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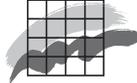
Factors affecting population size of Baltic Common Eiders *Somateria mollissima*

PhD thesis, 2008

Thomas Kjær Christensen



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Data sheet

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Abstract: In recent decades, the Baltic-Wadden Sea flyway population of Eiders has undergone marked changes, first experiencing a steep increase during the 1970s and 1980s, followed by a marked decline during the 1990s. There have been several reported incidences involving mass simultaneous mortality amongst this population during the period of decline, each of which were insufficient on their own to explain the overall level of decline.

The present thesis describes the overall population development in the Baltic-Wadden Sea flyway population of Eiders. In relation to the recent population decline, the thesis addresses the occurrence of epidemic disease, parasite infestations and the implications of hunting in relation to population development. The concept of body condition is introduced as a common currency, because the role of body condition in relation to population trends has not often been discussed in the literature. Finally, the synopsis is used to discuss the potential conservation measures that may be introduced and which might help in restoring the unfavourable development of the Baltic Eider populations.

Keywords: Common Eider, *Somateria mollissima*, population development, body condition, hunting, sea duck, Baltic Sea.

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1 Synopsis

1.1 Setting the scene

History and status of the Baltic-Wadden Sea Eider flyway population

Based on analyses of genetic variation, the Common Eiders *Somateria mollissima* (Linné 1758) in NW Europe apparently originate from a single Pleistocene refugium located in ice-free areas in the Kattegat/Skagerrak region during the last glacial period. This ancestral population has subsequently colonised the emerging Baltic Sea area, and spread to Sweden, Finland and the Baltic countries (Tiedemann & Noer 1998, Tiedemann et al. 2004). The same genetic analyses indicate a subsequent stepwise postglacial colonisation of NW Europe, via the North Sea to the Faroe Islands and to Iceland.

Given the contemporary migration patterns of present populations, Eiders breeding in the Baltic Sea area, Denmark, Germany and in the Netherlands constitute a discrete biological unit, a so-called flyway population, based on common wintering grounds (southern Baltic Sea, inner Danish waters and the Wadden Sea, Swennen 1990, Noer 1991). Eiders nesting in Denmark, western Sweden, Germany and The Netherlands are resident or partly migratory, whereas Eiders in southern Norway, eastern Sweden, Finland and the Baltic countries are completely migratory (Cramps & Simmons 1977, Noer 1991). Eiders in this flyway population rarely mix with Eiders originating from birds from the British Isles and other North Atlantic populations, of which many are strictly resident (Kear 2005).

Historically, Eiders in the Baltic-Wadden Sea flyway population seemingly underwent a southward expansion from their northern breeding areas to colonise the German North Sea coast in the late 18th and early 19th century (Bauer & Glutz von Blotzheim 1969). In 1906, the first nests were found in the Netherlands (van Heurn 1952). During the first half of the 20th century, expansion and growth of the colonies continued throughout the Baltic-Wadden Sea area (Almkvist et al. 1975, Hario & Selin 1988), although at a relatively slow rate. A marked increase in the Baltic populations has subsequently been observed at several colonies in the second half of the 20th century, and especially during the 1970s and 1980s (cf. Bregnballe et al. 2002, Hario & Selin 1988, 2002), an increase that likewise has been reflected in national breeding totals (**Paper 1**).

The reasons for the dramatic increases in populations during the 1970s and 1980s are not well known. The most obvious explanation proposed, is that increased environmental eutrophication during this period had led to an increase in primary production in coastal waters, and hence, resulted in improved foraging conditions for Eiders (cf. Hario & Selin 1988). Eutrophication and higher primary production improve conditions for filter feeding animals (e.g., Wolowicz et al. 2006), and of these blue mussels *Mytilus edulis* constitute an especially important prey species for the Eider (e.g., Madsen 1954, Nehls 1989, Nehls 1995, Leopold et al. 2001).

By the end of the 1980s and early 1990s, reports from different breeding populations showed that the increase had peaked and that numbers had begun to decrease. Estimates from Finland suggest that their colonies declined at a rate of 6-7 % annually from that time (Hario & Selin 2002, Hario & Rintala 2006), and a comparable decline of 38 % in breeding numbers between 1993 and 2000 has also been documented in a single Danish colony (Christensen & Noer 2001).

The overall magnitude of the decrease in the Baltic-Wadden Sea flyway population between c. 1990 and c. 2000, has been estimated at around 36% (**Paper 1**), based on midwinter counts of Eider. The number of wintering Eiders in Danish waters decreased during this period from c. 800 000 to c. 380 000 (Laursen et al. 1997, Pihl et al. 2001), suggesting that the overall population probably experienced a decrease from c. 1.2 mill. to c. 760 000 individuals (cf. Delaney & Scott 2002, Delaney & Scott 2006, **Paper 1**). On the basis of such a dramatic decline, the Eider in the Baltic-Wadden Sea flyway population may presently qualify as a species of conservation concern, even though there is evidence that the declines have stopped in some areas (Hario & Rintala 2006), and that the actual overall size of the Baltic-Wadden Sea population has probably been underestimated historically. Application of distance sampling modelling in 2004 to estimate population size rather than attempting to undertake complete counts as during previous winter surveys of waterfowl in Danish waters, suggest that the numbers present there are closer to 600 000 (Petersen et al. 2006) than to the 380 000 counted in the 2000 survey (Pihl et al. 2001). This may result in a revision of the overall Eider population estimates, because new areas were also included in the 2004 survey, but do not affect the overall magnitude of the population decline. It is unlikely that wintering Eiders in Danish waters have completely changed their former distributional pattern sometimes during the 1990s enough to affect the national totals (**Paper 1**).

Acknowledging the recent decreases in the Baltic-Wadden Sea, the Sea Duck Specialist Group of Wet-

land International arranged a workshop in Estonia in 2002 to compile information on the status and distribution of Eiders within the flyway, and likewise to discuss potential causes for the population decline. At that meeting, it became clear that the population decline, based on winter surveys, was not matched by comparable declines in breeding numbers monitored on different parts of the breeding grounds, which have shown remarkably stable trends throughout the range (**Paper 1**). To explain this discrepancy between reductions on the winter grounds and stable breeding numbers, five hypotheses were proposed. These were:

- (i) that earlier recruitment from the young (2-3 year old) non-breeding segment of the populations resulted in a reduction in age of first breeding that masked any change in absolute breeding numbers
- (ii) that major reductions in the Swedish breeding population had occurred unnoticed (e.g. because no complete surveys of the important breeding areas of the Stockholm archipelago had taken place since the early 1980s; Andersson 1985, Svensson et al. 1999),
- (iii) improved breeding survey methods in recent years had been more effective in locating proportionally more breeding birds, despite a real overall decline
- (iv) poorer coverage of Danish waters during recent winter surveys and/ or
- (v) there has been changes in winter distribution of Eiders (**Paper 1**).

Based on general assessments of survey techniques and survey coverage of both breeding and wintering Eiders, the two most likely explanations for the apparent discrepancy between wintering and breeding numbers were considered to be the result of shortcomings in our ability to monitor breeding and wintering number correctly and/or as a result of an unknown buffering effect of non-breeders recruiting into breeding classes, which would not feature as a change in breeding abundance over time (**Paper 1**). Assuming that the declines in the flyway populations are mainly related to a decrease in the female segment of the population (see below), this last hypothesis implies that an earlier breeding age amongst the young, normally non-breeding segment, may have compensated for an actual reduction in the numbers of older, experienced breeding element of the population, and in this way rendered breeding populations stable, assuming some kind of density dependence that controls the numbers of potentially available nest sites. In this way, the average age of first breeding will have fallen dramatically, but the abso-

lute numbers breeding may not have changed, despite the overall population decline which would have only been recognisable in the total population as a whole based on winter surveys.

There seems to be no obvious single explanation for the recent decline in the Baltic-Wadden Sea Eider population. On a large scale, continued eutrophication, global warming and commercial exploitation of mussels, may have had an adverse effect on foraging conditions for Eiders, which in turn may have consequences for both survival and reproduction. On a smaller scale, several Baltic populations have experienced increased local predation pressure from both mammalian (**Paper 1**) and avian predators (Kilpi & Öst 2002), outbreaks of epidemic diseases on the breeding grounds, affecting both adult female and juvenile survival (Hollmén et al. 1996, Hollmén et al. 2002, **Paper 2**, **Paper 3**). In addition, there have been frequent reports of parasite infections (Hario et al. 1992, Hario et al. 1995) and large scale 'die-offs' in some years on the wintering grounds (thought to be the result of starvation (Fleet 2001, Camphuysen et al. 2002). All of these factors have undoubtedly had some influence on population development of the Baltic Eiders.

The magnitude and speed of the population decline suggests that the declines cannot be explained by any one factor alone. However, the relative importance of factors such as epidemic diseases and parasite infestations, winter mass die-offs and increased predation may have increased accordingly. In the present thesis, I describe the overall population development in the Baltic-Wadden Sea flyway population of Eiders (**Paper 1**), and address the occurrence of epidemic disease (**Paper 2**, **Paper 3**), parasite infestations (**Paper 10**) and the implications of hunting (**Paper 4**, **Paper 5**) in relation to population development. To be able to assess the relative contribution of these various factors in relation to changes in both adult and duckling mortality and to reproductive ability and success, I introduce the concept of body condition as a common currency (**Paper 6**, **Paper 7**, **Paper 8**, **Paper 9**). Because the role of body condition in relation to population trends has not often been discussed in the literature, emphasis is placed on this element in the synopsis. I likewise discuss the potential conservation measures that may be introduced and which might help in restoring the unfavourable development of the Baltic Eider populations.

1.2 The significance of body condition

The Eider is a long-lived, seasonal monogamous and colonial breeding sea duck that is characterised by low annual reproductive rates and high annual adult survival rates (Coulson 1984, Swennen 1991b). The

Eider is considered to be a capital breeder (Meijer & Drent 1999), because females rely on endogenous energy stores accumulated during late winter and spring for reproduction. In preparation for breeding, female Eiders increase their body mass by c. 20% above winter levels during the period before breeding (Milne 1976), while investment of these stores in eggs (normally 4–5 per clutch) and in self-maintenance during the incubation period of c. 26 days, (when the females do not feed) results in loss of up to 40% of pre-laying body mass (Korschgen 1977, Parker & Holm 1990). Thus, by the end of incubation, female Eiders may be markedly emaciated, and some may even approach the critical level of c. 1,100 g where death by starvation is inevitable (Korschgen 1977). On top of their emaciated condition at the time of hatch, female Eiders face the task of rearing their ducklings in shallow water areas that often constitute suboptimal foraging habitats for adult Eiders (e.g. Gorman & Milne 1972), conditions that may add further energetic stress to brood tending Eider females.

Considering the energetic demands imposed by reproduction, it is perhaps not surprising that Eiders have been found to adjust their reproductive investment in accordance with their body condition, e.g., change clutch size (Erikstad et al. 1993, Hanssen et al. 2002, Hanssen et al. 2003a), abandon their nests (Burgeon et al. 2006), abandon ducklings or engage in brood care (Bustnes & Erikstad 1991, Öst 1999, Öst et al. 2002, Öst et al. 2005), and even skip breeding (cf. Coulson 1984, Swennen 1991b, Christensen & Noer 2001). Given their long life span of up to 25–30 years, these adjustments could be interpreted as adaptations to cope with the trade-off between current reproductive investment and safe-guarding their own long-term survival probabilities and hence secure life-time reproductive success, as predicted by life-history theory (e.g., Stearns 1992) and parental investment theory (e.g., Trivers 1972, Coleman & Gross 1991). The recent range of excellent studies revealing the condition related investment and behavioural reproductive strategies adopted by eider, has recently led to consideration of body condition acting as an ecological constraint, operating in a manner similar to extrinsic factors such as availability of breeding sites, food and mates (Öst et al. 2003b).

The dramatic energetic investment imposed by reproduction in Eiders emphasises the importance of the accumulation of resources for Eider females, the only sex which engages in direct reproductive investment (egg-laying, incubation and brood care). Given that more ducklings hatch and leave the nests from large clutches than from small clutches (Erikstad et al. 1993), and that duckling survival is higher amongst solitary broods than amalgamated broods (Öst et al.

2003a, Öst et al. 2003b), the best reproductive strategy for Eiders should be to lay large clutches and to care for own ducklings until fledging. Since large clutches and solitary brood care are positively correlated with female body condition, optimal resource accumulation is essential for optimal reproduction. Early pair formation (late autumn, early winter, Spurr & Milne 19776), stable pair bonds, and male mate guarding (Hario & Hollmén 2004, **Paper 6**) are all apparent strategies that enable females to secure undisturbed foraging time in preparation for reproduction.

Generally, an individual's ability to store resources is linked to its structural size. In birds, the benefits of being large relative to population mean range from direct superiority in competition for mates and resources, to benefits relating to other size-dependent physical and/or physiological relations such as a larger capacity for energy storage and endurance, lower relative heat loss and more effective utilisation of stored energy reserves (reviewed by Bluhm 1992, see references herein). Although there are obvious benefits associated with structural size, individuals of similar size may not always be of equal "quality". In fact, variation in the body condition of individuals, expressed as the body mass relative to structural size, can be a more reliable measure of the ability of an individual to meet its present and future needs. For instance, body condition is known to have a major influence on individual decision-making in many aspects of life (breeding, moulting, migration), and to influence on survival probabilities in both adults and juveniles, not only in birds, but in a wide range of animal species (e.g., Cargnelli & Neff 2006, Reading 2007, Roche et al. 2007, Wheatley et al. 2007). Blums et al. (2005) showed that among traits closely associated with fitness components in waterfowl, body condition covaries with both reproductive and survival components of fitness, whereas weaker correlations were found with measures of structural size. Consequently, in a given season or in relation to a given activity, measures of individual body condition may be considered a better predictor of individual quality than structural size alone.

As the body condition of an individual reflects the surplus or deficit of expendable energy resources that is available to an individual, changes in the average body condition probably have more wide-ranging implications on population development than just affecting reproduction. For example, Eiders are generally capable of mounting an immune response when experiencing infectious organism or extreme physiological stress that may affect individual fitness (Hanssen et al. 2003b). However, the cost of immunocompetence is high, and if mounted, the associated costs may have severe consequences on individual

survival (Hanssen et al. 2004). In the Eider, indications of immunosuppression have been shown in females of low body mass late in the incubation period and in females that subsequently abandon their brood (Hanssen et al. 2003b), suggesting that when stressed by the cost of their investment in breeding, females avoid mounting a costly immune response that would further jeopardise their energy balance. These results suggest that if the average body condition of female Eiders in a given population is lowered, these populations would in all probability be more vulnerable to stressors such as disease, parasite infection, contaminants (e.g., heavy metals) and poor foraging conditions, as they may be more reluctant to mount costly immune responses, or may even be unable to do so effectively.

1.3 Explanations for population increase

The marked increases in the Eider populations originating in the Baltic-Wadden Sea flyway during the 1970s and 1980s occurred along with a general increase in the level of eutrophication (see Rönkä et al. 2005). Since filter feeding bivalves, the main prey of Eiders, generally benefit from a higher primary production associated with eutrophication, Eiders may have benefited from increasing populations of bivalves (cf. Hario & Selin 1988). Better foraging opportunities would lead to enhanced reproductive output, i.e. individuals in better body condition lay larger clutch sizes (e.g., Hanssen et al. 2003a) and produce more ducklings that go on to survive (Öst et al. 2003b). That there has been an increase in average general body condition of Eiders in the Baltic-Wadden Sea flyway population during the period of population increase is supported by a marked increase in average clutch size recorded during this period (Hario & Selin 2002). Likewise, during the subsequent population decline, Eider females were found to have significantly smaller clutch sizes and weigh less than during the period of population increase, specifically amongst those cohorts recruiting during the population decrease (Hario & Selin 2002). Thus, it seems likely, that the population increase during the 1970s and 1980s has been related to a general improvement in foraging conditions of Eiders throughout the flyway that have for some reason enabled females to attain better body condition than in earlier times. This may well relate to enhanced food availability linked to the general eutrophication of Baltic waters, as indicated by Hario & Selin (1988).

That the population increase during this period has been substantial, is emphasised by the fact, that hunting of Eiders continued without a check to the population increase, and in Danish waters alone the

harvest accounted for between 130 000 and 150 000 individuals annually (Noer et al. 1995, **Paper 4**). Thus, the population increase occurred despite this substantial hunting off-take from the population, although the effect may have been to depress the rate of population increase below its potential (attained in the complete absence of hunting-related mortality), especially as adult birds constituted a high proportion of the total bag (Noer et al. 1995).

Although no other macro-environmental factor than the general increase in the level of eutrophication has been proposed as an explanation for this increase in the Eider populations, Eiders may have benefited from changes in human behaviour during the past 40-60 years. Historically, Eiders have been a natural resource providing supplementary meat, eggs and down to human households. However, the importance of such semi-subsistence exploitation has decreased or ceased in the Baltic area during the mid 20th century, potentially relaxing persecution that previously may have restrained the development of Eider populations. Likewise, a widespread practice of persecution of avian raptors during the 19th and early 20th century and extensive use of chemicals that affected survival and fecundity in top predators may have reduced the level of natural predation on Eiders, thereby providing conditions to enable population increase. Although there exists no detailed information of historical changes in human exploitation of Baltic Eiders and of historical changes in the level of avian predation, the population increase during the 1970s and 1980s may have benefited from such general changes.

1.4 Explanations for population decrease

Basically the decline in the overall size of the Baltic Eider population indicates that the current mortality rates among old established breeders are higher than the current reproductive output and associated recruitment rates. Thus, to explain the population decline, Eider populations may either have experienced increased adult mortality and/or decreased reproductive success.

1.4.1 Adult mortality

Generally the average adult survival of Eiders is high, ranging between 80 % and 95 % (Coulson 1984, Swennen 1991b, Hario & Selin 2002), and assessed from matrix population models (Caswell 1989), adult survival is the primary determinant of population dynamics of Eider populations (Noer et al. 1996). Thus even small changes in the average adult survival rate have large implications on population development, especially in the long term.

Disease

During the recent population decline, outbreaks of avian cholera epidemics have at least caused the death of 5–6000 breeding females in Danish and Swedish colonies. Although some colonies may have been affected without being known, and avian cholera unquestionable have had significant impact on survival rates in the local colonies, the total number succumbed during the recorded epizootics most probably only explain a fraction of the total population decline of c. 400000 birds. Consequently, avian cholera is probably of relatively little importance considering the present minimum population size of c. 250000 breeding pairs (which do not include Swedish birds, **Paper 1**).

Outbreaks of avian cholera, caused by the bacteria *Pasteurella multocida*, among European Eiders was first recorded in the Netherlands in 1984 (Swennen & Smit 1991), but has long been of concern among waterfowl in North America (c.f. Botzler 1991, Skerratt et al. 2005). In Denmark and Sweden, several Eider colonies were subject to outbreaks of avian cholera in 1996 and in 2001 and 2003, in which up to 90% of the breeding females in local colonies died (Ziesemer & R ger 1997, Persson 1998, **Paper 2**, **Paper 3**). Generally, females were found dead on full laid clutches early in the incubation period showing no sign of emaciation, suggesting that the cause of death was related to acute infection and not affected by individual differences in, e.g., body condition or age. Clinically, the cause of death was determined to multifocal, necrotising hepatitis (**Paper 2**).

Since no epidemics have been reported between 1984 and 1996 (**Paper 2**) despite intensive work in eider colonies during this period, and since the bacteria are only able to survive in water or soil for some month (Blanchong et al. 2006), the most probable explanation for the reoccurrence of cholera epizootics is that the bacteria was present in healthy carriers during the intermediate period (Botzler 1991, **Paper 2**). Such healthy

carriers have been documented among both wintering and breeding Eiders, although at an extremely low frequency (Korschgen et al. 1978). That healthy carriers of avian cholera probably are present within the Baltic Eider populations infer that new outbreaks may occur, and that this disease may have long-term implications for population development, although there is no indication that avian cholera is fully responsible for the recent population decline.

Avian cholera may be a recurrent disease in Eiders populations in the coming years, as indicated by the striking increase in outbreak frequency since the first record in 1984, the intervals between outbreaks being 12 years, 5 and 2 years, respectively. Hypothetically, such an increase in outbreak frequency may indicate that the long-term resistance of healthy carriers may have declined, e.g., carriers



Photo 1. A pile of dead Eiders (mostly females) which succumbed during the epizootic caused by avian cholera in the Stavns Fjord colony in Denmark in 1996. Some gulls (to the right) have probably died from scavenging on dead Eiders.

Photo: Thomas Kj er Christensen.

being more frequently stressed by, e.g., environmental factors, lowered food availability or high parasite loads, assuming that such stressors affects a general ability to depress latent diseases from emerging.

As avian cholera is highly contagious and infections are lethal, Eider populations are extremely vulnerable, as they are both colonially breeding and highly gregarious during winter. There seems no way that Eiders may mitigate or adjust to the presence of avian cholera to minimise the risk of epidemics, other than to loosen their gregarious behaviour. There exists some evidence of changed distributions of Eiders in the breeding areas in relation to increasing predator populations (**Paper 1**), and such changes may explain why avian cholera epizootics have not been recorded in breeding colonies since 2003. However, in the enormous Finnish and Swedish archipelagos, minor outbreaks among breeding Eiders may easily have taken place undetected, especially if Eiders breed increasingly dispersed, rather than in large conspicuous colonies. The spread of avian cholera from Danish wintering grounds to breeding colonies in the Baltic in 1996 was probably mediated by carriers becoming infectious on the common wintering grounds, which in 1996 was confined to relatively few open water foraging areas due to severe ice formation (DMI 1996), and hence resulted in very high bird densities. Thus the future risk of major outbreaks may be considered higher in years where severe ice conditions on the wintering grounds results in high Eider densities, as the disease subsequently may be carried into breeding colonies throughout the flyway, where avian cholera, by selectively removing the most fecund females, will have an enormous potential impact both qualitatively and quantitatively.

Winter mortality and parasites

Besides the outbreaks of avian cholera, a large number of Eiders succumbed to starvation during the massive die-offs recorded in the Dutch and German Wadden Sea during the winters 1999/2000 to 2001/2002 (Fleet 2001, Camphuysen et al. 2002, Ens et al. 2002, **Paper 1**). The most marked die-offs were recorded during 1999/2000, where c. 25 000 dead birds were estimated to be washed ashore, while somewhat lower numbers were recorded in the subsequent two winters (Camphuysen et al. 2002, Ens et al. 2002). Given that most birds that died were juvenile birds (based on recoveries of Danish and Finnish rings, see Camphuysen et al. 2002), the impact from these winter die-offs on the populations throughout the flyway may not have been immediately detectable in local surveys of breeding colonies. It seems more likely that the high mortality during these winters has affected subsequent recruitment rates throughout the range, an effect that would manifest in the years following the documented population decline mainly taken place during the 1990s, and likewise will contribute little to continued popula-

tion decline, as the die-offs involve relatively few fecund adult females.

Interestingly, Eiders that died during these winters were found to harbour very high loads of acanthocephalan parasites in their intestines (**Paper 10**), which lead to discussions of the potential contribution of parasites to the emaciated state of Eiders, and even whether high parasite infection levels were the primary cause of mortality (cf. Camphuysen et al. 2002).

Several parasite species have been described to cause lesions and disruptions to the alimentary tract (Watson et al. 1987, Connors & Nichol 1991), to cause alteration in metabolic rates (Connors & Nickol 1991, Delahay et al. 1995), reduce clutch size and breeding success (Hudson 1986) and weaken body condition (Keymer et al. 1991, Delahay et al. 1995) in their avian hosts. In consequence, it is generally acknowledged that parasite infestations have detrimental effects on their hosts. Parasite pathogenicity is, however, complex, and has been found to vary within species in relation to sex or age of the host, in relation to environmental condition and to parasite community structure within host individuals (e.g., Bosch et al. 2000). Likewise negative effects have been shown for some helminth species (Thompson 1985a, Keymer et al. 1991, Delahay et al. 1995), but not for others (e.g. Williams & Harris 1965, More & Bell 1983, Thomas 1986, Grey et al. 1989).

Parasites of the acanthocephalan order have been shown as being frequent macro-parasites of the small intestine in a large number of waterfowl species (e.g., Crompton & Harrison 1965, Ching 1989), including the Eider (e.g., Garden et al. 1964, Bishop & Threlfall 1974, Lysfjord 1981, Hario et al. 1992). In Eiders, acanthocephalan infestations have been reported throughout the breeding range and identified as both *Profilicollis botulus* (Van Cleave 1916) and *Polymorphus minutus* (Goeze 1782), which are obtained through ingestion of the infective cystacanths (intermediate larval stage) present in the shore crabs *Carcinus maenas* and small gammarid crustaceans, respectively (Rayski & Garden 1961, Thompson 1985b, 1985c, Nickol et al. 1999, Crompton & Harrison 1965, Itämies et al. 1980, Hario et al. 1992, Hollmén et al. 1996).

Heavy infestations with of *P. botulus*/*P. minutus* in Eiders have often been associated with poor body condition, marked emaciation and with incidents of increased mortality (Grenquist 1970, Thom & Garden 1955, Clark et al. 1958, Garden et al. 1964, Bishop & Threlfall 1974, Lysfjord 1981, Hario et al. 1992, Hollmén et al. 1996, Camphuysen et al. 2002). However, heavy infection levels have also been reported in apparently healthy Eiders showing no signs of ill-effects (Liat & Pike 1980, Thompson 1985a, **Paper 10**). In consequence, it has been suggested that the presence of high numbers of parasites contributes to a

poor body condition in otherwise weakened birds rather than being the primary cause of sickness and death (cf. Garden et al. 1964, Hario et al. 1995, Holmén et al. 1996).



Photo 2. A section of Eider intestine with the Acanthocephalan parasites *Profilicollis botulus*. Photo: Thomas Kjær Christensen.

In the Eiders that died in the Dutch and German Wadden Sea the levels of parasite infestations were 2-3 times larger than in apparently healthy Eiders collected by hunters in Danish waters (**Paper 10**). However, parasite infestations intensities were not correlated with the body condition of the dead Eiders, suggesting that the primary cause of mortality was related to poor foraging conditions as a result of commercial overexploitation of mussels, at least in the Netherlands, rather than to parasite infestations (Camphuysen et al. 2002, **Paper 10**). That increased levels of parasite infestations in some way may have contributed as a secondary or accelerating factor to a deterioration of the body condition of the starving Eiders seems a reasonable hypothesis (cf. Hanssen et al. 2003c), although their relative effect is presently unknown.

Since healthy Eiders do carry substantial parasite infestations this suggests that under normal circumstances, Eiders are capable of being parasitized, potentially without suffering serious fitness consequences. Whether the generally lower infection intensities in healthy, hunter-shot Eiders reflects that Eiders normally have a lower preference for prey species harbouring infective parasite cystacanths or are capable of depressing infestation levels below a critical level by mounting an immune response is not known. The emaciated state of the Eiders which succumbed during the winter die-offs suggests that the Eiders, in the

face of a collapsed food supply, had no alternative other than to prey on shore crabs that were very abundant (**Paper 10**). Despite the high energetic value of crabs (Guillemette et al. 1992), these easily obtained prey bring the risk of multiple parasite infection and hence contribute to a reduction in body condition amongst those individuals forced to feed upon them.

Given the potential of parasites to negatively affect the energetic resources or balance of their hosts, either as a result of direct loss of energy to parasites or indirectly through an increased cost of mounting an immune response, Eider populations are potentially vulnerable to changes in the general infection levels. Obviously, if parasite infestations add further energetic stress to Eiders, and the effects of infection is either proportional to parasite densities or are triggered when

densities reach some threshold level, the ability of Eider females to accumulate adequate resources for reproduction may be hampered. In addition, increased parasite infestations may render Eiders more susceptible to other stressors, such as from viral or bacterial infections, that potentially would result in slightly elevated mortality rates, which in turn may have major impacts on population development.

Even though our present understanding of the effects of parasite infection on mortality and reproduction rates is inconclusive, the intensity of parasite infection during winter periods could potentially indicate the general availability and quality of the main mussel prey in the ecosystem, as well as reflecting the general health status of the Eider populations. Further studies based on regular monitoring are needed to reveal the causal relationships between parasite infestation levels in winter and subsequent reproductive performance and survival probabilities of breeding female Eiders.

Predation

Very few natural predators prey on large sea ducks in the coastal and offshore areas of the Baltic Sea. Historically, White-tailed Sea Eagles *Haliaeetus albicilla* may be the only natural predator of Eiders, but the population of White-tailed Sea Eagles has until recently been very small (cf. Kilpi & Öst 2002), and probably not of significance to Eider populations,

especially not during the period of population increase. While almost unaffected by predators outside the breeding period, adult Eiders may occasionally have experienced predation from mammalian predators, such as the fox, martens and wild cats on the breeding grounds. However, the location of the breeding colonies on small islands and skerries, are generally acknowledged as an adaptation to avoid terrestrial predators.

In contrast, the levels of predation on breeding adult Eiders in the Swedish and Finnish breeding areas seem to have increased during recent years. This is due to range expansion of the introduced American Mink *Mustela vison* and of the native White-tailed Sea Eagle throughout the Baltic archipelagos (Kilpi & Öst 2002, **Paper 1**). Eider numbers have conspicuously declined in areas inhabited by mink and shifted their distribution away from traditional breeding islands to more distant and open, non-vegetated islands in the outer archipelago areas (**Paper 1**). On open islands, predation of females and eggs by eagles seems to be more successful than in vegetated areas, although the level of predation has increased everywhere (Kilpi & Öst 2002). Thus, Eider populations may presently be adversely affected by the rapid increase in White-tailed Eagle populations and from the expansion of Mink throughout the previously predator-free islands in the extensive Baltic archipelagos, relating both to a direct increase in mortality and to a reduced breeding success and/or decreasing availability of safe breeding sites.

Hunting

Eiders in the Baltic-Wadden Sea flyway are protected during the breeding season from hunting and egg collection. Outside the breeding period Eiders are exploited by hunters in autumn and winter in Finland, Denmark and Sweden. In Finland males have a short open season in spring, just prior to the breeding period.

The majority of the human hunting exploitation of the Baltic-Wadden Sea population of Eiders occurs in Denmark, where c. 60,000 to 80,000 Eiders are presently shot annually (The Danish Bag statistics 2005). The annual bag size of Eiders in Sweden amounts to 3-5,000 birds, and c. 25,000 in Finland where c. 70% are males (cf. **Paper 1**). In Finland, the bag size and the size of the breeding population are strongly correlated (Hario & Selin 1987), contrasting the situation in Denmark, where the declining bag size (from c. 140,000 during the 1970s and 1980s to the present level) was mainly related to the decrease in the number of sea duck hunters, and not to the decrease in the Eider population (**Paper 4**).

Acknowledging the potential impact of hunting on population size and trends, several legislative

actions have been implemented to protect Eiders in Danish waters, including area-specific bans on hunting from motorboats, bans of private sales of bagged Eiders, and closure of the hunt in February in specially protected areas designated under the EU Bird Directives. Most recently, in 2004, the open season has been reduced by c. 45 days for females and c. 15 days for males, with the specific aim of increasing survival of (locally breeding) adult females during the present population decline.

During the 1970s and 1980s the annual bag of Eiders in Danish waters accounted for between 130 000 and 150 000 individuals. Despite this substantial harvest, the Baltic populations increased markedly during this period, indicating that hunting had no effect on stopping population growth, although it very likely reduced the overall rate of expansion below the potential at that time. As hunting has declined concurrently with the recent population decline, the present impact from hunting is not precisely known, but hunting most probably has contributed by accelerating the population decrease.

There is some evidence that waterfowl hunters more frequently harvest individuals that are in poor condition (e.g., Greenwood et al. 1986, Reinecke & Shaiffer 1988, Dufour et al. 1993). This effect is referred to as the condition bias hypothesis (sensu Weatherhead & Greenwood 1981), that food stressed individuals are more easily attracted to decoys, and thus more susceptible to hunting. However, other types of sea duck hunting may likewise harvest poor condition individuals. Hunting from motor boats, the most frequent type of sea duck hunting in Danish waters (Clausager 2003, Clausager 2004), most often involves taking birds from smaller groups of birds in near-coastal areas, which may represent birds that for some reason are more stressed than those staging in the larger main flocks in more distant offshore areas, and which are more difficult to successfully approach by hunters (cf. **Paper 4**). If hunting in general affects individuals in poor condition, then the overall effect of hunting on both adult mortality rates and the reproductive potential of the populations may potentially be diluted (removing individuals of low reproductive potential and possibly relaxing density dependent effects), although in total, such an effect would in all probability be far from compensating the impact of the present annual harvest of 60 000 to 80 000 Eiders in Danish waters.

1.4.2 Reproductive success

The ultimate measure of reproductive success in Eider populations is the number of ducklings that survive and recruit to the breeding populations. However, studies of recruitment are few, as they

demand long term ringing programs and extensive recapturing programmes at the breeding colonies. Many more studies have assessed reproductive success by monitoring changes in clutch size, duckling survival and fledging success within populations (e.g., Swennen 1991b). These parameters are more easily obtained and are important determinants or components of reproduction and are highly predictive of reproductive success.

As previously mentioned, the investment in breeding is influenced by the body condition of the females, as the conditional state affects both clutch size and duckling survival (Hanssen et al. 2003a, Öst et al. 2003b). Hence the foraging conditions and ability to accumulate adequate resources for reproduction is an important component in assessments of reproductive success.

Clutch size

A general reduction in the average clutch size in Eider populations, normally ranging between 4 and 5 eggs, has been found amongst both Finnish and in Danish colonies (Hario & Selin 2002, Bregnballe 2002), reducing clutch sizes by 0.3 and 0.5 eggs respectively. Whereas the reduced clutch size in Finland has been associated with the population decrease and related to recruitment of poor cohorts of low body weight (Hario & Selin 2002), reduced clutch sizes in Danish colonies were not correlated with population changes. In the Danish colonies, clutch size reductions were found amongst old established breeders (ringed individuals), and hence assumed to be an immediate response to poorer foraging conditions and not to recruitment of less productive year classes (Bregnballe 2002).

Although lowered clutch sizes have implications for population development by reducing the total number of hatched ducklings, changes in clutch size may be more indicative of environmentally induced changes in foraging conditions, and ultimately the conditional status of the population, than indicative of reproductive success. Since hatching success is high, normally ranging between 80% and 95% (Swennen 1983, Erikstad et al. 1993), poor reproductive success

in years of low clutch size, is probably more affected by the poor condition of breeding females than by clutch size per se. Females in poor body condition at hatch more frequently abandon their broods to other brood tending females or engage in brood coalitions (e.g., Öst 1999), which are less successful strategies in terms of duckling survival, than if females care for their own broods (Öst et al. 2003b).

Duckling survival

Main sources of duckling mortality are predation and disease. Heavy duckling predation by gulls has been reported in many studies accounting for most mortality during the first days and weeks after hatch (e.g., Munroe & Bédard 1977, Mendenhall & Milne 1985, Swennen 1989). Assessed from an experimental study, ducklings predated by gulls were found to be otherwise weakened, leading to the conclusion that gull predation mostly removed unfit individuals, and hence, that the role of duckling predation was of low importance to population development (Swennen 1989). In his study, Swennen found that scarcity of food, leading to ducklings reacting differently to alarm calls by females upon predator attacks, were the main cause for predator success. Thus foraging conditions for ducklings seems a key factor for survival of ducklings between hatch and the first 10-12 days of life. For slightly older ducklings, parasites and diseases seems to be more important determinants of survival. Viral infections have been shown to account for much mortality in ducklings of up to 3 weeks old, and also resulted in recent mass die-offs in Finland (Hollmén et al. 2002), whereas the role of parasite infestations to duckling mortality seems less clear (Hario et al. 1992, Hario et al. 1995, Hollmén et al. 1996).

It seems questionable whether gull predation and the incidences of mass mortality of ducklings in Finland have had marked influence on the overall development of the Baltic-Wadden Sea population. Duckling survival is generally very low, resulting in long-term average fledging success of c. 0.342 ducklings per female per year (Swennen 1991a). However, fledging success is highly variable with occasional



Photo 3. Ducklings. Photo: Thomas Kjær Christensen.

years of very high success (Swennen 1989, Hario & Rintala 2006), such years being responsible for marked increases in colony size (cf. Coulson 1984). At times when adult survival is stable, fledging success or duckling mortality during the brood rearing period is probably the regulating factor of population growth in the Baltic-Wadden Sea flyway population (Hario & Rintala 2006).

In Eiders, years of high duckling survival occur infrequently, and have been reported at intervals of 2 to 6 years in a British colony (Coulson 1984). For Eiders in the Baltic-Wadden Sea population, single years of good reproduction have been found separated by poor periods lasting 12 years (Swennen 1991a, Hario & Rintala 2006). If years of good reproductive outputs are related in some way to years of good female condition, then it may be predicted, that the occurrence of such years may be even more infrequent, if the overall average female body condition has decreased. Thus, Eider populations suffering general difficulties in obtaining adequate resources for optimal breeding, most probably will experience long-term declines in population size, primarily as a result of reduced duckling survival.

Hunting

Eider hunting in Danish waters opens 1 October, and during the first phase, the proportion of young first year birds bagged by hunters is very high (Noer et al. 1995, **Paper 4**). Considering the low fledging success of Eiders, hunting thus seems to remove individuals that have managed to survive the first critical weeks when most duckling mortality takes place (e.g., Swennen 1989, Flint et al. 1998).

Based on recoveries of ducklings measured and marked during the first weeks after hatch, ducklings may be divided into three categories depending on their body condition. One group of the ducklings in poor condition, which are not recovered as either breeding birds in the colonies nor as shot by hunters, a second group of ducklings of intermediate body condition, which mainly are recovered as shot during the first hunting season, and a third group of good body condition, which mainly are recorded as breeding birds (**Paper 7**, **Paper 8**). This provides some evidence that hunting removes ducklings in poorest condition present at the time the hunting season opens, while the strongest individuals survive and recruit to the breeding populations. Most probably the poorest ducklings in each cohort have died during the first weeks or months post hatch prior to the hunting season.

However, duckling growth rates were not the same each year. Overall environmental conditions, as well as local habitat differences within years, affect the rate of growth and final duckling condition

between years (**Paper 9**), and indeed average body condition of duckling cohorts show marked variation from one year to another (**Paper 7**). The pattern of condition amongst three different groups of ducklings described above is likely to be manifest in a cohort of good average condition, but a different pattern emerges in a year when the average duckling cohort condition is poor. From a poor cohort, there is no difference in condition between individual shot by hunters or those that recruit as breeders. In a poor year, hunters shoot juvenile Eiders that otherwise would have had a high probability of recruiting to the breeding populations. The impact of hunting of juvenile Eiders on subsequent population development may consequently vary from year to year, depending on the growth pattern of ducklings in a given season (**Paper 8**).

1.5 Implications of body condition for population development

Even though Eider populations has been assumed to benefit from the general increase in eutrophication during the period of population increase, the size of Finnish population has not responded to recent eutrophication of the inner Baltic Sea (Rönkä et al. 2005). In the long term, continued eutrophication may have unfavourable effects on the prey of both adult and juvenile Eiders, by inducing changes in benthic communities or from extensive areas being frequently affected by oxygen depletion, thereby reducing overall prey abundance and availability (cf. Rönkä et al. 2005 and references herein).

Considering the general implications of poor body condition in relation to the reproductive output of females, e.g., reduced clutch size and duckling survival, an overall decreasing trend in body condition of Eider populations, as shown in Eiders in Finland during the period 1991–2004 (Lehikoinen et al. 2006), would predictably lead to a reduced level of reproductive output. Likewise, reproducing at a lower average body condition may infer a lower survival probability, if the pattern of markedly reduced survival rates found in several duck species when breeding at sub-optimal, as well as super-optimal, body conditions (Blums et al. 2005) also apply to Eiders. So far no general changes in adult survival have been reported from Baltic populations and related to decreases in breeding number (Hario & Rintala 2006, but see Christensen & Noer 2001). However, elsewhere, higher mortality rates have been documented in Eider females breeding in poor years (years of substantial non-breeding and low clutch size) (Coulson 1984), and in females that apparently “over-invested” by engaging in brood care (Hanssen et al. 2003a).

These results suggest that when breeding in both inadequate and in to good condition Eider females experience a cost in terms of reduced survival probability.

Females during the recent population decline in the Baltic-Wadden Sea population have experienced higher mortality rates than males as shown by changes in sex-ratio among adult Eiders in the Danish Bag Statistics/Wing Survey of Waterfowl, changing from a previously stable 60/40 male/female ratio to 70/30 ratio at present (**Paper 5**), and from a significant change from a female bias to a male bias during the spring migration of Eiders in the Golf of Finland (Kilpi et al. 2003, **Paper 5**). Calculated in relation to the overall population estimates (Delaney & Scott 2002, Delaney & Scott 2006), the change in the sex-ratio indicate that the female population segment has declined about 50% while the male segment has declined by c. 22 % during the 1990s. Acknowledging that the duties associated with reproduction infer increased cost to female Eiders in terms of decreased survival rates (Flint et al. 1998), this probably explains a skewed sex ratio of 60 % males and 40 % females previously recorded in the Baltic populations (Swennen et al. 1979). However, the recent change to a sex-ratio of 70 % males and 30% females (**Paper 5**) indicates that females presently experience higher mortality rates than expected from the cost of normal reproductive investments, which could relate to the lower average body condition documented by Lehtikoinen et al. (2006).

Even though Lehtikoinen et al. (2006) showed an almost significant decrease in long term trend in the average female body condition during 1991–2004, they also suggested that global warming may benefit Eider reproduction, as they showed that both clutch size and fledging success was significantly higher in years when ice break-up occurred early, and that female body condition were positively correlated with the North Atlantic Oscillation (NAO), an index of winter severity (Hurrell 1995, Hurrell et al. 2001). This result is not in agreement with an increasing global warming as the quality and growth of mussels is expected to decrease with higher average water temperature (Honkoop & Beukema 1997). One possible explanation for this discrepancy, and one which fits nicely with the overall resource allocation strategy of Eiders, may be, that the body condition of females deteriorates in relation to the duration of the period between arrival to the breeding grounds and start of egg laying in these migratory populations. In warmer years, females may start to breed shortly after arrival, whereas in cold years, females have to wait up to several weeks outside the breeding areas before ice break-up occurs, all the while expending stored energy, a difference that is probably not com-

pensated by a slightly later arrival in colder years (see Lehtikoinen et al. 2006). Consequently, if this interpretation holds, Eiders breeding in the northern Baltic area (Finland and Sweden) may benefit from global warming by earlier breeding, and not by an effect of winter conditions and female body condition. Thus, theoretically, Eider populations may increase as a result of global warming, as long as the benefits of earlier breeding and the associated higher reproductive outputs outweighs a potential increase in adult mortality related to a reduced average body condition.

Presently, very little is actually known about large-scaled and long-term changes in the foraging conditions of Eiders. Incidences of oxygen depletion linked to eutrophication and increased primary production have been reported to cause mussel die-offs (cf. Dolmer 1999), but areas most frequently affected by oxygen depletion are mainly shallow sheltered areas, such as narrow fjords, and deeper (>15 m) offshore waters (NERI 2004). However, in Danish waters, Eiders are generally distributed in coastal areas at depths of 2–10 meter (Petersen et al. 2006), a depth range that generally is not significantly affected by oxygen depletion, although mussels are known to have disappeared in some parts of the inner Danish waters (P.S. Kristensen pers. comm.). Thus mussel may have disappeared in some areas that probably have been within the reach of wintering Eiders. During the past 20 years, average sea water temperatures around Denmark have increased by c. 1–2° Celsius as a result of global warming (e.g., ICES 2006). The general effect of this temperature increase on mussel growth and condition is not known, although it is expected to decrease the energetic value of mussels as prey to Eiders (cf. Honkoop & Beukema 1997). However, in combination with a marked increase in commercial mussel fishery at about 1990 from below 10000 tonnes per year to a stable level of c. 30000 tonnes per year in inner Danish waters (Kristensen 1995, Kristensen & Hoffmann 2000), Eiders may thus have experienced a decline in prey profitability as well as a decrease in general availability, which may have affected foraging conditions to an extent that resulted in a decreased body condition.

Although it seems obvious that the foraging conditions of Eiders may be affected by both reoccurring episodes of oxygen depletion, higher sea water temperature and commercial mussel fishery, the significance of these variables in relation to the long-term development of the Baltic Eider populations has not yet been substantiated. Even though effects of such large scale changes are difficult to assess, future research should include these aspects given the potential of an ultimate effect on reproduction rates and survival of Eider populations.

1.6 Mitigation of the population decline

Management of Eiders in the Baltic-Wadden Sea flyway population is based on two major pillars, which are protection of the breeding habitats during the reproductive season and regulation of the hunt on the staging and wintering areas.

The common aim of protective actions is to secure a sustainable level of population size by allowing the population to reproduce as optimally as possible under prevailing environmental circumstances, and to balance exploitation of this natural resource (mainly recreational hunting) in order to harvest a population surplus without adversely affecting population size.

Protection of specific breeding grounds, involving restrictions in public access to reduce disturbance (with secondary egg loss to avian predators such as gulls and ravens) and removal of stationary predators (mink, fox, marten), may greatly increase reproductive success of a given population or colony. But,

even though such protective actions may increase in their relative value during periods of population decreases, or even are necessary as predators may benefit from more general changes in the environment while Eiders do not, it may be equally beneficial to Eider populations to expand protection to include foraging areas of high importance. Such areas may lay adjacent to breeding islands, but may also include larger coastal or offshore areas used mainly during winter and spring.

The importance of protecting critical feeding areas for Eiders will increase if global warming or continued eutrophication result in adverse impacts on food abundance. Year round restrictions on commercial mussel fishery, commercial gillnet fishery (by-catch of Eiders; cf. Merkel 2004), gravel extraction and hunting in traditionally important feeding areas will benefit Eiders by providing undisturbed feeding conditions, especially during late winter and spring. This approach would provide birds with the means of securing adequate resource accumulation, which

may contribute to increased reproductive success and survival rates of breeding females.

As protection of important winter and spring foraging sites are beneficial to adult Eiders in preparation for breeding, protective actions in areas used by brood tending females, may further be beneficial to duckling survival. Such actions should include restrictions on boating, as disturbances caused by fast moving boats and kayaks may be disruptive to Eider brood-rearing and may disperse broods increasing predation on ducklings, reducing foraging time or rendering favoured foraging habitats inaccessible (Bregnballe & Christensen 1993). Likewise, some restrictions may be put on eel-trap and gillnet fishing in traditional shallow water rearing areas in order to reduce the by-catch of ducklings, as many recoveries of ducklings drowned in fishing nets occur within the first month after hatch (own unpubl. obs.).



Photo 4. A young researcher with a marked female eider, Stavns Fjord 1989.

Photo: Thomas Bregnballe.

In many countries with an open season on waterfowl, sustainability in national harvest rates is generally assessed from current population status and developmental trends. Based on these assessments, current policies in most European countries have been to adjust the length of the open season or to close hunting on specific species in case of unfavourable population development. Elsewhere, recreational or sport hunting is regulated by means of daily bag limits (USA, Canada and Greenland) (e.g. Nichols et al. 1998).

Outside the breeding period, Eiders in the Baltic-Wadden Sea flyway population are predominantly hunted in Danish waters. Most recently (2004) the open season in Denmark has been shortened from 1 October to 28 February for both sexes, to 1 October to 15 January for female Eiders and 1 October to 15 February for males at present. In combination with a (1994) ban of hunting of Eiders within extensive EU bird protection areas in February, this action has markedly reduced the hunting pressure in late winter, especially on adult females, and at a time where Eiders are starting to accumulate resources necessary for successful breeding. The changes made in 2004, have crudely been assessed to have reduced the annual female Eider bag by c. 8.500 individuals. In a male-biased Eider population, a longer open season on males than on females would not jeopardise the reproductive potential of the population, as long as the sex-bias does not reverse as a result of sex-differentiated hunting (cf. Kokko et al. 1998).

From a reproductive viewpoint, reducing the hunting season in late winter should favour survival of individuals that are about to breed. Thus, the benefits of reducing the length of the open season compared to postponing the start of the hunting season, is greater in terms of reproductive potential, as a large proportion of Eiders shot during the first month of the season is composed of juvenile birds, while adults dominate the bag late in the season (Noer et al. 1995). Thus, from a conservation perspective, Eider populations, at least in Denmark, may experience increased recruitment and hence, potentially increase, if opening of the hunting season is postponed by one or two months in years of low average duckling body condition. At this time, the juvenile Eiders from Danish colonies probably are diluted by the massive arrival of Eiders from Sweden and Finland. Surely, Baltic breeding populations would not benefit from a change early in season in Danish waters, but similar actions may be worth considering for the Finnish populations in case of a high proportional juvenile kill early in the hunting season.

1.7 Conclusions

In recent decades, the Baltic-Wadden Sea flyway population of Eiders has undergone marked changes, first experiencing a steep increase during the 1970s and 1980s, followed by a marked decline during the 1990s. Whereas the population increase most probably related to improved foraging conditions, and occurred despite substantial and greater hunting pressure at that time, there is no one obvious explanation for the recent population decline. There have been several reported incidences involving mass simultaneous mortality amongst this population during the period of decline, each of which were insufficient on their own to explain the overall level of decline. Being a long lived species with relatively low and highly fluctuating reproductive success, the population size of the Eider is extremely sensitive to even small increases in annual mortality, but is highly insensitive to large changes in annual reproductive output. Its long-lived population buffers annual changes in reproduction more effectively because annual survival probability is so high. Hence, taken together, the mass mortality of birds through starvation on the Netherlands wintering grounds and from avian cholera outbreaks may not be numerically great, but could together constitute a compound contribution to the causes of the decline. Hence, although the total impact on the populations from these episodes most probably collectively accounted for much less than one quarter of an estimated decline of c. 400,000 individuals in the total flyway population, it seems reasonable to assume, that Eiders have experienced general increases in mortality and/or decreases in reproductive success, related to other factors than those recorded in relation to disease and winter starvation, although such general changes have not yet been documented.

Female Eiders have been found to lay increasingly smaller clutches and have shown a decreasing average body weight during the period of recent population decrease, indicating that Eiders in the Baltic-Wadden Sea populations may have experienced poorer foraging conditions which have affected their ability to accumulate adequate resources for optimal reproduction. Since mortality and reproductive success in female Eiders is largely influenced by the body condition of individuals, deteriorating foraging conditions of Eiders thus seems an obvious explanation for, or at least a substantially contributing factor to, the recent population decline. Likewise, a lower average body condition of Eiders may lead to a general reduction in energetically costly immunocompetence, which might explain the apparent increase in frequency of avian cholera epizootic

recorded recently and the more frequent reports of parasite infestations in both adults and juvenile Eiders, as well as outbreaks of viral diseases in ducklings. Presently, immunology is a growing topic in ecological studies, but few studies have so far coupled the cost of immunity to life history traits and population developmental trends (cf. Hanssen 2006).

Although there is little existing documentation of long-term declines in the average adult mortality rates or in reproductive success in Baltic Eider populations related to deteriorating foraging conditions, the incidences of mass starvation in the Wadden Sea area during the winters 1999/2000–2001/2002 related to poor foraging conditions (Camphuysen et al. 2002, Ens et al. 2002, **Paper 10**), indicates that Eiders are susceptible to such changes. Consequently, in the face of changing food availability and or food quality, Eider populations may be adversely affected by continued eutrophication and associated incidences of oxygen deficits in the water column in coastal marine areas, global warming and by increasing commercial exploitation of their main prey, mussels.

Presently, the marked decline of the Baltic-Wadden Sea Eider flyway population assessed from winter surveys has not been matched by similar reductions in national surveys of breeding numbers, although several local populations have shown marked declines. This discrepancy may be explained if Eiders presently start to breed at a younger age, and such behavioural change may have taken place due to relaxed density dependent regulation for breeding sites as the populations have declined. However, if the stable breeding numbers reflects a younger recruitment age, then the non-breeding (young) segment of the populations is correspondingly reduced. A reduction in breeding numbers may thus be expected to emerge in the near future as the non-breeding segment most probably will be slowly depleted, if not compensated by increased reproductive success from earlier breeding or from relaxed density dependent regulation of fledging success. Likewise, the sensitivity of the populations to future incidences of mass mortality, e.g., avian cholera epizootics, is increased.

The pattern of population development in the Gulf of Finland shows remarkable similarities with a logistic growth trajectory with an overshoot, but whether such a development applies to the overall Baltic population is an open question. The tendency of poorer body condition in breeding females indicates, however, that the Eider populations will decline to a level where relaxed density dependent effects offsets associated lower adult mortality rates and lower clutch sizes, as may already be the case in the Gulf of Finland.

The challenge for future research into Eider population dynamics will be to describe the changes in demographic parameters that most probably have or will occur in relation to general environmental changes, and which will be determinants of population trajectories in the coming years. To do so, continued individual marking of Eiders in combination with extensive breeding surveys, will be required to explore and document changes in the age composition of breeding populations and to obtain information on reproductive performance on both a cohort and individual basis. By conducting such research programmes, an ultimate goal should be to establish individual (quality) based population modelling, from which future population development, as well as population sensitivity to both small and large scale environmental changes and hunting, can be assessed. Since the most important demographic parameters, reproductive value and survival, are influenced by the body condition of individuals, variation in body condition, on both an individual and cohort level, and the interaction between foraging conditions and resource accumulation strategies in Eiders, would be central parameters in such models. Considering the potential implications of, e.g., global warming, eutrophication and commercial mussel fishery on the availability and quality of the main prey of Eiders, the need for more detailed data and robust population models will certainly increase markedly in the near future. The relevance of developing new management tools is further emphasised by the fact that Eiders in the Baltic population are heavily hunted, and consequently demands special considerations in relation to sustainable exploitation, especially given the present declining status of this flyway population.

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2 List of papers

- 1) Desholm, M., Christensen, T.K., Scheiffarth, G., Hario, M., Andersson, Å., Ens, B.J., Fox, A.D., Nilsson, L., Waltho, C.M., Lorentsen, S.H., Kuresoo, A., Camphuysen, K.C.J., Kats, R.K.H. 2002. Status of the Baltic-Wadden Sea population of the Common Eider *Somateria m. mollissima*. – *Wildfowl* 53: 167-203.
- 2) Christensen, T.K., Bregnballe, T., Andersen, T.H. & Dietz, H.H. 1997. Outbreak of Pasteurellosis among wintering and breeding common Eiders *Somateria mollissima* in Denmark. – *Wildlife Biology* 3: 125-128.
- 3) Pedersen, K., Dietz, H.H., Jørgensen, J.C., Christensen, T.K., Bregnballe, T. & Andersen, T.H. 2003. *Pasteurella multocida* from outbreaks of avian cholera in wild and captive birds in Denmark. – *Journal of Wildlife Disease* 39(4): 808-816.
- 4) Christensen, T.K. 2005. Factors affecting the bag size of the Eider *Somateria mollissima* in Denmark 1980-2000. – *Wildlife Biology* 11(2): 89-99.
- 5) Lehikoinen, A., Christensen, T.K., Kilpi, M., Öst, M., Saurola, P. & Vattulainen, A. Large-scale changes in secondary sex ratio in a declining population of Common Eiders *Somateria mollissima* (submitted to *Wildlife Biology*).
- 6) Christensen, T.K. 2000. Female pre-nesting foraging and male vigilance in Common Eider *Somateria mollissima*. – *Bird Study* 47: 311-319.
- 7) Christensen, T.K. 1999. Effects of cohort and individual variation in duckling body condition on survival and recruitment in the Common Eider *Somateria mollissima*. – *Journal of Avian Biology* 30: 302-308.
- 8) Christensen, T.K. 2001. Effects of duckling body condition on hunting vulnerability in juvenile and immature common Eiders *Somateria mollissima*. – *Wildlife Biology* 7: 97-104.
- 9) Christensen, T.K. 2002. Variation in growth rate and body condition of common Eider *Somateria mollissima* ducklings within and between years. – *Danish Review of Game Biology* 16: 25-32.
- 10) Kats, R.K.H., Christensen T.K., Bækgaard, H., Borgsteede, F.H.M., Ens, B.J., Camphuysen, K.C.J., Meesters, E.H.W.G., Leopold, M.F. & Drent, R.H. in prep. 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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In recent decades, the Baltic-Wadden Sea flyway population of Eiders has undergone marked changes, first experiencing a steep increase during the 1970s and 1980s, followed by a marked decline during the 1990s. There have been several reported incidences involving mass simultaneous mortality amongst this population during the period of decline, each of which were insufficient on their own to explain the overall level of decline.

The present thesis describes the overall population development in the Baltic-Wadden Sea flyway population of Eiders. In relation to the recent population decline, the thesis addresses the occurrence of epidemic disease, parasite infestations and the implications of hunting in relation to population development. The concept of body condition is introduced as a common currency, because the role of body condition in relation to population trends has not often been discussed in the literature. Finally, the synopsis is used to discuss the potential conservation measures that may be introduced and which might help in restoring the unfavourable development of the Baltic Eider populations.