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Hidden survival heterogeneity of three Common eider populations in response to climate fluctuations

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Summary

1. Understanding how individuals and populations respond to fluctuations in climatic conditions is critical to explain and anticipate changes in ecological systems. Most such studies focus on climate impacts on single populations without considering inter- and intra-population heterogeneity. However, comparing geographically dispersed populations limits the risk of faulty generalizations and helps to improve ecological and demographic models.

2. We aimed to determine whether differences in migration tactics among and within populations would induce inter- or intra-population heterogeneity in survival in relation to winter climate fluctuations. Our study species was the Common eider (*Somateria mollissima*), a marine duck with a circumpolar distribution, which is strongly affected by climatic conditions during several phases of its annual cycle.

3. Capture-mark-recapture data were collected in two arctic (northern Canada and Svalbard) and one subarctic (northern Norway) population over a period of 18, 15, and 29 years respectively. These three populations have different migration tactics and experience different winter climatic conditions. Using multi-event and mixture modelling, we assessed the association between adult female eider survival and winter conditions as measured by the North Atlantic Oscillation (NAO) index.

4. We found that winter weather conditions affected the survival of female eiders from each of these three populations. However, different mechanisms seemed to be involved. Survival of the two migrating arctic populations was impacted directly by changes in the NAO, whereas the subarctic resident population was affected by the NAO with time lags of 2–3 years. Moreover, we found evidence for intra-population heterogeneity in the survival response to the winter NAO in the Canadian eider population, where individuals migrate to distinct wintering areas.

5. Our results illustrate how individuals and populations of the same species can vary in their responses to climate variation. We suspect that the found variation in the survival response of birds to winter conditions is partly explained by differences in migration tactic. Detecting and accounting for inter- and intra-population heterogeneity will improve our predictions concerning the response of wildlife to global changes.

Key-words: Arctic, hidden states, life-history strategy, mixture models, multi-event, NAO, seabirds

Introduction

Reported impacts of climate warming on free-living populations typically focused on a single population (e.g. see review in Barbraud 2010; Oro 2014 but see Forchhammer *et al.* 2002; Harris *et al.* 2005; Jenouvrier *et al.* 2009). Populations of the same species may be characterized by various life-history strategies (e.g. Schultner *et al.* 2013) and exposed to diverse environmental conditions. As a consequence, they may respond differently to changing

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environmental conditions, particularly among migratory species where the effects of winter conditions on vital rates and population dynamics may depend on their migration tactic (Sedinger *et al.* 2011; Alves *et al.* 2013). For instance, migration could by itself jeopardize survival and reproductive success because of high energetic or physiological costs (e.g. Wikelski *et al.* 2003) and these costs may be exacerbated by harsh winter conditions. Demographic responses to winter conditions can thus differ between populations depending on their migration tactics.

The apparent link between changes in the environment and the demographic response of a given population may also be affected by among-individual heterogeneity within the same population. For example, birds migrating through geographical locations that are characterized by different environmental conditions can induce important variation among individuals originating from the same population. These differences can have a direct effect on individual survival and/or carry-over effects on their subsequent breeding phenology (Alves *et al.* 2013), breeding success (Norris *et al.* 2004), or breeding probability (Sedinger *et al.* 2011). Such individual heterogeneity may strongly affect our understanding of population responses to environmental change. Indeed, in the extreme scenario where some individuals winter in an area in which environmental conditions improve while others winter in an area where conditions deteriorate, the relationship between environmental conditions and vital rates or population dynamics may be difficult to detect and interpret. Individual heterogeneity in migratory behaviour thus needs to be taken into account when considering population responses to global change.

Large-scale climate indices, such as the North Atlantic Oscillation (NAO; Hurrell *et al.* 2003) are often used as proxies of environmental conditions. Examining how populations respond to such indices could help in understanding the complex interactions between weather and ecological processes (Stenseth *et al.* 2003; Hallett *et al.* 2004; Straile & Stenseth 2007), particularly for migratory species that use very large geographical areas. The NAO is known to be a strong driver of climate variability in the north Atlantic Ocean and particularly so in winter (Hurrell & Deser 2009). It integrates both temporal and spatial components of several weather variables including air temperature, wind, and precipitation (Stenseth & Mysterud 2005). In birds, the NAO may influence winter distributions (Zipkin *et al.* 2010), breeding success (Lehikoinen, Kilpi & Öst 2006; Sandvik & Erikstad 2008), adult survival (Grosbois & Thompson 2005; Sandvik *et al.* 2005; Sandvik & Erikstad 2008), and population dynamics (Thompson & Grosbois 2002; Morrissette *et al.* 2010). However, the winter NAO can be associated with different local climatic conditions depending on the specific geographical area considered. For example, links between the NAO and local sea surface temperatures vary between the northeast and northwest North Atlantic (Sandvik, Coulson & Sæther 2008). Hence, for species characterized by strong heterogeneity in migratory behaviour, this spatial variation of the NAO effects should be taken into account when interpreting wildlife population dynamics.

In this study, we analysed the associations between the winter NAO and female adult survival among three Common eider (*Somateria mollissima*) populations, two arctic and one subarctic. Birds from these three populations disperse over a wide geographical range within the North Atlantic during winter, and have different post-breeding migration tactics (Mosbech *et al.* 2006; Hanssen *et al.* 2016). The links between the regional climatic fluctuations and the winter NAO differ among eider wintering areas (Table 1) and we would thus expect inter- and intra-population heterogeneity in the association between eider survival and the winter NAO. More specifically, the survival of eiders breeding in the Canadian Arctic should be negatively correlated with the positive winter NAO, as positive values are associated with greater storm activity and lower air temperatures on the wintering areas of this population (Gillett, Graf & Osborn 2003; Hurrell & Deser 2009). Most eiders breeding in Svalbard overwinter in Iceland where a positive NAO is characterized by strong winter storms (Table 1). Their adult survival should therefore also be negatively and directly associated with the winter NAO. Conversely, we predicted a positive effect of the winter NAO on the survival of eiders breeding in northern Norway, where positive winter NAO is characterized by higher air and sea surface temperatures for this resident population (Table 1). Finally, we expected intra-population heterogeneity in the survival response to the winter NAO fluctuations within the Canadian population whose individuals can migrate to two distinct wintering areas (Mosbech *et al.* 2006). Our limited dataset did not allow us to test for individual heterogeneity in response to winter conditions in Svalbard, where individuals also migrate to two different wintering areas.

Materials and methods

STUDY SITES AND EIDER POPULATIONS

The Common eider (*Somateria mollissima*) is the largest sea-duck species in Europe and North America, mostly breeding in the Arctic. We worked on female eiders only, which are strongly philopatric (e.g. Sonsthagen *et al.* 2009) and start breeding at 2–3 years old (Baillie & Milne 1982). Although the exact age of individuals was unknown, all birds used in our analyses are adults as they were captured at the breeding colony during the nesting period. Data available from the Dryad Digital Repository: https://doi.org/10.5061/10.5061/dryad.n026d

Canadian Arctic, East Bay Island

Fieldwork was conducted on a small rocky island (Mitivik Island; 0·19 km^2) within the East Bay Migratory Bird Sanctuary, Southampton Island, Nunavut, Canada (64° 02′ N, 81° 47′ W;

Fig. 1) from 1996 to 2013. An average of 545 female eiders (range from 209 to 1035) were captured and measured annually just before or after the incubation period. Each year, birds were also resighted and their leg bands read from observation blinds during the laying and incubation periods. Blinds were distributed at the periphery of the colony, which could have, in addition to the rolling topography of the island, created some detection heterogeneity among birds, as eiders breeding far from the blinds were likely less visible. About 78% of the female eiders originating from East Bay Island winter in southwest Greenland and 22% in southern Atlantic Canada along southern Labrador, Newfoundland, and south to the Gulf of Saint-Lawrence (Mosbech *et al.* 2006; Fig. 1). Because of different associations between the winter NAO and local conditions in these areas, individuals could experience different winter conditions. For example, an increase in the winter NAO leads to a greater increase of the storm activity in the Gulf of Saint-Lawrence than in the southwest Greenland (Table 1). Wintering areas (December-March) of 26 eider females were defined using satellite transmitters implanted in 2001, 2003, 2012, and 2013 (Fig. 1). The procedures for capturing, marking, and band reading at East Bay are described in detail by both Mosbech *et al.* (2006) and Descamps *et al.* (2010). In addition, avian cholera outbreaks of different severities have occurred regularly in the Canadian population since 2005, which strongly affected eider survival (Descamps *et al.* 2009, 2012). Birds infected by cholera typically die very quickly (Buttler 2009), and all eider carcasses of marked individuals were recovered each year on the island through a systematic survey at the end of the nesting season. To remove this cause of mortality from the analysis, we right-censored the 1119 recovered individuals that died during cholera outbreaks as this might obscure other mortality sources such as climate.

Svalbard, Prins Heinrich Island

Fieldwork was carried out on Prins Heinrich Island (78° 55′ N, 12° 00′ E; Fig. 1) on the west coast of Svalbard from 1999 to 2013. The substrate of this small island of 0·06 km^2 in Kongsfjorden is rock and tundra. Here, on average, 55 females (range: 0–136) were captured annually on the nest with a noose pole. Only physical recaptures occurred at this site (no band reading at a distance). Females nesting in Svalbard breed on a flat, homogeneous island and are thus considered equally detectable. The eiders from this colony migrate to either northern Iceland (about 75%) or northern Norway (Hanssen *et al.* 2016; Fig. 1). Like the eiders from the Canadian Arctic, eiders originating from Svalbard could be exposed to different local conditions associated with the winter NAO. For example, an increase in the winter NAO leads to a greater increase in the storm activity in Iceland than in the northern Norway (Table 1).

Northern Norway, Grindøya Island

Fieldwork was conducted from 1985 to 2013 on Grindøya near Tromsø, northern Norway (69° 49′ N, 18° 15′ E, Fig. 1). Grindøya is an island of 0·65 km^2, where 200–500 pairs of Common eiders breed annually in habitats including beach, stunted forest or bushes. This variation in nesting habitats could induce individual heterogeneity in detection rate. An average of 106 female eiders (range: 42–235) were captured on the nest annually with a noose pole during the incubation period. Only physical recaptures occurred at this site

Table 1. Changes in winter (December-March) environmental variables on Common eider wintering grounds associated with an increase of 1 unit in the winter North Atlantic Oscillation (NAO). Eiders nesting in the Canadian Arctic (East Bay) migrate to their wintering areas located in southwest Greenland, Labrador, Newfoundland or Gulf of St-Lawrence. Birds nesting in Svalbard (Prins Heinrich) migrate and spend the winter either in northern Iceland or in northern Norway. Finally, eiders nesting in northern Norway (Grindøya) are resident and winter in the vicinity of their breeding site. Storm activity stands for mean storm track anomalies expressed in terms of amplitude (gpm: geopotential meters = m^2 s^{-2})

	Southwest Greenland	Northern Labrador	Southern Labrador	Gulf of St-Lawrence and Newfoundland	Northern Iceland	Northern Norway	References
Surface temperatures (1900–2009)	**Negative** −0·5 to −0·3 °C	**Negative** −0·5 to −0·4 °C	**Negative** −0·25 to −0·15 °C	**Negative** −0·2 to −0·1 °C	**Null**	**Positive** 0·1 to 0·2 °C	Møller, Fiedler & Berthold 2010 (Fig. 2·8)
Precipitation (1979–2013)	**Positive** 0 to 0·15 mm day^{-1}	**Negative** −0·15 to −0·3 mm day^{-1}	**Negative** −0·15 to −0·3 mm day^{-1}	**Negative (north)** 0 to −0·15 **Positive (south)** 0 to 0·3 mm day^{-1}	**Positive** 0·3 to 0·6 mm day^{-1}	**Positive** 0 to 0·3 mm day^{-1}	Hurrell & Deser 2015 (Fig. 2)
Storm activity (1958–1998)	**Positive** 0 to 4 gpm	**Positive** 0 to 2 gpm	**Positive** 4 to 6 gpm	**Positive** 4 to 8 gpm	**Positive** 5 to 7 gpm	**Positive** 4 to 6 gpm	Hurrell & Deser 2009 (Fig. 12)

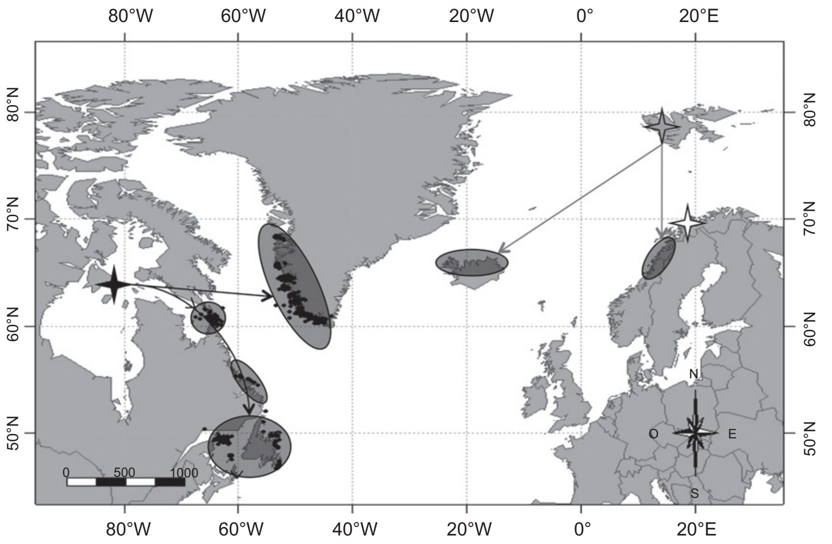

Fig. 1. Approximate winter (Dec–Mar) distribution (ellipses) of female Common eiders breeding in Canada (black star), Svalbard (grey star), and northern Norway (white star) islands. Note that winter distribution of some birds breeding in Svalbard and those breeding in northern Norway partly overlapped in winter in northern Norway. Black dots showed the winter locations of 26 females marked in Canada (East Bay) and tracked with satellite transmitters.

(no band reading at distance). Females from Grindøya are resident and spend the winter in the vicinity (within 50 km) of their breeding location in northern Norway (Bustnes & Erikstad 1993) where all birds are exposed to the same winter conditions.

WINTER NORTH ATLANTIC OSCILLATION

Winter NAO values are based on the difference in normalized sea level pressure between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland. Data from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based were used in the analysis. We defined the winter NAO as monthly NAO values averaged from December to March, when all the birds were on their wintering grounds. We considered winter NAO with and without time lags of 1–3 years. For each wintering area, the associations between the local climatic variables and the winter NAO are presented in Table 1.

MARK-RECAPTURE MODELLING PROCEDURE

Goodness-of-fit

The first step of survival modelling is to check the fit of our dataset to the reference model with goodness-of-fit (GOF) tests. These tests indicate whether or not heterogeneity among individuals is statistically significant. GOF tests are well developed for single-state capture-recapture models (Lebreton *et al.* 1992; Pradel, Gimenez & Lebreton 2005) but not for multi-event ones (Pradel 2005). Thus, for each colony, we first performed a standard GOF test for the single-state Cormack-Jolly-Seber (CJS) model (Burnham *et al.* 1987), where individual heterogeneity in detection probability tends to induce both apparent transience (Pradel *et al.* 1997) and apparent trap-happiness (Pradel 1993). In case these transience (test 3.SR) and trap-happiness (test 2.CT) components of the GOF test for CJS-models were statistically significant and when individual detection heterogeneity is expected (Canadian and northern Norway populations), we derived an approximate GOF for models where individual detection heterogeneity (IDH-models, models including two mixture classes of heterogeneity in the detection, see below) was accounted for, following Péron *et al.* (2010). If this corrected test was still statistically significant (i.e. if some unexplained lack of fit remains even after accounting for individual heterogeneity), this was taken into account using an overdispersion coefficient ($\hat{c}$) for the calculus of the model selection criterion (see below). $\hat{c}$ was calculated for each colony as the ratio between the overall non-directional χ^2-statistic (obtained by removing the squared directional test statistics z^2 from their respective main components 3.SR and 2.CT of the standard GOF test) and the corresponding degrees of freedom (Péron *et al.* 2010). All the GOF test components were computed using U-CARE (Choquet *et al.* 2009).

GOF tests results are presented in Appendix S1 (Table S1, Supporting Information). The directional tests for transience (3.SR) and trap-happiness (2.CT) were both statistically significant for the Canadian and Norwegian populations, supporting our prediction that individual heterogeneity in detection may occur in those two populations. For the Canadian population, the overall corrected GOF test of the IDH-model still proved statistically significant, and we thus used a $\hat{c}$ of 2·79. For the Svalbard population, the CJS-model fitted the capture-recapture data despite a moderate but statistically significant transience effect. Our umbrella model was thus a model including two survival groups: survival of the first transient-group corresponds to the survival from the first capture to the subsequent year, and includes all the bias because of the presence of transients. Survival of the second transient-group (i.e. survival from 1 year after the first capture onwards) is an unbiased survival estimate of residents (Pradel *et al.* 1997). The inclusion of a transient effect in the survival for eiders from Svalbard did not significantly improve the model fit (Table S2 in Appendix S1). This means that the chance of recapturing individuals that have only been caught once before compared with those captured several times did not markedly differ. This transient effect was thus not included in subsequent models when testing for the winter NAO effects for the Svalbard population (Table 2). For the northern Norwegian population, the corrected 3.SR and 2.CT tests as well as the overall corrected GOF test of the IDH-model proved statistically significant. To take this remaining lack of fit into account, we performed our model selection using a $\hat{c}$ of 1·49.

Individual heterogeneity modelling

Individual heterogeneity in the detection rates may bias survival estimates if not accounted for (Pradel *et al.* 1997) because it violates the fundamental assumption of parameter homogeneity in Capture-mark-recapture (CMR) models (Lebreton *et al.* 1992) and can lead to flawed inferences (Burnham & Anderson 2003). *A priori* knowledge on the study system should be the most reliable cue when deciding which form of individual heterogeneity to incorporate in CMR models (Péron *et al.* 2010). We had *a priori* reasons to expect heterogeneity in the survival response to the winter NAO between two groups within the migratory Canadian population, as individuals can use two distinct wintering areas with different weather conditions. We thus built CMR multi-event (Pradel 2005) models with a finite mixture structure (Pledger, Pollock & Norris 2003) in detection (Pradel *et al.* 2009; Péron *et al.* 2010; called individual detection heterogeneity or IDH-models) and/or in survival probabilities as required by the particular dataset (see study sites and populations description). Mixture models are known to be an efficient way to account for heterogeneity of undetermined origin and using two classes is generally considered sufficient (Pledger, Pollock & Norris 2003). When, like here, a specific form of heterogeneity is expected, there is no guarantee that the two classes correspond to the hypothesized groups. The detection of two classes by model selection should thus not be taken as evidence that these groups are indeed present. In particular, if individuals known to belong to the same hypothesized group are not classified similarly, or if, while put in the same class, the class attributes depart from what is expected, the classes most likely do not reflect the hypothesized groups. Conversely, if the class attributes fit closely the attributes expected, this is some indication that the hypothesized groups may indeed structure the population. In this study, we examined if the frequency of the classes and the response of survival to the winter NAO within each class fit the expectations for the two migration groups known to exist within the Canadian population. We thus considered two discrete classes of heterogeneity (hereafter 'hidden classes'; we also built a model with three classes, see Table S5 in Appendix S1) with no possible transitions between them, as in survival probabilities the two classes intended to reflect individually fixed migration behaviour. Indeed, individual female common eiders tracked by satellite from two of our study populations appeared to have consistent wintering areas from year to year (G. Gilchrist unpublished data for Canada and Hanssen *et al.* 2016 for Svalbard). Moreover, these two survival groups were expected to respond differently to the winter NAO (see Introduction).

In a preliminary analysis, we tested whether heterogeneity occurred independently in survival and detection rates (description of independent and dependent model structures in Appendix S1; Table S5) for the populations from Canada and northern Norway. This preliminary analysis showed that, in both populations, models performed better (lower QAIC) when heterogeneities in detection and survival were linked (Table S6 in Appendix S1). Our model selection was therefore based on heterogeneity with the dependent model structure (Table S6 in Appendix S1). This apparent association between heterogeneity in detection and in survival is discussed (see below). Preliminary analyses (Table S2 in Appendix S1) confirmed our assumptions of individual heterogeneity in detection for the Canadian Arctic and northern Norway populations. We thus modelled time-variation in detection rates with an additive effect between the two 'hidden classes', which means that one class was more detected than the other and the detection of both classes fluctuated over time in parallel. In Svalbard, eider detection rates varied over time and no heterogeneity was included.

Model selection

We investigated the effect of winter NAO on survival with and without taking survival heterogeneity among individuals into account. We considered that variations in the NAO affected the different classes of eiders either additively [i.e. the link between survival and the NAO is the same in the two classes (same slope) but one class has higher rates than the other (different intercept), noted '+' in Table 2], in interaction [i.e. survival of the two classes responds differently to the NAO (different slope and different intercept), noted '*' in Table 2] or in the same way [i.e. both classes have the same survival with the same answer to variations in the NAO (same slope and same intercept), Table 2].

We used the Akaike's information criterion to rank our models (Burnham & Anderson 2003), adjusted for overdispersion (Quasi-Akaike's information criterion, QAIC) for the Canadian population, adjusted for small sample size (Second-Order Akaike's information criterion, AICc) for the Svalbard population and adjusted for both overdispersion and small sample size (QAICc) for the Norwegian population, in which small sample size issue ($n/K < 40$ with n the number of observations and K the number of estimable parameters; Burnham & Anderson 2003) were detected only in models without covariate and with time interaction. The lower the AIC, the better the trade-off between prediction bias and parsimony. If the difference in AIC values between two models is <2, the models are deemed to have equal statistical support and in the case of nested models, the simplest was preferred (Burnham & Anderson 2003).

In a second step, we performed the analyses of deviance (ANODEV, Grosbois *et al.* 2008) to test whether or not variations in NAO were associated with variation in eider survival in each population (Grosbois *et al.* 2008) and we calculated the proportion of deviance (Dev) explained by a given covariate as: $R^2_{\mathrm{Dev}} = \frac{\mathrm{Dev}(\mathrm{F_{cst}}) - \mathrm{Dev}(\mathrm{F_{co}})}{\mathrm{Dev}(\mathrm{F_{cst}}) - \mathrm{Dev}(\mathrm{F_t})}$; F_{cst}, F_{t} and F_{co} refer, respectively, to models with constant, time and covariate effects (results in Table 2). These models need to be comparable in the calculus of the R^2_{Dev}, e.g. the ANODEV test of the model $\varphi(\mathrm{h*NAO})\ \mathrm{p_{h+t}}$ used the deviance of the constant model $\varphi_{\mathrm{h}}\ \mathrm{p_{h+t}}$ and the temporal model $\varphi_{\mathrm{h*t}}\ \mathrm{p_{h+t}}$ whereas the ANODEV test of the model $\varphi(\mathrm{NAO})\ \mathrm{p_{h+t}}$ used the deviance of the constant model $\varphi.\ \mathrm{p_{h+t}}$ and the temporal model $\varphi_{\mathrm{t}}\ \mathrm{p_{h+t}}$. Thus, the R^2_{Dev} of models with and without heterogeneity are not comparable. The model including environmental covariates (F_{co}) gives us the slope and the intercept of the relationship between survival and the winter NAO, so we can look at the slope to define the relation.

Table 2. Analysis of deviance (ANODEV) results of the effect of winter North Atlantic Oscillation (NAO) without or with time lag of one (NAO1), two (NAO2) or three (NAO3) years on the female adult survival (φ) of Common eider breeding in Canada (East Bay 1996–2013), Svalbard (Prins Heinrich 1999–2013) or northern Norway (Grindøya 1985–2013). Because of a lack of data for Prins Heinrich (see above), two groups of heterogeneity were considered only for Grindøya and East Bay, additively (e.g. h+NAO) or in interaction (e.g. h*NAO) with the covariate. 'np' is the number of parameters

Model	np	Deviance	Criterion	ΔCriterion	$F_{j-1,\,n-j}$	P	R^2_{Dev}	Weight
Canada			$\mathrm{QAIC_c}$	$\Delta\mathrm{QAIC_c}$				
(East Bay) $\hat{c}$ = 2·79								
φ(h*NAO) p_{h+t}	**23**	**21 372·49**	**7704·85**	**0·00**	**4·66**	**0·009**	**0·32**	**0·903**
φ(h+NAO) p_{h+1}	22	21 390·69	7709·36	4·51	3·25	0·067	0·30	0·095
φ(h*NAO1) p_{h+t}	23	21 407·93	7717·55	12·70	2·47	0·081	0·20	0·002
φ(NAO) p_{h+t}	**21**	**21 426·26**	**7720·10**	**15·25**	**6·77**	**0·020**	**0·31**	**0·000**
φ(h+NAO1) p_{h+t}	22	21 444·44	7728·62	23·77	0·72	0·502	0·09	0·000
φ(h+NAO3) p_{h+t}	22	21 463·82	7735·57	30·72	0·08	0·925	0·01	0·000
φ(h*NAO2) p_{h+1}	23	21 459·83	7736·15	31·30	0·23	0·876	0·02	0·000
φ(h+NAO2) p_{h+t}	22	21 465·57	7736·20	31·35	0·03	0·975	0·00	0·000
φ(h*NAO3)p_{h+1}	23	21 461·59	7736·78	31·93	0·17	0·918	0·02	0·000
φ(NAO1)p_{h+t}	21	21 478·13	7738·69	33·84	1·53	0·235	0·09	0·000
φ(NAO3) p_{h+t}	21	21 498·19	7745·88	41·02	0·12	0·732	0·01	0·000
φ(NAO2) p_{h+t}	21	21 499·51	7746·35	41·50	0·04	0·850	0·00	0·000
Svalbard			AICc	ΔAICc				
(Prins Heinrich) $\hat{c}$ = 1·00								
φ(NAO) p_t	16	1704·12	1736·79	0·00	4·55	0·054	0·27	0·627
φ(NAO2) p_t	16	1706·58	1739·24	2·46	2·21	0·163	0·16	0·184
φ(NAO3) p_t	16	1707·43	1740·10	3·31	1·54	0·238	0·11	0·120
φ(NAO1) p_t	16	1708·53	1741·19	4·41	0·78	0·395	0·06	0·069
Northern Norway			QAICc	ΔQAICc				
(Grindøya) $\hat{c}$ = 1·49								
φ(NAO2) p_{h+t}	**32**	**8419·57**	**5719·96**	**0·00**	**12·13**	**0·002**	**0·32**	**0·624**
φ(h + NAO2) p_{h+t}	**33**	**8419·34**	**5721·86**	**1·89**	**5·96**	**0·007**	**0·31**	**0·242**
φ(h*NAO2) p_{h+t}	**34**	**8418·45**	**5723·31**	**3·34**	**6·70**	**0·001**	**0·28**	**0·117**
φ(NAO3) p_{h+t}	**32**	**8432·14**	**5728·41**	**8·44**	**7·29**	**0·012**	**0·22**	**0·009**
φ(h*NAO3) p_{h+t}	**34**	**8428·55**	**5730·09**	**10·12**	**4·59**	**0·006**	**0·21**	**0·004**
φ(h + NAO3) p_{h+t}	**33**	**8432·08**	**5730·41**	**10·45**	**3·53**	**0·044**	**0·21**	**0·003**
φ(NAO1) p_{h+t}	32	8446·39	5737·98	18·02	3·09	0·090	0·11	0·000
φ(h*NAO1) p_{h+t}	34	8444·76	5739·68	19·71	1·88	0·240	0·10	0·000
φ(h+NAO1) p_{h+t}	33	8445·88	5740·98	21·01	1·51	0·145	0·10	0·000
φ(NAO) p_{h+t}	32	8459·51	5746·79	26·83	0·07	0·789	0·00	0·000
φ(h+NAO) p_{h+t}	33	8458·70	5748·30	28·33	0·03	0·973	0·00	0·000
φ(h*NAO) p_{h+t}	34	8458·70	5750·33	30·37	0·03	0·992	0·00	0·000

Significant ANODEV results are in bold, n is the number of survival estimates obtained from model F_t (fixed-effect model with a time effect, see formula above), j the number of parameters required to describe the relationship between survival and the focal climatic covariate (equal to two in simple cases: a slope and an intercept), $F_{j-1,\,n-j}$ the ANODEV test statistic following a Fisher-Snedecor distribution with $j-1$ and $n-j$ degrees of freedom, P the P-value of the ANODEV test and R^2_{Dev} the proportion of the survival variation explained by the covariate [see Grosbois *et al.* (2008) for details on these tests].

Post-hoc validation

To test our hypothesis that survival heterogeneity was related to different wintering grounds for the Canadian population, we considered the 26 females tracked by satellite and compared their wintering area with the survival class they belong to. Indeed, for each mixture model, E-Surge program computes the probability that each female (or, more exactly, each capture history) belongs to one class or the other. We can thus obtain *a posteriori* their allocation to the two 'hidden' classes ('history state dependent probability' in Choquet & Nogue 2011).We then used this post-hoc allocation probability to determine whether or not females with similar migration tactics would be merged together in the same class. We arbitrarily defined a threshold probability of 80%, at which we considered a female reliably assigned to one or the other class. Although implanting eider females with transmitters could potentially impact their survival (Fast *et al.* 2011), preliminary analysis showed that incorporating females tracked by satellite did not affect our results for the Canadian population.

We analysed 3890, 515, and 1312 individual encounter histories of female Common eiders respectively from the Canadian Arctic (East Bay), Svalbard (Prins Heinrich), and northern Norway (Grindøya). Models were implemented in program E-SURGE (Choquet, Rouan & Pradel 2009). The implementation in practice of the CMR mixture models in program E-SURGE is given in Appendix S2.

Results

HETEROGENEITY BETWEEN POPULATIONS IN THEIR RESPONSE TO THE WINTER NAO

In the Canadian Arctic population, adult eider survival was negatively related, with no time lag, to a positive winter NAO [$R^2_{\mathrm{Dev}} = 0{\cdot}31$; slope on a logit scale = −0·47 ± 0·10SE; model φ(NAO) p_{h+t}; Table 2; Fig. 2a], which is associated with colder temperatures and higher storm activity in their wintering areas (Table 1). Positive winter NAO with a 1- to 3-year time lag did not influence adult female survival [models φ(NAO1 to NAO3) p_{h+t}; Table 2].

In Svalbard, the survival of eiders from Svalbard tended to be negatively associated with a positive winter NAO (higher precipitation and storm activity in their winter location) with no time lag [$R^2_{\mathrm{Dev}} = 0{\cdot}28$; slope on a logit scale = −0·76 ± 0·40 SE; model φ(NAO)p_t; Table 2; Fig. 2b]. As in Canada, no effect of the winter NAO with any time lag was detected (Table 2).

In northern Norway, survival was positively linked to a positive winter NAO (warmer temperatures and higher storm activity, Table 1) with a lag of 2 years [$R^2_{\mathrm{Dev}} = 0{\cdot}32$; slope on a logit scale = 0·46 ± 0·07 SE; model φ(NAO2)p_{h+t}; Table 2; Fig. 2c] although also positively linked to winter NAO with a lag of 3 years [$R^2_{\mathrm{Dev}} = 0{\cdot}22$; slope on a logit scale = 0·53 ± 0·09 SE; model φ(NAO3)p_{h+t}; Table 2]. There was no relationship between the winter NAO with no time lag and survival [$P = 0{\cdot}79$; model φ(NAO)p_{h+t}; Table 2].

HETEROGENEITY BETWEEN EIDERS OF THE SAME POPULATION IN THEIR RESPONSE TO WINTER NAO

In the Canadian breeding colony, we found detectable heterogeneity in the survival response of the eiders to the winter NAO with no time lag. Indeed, including individual heterogeneity greatly improved the model fit [i.e. lowering QAIC by >15 units and higher QAIC weight; models φ(h*NAO)p_{h+t} vs. φ(NAO)p_{h+t}; Table 2; Fig. 3], suggesting that different individuals (in terms of survival) are present in this population and respond differently to the covariate. Although survival of all individuals responded negatively to the colder temperatures and stronger storms associated with positive winter NAO, the relationship between survival and the winter NAO differed between them. Indeed, in our model, the survival of c. 78% ± 0·06 SE of individuals (class H1) declined moderately with increasing winter NAO (slope of −0·33 ± 0·10 SE on a logit scale), whereas the other class (H2) responded more strongly [slope of −1·98 ± 0·75 SE on a logit scale (Fig. 3)]. The average survival from these two classes of females [φ(h*NAO), Table 2] differed by c. 10% (0·83 ± 0·01 SE for class H1 corresponding to 78% of the females and 0·91 ± 0·02 SE for class H2 corresponding to 22% of the females; $P = 0{\cdot}0001$; Table S4 in Appendix S1). Their average detection probabilities were also different (0·58 ± 0·02 SE for class H1 and 0·24 ± 0·04 SE for class H2; Table S4 in Appendix S1). These results prove the existence of heterogeneity, but are not evidence of two classes. However, using the post-hoc allocation probabilities (i.e. the probability of being associated to one of these two groups), we found that 54% (14 of 26) of the females tracked with satellite transmitters could be associated by our model to one of these two classes with a probability ≥80% (Table S3 in Appendix S1). Among these 14 females, 13 (93%) belonged to class H1 and 12 of them migrated to southwest Greenland and northern Labrador, which are areas similarly impacted by the winter NAO (Table 1).

In northern Norway, we detected individual heterogeneity in the survival response to the 2-years-lagged winter NAO with an additive effect [$R^2_{\mathrm{Dev}} = 0{\cdot}31$; model φ(h+NAO2) p_{h+t}; Table 2], although this model was not markedly different from the model without heterogeneity in terms of QAICc [φ(NAO2)p_{h+t}; Table 2]. This means that all individuals responded in the same way to the 2-years-lagged winter NAO fluctuations (same slope of 0·46 ± 0·09 SE on

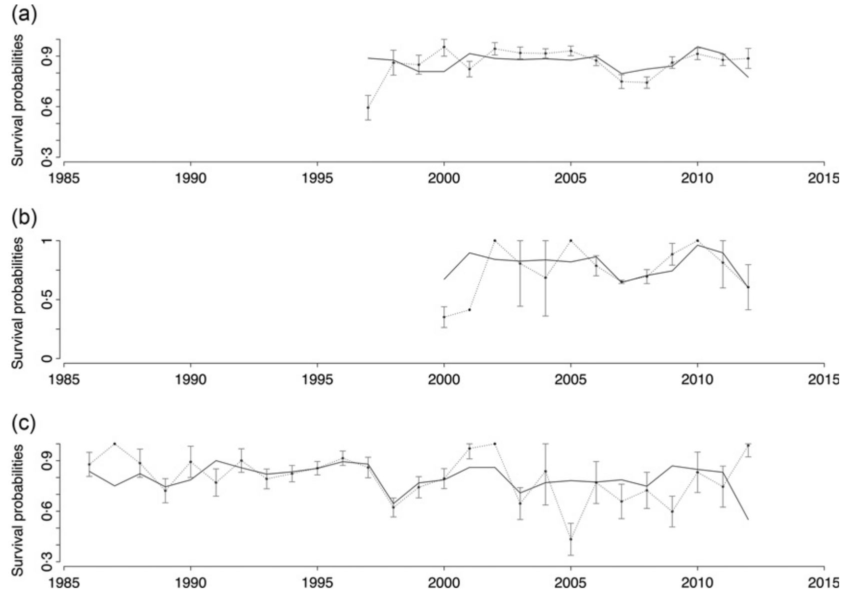

Fig. 2. Survival probabilities (±SE) of eiders breeding in (a) Canada (b) Svalbard, and (c) northern Norway from the time-dependent models (dashed line; models $\varphi_t p_{h+t}$, $\varphi_t p_{h+t}$, and $\varphi_t p_t$; Table S2 in Appendix S1) and winter North Atlantic Oscillation (NAO) models with a 2-years time lag [solid line; northern Norway; model φ(NAO2); Table 2] and without time lag [solid line; Canada and Svalbard; model φ(NAO); Table 2].

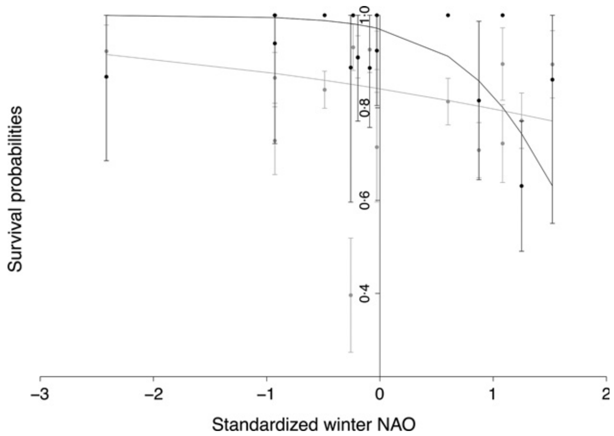

Fig. 3. Survival estimates (±SE) of adult females breeding in the Canadian Arctic (*y*-axis) from the time-dependent model with heterogeneity (isolated points; model $\varphi_{h.t}p_{h+t}$; Table S2 in Appendix S1) and predicted lines from the winter North Atlantic Oscillation (NAO) model with heterogeneity [model φ(h*NAO); Table 2] as a function of the standardized winter NAO without time lag (*x*-axis). Group H1 estimates are in grey and group H2 estimates in black. No estimate of SE is provided by program E-SURGE for points on the boundary.

a logit scale), but some had a slightly higher survival on average than others (0·80 ± 0·01 SE vs. 0·79 ± 0·02 SE).

Discussion

HETEROGENEITY BETWEEN POPULATIONS RESPONSE TO THE WINTER NAO

Female eider survival was associated with the winter NAO in all three populations examined. This adds to the growing body of evidence suggesting that large-scale climate variation influences seabird population dynamics (Grosbois & Thompson 2005; Harris *et al.* 2005; Sandvik *et al.* 2005; Hovinen *et al.* 2014; Descamps *et al.* 2015a). In each case, the winter NAO explained c. 30% of the inter-annual variation in survival rates. However, the underlying mechanisms seem to have differed between these three geographically dispersed populations (Fig. 1). The different associations between the winter NAO and survival were consistent with a previous study reporting a direct NAO effect on the female eider pre-laying body mass in the Canadian Arctic but a delayed effect in northern Norway (Descamps *et al.* 2010). In the present study, we found that the survival of the eiders breeding in Canada (and Svalbard) was negatively influenced by the winter NAO with no time lag, indicating direct effect of winter conditions. By contrast, survival of non-migratory eiders nesting in northern Norway was positively linked to winter NAO with lags of 2 or 3 years (Fig. 2).

As predicted, the association between survival and the winter NAO could be explained by the links between the winter NAO and local weather experienced by eiders on their wintering grounds. Indeed, eiders from the Canadian Arctic, whose survival was negatively impacted by the direct winter NAO, migrated to wintering areas where high positive winter NAO values were associated with cold sea surface and air temperatures, as well as high storm activity. Similarly, eiders originating from Svalbard wintered in areas where high positive winter NAO values were associated with frequent storm activity (Table 1). Such conditions could directly lower eider overwinter survival. However, while low winter air and water temperatures may not necessarily be unfavourable to wintering eiders (Jenssen, Ekker & Bech 1989), storm activity may be detrimental. Storms can potentially increase costs of foraging (Heath & Gilchrist 2010) and lower energetic gain, or directly decrease survival. Moreover, storms can destroy bivalves' beds at shallow depths (Reusch & Chapman 1995; Carrington 2002; Carrington *et al.* 2009) and hence immediately decrease food availability. Previous studies have shown a negative association between the survival and winter storms among migratory Mediterranean Cory's shearwaters, a long-lived seabird (Boano, Brichetti & Foschi 2010; Genovart *et al.* 2013; Descamps *et al.* 2015b). The proximate mechanisms linking storms and seabird demographic parameters can likely vary among species and deserves further investigation.

By contrast, the survival of eiders breeding and wintering in sheltered fjords in northern Norway, where the winter NAO values were positively correlated with the sea surface and air temperatures (Table 1), was positively linked with lagged winter NAO. Such lagged effects likely reflect the indirect effect (through the food chain) of oceanographic conditions on the eider food availability and/or food quality (Menge, Chan & Lubchenco 2008; Descamps *et al.* 2010).

Although the observed inter-population heterogeneity can be explained by differences in the wintering locations (and thus winter conditions encountered), we suggest that migration tactics could also explain, at least in part, of the differences in the observed responses to the winter NAO. Unlike migrating eiders, the survival of resident eiders from northern Norway was not directly affected by winter conditions. As they do not have to deal with the high energetic and physiological costs of migration (e.g. Wikelski *et al.* 2003), they may enter the winter in better body condition (more energetic reserves), which could buffer variation in winter conditions. On the other hand, eiders breeding in the Canadian Arctic may be more vulnerable because they have to complete their fall migration before coping with relatively low temperatures and strong storms during winter.

HETEROGENEITY AMONG EIDERS OF THE SAME POPULATION IN THEIR RESPONSE TO THE WINTER NAO

We expected intra-population heterogeneity in the survival response to the winter NAO fluctuations within the migratory Canadian population but not in resident birds in the northern Norway population. Our results support these predictions. Indeed, individuals of the Canadian eider population respond differently to variation in winter conditions. Even if it is possible that the regressions results could be driven by some years, the models with heterogeneity were largely supported in terms of AIC. The survival of some eiders ('class' H1) was more affected (6 fold) by fluctuations in the winter NAO than others (slope of $-0{\cdot}33 \pm 0{\cdot}10$ SE vs. $-1{\cdot}98 \pm 0{\cdot}75$ SE on a logit scale). One possible explanation would involve different local effects of winter NAO on geographically distinct wintering grounds used by these birds (e.g., higher storm activity and potentially more challenging weather conditions in southern Atlantic Canada when compared with southwest Greenland, Table 1). Several results support this interpretation. First, even if the attribution of individuals to a particular group may be inaccurate (Pledger, Pollock & Norris 2003), the proportions of individuals associated to each group of our model (78% of individuals were in the group H1 compared with 22% in the group H2) were identical to the proportions of eiders using the two wintering areas (78% in southwest Greenland and 22% in southern Atlantic Canada), as shown by the previous study of Mosbech *et al.* (2006) with autumn migration satellite tracking of 18 females breeding at East Bay. Second, considering only individuals with a high assignment probability, 85% ($n = 12/13$) of the satellite tracked individuals associated with class H1 (based on capture history) overwintered under the exact same wintering conditions (i.e., southwest Greenland and northern Labrador). Under our hypothesis, these results suggest that individuals from class H1 would overwinter in southwest Greenland and northern Labrador. Their lower average survival probability (Table S4 in Appendix S1) could also be explained by higher harvesting pressure in Greenland compared with southern Atlantic Canada (Gilliland *et al.* 2009). To explain the link between detection and survival probabilities, we suggest that eiders wintering in a more favourable environment (in Greenland) would be in better average body condition when they arrive at the breeding grounds and would hence be more likely to initiate breeding than eiders wintering under less favourable conditions (F. Jean-Gagnon, P. Legagneux, G. Gilchrist, S. Bélanger, O.P. Love & J. Bêty, submitted). Higher breeding propensity very likely results in higher detection probability at the breeding colony. This remains speculative and further investigations would be needed.

Indeed, we recognize that interpreting hidden heterogeneity in the survival response to the environmental conditions can be difficult as many factors could contribute to inter-individual differences. For instance, intra-population heterogeneity could result from the cost of reproduction and its link to environmental conditions (Descamps *et al.* 2009) or age of individuals (Coulson *et al.* 2001), where, for example, the survival of senescent individuals would be more impacted by environmental conditions than prime-age ones. Therefore, while other alternatives may exist to explain our results, differences in migratory tactics are one likely explanation for the observed intra- and inter-population heterogeneity. Indeed, in addition to the results in the Canadian population, eiders breeding and wintering in northern Norway faced the same winter environmental conditions and we found that the lagged winter conditions had the same impact (same slope) on survival of all birds. Thus, heterogeneity was not detected in the survival response to the winter NAO, but only in the survival with one group tending to have a slightly higher mean survival than the other. This could rather be explained by differences between the females in terms of reproduction cost and/or nesting habitats (e.g. sheltered vs. exposed females, Høyvik Hilde *et al.* 2016). Further investigations would be needed to better study such potential interactions.

Conclusion

Our study led to two key findings. Within a given species, the response of birds to winter climate fluctuations can vary substantially; some populations were affected by the NAO directly in a given year, while another was affected indirectly, most likely through delayed changes in the food web. Also, the strength of the association between the survival and winter conditions can differ not only between populations (such as in Harris *et al.* 2005) but also among individuals within the same population, likely due, here, to variation in migration tactics. Our study is unique because we used a reverse procedure based on capture history: using individual data in post-hoc analyses could provide a way to confirm individual heterogeneity, *a priori* suspected, and identify its potential sources.

All results of our study taken together provide several clues to support our *a priori* hypothesis that the differences in individual life-history strategies would introduce individual heterogeneity in the survival response to winter conditions. The existence of such inter- and intra-population heterogeneities in the response to climatic fluctuations can affect the demographic modelling and viability analyses (Coulson *et al.* 2001; Kendall *et al.* 2011). Hence, to better understand and anticipate the effects of global changes, heterogeneity should be incorporated into population models when *a priori* knowledge and empirical tests support its existence.

Overall, the general modelling approach we used could be extended to any other discipline where, in addition to large CMR dataset, individual information is available to confirm the potential 'hidden' groups present among or within populations. This could open applications and perspectives, particularly in population ecology. Not only to better understand migratory connectivity, which is particularly challenging because of the difficulty to follow each individual and population year round (Webster *et al.* 2002), and which could be related to genetic variance among groups (Sonsthagen *et al.* 2009) and its link with life-history differences; but also for example in eco-epidemiology (Bansal, Grenfell & Meyers 2007) or disease ecology studies (Lloyd-Smith *et al.* 2005) as soon as heterogeneity is suspected. One could imagine detecting groups from CMR data and combine them with satellite telemetry, genetic analyses, stable isotope information or serological data that may allow validation of the classification of individuals as a function of their wintering area, feeding behaviour or physiological and immunological status.

Authors' contributions

L.G., S.D., R.P. and J.B. conceived the ideas and designed methodology; S.A.H., K.E.E., G.G. and G.W.G. provided the data; L.G. analysed the data; L.G. led the writing of this paper. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.n026d (Guéry *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Supporting tables including goodness-of-fit tests results, results of the first step of the model selection procedure, PTT-wearing female informations, comparison of demographic rates, results with 3 heterogeneity classes and the model structure description.

Appendix S2. Practical implementation in the E-SURGE program of multi-event models with dependent heterogeneity in the survival and detection probabilities.