

# The effect of climate on adult survival in five species of North Atlantic seabirds

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## Summary

1. In long-lived species, adult survival is an important life-history trait. Better knowledge of the effects of non-catastrophic climate variation on the adult survival of long-lived seabirds is therefore needed. However, documentation of such effects is still rare.
2. Using capture–mark–resighting data, we modelled the annual survival rates of five species of seabirds, the common guillemot (*Uria aalge*), Brünnich's guillemot (*Uria lomvia*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*) and black-legged kittiwake (*Rissa tridactyla*). The data spanned 14 years of observation at a colony on Hornøya, off Northern Norway in the western Barents Sea.
3. A method of taking into account ring-loss of marked individuals is proposed. This approach made it possible to keep many observations which otherwise would have to be discarded.
4. The estimated survival rates were higher and less variable than most estimates for the same species from other colonies. There was extensive resighting heterogeneity. Ignoring this effect would have underestimated breeding life span by more than 50% in some species.
5. The analysis presented is the first study to document a correlation between the North Atlantic Oscillation (NAO) index and adult survival in North Atlantic seabirds. Other environmental variables considered were sea surface temperatures (SST) and prey stocks. In most of the species, models incorporating climatological variables were considerably better supported than models with constant survival, time-dependent survival or prey effects. SSTs tended to explain more of the variability in seabird survival than did the NAO.
6. The importance of prey availability was evident in some of the species, but climate was generally a better predictor of survival. Nevertheless, the evidence suggests that meteorological parameters affect seabird mortality only indirectly, possibly through the food chain. This conclusion rests on the observations that most NAO effects are lagged, and that survival rates decreased with increasing SSTs.

*Key-words:* adult mortality, Barents Sea, fish stock biomass, North Atlantic Oscillation, sea surface temperature.

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## Introduction

Many aspects of seabird life history respond to climatic

conditions (Ainley & Divoky 2001; Schreiber 2002; Durant *et al.* 2004). The most dramatic examples come from the effect of the El Niño–Southern Oscillation, which regularly causes total breeding failure and high mortality (e.g. Barber & Chavez 1983; Duffy 1990; Chastel, Weimerskirch & Jouventin 1993). The effect of the El Niño–Southern Oscillation is most pronounced in the south-eastern Pacific Ocean, although other

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**Table 1.** Explanatory variables examined. For each variable, the expected sign of the correlation and the reason is provided

Explanatory variable	Expected correlation	Reason
Extended winter NAO index, time lag zero	Positive	Direct effect of meteorological parameters (wind speed) on survival
Extended winter NAO index, time lags 1–4 years	Positive or negative	Indirect effect(s) of meteorological or oceanographic parameters mediated by the food chain
Sea surface temperature (SST) during August–October	Positive or negative	Indirect effect: food availability during flightlessness (moult)
Sea surface temperature (SST) during November–March	Positive or negative	Indirect effect: food availability when conditions (wind) are most severe
SST around Hornøya during April–August	Positive or negative	Indirect effect: food availability during the breeding season
Barents Sea capelin stock mass in the previous autumn	Positive	Main food source
Barents Sea herring 0-group index 1 year earlier	Positive	Food source
Barents Sea cod 0-group index in the previous autumn	Weakly positive	Food source of minor importance

parts of the Pacific (Ainley 1990; Ainley *et al.* 1994), the Southern Ocean (Chastel *et al.* 1993; Guinet *et al.* 1998) and even the Indian Ocean (Barbraud & Weimerskirch 2003; Crawford, Cooper & Dyer 2003) and Southern Atlantic (La Cock 1986; Duffy 1990) are also affected. Other, less pronounced climatic oscillations are known from other oceanic regions, the most well-studied of which is the North Atlantic Oscillation (NAO; e.g. Hurrell *et al.* 2003; Hurrell & Dickson 2004). However, those oscillations do not entail phenomena as catastrophic as during El Niño years. It may be partially for this reason that documentation of an influence of climatic variability on seabird life histories is rarer in the North Atlantic.

Although recent reviews have attempted to summarize the effects of the NAO on life-history traits of Atlantic seabirds (Reid, Becker & Furness 1999; Durant *et al.* 2004), no clear pattern has yet emerged. Several life-history traits have been shown to vary with climatic conditions in the North Atlantic (Aebischer, Coulson & Colebrook 1990; Montevecchi & Myers 1997; Barrett 2001a; Durant, Anker-Nilssen & Stenseth 2003), but adult survival has not been among these (but see Frederiksen *et al.* 2004). Responses of seabird adult survival rates to climate have so far been demonstrated only in the South and North Pacific and the Southern (Indian) Ocean (e.g. Barbraud *et al.* 2000; Barbraud & Weimerskirch 2001; Jones, Hunter & Robertson 2002; Barbraud & Weimerskirch 2003; Jenouvrier, Barbraud & Weimerskirch 2003).

According to life-history theory, adult survival is the parameter that has the highest elasticity – and thus importance – in long-lived species (Lebreton & Clobert 1991; Stearns 1992; Wooller, Bradley & Croxall 1992). Adult survival is therefore expected to be the life-history trait in which an effect of climatic variability should be least apparent (see Gaillard & Yoccoz 2003). The unwillingness of seabirds to jeopardize their survival has for instance been invoked to explain why the main effect of sea surface temperatures (SSTs) on alba-

ross population size acts through recruitment of new breeders rather than adult survival (Weimerskirch *et al.* 2003).

On the other hand, it would be surprising if adverse weather conditions did not affect survival at all. Many so-called seabird wrecks seem for instance to be related to periods of stormy weather (Hudson 1985). In addition to these direct causes of mortality, indirect effects, operating through the food chain, certainly affect seabirds in one way or another, especially as the effects of climate on marine invertebrates (Fromentin & Planque 1996; Heath *et al.* 1999) and fish stocks (Alheit & Hagen 1997; Ottersen & Loeng 2000; Hjermmann, Stenseth & Ottersen 2004) are increasingly well documented.

In this study, we set out to test whether and, if so, how climatic variability affects adult mortality patterns of five North Atlantic seabird species. We included both climatological variables (NAO, SSTs) and prey abundance data (Table 1), and assessed their relative importance by means of model averaging and variance components. All the variables, especially SSTs, were shown to be important in at least some of the species.

## Materials and methods

### FIELD METHODS

The study was carried out on Hornøya, an island off the north-east coast of Norway (70°22' N, 31°10' E), where *c.* 2000 breeding pairs of common guillemots *Uria aalge* (Pontoppidan), 600 pairs of Brünnich's guillemots *Uria lomvia* (L.), 300 pairs of razorbills *Alca torda* L., 5000 pairs of Atlantic puffins *Fratercula arctica* (L.), and 15–20 000 pairs of black-legged kittiwakes *Rissa tridactyla* (L.) breed (Anker-Nilssen *et al.* 2000; Barrett 2001b).

Our study of the demography of these five species started in 1989 with common and Brünnich's guillemots (i.e. 14 years of observation); puffins and kittiwakes have been studied since 1990 and the razorbill

since 1995. Observations of one species, the Brünnich's guillemot, were terminated in 2002 because birds were being displaced by an expanding common guillemot population.

Our samples consisted of breeding birds which were caught initially using noose-poles. Each bird was ringed with a numbered stainless steel ring and marked with a unique colour ring combination consisting of three or five Darvik rings. In subsequent years the colony was searched for ringed birds using binoculars. In addition to adult birds, we also marked two cohorts of puffin chicks (1994 and 1995), which entered the data base at an age of four years.

During the course of the study, a total of 136 common guillemots, 124 Brünnich's guillemots, 116 razorbills, 848 puffins and 949 kittiwakes were marked. The sample sizes in each year are given in Appendix I (Table A1).

#### CAPTURE-RECAPTURE ANALYSIS

Calculation of apparent survival probabilities  $\phi$  can be grossly biased when it is ignored that the probability  $p$  of recapturing any individual that has survived is not normally unity. The data were therefore analysed in a capture-mark-recapture framework, using program MARK (White 2003; for documentation, cf. White & Burnham 1999). The analyses utilized live resightings of marked individuals, a situation in which the Cormack-Jolly-Seber (hereafter CJS) model is an appropriate starting point (Cormack 1964; Jolly 1965; Seber 1965). Apparent survival rates  $\phi$  will, for simplicity, be referred to as survival in the remainder of the article, i.e. this measure includes permanent emigration, which could not be assessed separately with our data set.

Initial data inspection consisted of testing whether the CJS model fitted the data; that is, whether the 'iii assumption' was met (independence of fates and identity of rates among individuals). This was performed using RELEASE (as implemented in MARK; for documentation, cf. Burnham *et al.* 1987). This program evaluates the goodness-of-fit (GOF) of the CJS model by means of three tests, as follows.

Test 1 is applicable only when there are different treatment or attribute groups, and tests whether  $\phi$  or  $p$  differ between or among those groups. It was used to verify that puffins marked as adults and puffins aged 4 years or more that have been marked as chicks, could be pooled. Estimated rates did not differ between those groups neither for the 1994 cohort ( $\chi^2_{11} = 14.92$ ) nor for the 1995 cohort ( $\chi^2_9 = 12.46$ ). Test 1 was also used to assess whether 'problematic birds' could be included (see below).

Test 2 tests for deviations from the assumption that  $\phi$  and  $p$  are independent of specific sampling occasions. That assumption was violated in all species ( $\chi^2/\text{d.f.} > 1.5$ ,  $P < 0.12$ ) except Brünnich's guillemot ( $\chi^2_8 = 4.14$ ). In the common guillemot and the razorbill this heterogeneity was not interpretable because the data were insufficient. For the remaining two species, puffin and

kittiwake, however, the CJS model was clearly rejected ( $\chi^2_{19} = 179.08$  and  $\chi^2_{21} = 134.22$ , respectively).

One major reason for this deviation from the CJS model could be resighting heterogeneity, also known as trap dependence. This factor was corrected for using the method suggested by Pradel (1993), i.e. by breaking up capture histories into pieces containing two sightings, and removing each bird from the data set after the second sighting. This made it possible to treat trap dependence simply as age dependence in resighting rates. Decisions of how many years of trap dependence had to be accounted for were based on the Akaike information criterion corrected for small sample sizes ( $\text{AIC}_C$ ) (see below) and the overdispersion factor  $\hat{c} = (\chi^2_{\text{Test2}} + \chi^2_{\text{Test3}})/(\text{d.f.}_{\text{Test2}} + \text{d.f.}_{\text{Test3}})$ .

A likelihood ratio test (LRT) between the models  $\{\phi_t, p_t\}$  and  $\{\phi_t, p_{t+h_1}\}$ , where  $t$  is time (year) and  $h_1$  is resighting heterogeneity extending to the first year after the previous sighting, indicated that resighting dependence was indeed present ( $\chi^2_1 > 9$ ; but not in Brünnich's guillemot,  $\chi^2_1 > 0.30$ ). Guided by  $\text{AIC}_C$  values, we found that the 'trap happiness' extended over 2 years in the common guillemot and kittiwake and 4 years in the puffin. These models achieved acceptable overdispersion factors (all  $\hat{c} < 1.2$ ) and GOF test values (all  $P > 0.3$ ; approximated by subtracting the LRT  $\chi^2$  statistic from the original GOF  $\chi^2$  statistic; Lebreton *et al.* 1992) for all species.

Finally, Test 3 checks whether  $\phi$  and  $p$  are independent of prior capture histories. That was the case (all  $\chi^2/\text{d.f.} < 0.6$ ,  $P > 0.9$ ).

Model selection started with the most general model, namely  $\{\phi_t, p_{t+h_1}\}$ . Subsequent simplifications of the initial model were guided by Akaike's (1973) information criterion corrected for small sample sizes ( $\text{AIC}_C$ ; Sugiura 1978), where a given model's  $\Delta\text{AIC}_C$  refers to the difference between the  $\text{AIC}_C$  of the respective model and the optimal model. Resighting rates  $p$  were simplified first, followed by survival rates  $\phi$ . After testing the neighbourhood of the final model, this model was chosen for further analysis.

To take account of model uncertainty, the estimates of survival rates provided are based on model averaging. Models were weighted using their  $\Delta\text{AIC}_C$  as described by Buckland, Burnham & Augustin (1997). The standard errors provided with those estimates are unconditioned, i.e. they incorporate model uncertainty.

In calculating the temporal variance  $\tau^2$  of survival estimates, it has to be taken into account that the total observed variance  $S^2$  is a combination of both biologically relevant and of sampling variance. Utilizing the variance-covariance matrices provided by MARK, it was possible to separate those variance components following the approach described by Burnham *et al.* (1987; cf. Gould & Nichols 1998).

A special problem, caused by loss of colour rings, occurred in both the puffin and the kittiwake data sets, resulting in observations of incomplete colour ring combinations. Unless the ring number could be read, it

was impossible to tell which bird of a given colour ring series was the one that had lost its ring. Two options are available to address this problem: (i) all 'problematic' birds, i.e. all birds that belong to a colour ring series that could have given rise to the incomplete observation, are excluded from all further analyses. This drastically reduces the sample size (from 718 to 279 in puffins, and from 949 to 792 in kittiwakes). (ii) Birds are retained until the last 'unproblematic' year, i.e. until the last year before an incomplete colour ring combination that they could have given rise to, is observed. To avoid biasing the calculation of survival and resighting rates, those rates must not be calculated for problematic birds after they were last seen with complete colour combinations. Coding these years as 0 would artificially lower the estimated rates. Coding the respective birds as -1 in the encounter histories (which MARK interprets as 'not released' so as to ignore subsequent years) is not possible either, because the birds need not have been resighted during their last unproblematic year.

The solution is to code problematic years differently in the parameter index matrix (PIM). This is accomplished by using different attribute groups for birds that are unproblematic and every class of birds that are excluded starting from the same year. In the case of puffins, this means: one attribute group for unproblematic birds, and one group each for birds that are retained until 2001 (i.e. whose colour ring combination could have given rise to an incomplete combination observed for the first time in 2002), until 1999, until 1998 and until 1997. For kittiwakes, the respective attribute groups are: unproblematic, retained until 2001, and retained until 1997. The PIMs of all groups are then coded identically up to and including the last unproblematic year of any attribute group. The remaining years in the PIMs of problematic birds are filled by an additional fixed parameter. The values chosen ( $\phi = 0.5$ ,  $p = 0.0$ ) are arbitrary and do not influence the estimates of the other parameters.

In order to test whether it was legitimate to pool those attribute groups (up to and including the last 'unproblematic' year), Test 1 of RELEASE was run for data sets containing the unproblematic birds, adding one problematic group at a time, starting with the longest series, and terminating the data set at the last year that was unproblematic for all birds. In this way, Test 1 revealed that all attribute groups of puffins could be pooled ( $\chi^2/\text{d.f.} < 0.80$  and  $P > 0.70$  in all four tests). In kittiwakes, it was legitimate to add the birds that were unproblematic until 2001 ( $\chi^2_{21} > 18.91$ ), but not the birds that were unproblematic until 1997 ( $\chi^2_{25} > 42.59$ ). The latter group of individuals was thus excluded from further analysis.

#### ENVIRONMENTAL EFFECTS

To assess the effect of environment on survival rates, we included both climatic and biotic variables in the ana-

lysis after choosing an otherwise optimal model. Table 1 lists the variables used and the rationale for including them into the analysis. The first such variable was the North Atlantic Oscillation (NAO) index, which is known to correlate with many ecologically relevant parameters in many habitats (e.g. Ottersen *et al.* 2001; Stenseth *et al.* 2003). The index used was the principal component-based extended winter (i.e. December–March mean) NAO index (Hurrell 2003), because the signal : noise ratio of the NAO is strongest in winter (Barnston & Livezey 1987; Hurrell *et al.* 2003). In the initial model in this part of the analysis, the time effect in  $\phi$  was replaced by NAO index values at time lags of 0–4 years. Larger time lags were not considered because their existence did not seem biologically plausible. Subsequent simplification followed the procedure outlined above.

We also assessed the effect of sea surface temperatures (SST) on survival rates. Using optimum interpolation SST data available on a  $1^\circ \times 1^\circ$  grid (Reynolds, Stokes & Smith 2004a; cf. Reynolds *et al.* 2004b), we averaged SSTs for different subregions of the North Atlantic and for different seasons. The regions considered were the Barents Sea, the Norwegian Sea, the North Sea, the North-Eastern Atlantic Basin (i.e. west of the European, including Irish and Icelandic, west coasts, and east of Kap Farvel, Greenland) and the north-western area (west of Kap Farvel, i.e. off Newfoundland and the Labrador Sea). The periods considered were autumn (August–October) and winter (November–March). For the summer (April–August), the SSTs around Hornøya were also included.

Finally, the effect of prey abundance on survival rates was assessed by using stock estimates of some of the most important prey species of seabirds: for Barents sea capelin (*Mallotus villosus*) we used estimates of stock mass obtained in autumn acoustic surveys (ICES 2003a); autumn trawl surveys were the source of 0-group cod (*Gadus morhua*) indices (ICES 2003b); abundance of Norwegian spring-spawning herring (*Clupea harengus*) was represented by 0-group indices as measured in the previous year (ICES 2003a).

All environmental variables were normalized prior to analysis. Effects of these environmental variables are given as  $\beta$  estimates  $\pm$  corrected 95% confidence intervals (see below), and their effect is measured in terms of the variance explained by each variable. The latter was designated  $r^2$  and calculated as the proportion  $(\text{DEV} - \text{DEV}_{ev})/(\text{DEV} - \text{DEV}_0)$ , where DEV is the deviance (i.e. minus two times the log-likelihood) of the model assuming constant survival rates,  $\text{DEV}_{ev}$  is the deviance of the fully time-dependent model and  $\text{DEV}_0$  is the deviance of the model assuming a linear effect of an environmental variable. Following Breslow (1990), confidence intervals of the  $\beta$  estimates supplied by MARK were corrected for sampling variability by multiplication with  $\sqrt{(\text{DEV}_{ev} - \text{DEV}_0)/(\text{d.f.}_t - \text{d.f.}_{ev})}$ .

Covariation among species was tested using Pearson's product-moment and Spearman's rank correlation of

the logit-transformed real estimates that were obtained by model averaging of all relevant time-dependent models. The rationale behind the non-parametric method was to dampen the effect of large estimated survival rates (with real estimates close to unity).

The R language was used for statistical calculations (R Development Core Team 2003).

## Results

### TIME EFFECTS

Table 2 summarizes the mean survival rates for the five species and compares them to other colonies. Year-by-year results are given in Fig. 1 and Appendix I (Table A1). All estimates are based on weighted averages of the best models (see Materials and methods). Details on model selection are also provided in the Appendix (Table A2).

Resighting rates were high and, according to the optimal model of those species, constant in the common guillemot (94.5%, SE 0.8%), Brünnich's guillemot (92.6 ± 1.1%) and razorbill (95.3 ± 1.0%). In the remaining two species, resighting rates were lower and more variable (puffin, 76.2 ± 0.9%, range 9.2–90.2%; kittiwake, 84.2 ± 0.7%, range 40.0–91.7%). The kittiwake was also the only species where the model with fully time-dependent survival performed best. In both common and Brünnich's guillemots, models with negative linear trends in survival received more support than constant survival. Also in razorbills, a negative linear trend in survival was among the candidate models, even though it had a higher AIC<sub>C</sub> than the model with constant survival. In the puffin, the best model had constant survival.

Choosing among time-dependent and time-independent models makes temporal variability an either/or affair, which in the real world it is not. Therefore,

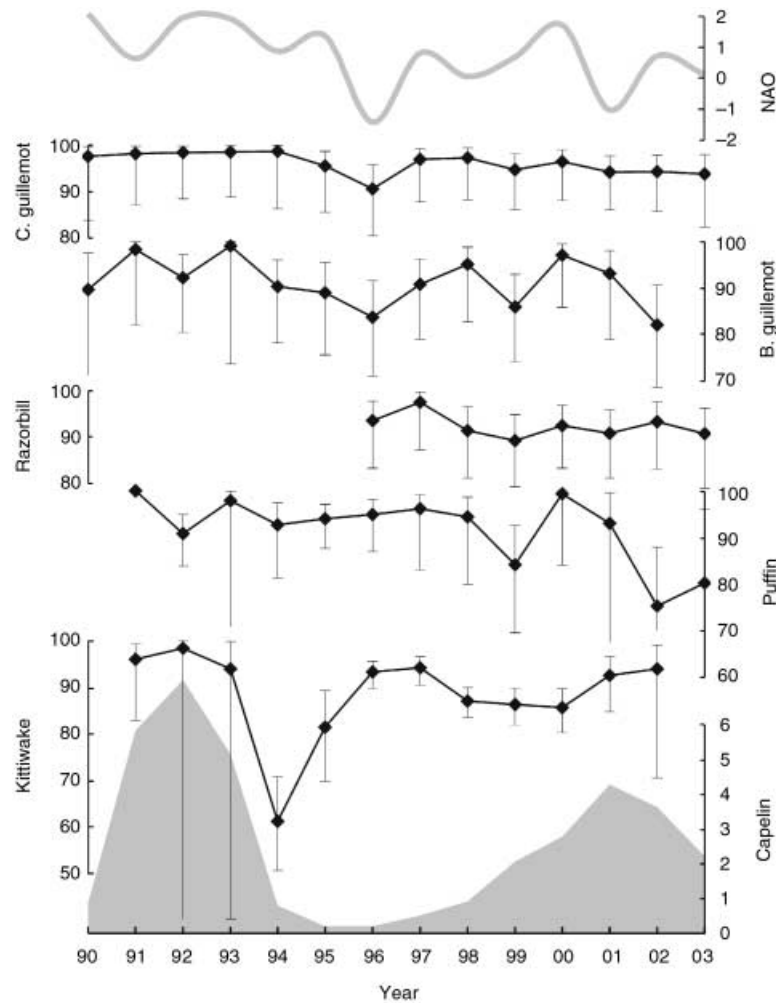
**Table 2.** Mean survival estimates ( $\phi$ ) and their variability ( $S$ ,  $\tau$ ) for Hornøya (boldface) and some other colonies, sorted in decreasing order of  $\phi$ . All measures are given as percentage. Survival rates ( $\phi$ ) of this study are based on model averaging;  $S$  and  $\tau$  are standard deviations ( $S$ , square root of the total variance;  $\tau$ , square root of the temporal variance<sup>a</sup>; see Materials and methods). Years indicate the range of observation (i.e. sample size = number of years – 1)

Species/colony	$\phi$	$S$ ( $\tau$ )	Years	Reference
<b>Common guillemot</b>				
Colonsay, Scotland, UK	96.4	6.4	1991–1996	Harris <i>et al.</i> (2000b)
<b>Hornøya</b> , Finnmark, Norway	<b>96.1</b>	<b>2.3 (0.0)</b>	1989–2003	This study
Isle of May, Scotland, UK	95.2	22.8	1986–1997	Harris, Wanless & Rothery (2000a)
SE Farallon Islands, California, USA	93.9 <sup>b</sup>	5.2	1986–1991	Sydeman (1993)
Canna, Scotland, UK	93.9	4.1	1984–1996	Harris <i>et al.</i> (2000b)
Skomer, Wales, UK	87.1 <sup>b</sup>	7.6	1972–1975	Birkhead & Hudson (1977)
Stora Karlsö, Gotland, Sweden	85.9	–	1962–1997	Olsson, Nilsson & Fransson (2000)
<b>Brünnich's guillemot</b>				
<b>Hornøya</b> , Finnmark, Norway	<b>91.6</b>	<b>5.3 (3.2)</b>	1989–2002	This study
Upernavik, Kitaa, Greenland	87.5	–	1961–1979	Kampp (1991)
Coats Island, NW Territ., Canada	87.3	5.5	1989–1993	Gaston <i>et al.</i> (1994)
<b>Razorbill</b>				
<b>Hornøya</b> , Finnmark, Norway	<b>91.9</b>	<b>2.5 (0.0)</b>	1995–2003	This study
Isle of May, Scotland, UK	90.5	7.0	1986–1997	Harris <i>et al.</i> (2000a)
Skomer, Wales, UK	90.1	–	1972–1995	Poole <i>et al.</i> (1998) <sup>c</sup>
Gulf of St Lawrence, Que., Canada	89.5	7.1	1989–1995	Chapdelaine (1997)
Shiant Islands, Scotland, UK	77.0	21.1	1971–1977	Steventon (1979)
<b>Puffin</b>				
<b>Hornøya</b> , Finnmark, Norway	<b>94.6</b>	<b>7.5 (4.9)</b>	1990–2003	This study
Isle of May, Scotland, UK	91.6	5.1	1986–1997	Harris <i>et al.</i> (2000a)
Skomer, Wales, UK	91.3	–	1972–1995	Poole <i>et al.</i> (1998) <sup>c</sup>
Røst, Nordland, Norway	89.6	5.8	1990–2003	Anker-Nilssen & Aarvak (2004), Anker-Nilssen pers. comm
<b>Kittiwake</b>				
Prince William Sound, Alaska, USA	92.2 <sup>b</sup>	–	1991–1995	Golet, Irons & Estes (1998)
Middleton Island, Alaska, USA	91.2	2.4	1987–1990	Hatch, Roberts & Fadely (1993)
Isle of May, Scotland, UK	88.2	5.5	1986–1997	Harris <i>et al.</i> (2000a)
<b>Hornøya</b> , Finnmark, Norway	<b>88.0</b>	<b>10.0 (9.0)</b>	1990–2002	This study
Fair Island, Shetland, UK	83.2	11.8	1986–1998	Rothery <i>et al.</i> (2002)
Foula, Shetland, UK	80.1	13.2	1986–1997	Oro & Furness (2002)
Brittany, France	79.5	6.5	1980–1994	Cam <i>et al.</i> (1998)
Tyne & Wear, UK	79.0 <sup>b</sup>	14.0	1954–1998	Coulson & Strowger (1999)

<sup>a</sup>When temporal variance were estimated to be negative, we assumed them to be zero.

<sup>b</sup>Those estimates were based on simple resightings rather than capture-recapture methodology.

<sup>c</sup>Cited in Harris *et al.* (2000a).



**Fig. 1.** Apparent annual adult survival estimates (%) of five species of seabirds at Hornøya, northern Norway (common guillemot, Brännich's guillemot, razorbill, puffin and kittiwake), and two environmental variables, namely the extended winter NAO index (top) and Barents Sea capelin stock biomass (shaded area at bottom,  $10^9$  kg). Survival estimates are based on model averaging; error bars are unconditional 95% confidence intervals. The large error intervals for near-unity estimates are computational artefacts; on the other hand, the increasing confidence intervals towards the end of the period mirror true uncertainty due to capture heterogeneity. Note also the exceptionally large confidence intervals in the kittiwake in 1992 and 1993 (especially compared to the period from 1996 to 2000), which are probably caused by the crash in 1994 in combination with capture heterogeneity (i.e. because of the presence of many difficult to observe birds, it was impossible to estimate whether they had died during the crash or 1 or 2 years earlier).

Table 2 presents the temporal standard deviations ( $\tau$ ) alongside with the survival estimates and the total standard deviations ( $S$ ). The highest temporal variability was found in the kittiwake (9%), which is in accordance both with the optimal model chosen and with Fig. 1. There was also some temporal variability among puffins (5%) and Brännich's guillemots (3%), even though the optimal models did not include time as a variable.

From visual inspection of Fig. 1 it seems that there is some covariation among the alcid species: all four species shared a local minimum in 1999 and a local maximum in 2000, both species of guillemots and possibly the razorbill shared a minimum in 1996, and both Brännich's guillemot and puffin experienced a minimum in 1992 and a maximum in 1993. However, only the temporal correlations of the Brännich's guillemot with the common guillemot and the puffin were signif-

icant (Table 3). However, it is remarkable that most correlations have positive signs (nine of 10, sign test  $P = 0.00098$ ).

#### CLIMATE EFFECTS

The effects of environmental variables are summarized species-wise in Tables 4–8. In both species of guillemot and the puffin several climate models achieved a lower  $AIC_C$  than any of the constant or time-dependent models, the  $\Delta AIC_C$  between the best climate model and the best model without climate being 2.86 in the common, 3.18 in Brännich's guillemot and 1.22 in the puffin (Tables 4, 5, and 7). In razorbills, constant survival was still the best model; however, its  $AIC_C$  differed only by 0.73 from the best climate models (Table 6). In the common guillemot, a single climate variable was able to account for approximately half the temporal variation

**Table 3.** Temporal correlation between adult annual survival rates in five species of seabirds on Hornøya, northern Norway. Above the diagonal: Pearson product-moment correlation coefficients, below the diagonal: Spearman rank correlation coefficients. (Significance levels are indicated by an asterisk:  $0.10 > p^+ \geq 0.05 > p^* \geq 0.01$ ; degrees of freedom are given in brackets). Data used are the logit-transformed real estimates provided in Table A1 in Appendix I)

Species	Common guillemot (CG)	Brünnich's guillemot (BG)	Razorbill (RB)	Puffin (PU)	Kittiwake (KI)
CG	1	+0.57* (11)	+0.32 (6)	+0.33 (10)	+0.02 (10)
BG	+0.55 <sup>+</sup> (11)	1	-0.09 (5)	+0.62* (10)	+0.18 (10)
RB	+0.12 (6)	-0.29 (5)	1	+0.21 (5)	+0.62 (5)
PU	+0.23 (10)	+0.70* (10)	+0.46 (5)	1	+0.24 (10)
KI	+0.08 (10)	+0.17 (10)	+0.71 (5)	+0.13 (10)	1

**Table 4.** Environmental effects on annual adult survival of common guillemots. All models containing prey species and the best climatic models are shown. ( $n_p$ , number of parameters; DEV, deviance;  $\Delta AIC_C$ , difference between the  $AIC_C$  of the current model and the minimum  $AIC_C$ ; ER, evidence ratio, i.e. the ratio of the  $AIC_C$  weights of the current model and the best model, equivalent to model likelihood given the set of models; estimate,  $\beta$ -estimates of the effect  $\pm$  corrected 95% confidence intervals, both multiplied by 1000;  $r^2$ , variance explained. See Materials and methods for details.) The  $AIC_C$  weight of the best model was  $w_0 = 0.100$  (any other  $w_i$  can be found by multiplication of  $w_0$  with the model's evidence ratio)

Effect <sup>a</sup>	$n_p$	DEV	$\Delta AIC_C$	ER	Estimate	$r^2$
Time	17	404.94	17.57	0.000		1.00
Cod	5	415.78	5.85	0.054	+58 $\pm$ 335	0.01
Capelin	5	414.52	4.59	0.101	+219 $\pm$ 337	0.12
Constant	4	415.88	3.93	0.140		0.00
Herring	5	412.19	2.26	0.329	+544 $\pm$ 460	0.34
Trend	5	411.76	1.83	0.400	-388 $\pm$ 285	0.38
NAO/0 +1	6	408.92	1.02	0.600	+442 $\pm$ 210 +117 $\pm$ 162	0.64
SST/North, autumn + NAO/0	6	408.85	0.95	0.621	-305 $\pm$ 642 +231 $\pm$ 263	0.64
SST/West, winter	5	410.55	0.62	0.733	-493 $\pm$ 305	0.49
NAO/0	5	409.99	0.06	0.971	+403 $\pm$ 210	0.54
SST/North, autumn	5	409.93	0.00	1.000	-499 $\pm$ 275	0.54

<sup>a</sup>NAO, North Atlantic Oscillation (with the time lags given); SST, sea surface temperature (for the ocean and season given; East, North-East Atlantic Basin; West, North Atlantic west of Greenland; North, North Sea).

**Table 5.** Environmental effects on annual adult survival of Brünnich's guillemots. The  $AIC_C$  weight of the best model was  $w_0 = 0.328$  (see legend of Table 4 for explanations)

Effect	$n_p$	DEV	$\Delta AIC_C$	ER	Estimate	$r^2$
Time	14	444.25	10.43	0.005		1.00
Cod	3	465.24	8.82	0.012	+82 $\pm$ 399	0.01
SST/West, winter	3	463.71	7.29	0.026	-238 $\pm$ 469	0.09
Constant	2	465.54	7.11	0.029		0.00
Trend	3	463.43	7.01	0.030	-229 $\pm$ 604	0.10
SST/North, winter	3	462.78	6.36	0.042	-215 $\pm$ 326	0.13
NAO/1	3	461.79	5.37	0.068	+255 $\pm$ 316	0.18
Capelin	3	460.66	4.24	0.120	+327 $\pm$ 373	0.23
Herring	3	460.43	4.01	0.135	+506 $\pm$ 563	0.24
NAO/0 +1	4	458.23	3.83	0.147	+269 $\pm$ 327 +273 $\pm$ 296	0.34
Herring + Capelin	5	454.39	0.00	1.000	+600 $\pm$ 438 +405 $\pm$ 63	0.52

in survival (54%), while the amount of variation explained by climate was substantially lower in Brünnich's guillemot (34%), the razorbill (32%), the puffin (19%) and the kittiwake (15%). The kittiwake was also the only species where a fully time-dependent model was

substantially better ( $\Delta AIC_C > 20$ ) than any model incorporating climate effects (Table 8). The time lags of the best NAO models were 0 years in the common guillemot and the kittiwake, 1 year in Brünnich's guillemot and the razorbill and 2 years in the puffin.

**Table 6.** Environmental effects on annual adult survival of razorbills. The AIC<sub>C</sub> weight of the best model was  $w_0 = 0.064$  (see legend of Table 4 for explanations)

Effect	$n_p$	DEV	$\Delta AIC_C$	ER	Estimate	$r^2$
Time	10	334.22	10.26	0.006		1.00
Herring	4	337.74	1.44	0.486	$-333 \pm 687$	0.07
Capelin	4	337.64	1.35	0.510	$-221 \pm 396$	0.17
Trend	4	337.60	1.30	0.521	$-157 \pm 269$	0.18
SST/Norwegian, winter	4	337.29	1.00	0.606	$-148 \pm 195$	0.25
NAO/1	4	337.18	0.97	0.643	$-183 \pm 241$	0.28
Cod	4	337.06	0.77	0.680	$+196 \pm 239$	0.31
SST/East, autumn	4	337.02	0.73	0.693	$-285 \pm 342$	0.32
Constant	3	338.32	0.00	1.000		0.00

**Table 7.** Environmental effects on annual adult survival of puffins. The AIC<sub>C</sub> weight of the best model was  $w_0 = 0.113$  (see legend of Table 4 for explanations)

Effect	$n_p$	DEV	$\Delta AIC_C$	ER	Estimate	$r^2$
Time	29	1715.97	6.88	0.032		1.00
Herring	19	1732.55	3.03	0.220	$+124 \pm 692$	0.01
Cod	19	1732.40	2.88	0.236	$+144 \pm 548$	0.02
Capelin	19	1731.86	2.34	0.310	$-138 \pm 340$	0.05
Trend	19	1731.45	1.93	0.380	$+410 \pm 916$	0.08
Constant	18	1732.77	1.22	0.543		0.00
SST/East, winter	19	1730.30	0.78	0.678	$+418 \pm 707$	0.15
SST/Norwegian, autumn	19	1729.60	0.08	0.960	$-679 \pm 522$	0.19
NAO/2	19	1729.52	0.00	1.000	$-530 \pm 1001$	0.19

**Table 8.** Environmental effects on annual adult survival of kittiwakes. The AIC<sub>C</sub> weight of the best model was  $w_0 = 0.998$  (see legend of Table 4 for explanations)

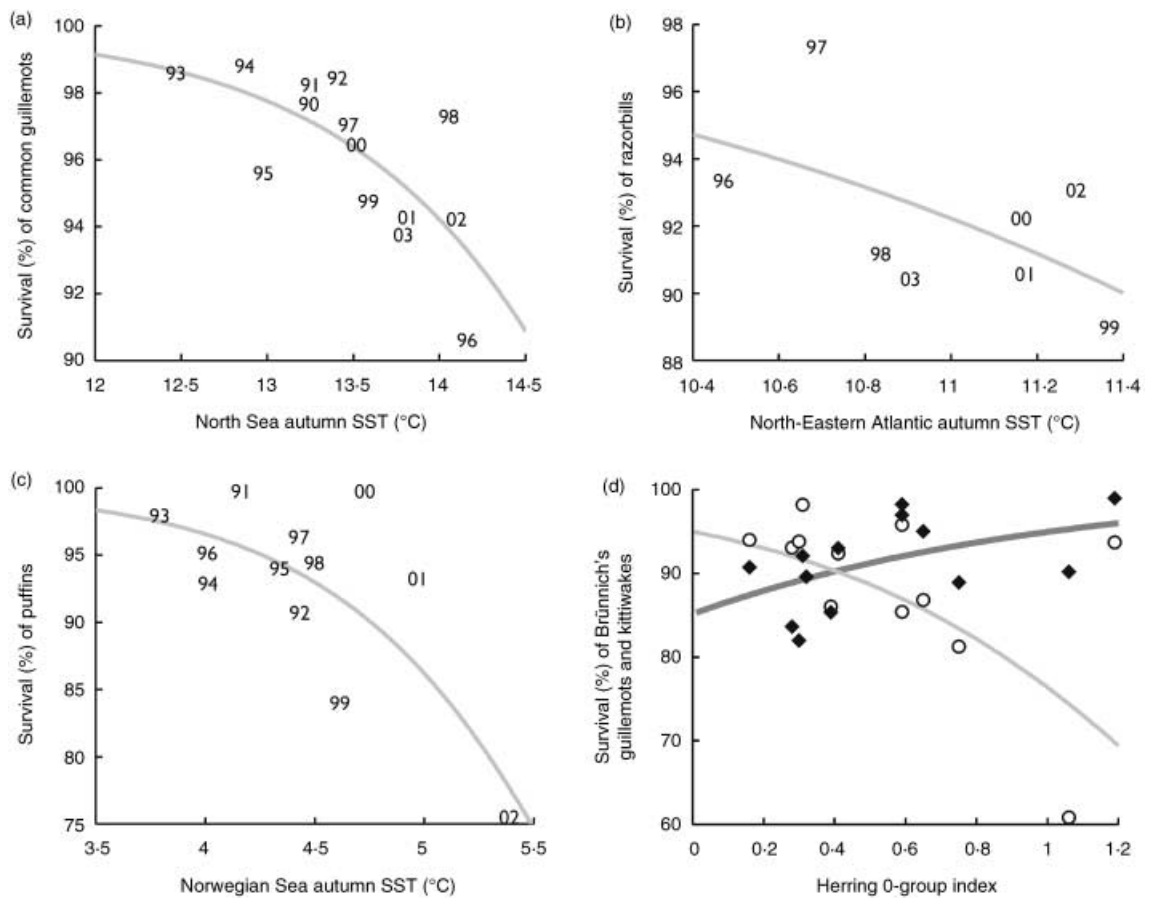
Effect	$n_p$	DEV	$\Delta AIC_C$	ER	Estimate	$r^2$
Constant	16	5762.67	56.96	0.000		0.00
Capelin	17	5761.81	56.38	0.000	$+81 \pm 495$	0.01
SST/Barents, autumn	17	5747.88	44.18	0.000	$+244 \pm 325$	0.19
SST/North, autumn	17	5745.69	41.99	0.000	$+328 \pm 379$	0.26
Cod	17	5745.03	41.33	0.000	$+269 \pm 203$	0.22
NAO/all five time lags	21	5719.16	23.55	0.000		0.55
Herring	17	5715.78	12.08	0.002	$-754 \pm 387$	0.59
Time	27	5683.46	0.00	1.000		1.00

SSTs tended to account for more variation in survival than did NAO, and autumn SSTs for more than winter SSTs. Also the subregions of the North Atlantic for which the SSTs in the best SST model were calculated differed between species; namely the North Sea for the guillemots (Fig. 2a, Tables 4 and 5), the North-Eastern Atlantic Basin for razorbills (Fig. 2b, Table 6) and, to a lesser extent, for puffins, which showed a strong relation to SSTs in the Norwegian Sea (Fig. 2c, Table 7). SSTs around Hornøya during the breeding season did not affect survival to the subsequent year in any of the species (all  $\Delta AIC_C > 2.40$ , all  $r^2 < 0.05$ ).

Most coefficients of the unlagged NAO effect were positive (and all with evidence ratios, or model likelihoods, larger than 0.25 were). The opposite was true of SSTs: most coefficients of SST effects had negative signs (and all with evidence ratios  $> 0.7$  had).

#### BIOTIC EFFECTS

In Brünnich's guillemot, a combined herring and capelin effect on survival was the overall best model. In the razorbill, a cod model achieved a  $\Delta AIC_C$  of 0.77. In the remaining species, however, models incorporating prey species abundance performed more poorly ( $\Delta AIC_C > 2$ , evidence ratios  $< 0.33$ ). Among prey species, and across bird species, herring accounted for most variation: 24% in Brünnich's guillemots, 34% in common guillemots and 59% in kittiwakes (even though the herring model was far less parsimonious than the time-dependent model in the latter species,  $\Delta AIC_C > 12$ ). While the sign of the estimate was positive in the guillemots, it was negative in the kittiwake (Fig. 2d). Capelin never explained more than 23% of variation in survival, and all corresponding evidence ratios were smaller than 0.6.



**Fig. 2.** Selected relationships between adult survival in seabirds from Hornøya and environmental factors. The factors chosen are the ones which accounted for most variation in survival of the respective species. Note that all relations between temperature and survival were negative. Regression lines appear curved in the figures; however, they are linear on a logit scale. See Tables 4–8 for estimates of the slopes and  $r^2$ . (a) A strongly negative relation between sea surface temperatures (SSTs) in the North Sea during autumn (August–October) and common guillemot survival. (b) A weakly negative relation between SSTs in the North-Eastern Atlantic Basin during autumn and razorbill survival. (c) A negative relation between SSTs in the Norwegian Sea during autumn and puffin survival. (d) Herring 0-group index and survival of Brännich's guillemot (black diamonds and dark grey curve) and kittiwake (open circles and light grey curve): weakly positive and negative relations, respectively.

## Discussion

Using capture–mark–recapture analysis we found that environmental variables can account for substantial proportions of the variation in apparent adult survival of three alcid species, the common, the Brännich's guillemot and the puffin (Tables 4, 5 and 7). In a fourth alcid, the razorbill, constant survival was the best and most parsimonious model; however, several models incorporating environmental variables performed nearly as well (Table 6), their AIC<sub>C</sub> deviating by less than unity from the optimal model. In the kittiwake, temporal variation in survival was much more pronounced than in the alcid species (Fig. 1, Table 2) and not readily accounted for by environmental variables (Table 8). There was only weak covariation in survival among the species (Table 3, Fig. 1).

Viewed in a life-history context adult survival is the parameter that has the highest elasticity, or that explains most variation in the lifetime reproductive success of long-lived species (Lebreton & Clobert 1991; Stearns

1992; Wooller *et al.* 1992). Seabirds, with their comparatively long breeding life span and low annual reproductive output, are often used as model species of such life-history strategies (e.g. Johnsen, Erikstad & Sæther 1994; Erikstad *et al.* 1998a; Weimerskirch, Zimmermann & Prince 2001). The unwillingness of seabirds to jeopardize their survival (and, thereby, future reproduction) should thus be expected to be visible in their responsiveness to climatic fluctuations (cf. Gaillard & Yoccoz 2003). In accordance with this expectation, there are many findings that relate different aspects of seabird breeding biology to climate, such as timing of breeding, breeding success or recruitment (e.g. Lyver, Moller & Thompson 1999; Kitaysky & Golubova 2000; Periman *et al.* 2000; Barrett 2001a; Durant *et al.* 2003; Inchausti *et al.* 2003). Adult survival is also known to be affected by extreme El Niño events (e.g. Barber & Chavez 1983; La Cock 1986; Jones *et al.* 2002). However, to our knowledge the findings reported here are the first documentation of a correlation between the NAO and survival of a marine top predator.

In comparison with other colonies of the seabird species studied, our survival estimates are high and show little temporal variation (Table 2). All survival rates estimated in this study are in the upper part of the range found by other studies. Except for the kittiwake and the puffin, our estimates are also the least variable among all colonies. With the data at hand, no explanation other than on an *ad-hoc* basis can be given. It has, for instance, been hypothesized that a local stock of capelin in the Varangerfjord may be an explanation of breeding success being comparatively high on Hornøya (Barrett & Furness 1990). If this is correct, it may also have a positive impact on adult survival by relieving them from food stress during the breeding season. Also the comparatively small colony size may relieve birds from competition for food.

Another explanation may be purely methodological: Prévot-Julliard, Lebreton & Pradel (1998: 85) warned that 'heterogeneous capture probabilities independent of survival probabilities tend to negatively bias survival estimates'. To find a model that fitted the resighting data of all species but the Brünnich's guillemot, we had to take into account trap dependences spanning 1–4 years. The effect of ignoring resighting heterogeneity is also emphasized by a comparison with earlier survival estimates on Hornøya (Erikstad *et al.* 1998b): for kittiwakes and puffins, the previous survival estimates were 8–9% lower, leading to severe underestimates of the average breeding life spans (puffins, 7 instead of 18 years; kittiwakes, 5 instead of 8 years).

The main explanation for the resighting heterogeneity in our study may be that individual birds differ in how well their nesting sites are protected and that, due to the high nest-site fidelity of the species (e.g. Ashcroft 1979; Fairweather & Coulson 1995; Harris, Wanless & Barton 1996; but see Boulinier *et al.* 2002), birds overlooked in one year have a higher probability of also being overlooked in subsequent years. This explanation is reinforced in puffins by their hole-nesting habits, which makes them the most difficult-to-observe species in our study, and the one with the most extensive resighting heterogeneity (4 years).

#### CLIMATE EFFECTS

The North Atlantic Oscillation (NAO) affects biological phenomena as diverse as flowering time of vascular plants, sex ratio in ungulates or spawning time of amphibians (Forchhammer, Post & Stenseth 1998; Post & Stenseth 1999; Post *et al.* 1999; see review by Ottersen *et al.* 2001). It has recently become evident that not only terrestrial and limnic systems and marine invertebrates but also marine top predators are affected by the NAO (Thompson & Ollason 2001; Thompson & Grosbois 2002; Durant *et al.* 2004). However, causal pathways of these interactions are not easily identified. The NAO is defined as a temporal fluctuation of sea level pressure anomalies (Hurrell *et al.* 2003) and can as such hardly be said to be the cause of any of these

responses. Rather it is convenient to treat the NAO as a 'proxy' for different climatic processes (Stenseth *et al.* 2003). A full understanding of any climate-related response requires that one identifies the factors that cause it. In the case of seabird survival, those factors could be wind and/or prey availability. While harsh weather conditions can be considered a direct cause of mortality, the latter factor is indirect, in that the climate effect is mediated through the food web.

We found evidence that climatic factors, as measured by the NAO extended winter index, influence adult survival of at least the auks studied, accounting for 12–54% of the variation in survival. Several lines of evidence suggest that these effects are indirect rather than direct. First, the presence of time lags in the NAO effect indicates that adverse weather conditions cannot be a major cause of climate-related mortality. Although the strongest NAO effect (in the common guillemot) was not lagged, there is evidence of a time lag of 1 year in Brünnich's guillemots and razorbills, and a time lag of 2 years in puffins. As judged by their evidence ratios, those models are either better (Brünnich's guillemot, puffin) or not substantially poorer (razorbill) than the best model without climate. The positive correlation with NAO at time lag 0 in the common guillemot is the only arguable sign of a direct climate effect (cf. Table 1). A causal link could lie in the fact that wind speed is positively correlated with NAO across most of the north-eastern North Atlantic (Durant *et al.* 2004), and that wind is known to have adverse effects on survival of seabirds (Hudson 1985; cf. Finney, Wanless & Harris 1999).

Secondly, even in the species with an unlagged NAO effect, most coefficients of sea surface temperature (SST) effects are negative, i.e. lower temperatures coincide not with reduced, but with higher survival rates. This also indicates that it is not temperature *per se*, but a mediated effect, presumably through the food chain, that triggers mortality (cf. Table 1). Weimerskirch *et al.* (2003) found for instance that population size of several albatross species in the Southern Ocean was positively affected by low SSTs, and invoked as explanation that krill abundance is positively correlated with sea ice cover (cf. Barbraud & Weimerskirch 2001; Jenouvrier *et al.* 2003). With some modifications (there is, for instance, no sea ice in the North Sea), a similar explanation will most probably be valid in the North Atlantic system as well. In the Barents Sea, a recent study has shown positive correlations between sea temperatures and herring recruitment and stock biomass (Hjermann *et al.* 2004). Herring, however, preys upon the preferred food source of Hornøya seabirds, the capelin, and thereby lowers the total biomass available for seabirds to prey upon (Hjermann *et al.* 2004). This shows that causal pathways can go in previously unexpected directions. The exceptionally bad breeding season that Scottish seabirds experienced in 2004 points in the same direction: warm water conditions in the North Sea have led to a crash in sand eel (*Ammodytes* spp.)

stocks (RSPB, unpubl. data; cf. Frederiksen *et al.* 2004). It will therefore be interesting to see whether the survival from 2004 to 2005 of Norwegian seabirds that winter in the North Sea will be affected as well.

Whatever the exact causes may be, their effects are dramatic at least for some species. In the common guillemot, for example, North Sea SST explains 54% of the variation in survival. This might not seem dramatic, given that the total variation in survival was low. However, for species with high adult survival and low fecundity, reductions in survival of even a few percentage points can have large effects on the lifetime reproductive success of individuals and, thereby, on population trends. The Hornøya population may be buffered to a certain degree by local fish stocks (see above), so it has still been increasing after a crash in 1987 (Lorentsen 2002; R.T.B. personal observation). However, other Norwegian colonies have shown steady and partly steep decreases, some even by 96% (Lorentsen 2002). Survival rates have not been studied in those colonies; however, if the results from Hornøya are representative, the situation will further aggravate, especially given that SSTs are predicted to further increase in the near future (IPCC 2001).

#### PREY

One obstacle in explaining seabird winter mortality is their widespread distribution across vast oceanic ranges (Fauchald & Erikstad 2002). Not only do environmental variables, both climatic and biotic, differ spatially and temporally between these areas, but seabirds can also move between them. In contrast to many other species, seabirds can simply leave an area with adverse weather or trophic conditions. This lowers the probability of finding effects of any one variable that is calculated for large oceanic ranges as a whole.

Bearing these precautions in mind, the comparatively weak effects of prey abundance found are not surprising. The estimates are built upon surveys in the Barents and the Norwegian Sea, and need not be representative of prey availability in the wintering areas. Furthermore, data were unavailable for one important prey, namely sand eels. This fish makes up a large part of the diet of some species during the breeding season (Barrett 2002), but stock estimates do not exist for the Barents Sea.

Of the three prey species we analysed, herring was clearly the species which explained most variance in seabird survival. This is somewhat surprising, given that herring did not make up much of the seabirds' diet during the breeding season at Hornøya before the crash in capelin stocks in 1994 (Barrett & Krasnov 1996). However, the sign of the estimates of herring effects are positive in both guillemot species, where it explains a third (common) and a fourth (Brünnich's) of survival variation, respectively. A positive correlation should be expected if the causal factor of variability in survival is the availability of this food source (Table 1).

In the kittiwake, however, herring, while accounting for nearly 60% of the birds' survival, was negatively correlated with survival (Fig. 2d). The effect of herring on the kittiwake might be indirect, namely by displacing the main prey species of the kittiwake (Anker-Nilssen, Barrett & Krasnov 1997; Hjermann *et al.* 2004). The Kittiwake also deviated somewhat in other regards from the four alcid species: the optimal model was time-dependent, no model with environmental variables achieved an acceptable  $\Delta\text{AIC}_C$  and the temporal variance was decidedly highest (Table 2). However, this difference from the auks seems to be due to the crash in survival between 1993 and 1994 alone (Fig. 1). In this year, survival was reduced to 61%, which is a nearly threefold increase in mortality compared to the remaining years. This event coincided with a crash in Barents Sea capelin stocks (Fig. 1). However, capelin was a poor predictive variable for kittiwake survival over the entire period of observation. If there was a causal relation between the crash in the two species, which is probable given the data on food preference of kittiwakes breeding at Hornøya (Barrett & Krasnov 1996), the birds nevertheless recovered both much faster and more completely than their main prey. This indicates that kittiwakes may have been able to switch to another prey. Why this switch did not happen instantaneously but required about 2 years is an open question.

Of the prey species considered, cod is the least prevalent among diet items during the breeding season (Barrett 2002). In accordance with this fact, we find that cod 0-group indices only explain minor amounts of variability in seabird survival (cf. Table 1). Only in the razorbill was the variance explained as much as 31% and the  $\Delta\text{AIC}_C$  as low as 0.77.

#### WINTERING AREAS AND TIMING OF MORTALITY

From ringing returns, direct observation and oil-spill-caused mortality, the wintering areas of the auks in our study are more or less well known (Brown 1985; Nikolaeva, Krasnov & Barrett 1996; Gaston & Jones 1998). What is far less established is whether the different breeding populations mix during winter or whether they have wintering areas more or less distinct from the ones of conspecifics from other breeding colonies.

In this context, it is noteworthy that the oceanic regions identified in our analysis of SSTs to be the most relevant (Tables 4–8) coincide with the areas that have been known to be wintering areas of those birds. It is tempting to interpret our findings as evidence of the wintering areas of the Hornøya population of the species concerned; however, the high number of oceanic regions tested in our (pre)analyses and the risk for data dredging preclude this. A look at the best-supported models nevertheless proves informative: for three of the alcid species in our analyses (common guillemot, razorbill and puffin), at least one model incorporating SSTs is among the set of optimal ones ( $\Delta\text{AIC}_C < 2$ ,

evidence ratios > 0.6). The respective oceanic regions are the North Sea and western North Atlantic for common (and Brünnich's) guillemots, and the North-Eastern Atlantic Basin and the Norwegian Sea for both razorbills and puffins.

By analysing the effects of SSTs separately for autumn (August–October) and winter (November–March), we hoped to answer the question of when in the life cycle of seabirds mortality predominantly occurs. It has long been assumed that mortality occurs mainly during winter (e.g. Newton 1998), and this is supported by recent empirical evidence (Barbraud & Weimerskirch 2003; Gaston 2003; Jenouvrier *et al.* 2003). The two periods were chosen in order to be able to distinguish between mortality during moult (autumn) and during the period of the harshest weather (winter). The results suggest that variation in survival is better accounted for by autumn SSTs than by winter SSTs. This may indicate that flightlessness during moult is a crucial period in the alcid life cycle. This is compatible with the interpretation that not being able to evade adverse conditions places more severe constraint on survival than the on average harsher weather conditions during winter.

### Conclusion

To conclude, we found clear evidence of climate and/or prey effects on adult survival of the four auk species analysed, but not in the kittiwake. Thereby we were able to corroborate several of our initial expectations (Table 1). Although survival rates were generally higher and more stable than in most other colonies where these species have been studied, the amount of variation in survival explained by environmental variables was surprisingly high. Considering that even small changes in adult survival will have dramatic effects on long-lived species, our findings are alarming. This is aggravated by the fact that survival decreases with increasing sea surface temperature, a condition which will occur more often in the future.

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### Supplementary material

The following supplementary material for this article is available online at <http://www.evol.no/hanno/05/JAESuppl.pdf>

**Table A1.** Year-by-year estimates of the apparent adult survival of five species of seabirds at Hornøya.

**Table A2.** Model selection. The optimal model, its neighbourhood, and some further relevant models are shown for each species.

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