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Winter climate affects subsequent breeding success of common eiders

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Abstract

The phenology of spring migration depends on the severity of the preceding winter and approaching spring. This severity can be quantified using the North Atlantic Oscillation (NAO) index; positive values indicate mild winters. Although milder winters are correlated with earlier migration in many birds in temperate regions, few studies have addressed how climate-induced variation in spring arrival relates to breeding success. In northern Europe, the NAO-index correlates with ice cover and timing of ice break-up of the Baltic Sea. Ice cover plays an important role for breeding waterfowl, since the timing of ice break-up constrains both spring arrival and onset of breeding. We studied the effects of the winter-NAO-index and timing of ice break-up on spring migration, laying date, clutch size, female body condition at hatching and fledging success of a short-distance migrant common eider (*Somateria mollissima*) population from SW Finland, the Baltic Sea, 1991–2004 (migration data 1979–2004). We also examined the correlation between the NAO-index and the proportion of juvenile eiders in the Danish hunting bag, which reflects the breeding success on a larger spatial scale. The body condition of breeding females and proportion of juveniles in the hunting bag showed significant positive correlations with the NAO, whereas arrival dates showed positive correlations and clutch size and fledging success showed negative correlations with the timing of ice break-up. The results suggest that climate, which also affects ice conditions, has an important effect on the fledging success of eiders. Outbreaks of duckling disease epidemics may be the primary mechanism underlying this effect. Eider females are in poorer condition after severe winters and cannot allocate as much resources to breeding, which may impair the immune defense of ducklings. Global climate warming is expected to increase the future breeding success of eiders in our study population.

Keywords: breeding success, clutch size, common eider, condition, immune defense, migration, NAO-index, spring arrival, the Baltic Sea, timing ice break-up

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Introduction

Two hypotheses have been proposed regarding the effect of climate on avian populations: the tub hypothesis suggests that climate determines the number of birds surviving the critical nonbreeding period of the year because of density dependence and weather conditions. The tap hypothesis predicts that annual variation in population size is related to the weather during the breeding season, because this will influence the influx of new recruits into the population in subsequent years (Sæther *et al*., 2004). According to Sæther *et al*. (2000, 2004), recent results in the temperate region support the first hypothesis.

The phenology of spring migrating birds and other animals is dependent on the severity of the preceding winter and approaching spring (Zhou *et al*., 1995; Sims *et al*., 2001; Forchhammer *et al*., 2002; Hüppop & Hüppop, 2003; Stefanescu *et al*., 2003; Lehikoinen *et al*., 2004; Vähätalo *et al*., 2004). This severity can be quantified using large-scale climatic indices such as the North Atlantic Oscillation (NAO) index in Western Europe (Hurrell, 1995; Hurrell *et al*., 2001); positive values indicate mild winters. These fluctuating indices may also be used as mimics of persistent climatic change,

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given that they prevail in one mode – positive or negative – for several years in a row. Short-distance migrants especially have been noted to respond strongly to climate variation (Hubalek, 2003; Lehikoinen *et al*., 2004). Despite the common knowledge that milder winters in recent years are correlated with persistently earlier migration and laying dates in many birds in temperate regions (Brown *et al*., 1999; Marra *et al*., 2005; Sparks *et al*., 2005), few studies have been published concerning the effect of climate on variation in spring arrival and how this variation relates to breeding success. Sparks *et al*. (2005) have urged the need for studies which document how climate change affects bird populations now and in the future.

Ideally, the effect of climate change should be studied at appropriate time and geographical scales for each bird species and population concerned (Ahola *et al*., 2004). The effects of climate change on the breeding success of birds have been equivocal. The NAO-index correlated negatively with the hatching and fledging success of northern fulmars *Fulmar glacialis* in Scotland (Thompson & Ollason, 2001), as did increased sea temperature with the growth rate and fledging success of tufted puffins *Fratercula cirrhata* (Gjerdrum *et al*., 2003). In British Columbia, survival and breeding success of adult yellow warblers *Dendroica petechia* was positively correlated with the Southern Oscillation Index (SOI), suggesting that global climate change may negatively affect populations (Mazerolle *et al*., 2005). On the contrary, higher productivity in red-winged blackbirds *Agelaius phoeniceus* in Ontario was associated with higher winter NAO values (Weatherhead, 2005). In line with this finding, pied flycatchers *Ficedula hypoleuca* in northern Germany started breeding progressively earlier, and also the clutch size and number of fledged young increased from 1970 to 1995 (Winkel & Hudde, 1997). Finally, in the collared flycatcher *Ficedula albicollis*, the laying date was negatively correlated with the NAO-index, whereas clutch size and fledging success were not (Przybylo *et al*., 2000).

In the northern hemisphere, winter temperatures are suggested to increase disproportionately due to climate change (e.g. Tol, 1994; Serreze *et al*., 2000). In Northern Europe, the winter NAO-index correlates negatively with the maximum ice cover of the Baltic Sea (Koslowski & Loewe, 1994; Omstedt & Chen, 2001; Chen & Li, 2004), and larger ice cover is associated with later ice break-up. Ice cover plays an important role for sea-breeding waterfowl, since they cannot arrive on their breeding areas before ice break-up and breeding cannot commence as long as there is an ice bridge to the mainland and between larger islands, because of increased risk of mammalian predation. We explored how the NAO and timing of ice break-up affect the breeding success of a short-distance migrant, the common eider *Somateria mollissima*, which is the most numerous breeding waterfowl in the Baltic Sea area (Delany & Scott, 2002). Variation in the quality of wintering habitats may produce differences in the individual condition of migratory birds that can have carry-over effects on subsequent stages of the annual cycle (Studds & Marra, 2005). Because the common eider is a pure 'capital' breeder (Drent & Daan, 1980), which uses stored resources for egg production and during incubation (Meijer & Drent, 1999; Hario & Öst, 2002; Waldeck *et al*., 2004), it is well suited as a study species for examining how winter conditions may affect subsequent breeding success.

Material and methods

Study area

The study area is situated in the archipelago off the Hanko peninsula, in the Gulf of Finland, south-west Finland, Baltic Sea (Fig. 1). The area consists of a complex of islands and islets in an area roughly $10 \times 10\,\text{km}^2$ in size (Öst & Kilpi, 1999). The study area is described in more detail by Kilpi & Lindström (1997), Öst & Kilpi (2000) and Kilpi *et al*. (2001).

Climate indices

We used the extended winter NAO-index (December–March) of Hurrell (1995) that is continuously updated (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) to describe the winter and early spring climate (see also Sparks *et al*., 2005).

The waters off our study area are frozen during an average year, whereas in mild winters there is little or no ice. Thus, the extent of the ice cover ultimately determines when eiders arrive at the study area. We used the Julian date of ice break-up at Jussarö, Gulf of Finland as an index of ice conditions in the breeding area and in the Baltic (Kalliosaari, 1982; Kalliosaari & Seinä, 1987; Seinä & Kalliosaari, 1991; Seinä *et al*., 1996, 2001, in press) (Fig. 1). In 1979–2004, the average date of break-up was 16 March ± 41 days varying from no ice cover to the latest break-up on 30 April. When analyzing the breeding success over the entire Baltic Sea as judged by Danish hunting bag data, we used the log-transformed maximum ice-cover of the Baltic Sea (Seinä & Kalliosaari, 1991; Seinä *et al*., 1996, 2001, unpublished) as a general indicator of ice conditions. In the winters 1986–2004, the average maximum ice-cover of the Baltic Sea was $154\,000\,\text{km}^2$, and varied from 52 000 to $405\,000\,\text{km}^2$. The timing of ice-break at Jussarö and maximum ice-cover of the Baltic Sea were tightly

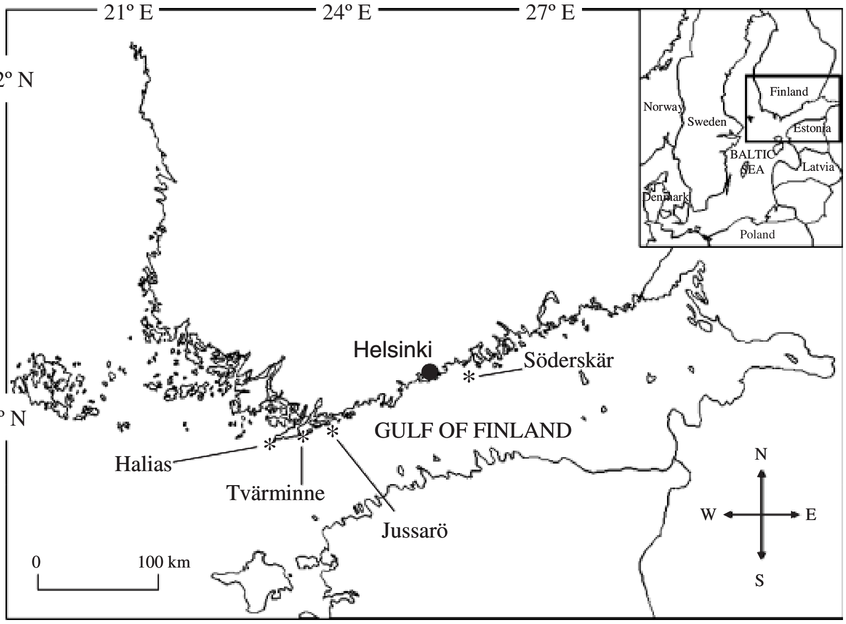

Fig. 1 Map of northern Baltic Sea and the study sites Hanko Bird Observatory (Halias) and Tvärminne and Jussarö archipelagos. The easternmost large occurrence of eiders in the Baltic Sea (Söderskär) is also shown on the map.

negatively correlated with the winter NAO-index during the whole study period 1979–2004 ($r_s = -0.61$, $n = 26$ years, $P = 0.001$; $r_s = -0.71$, $n = 26$ years, $P < 0.001$, respectively).

Eider data

Eiders in our study population winter in Danish waters (Kilpi *et al.*, 2003). We counted migrating eiders within identification distance at Hanko Bird Observatory (HALIAS; 59°49′N, 22°54′E) (Fig. 1) by means of spotting scopes (20–60 ×) every spring during 1979–2004 (excluding 1990). One to six persons counted birds in migratory flight at the Observatory using standardized routines including four hours of standardized counts beginning at sunrise (Lehikoinen & Vähätalo, 2000). Observation activity covered 75% (mean range 38–100%) of the days between 15 March and 10 May. The cut-off day of the migration data was 10 May. The median migration of eiders at HALIAS occurs between 1 and 28 April (Lehikoinen & Vähätalo, 2000). The median date of observation showed a clear advancing trend ($r_s = -0.62$, $n = 25$, $P = 0.001$). However, when analyzed during the main migration period, i.e. 1–28 April, the observation activity did not show any trend ($r_s = -0.15$, $n = 25$, $P = 0.47$).

The timing of the early (first arrival date (FAD)) and the median (median migration date (MID)) phase of migration were defined as the Julian dates when the season's cumulative bird sum reached 5% and 50%, respectively (see also Lehikoinen & Vähätalo, 2000). The relationship between the arrival date and the date of ice break-up at Jussarö may be biased if observation activity was dependent on the timing of ice-break. We checked for this possibility by calculating the dates when the cumulative number of observation days reached 5% and 50% of the total number of observation days each spring, and measured Spearman rank correlations between these dates and the ice-break at Jussarö. Early observation activity (5%) did not depend on the timing of ice-break ($r_s = 0.17$, $n = 25$, $P = 0.39$), but the median of the observation activity days showed a significant positive correlation with the timing of ice break-up ($r_s = 0.59$, $n = 25$, $P = 0.002$). However, when observation activity dates were analyzed during the main migration period of eiders (i.e. 1–28 April (Lehikoinen & Vähätalo, 2000)), the observation activity was no longer dependent on the timing of ice-cover (5% dates: $r_s = 0.160$, $P = 0.445$; 50% dates: $r_s = 0.015$, $P = 0.94$).

We monitored eider breeding phenology and breeding success in the Tvärminne (TVM) study area in 1991 and 1993–2004 (except for breeding success in 1993) (Kilpi & Lindström, 1997; Öst, 1999, Fig. 1). We assessed the population size by (1) nest counts on census islands ($n = 33$) in the area, and by (2) large-scale brood counts at the time when duckling have hatched (Öst, 1999). This information was used to assess the number of fledglings produced each year per the number of females found breeding (up to 1998; Öst, 1999) or at sea once the ducklings have hatched (from 1998 onwards). Fledged ducklings refers to juveniles at least 50 days old (fledging occurs at ca. 70 days; Cramp & Simmons, 1977).

We also assessed whether climate affects the breeding success on a larger scale by using data on the Danish hunting bag in the wintering areas during the winters 1986–2005. Wings of shot eiders were collected by hunters, which yield a measure of annual proportion of juvenile birds. The annual proportion of juveniles of all hunted eiders in the wintering area reflects the breeding success of the previous summer (Noer *et al.*, 1995). Wing data were obtained from Noer *et al.* (1995), yearly reports published by Danmarks Miljöundersögelser (www.dmu.dk) and Anthony D. Fox (personal communication). We analyzed the correlations between the NAO, maximum ice-cover and proportion of juveniles in the Danish hunting bag the next winter.

Breeding females were annually trapped with handnets at the nest, under license from local authorities. Trapping was mostly done a few days before hatching: we recorded (1) the size of the full clutch and (2) the incubation stage of the clutch using an egg floatation test to determine the laying date to an accuracy of ± 1 day (Kilpi & Lindström, 1997). We also (3) weighed each female to the nearest 10 g, and (4) measured the length of the radius-ulna to the nearest 1 mm. This procedure allows us to estimate the hatching weight of the female by regressing log-transformed body weight on log-transformed incubation time (see Kilpi & Lindström, 1997), and using this information we derived a mean daily weight loss. We also determined a body condition index; condition indices were derived as standardized residuals of actual body masses from those predicted from regression of log-transformed body mass on log-transformed length of the radius-ulna (Ormerod & Tyler, 1990). Females are also given unique colored tags attached to one of the primaries (Kilpi *et al.*, 2001), and broods hatched in the TVM area stay close to their nesting island throughout the breeding season (Öst & Kilpi, 2000). Hence, our measure of reproductive success is specific for the TVM population.

Statistical methods

We controlled for the effect of one variable (e.g. timing of ice break-up or maximum ice cover) when analyzing the effect of another (e.g. the NAO) and vice versa by conducting partial correlation analyses. We used partial linear correlation when data were normally distributed (climate indices during 1986–2004, clutch size, body condition and fledging success), and Kendall partial rank-order correlation (Siegel & Castellan, 1988) when the assumption of normality was not met (ice break-up during 1979–2004, laying date and mean daily weight loss). Temporal trends were tested by Spearman rank correlation and extent of annual variation of the breeding variables was analyzed by Kruskal–Wallis ANOVA.

Results

The climate indices

The NAO-index did not show a significant trend over time, whereas ice break-up occurred earlier with time (Table 1). The two indices were significantly negatively correlated with each other (Table 1). The NAO-index was significantly above zero during the study period (one-tailed *t*-test: $t_{25} = 2.76$, $P = 0.01$).

Climate and eider migration

Eiders showed a strong positive trend towards earlier migration over the study period (Table 2), in all aspects studied here (FAD and MID) (Figs 2 and 3). FAD ranged from 17 March to 16 April.

When the NAO and the timing of ice break-up were considered separately, both climatic indices were correlated with the timing of migration (FAD and MID) (Figs. 2 and 3), showing that milder winters with earlier ice-break result in earlier migration. However, the timing of migration (FAD and MID) was more tightly linked to

Table 1 Descriptive statistics of the winter NAO-index, the timing of ice break-up at Jussarö and maximum ice-cover of the Baltic Sea during the period 1979–2004

Index	Mean ± SD	Range	Trend 1979–2004	*P*-value
Winter NAO- index	1.12 ± 2.08	−3.78 to + 5.08	None, $r_s = -0.07$	0.75
Ice-break at Jussarö	16 March ± 41 days	No ice – 30 April	$r_s = -0.44$	0.02
Maximum ice-cover	177 000 km^2	52 000 ± 405 000 km^2	$r_s = -0.36$	0.08

Trends are based on Spearman rank correlations for the entire data set.
NAO, North Atlantic Oscillation.

Table 2 Descriptive statistics of the indices describing the migration of eiders at HALIAS in 1979–2004 (excluding 1990)

Indices	Mean ± SD	Range (CV%)	Trend	*P*-value
FAD	30 March ± 10 days	16 March–15 April (11.0)	$r_s = -0.64$	< 0.001
MID	10 April ± 6 days	27 March–19 April (5.6)	$r_s = -0.58$	0.003
FAD to MID	11 ± 6 days	2–24 days (57.5)	$r_s = 0.62$	0.001

Given are first arrival (FAD), median migration date (MID) and the time lapse between these two dates (FAD to MID). Annual trends are analyzed with Spearman rank correlation.

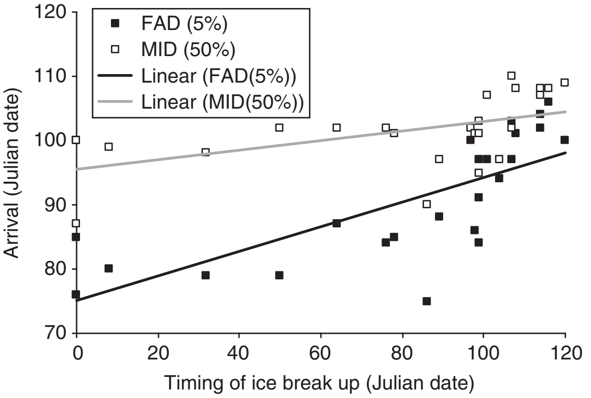

Fig. 2 Annual arrival dates (FAD, first 5% of the annual sum of migrants; MID, median migration date) of eiders at the Hanko Bird Observatory in relation to ice break-up at Jussarö, Gulf of Finland. Linear trend lines illustrate positive correlations between the timing of migration and ice break-up (FAD: $r_s = 0.86$, $n = 25$, $P < 0.001$; MID: $r_s = 0.68$, $n = 25$, $P < 0.001$).

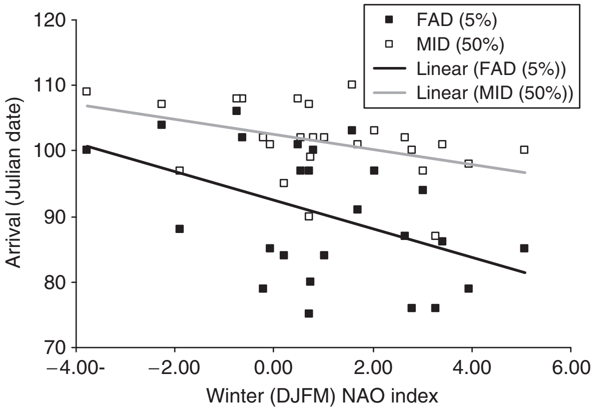

Fig. 3 Annual arrival dates (FAD, first 5% of the annual sum of migrants; MID, median migration date) of eiders at the Hanko Bird Observatory in relation to the North Atlantic Oscillation (NAO)-index. Linear trend lines illustrate negative correlations between the timing of migration and the NAO (FAD: $r_s = -0.44$, $n = 25$, $P = 0.029$; MID: $r_s = -0.42$, $n = 25$, $P = 0.035$).

the timing of ice break-up than to the NAO-index. Thus, the timing of migration was significantly positively correlated with the timing of ice break-up (Kendall partial rank-order correlation: FAD: $T = 0.67$, $n = 25$, $P < 0.001$; MID: $T = 0.44$, $n = 25$, $P < 0.001$, NAO held constant), whereas the timing of migration was unaffected by the NAO (FAD: $T = -0.024$, $n = 25$, $P > 0.25$; MID: $T = -0.13$, $n = 25$, $P > 0.25$, timing of ice break-up held constant). The time lapse between FAD and MID was strongly positively correlated over the years (Table 2), so that subsequently earlier ice break-up and migration both independently produced a less synchronous migration period over the years ($T = -0.25$, $n = 25$, $P < 0.05$, when holding the timing of FAD constant, $T = -0.46$, $n = 25$, $P < 0.001$, when holding the timing of ice break-up constant, respectively). In contrast, the NAO-index and the FAD–MID interval were not significantly correlated, when holding the timing of ice break-up constant ($T = -0.07$, $n = 25$, $P > 0.25$).

Eider breeding characteristics

None of the breeding variables (laying date, clutch size, weight loss, body condition, productivity) showed any significant temporal trends over the 1991–2004 study period (Spearman rank correlations, all P's > 0.09, Table 3). However, both mean laying dates and body condition at duckling hatch showed significant variation between the years (laying date: Kruskal–Wallis ANOVA, $H = 538.2$, df $= 12$, $n = 1322$, $P < 0.001$; body condition: ANOVA $F_{12,1309} = 20.8$, $P < 0.001$). In contrast, clutch size did not vary significantly between years (Kruskal–Wallis ANOVA $H = 17.7$, df $= 12$, $n = 1321$, $P = 0.12$). However, clutch size significantly decreased with laying date during the breeding season (ANOVA $F_{11,1311} = 3.28$, $P < 0.001$). We were unable to statistically test for annual variation in mean daily weight loss and fledging success, because only one average value was derived for each year. Judged by these annual averages, however, the variation in the number of fledglings produced per incubating female (range 0.07–1.48) and mean daily weight loss (range 15.0–27.6 g) is considerable (Table 3).

Climate and eider breeding characteristics

Neither NAO nor the timing of ice break-up were correlated with mean laying date (Kendall partial

Table 3 Variables relating to eider breeding and breeding success in 1991–2004

Variable	Mean ± SD	Range (CV %)	Trend 1991–2004	*P*-value
Mean laying date	28 April ± 5	23 April–13 May (18.1)	None, $r_s = 0.22$	0.47
Average clutch size	4.77 ± 0.14	4.42–4.96 eggs (2.9)	None, $r_s = 0.44$	0.14
Average weight loss	23.9 ± 3.2	15.0–27.6 g (13.7)	None, $r_s = 0.07$	0.82
Mean condition	0.07 ± 0.51	−0.82 to +1.22 (573)	None, $r_s = -0.49$	0.09
Productivity	0.65 ± 0.47	0.07–1.48 young (72.3)	None, $r_s = 0.39$	0.22

Shown are averages of annual mean clutch size (13 years), mean laying dates (13 years), average daily weight loss of incubating females in grams (13 years), average standardized condition of females when duckling hatch and average productivity expressed as fledged ducklings per incubating female (12 years, see Material and methods).

rank-order correlation, NAO: $T = -0.19$, $n = 13$ years, $P > 0.1$, timing of ice break-up held constant; ice break-up: $T = 0.21$, $n = 13$ years, $P > 0.1$, NAO held constant, Fig. 4). However, the synchrony of laying dates (SD) showed a significant negative correlation with the NAO when timing of ice break-up was held constant ($T = -0.40$, $n = 13$ years, $P < 0.05$), whereas the timing of ice break-up did not show any correlation with laying synchrony when the NAO was held constant ($T = -0.27$, $n = 13$ years, $P > 0.1$). Correspondingly, the annual average daily weight loss of females was not correlated with the NAO-index nor the timing of ice break-up (NAO: $T = 0.08$, $n = 13$ years, $P > 0.25$, timing of ice break-up held constant; ice-break: $T = 0.12$, $n = 13$ years, $P > 0.25$, NAO held constant). However, smaller clutch sizes tended to be associated with later ice break-up (partial linear correlation: NAO held constant: $r = -0.50$, $n = 13$ years, $P < 0.1$, Fig. 4), whereas the NAO was not correlated significantly with mean clutch size ($r = 0.15$, $n = 13$ years, $P = 0.64$, timing of ice break-up held constant).

The NAO-index was significantly positively correlated with mean condition of females when ducklings hatched ($r = 0.83$, $n = 13$ years, $P = 0.001$, timing of ice break-up held constant), whereas the timing of ice break-up was not ($r = 0.46$, $n = 13$ years, $P = 0.14$, NAO held constant, Fig. 4). On the contrary, the timing of ice break-up was significantly negatively correlated with average fledging production at Tvärminne ($r = -0.611$, $n = 12$ years, $P = 0.046$, NAO held constant, Fig. 4), whereas no such correlation existed for the NAO ($r = -0.04$, $n = 12$ years, $P = 0.89$, timing of ice break-up held constant, Fig. 4). However, the NAO-index showed a nearly significant positive correlation with the subsequent proportion of juveniles in the Danish hunting bag ($r = 0.44$, $n = 19$, $P = 0.07$, maximum ice cover held constant, Fig. 5), whereas maximum ice cover was not correlated with the proportion of juveniles ($r = 0.06$, $n = 19$, $P = 0.80$ NAO held constant). The fledging success at Tvärminne and the proportion of juveniles in the Danish hunting bag the next winter showed a significant positive correlation (Pearson linear correlation, $r_p = 0.61$, $n = 12$, $P = 0.034$). Neither FAD nor MID showed any significant correlations with the five breeding variables.

Discussion

Both female body condition and fledging success were correlated with at least one of the two winter climate indices, indicating that the severity of the preceding winter and approaching spring affects the breeding success of eiders. The NAO-index describes the winter climate on a large scale from the eastern seaboard of the United Stated to Siberia (Hurrell, 1995), and is thus an adequate indicator of the severity of conditions at the wintering areas of eiders, whereas the timing of ice break-up more accurately reflects local conditions at the breeding areas. The NAO was correlated more strongly with body condition, which to a large part is acquired in the wintering areas in Danish waters (Hario & Öst, 2002). Nonbreeding is common in eiders, and is assumed to be linked to insufficient body reserves for breeding (Coulson, 1984). Similarly, the timing of ice break-up at the breeding area was more strongly correlated with fledging success at Tvärminne. The NAO-index was positively correlated with the proportion of juveniles in the Danish hunting bag, which suggests that climate affects the breeding success of the entire Baltic Sea area. Based on the results, global climate warming is expected to increase the breeding success of eiders in the Baltic Sea area in the future.

The results are similar to those of Gaston *et al.* (2005b), who found that Arctic thick-billed murres *Uria lomvia* and black-legged kittiwakes *Rissa tridactyla*, were able to shorten their food-finding visits with earlier ice break-up, resulting in increased growth and survival of young. Gaston *et al.* (2005a) suggested that global warming should benefit birds that are breeding on the northern limit of the species' range. Baltic eiders are not situated in the northern limit of species distribution (range in the Baltic 54–65°N), because breeding eiders can be found as far north as Svalbard (80°N) and Franz

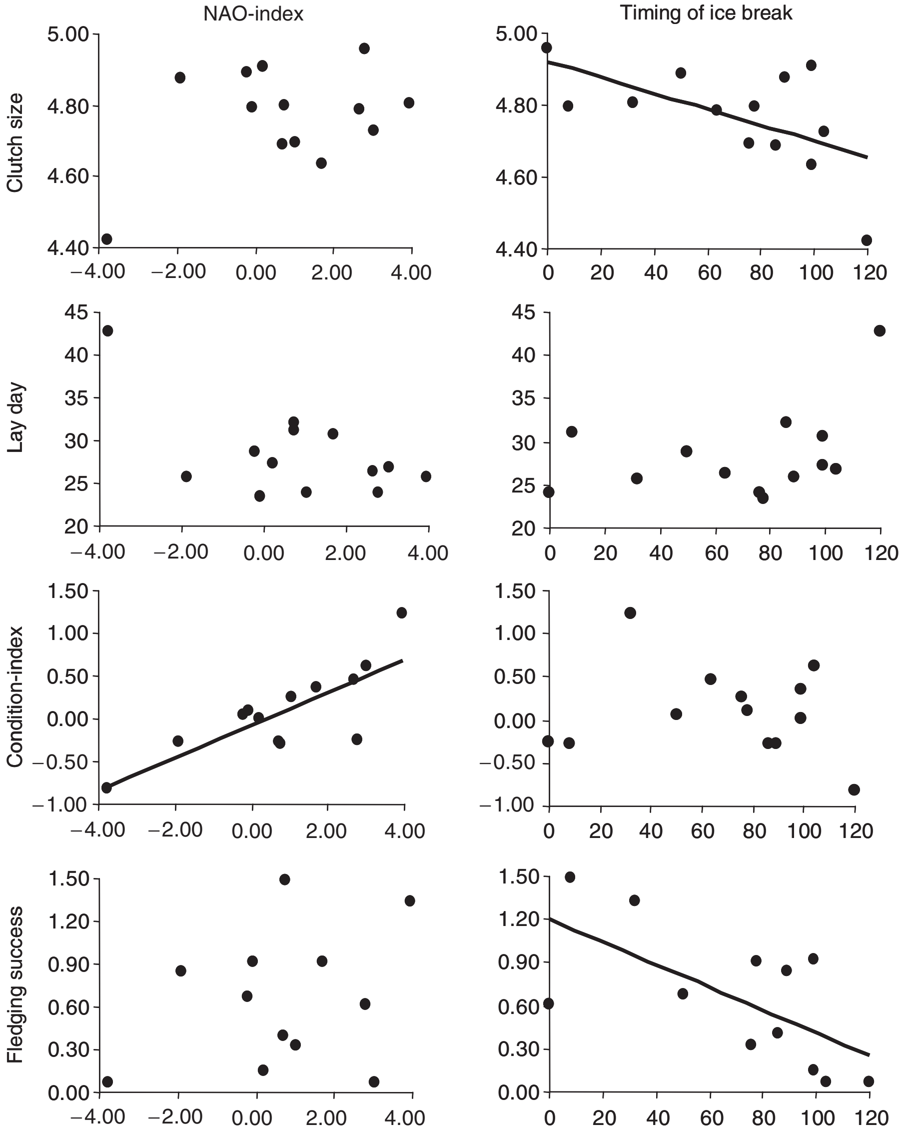

Fig. 4 Average clutch size, laying day, standardized condition of females and fledging success (see Material and methods) of eiders breeding at Tvärminne in relation to the North Atlantic Oscillation-index and the timing of ice break-up (Julian dates). Linear trendlines illustrate significant correlations between variables.

Joseph Land (81°N) (Cramp & Simmons, 1977). Our results are opposite to those presented in some other recent studies (Thompson & Ollason, 2001; Gjerdrum *et al*., 2003; Mazerolle *et al*., 2005). The reason for these differences could be that the breeding performance of common eiders is to such a large extent condition dependent (Kilpi *et al*., 2001; Öst *et al*., 2003), and severe climate inevitably has a negative effect on the condition of nesting eider females (Kilpi & Lindström, 1997). In contrast, in some other sea birds such as tufted puffins (Gjerdrum *et al*., 2003) and fulmars (Thompson & Ollason, 2001), climate warming has a detrimental effect on available food resources.

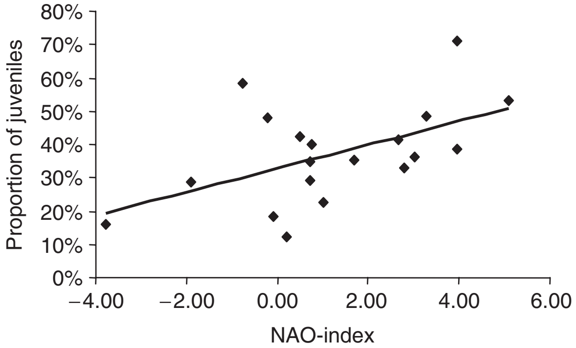

Fig. 5 Proportion of juvenile eiders in the Danish hunting bag in relation to the North Atlantic Oscillation-index of the preceding winter.

The timing of migration (FAD and MID) of eiders showed a clearly advancing temporal trend and the timing of migration correlated with both the NAO and the timing of ice break-up when each index was analyzed without statistically controlling for the confounding effect of the other. However, our partial correlation analysis indicated that the timing of ice break-up may be the main factor affecting the migration pattern. This supports the widely held view that timing of bird spring migration is related to the climate (Forchhammer *et al*., 2002; Cotton, 2003; Lehikoinen *et al*., 2004; Vähätalo *et al*., 2004), and that spring arrival has advanced during recent decades (Cotton, 2003; Lehikoinen *et al*., 2004; Marra *et al*., 2005; Sparks *et al*., 2005). Even though the NAO-index did not show any temporal trend over the study period 1979–2004, it was persistently significantly positive over the period. This mimics global warming, since the standardized average of the NAO-index during 1864–1994 was zero (Hurrell, 1995). This is supported by the fact that timing of ice break-up has advanced and the maximum ice-cover of the Baltic Sea has shown a nearly significant decreasing trend (Table 1). The mean ice extent of the Baltic Sea is predicted to decrease in the future (Meier, 2002), allowing even earlier eider migration.

Neither the NAO nor the timing of ice break-up were significantly correlated with the timing of egg laying, which is interesting, because many other studies have reported advanced or climate-related timing of egg laying (Brown *et al*., 1999; Przybylo *et al*., 2000; Both & Visser, 2001; Coppack & Both, 2002). This discrepancy may partly be due to the fact that earlier migration and earlier ice break-up both produced a less synchronous migration period. In pied flycatchers, selection for earlier laying is evident, which reduces the time interval between arrival and laying (Both & Visser, 2001; Coppack & Both, 2002). Because eiders are long-lived birds capable of breeding for more than 20 years (Coulson, 1999), selection for earlier breeding likely does not occur as swiftly as in passerines with shorter generation times. Our study period is too short to observe selection for earlier breeding, and reflects behavioral plasticity. Although the mean timing of laying was unaffected by climatic indices, the variation in laying dates decreased with increasing NAO-values. This suggests that there may be larger between-individual variation in the rate of body reserve acquisition following severe winters, and this in turn may be reflected on a larger spread of laying dates in the population.

The mean daily weight loss during incubation did not correlate with any of the climate indices. This suggests that local weather conditions during incubation rather than winter climate affects weight loss (cf. Kilpi & Lindström, 1997; Öst *et al*., 2003). Interestingly, however, the body weight of females at the end of incubation showed a significant positive correlation with the NAO. Our conclusion is that the amount of body reserves acquired at the wintering quarters in Denmark is a significant predictor of female condition when ducklings hatch, despite the confounding effect of local climate during incubation (cf. Hario & Öst, 2002). The common eider is a short-distance migrant like many other waterfowl of northern Europe (Cramp & Simmons, 1977), but it differs from most other ducks in being a pure ’capital’ breeder (Drent & Daan, 1980), using stored resources for egg production and during incubation (Meijer & Drent, 1999; Hario & Öst, 2002; Waldeck *et al*., 2004). Based on our results, winter severity in northern Europe affects the condition of females and, thus, the resources available for breeding. Hence, eider females cannot allocate as much resources into breeding after a severe winter compared with a milder one.

The variation of fledging success was much larger than the variation of clutch size (cf. Coulson, 1999), though both variables were negatively correlated with the timing of ice break-up. The smaller clutch size following later ice break-up could be partly explained by later egg laying, which decreases clutch size, even though the laying date itself did not correlate with climate indices. The fledging success of eiders in the Gulf of Finland is strongly affected by epidemics, which may cause as high as 99% mortality of ducklings during their first 4 weeks of life in some years (Hollmén *et al*., 2002). Epidemics seem ultimately caused by viral agents (Hollmén, 2002), which result in large-scale die-offs because of secondary infections. Viral agents identified by Hollmén *et al*. (2002) and Hollmén (2002) cause a break-down of duckling immune defence after an initial phase of several days or weeks during which time ducklings rely on induced immune defense, which is a maternal effect. Our results may indicate that following mild winters, females may be better able to reduce the likelihood of duckling epidemics because of their better body condition. Because immune defense and body condition are positively linked (Moreno *et al*., 1998; Møller *et al*., 2003, 2004; Mougeot & Redpath, 2004), this carry-over effect on ducklings may be produced by the capacity of good-condition females to produce antioxidants (such as carotenoids) in eggs, raising the level of induced immune defense, and thus reducing the risk of disease (Blount *et al*., 2003).

The scenario described above may be one possible mechanism explaining how climate could affect the immune defense of birds and ultimately their breeding success. Other mortality factors of ducklings in the Gulf of Finland are low food availability, predation by large gulls and weather conditions during brood-rearing, but the effects of the latter two factors for overall fledging success are considered fairly small (Hario & Selin, 1991). Annual variation in the availability of duckling foods could affect duckling condition, and this in turn may affect the ducklings' susceptibility to disease and predation (Swennen, 1989). The main food of ducklings are gammarid shrimps *Gammarus* spp. and blue mussels *Mytilus edulis* (Hario & Selin, 1991), both of which are ubiquitous in the western part of the Gulf of Finland (Särkkä, 1986, Westerbom *et al*., 2002), but there are no data available from our study population on how annual variation in these food resources is linked to variation in duckling body condition. However, data from a Danish common eider population suggest that significant annual variation in mean duckling body condition was unrelated to fledging success and recruitment into the breeding population, whereas relative body condition attained as ducklings within cohorts was positively correlated with subsequent recruitment (Christensen, 1999, 2002).

As a conclusion, when studying the effects of global climate change on breeding success of migratory birds, climatic effects in both wintering and breeding areas, along with the precise factors affecting the quality of offspring produced, need to be considered. In our case, female brood-rearing behaviour is linked to offspring survival and condition (Bustnes & Erikstad, 1991; Kilpi *et al*., 2001; Öst *et al*., 2003; M. Öst, B. D. Smith and M. Kilpi, in preparation), and female condition may also be directly linked to offspring quality in terms of yearly survival.

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