Nu terug naar het heden. Allereerst dank ik mijn promotor, Rudi Drent, voor zijn inspirerende inzet en vertrouwen, die vooral tijdens de laatste fase van het opschrijven en de afronding op mij een enorme indruk heeft gemaakt. Ik kijk daarom met veel plezier terug op onze gezamenlijke bijeenkomsten op Texel en in Haren, waarin je me steeds bij de kern hebt gehouden. Je hebt me enorm gestimuleerd om ook de locale broedvogels bij het onderzoek te betrekken en keer op keer de grote waarde van het populatie model benadrukt. Hieruit is nog maar weer eens gebleken dat langjarig onderzoek van groot belang is voor beleidsrelevant onderzoek. Verder bedank ik Joost Tinbergen, Simon Verhulst en Jan Komdeur voor de

kritische opmerkingen en discussies, Suus Bakker voor de regelzaken in Groningen en als laatste Dick Visser voor de vormgeving van dit proefschrift, en Wim Wolff, Patrick Meire en Tony Fox als leden van de leescommissie

De overlevingsanalyse van het langjarige ringwerk in de kolonie op Vlieland is natuurlijk alleen maar mogelijk geweest dankzij de enorme erfenis van Kees Swennen, die al in de jaren 60 is begonnen met het ringwerk aan eidereenden. Ik heb met veel genoegen de uitkomsten op de Hoge Berg met je doorgenomen en een aantal hypotheses in je proefschrift kunnen uitdiepen. Verder wil ik Piet Duiven bedanken voor zijn enorme enthousiasme en deskundigheid, maar ook het verstrekken van praktische informatie bij allerlei aspecten in dit proefschrift, zoals de dissecties en experimenten. Vooral de hulp en het plezier bij het ringwerk in de kolonie op Vlieland zal ik nooit vergeten. Bedankt hoofdpiet! Henk van der Jeugd bedank ik voor het wijzen van de weg naar MARK.

Als RuG-promovendus ben ik gedetacheerd geweest bij IMARES (voorheen Alterra voorheen IBN) op Texel. Allereerst wil ik mijn twee begeleiders bedanken, Bruno Ens en Mardik Leopold. Beide hebben mij weg wijs gemaakt in de shellfish scene. Mijn long-term begeleider, Bruno, wil ik bedanken en mijn waardering uitspreken voor zijn volhardende rol in de loop van de jaren met de nodige hectiek vooral rond EVA2. Ik ben je enorm dankbaar dat je steeds weer de tijd en energie kon vinden om me dichter bij de afronding te brengen. Mardik Leopold wil ik bedanken voor zijn enorme enthousiasme voor de vogels van de zee en inzicht in de arena van de toegepaste onderzoekswereld met de vele belanghebbende belangen. Never a dull moment met jou aan de koffietafel! Door de jaren heen heb ik de medewerkers binnen het huidige IMARES op Texel (voorheen Alterra voorheen IBN) leren kennen die een voor mij onuitwisbare rol hebben gespeeld in dit onderzoek of indruk hebben gemaakt: Kees Kersting, Bert Brinkman, Cor Smit, Oscar Bos, Jan-Andries van Franeker, Norbert Dankers, Peter Reijnders, Kees Dijkema, Jenny Cremer, Elze Dijkman, Sophie Brasseur, Frouke Fey, Hans Verdaat, Kees Oosterbeek, Hauke Flores, Piet-Wim van Leeuwen, Aad Sleutel, Koos Zegers, Andre Meijboom, Martin de Jong, Erik Meesters, Wilem van Duin, Martin Baptist, Han Lindeboom, Michaela Scholl, Ingrid de Raad. Speciale dank gaat uit naar de beide paranimfen Piet-Wim ('workshop' kooienbouwen, 'kingetje' met de 'King of the Bush' op Vlieland en lange avonden in de Eemshaven) en Erik (de kunst van de statistiek en de rust), Sophie, Andre, Martin, Hauke en Ingrid voor hun erg plezierige aanwezigheid. Marcel Klaassen heeft me met zuurstofmetingen wegwijs gemaakt in de wereld van de energiehuishouding en ik hoop dat dit gedeelte een vervolg gaat krijgen. Als student of vrijwilliger hebben Grietje Zijlstra, Rogier van Viegen, Karsten Rook, Joost Oonk, Rein Planting, Jeroen Haas, Inge Hollander, Charles Showers, Rieneke de Jager, Laurens van Kooten, Peter Spannenburg, Annemarie Teunissen en Rob van Veghel mij geholpen bij veldwerk op Vlieland, benthos bemonsteringen en de verwerking ervan, en voedselkeuze experimenten. Een consequentie van dit fascinerende werk waren de

vliegtuigtellingen aan de eidereenden in de winter met de piloten Simon IJspeert en Brien van Wijk. Het was erg bijzonder om de Waddenzee in vogelvlucht te mogen zien.

De nabijheid van het NIOZ heeft een inspirerende invloed gehad door de aanwezigheid van Kees Camphuysen, Ane Dekkinga, Rob Dekker, Bernard Spaans, Casper Kraan, Jeroen Reneerkens, Piet den Hout, Katja Phillipart, Tanya Compton, Anne-Claire Baudoux, Micha Rijken en mede door de literatuur discussies in het interferentieclubje met Anne Rutten, Theunis Piersma, Isabel Smallegange, Jan Jaap Poos, Wouter Vahl, Bruno Ens, en Jaap van der Meer. I thank Alina Stadnitskaia for translating russian literature.

Een groot deel van het onderzoek in dit proefschrift is mede tot stand gekomen dankzij de multidisciplinaire samenwerking, o.a in het kader van NWO-SUSUSE, EVA2 en ESSENSE, tussen verschillende instituten, overheden, organisaties en personen en aan dit onderzoek hebben bijgedragen in de vorm van data en faciliteiten: RIVO/Imares (Aad Smaal, Tammo Bult, Johan Craeymeersch, Jack Perdon, Pauline Kamermans), Marnix van Stralen, Vogeltrekstation (Gerrit Speek), RIKZ (Cor Berrevoets, Jaap de Vlas), SOVON (Peter de Boer, Ben Koks, Lieuwe Dijksen, Michiel van der Weide), LNV-Noord (Syste Braaksma, Gerard Mast), LNV Boten (Phoca: Jan van Dijk, Bram Fey, Dirk Kuiper; Cornelis Bos: Eelke Boersma, Floris Sinnema; Stormvogel: Nico Laros; Harder: Klaas Kruier, John de Boer), ID-Lelystad (Fred Borgsteede), Diergeneeskunde, Universiteit van Utrecht (Gerry Dorrestein), Dirk Kuiken, Folkert Jansen, SBB (Texel: Eric Menkveld, Vlieland: Carl Zuhorn, Piet Schaper, Gerrit Wierda; Terschelling: Harry Horn, Hildebrand van Dijk, Ameland: Piet Visser; Schiermonnikoog & Griend: Otto Overdijk: Rottum: Bert Corte, Anneke Bouwman, Dries Olsthorn, Nelly van Brederode, Hans Roersma, Marit Heegstra, Roelof Hovinga), Fryske Gea (Richard Kiewiet), Freek Niewold, Chris Pool, Henk van der Jeugd, Kees Rappoldt, Hein Sas, Jaap en Rienk Nadema, Georg Nehls, Gregor Scheiffarth, Henrik Baekgaard en Thomas Christensen.

Tenslotte is dit proefschrift tot een afronding gekomen dankzij het volste vertrouwen en de liefde van Sandra, Henk, Minke en Jelliena, en de komst van mijn mooie jongens, Sverre en Meinte, ook al ging het daardoor een tandje langzamer.

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