

Winter extra-tropical cyclones as a driver of seabird survival: variation between and within Common eider populations

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Title: Winter extratropical cyclone influence on seabird survival: variation between and within common eider populations

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1. Abstract

Extratropical cyclones (ETCs) play a primary role in determining the variation in local weather and marine conditions in the mid-latitudes. ETCs have a broad range of intensities, from benign to extreme, and their paths, frequency, and intensity may change with global warming. However, how ETCs, and cyclones in general, currently affect marine wildlife is poorly studied and remains substantially unexplored. To understand how winter ETCs affect the inter-annual variability of adult seabird survival, we used capture-mark-recapture datasets collected in two arctic (northern Canada and Svalbard) and one subarctic (northern Norway) breeding populations of common eider, *Somateria mollissima*, over periods of 19, 16 and 30 years, respectively. We found significant negative correlations between winter ETC activity and female eider survival, but different mechanisms appear to be involved in the different studied populations. The number of winter ETCs, extreme or not, was found to be linked to survival without lags in the Canadian population, whereas amplitude and duration of extreme winter ETCs (with time lags) impacted female adult survival in the Svalbard and northern Norway eider breeding populations. We hypothesise that fjords in the wintering grounds of some populations act as climatic shelters and provide natural protection, and hence could partly explain inter-population heterogeneity in the response to ETCs. We suggest that ETCs represent a likely mechanism behind the frequently reported relationship between North Atlantic Oscillation and seabird survival in the North Atlantic.

2. Introduction

Understanding how individuals and populations respond to fluctuations in climatic conditions is critical in order to explain and anticipate changes in ecosystems. This requires

1 identifying relevant climatic parameters that affect demographic rates (e.g. survival, recruitment
2 or breeding success; Jenouvrier 2013) throughout the annual cycle. The winter period is one of
3 the critical stages influencing annual survival of migratory seabirds (Barbraud et al. 2000,
4 Sandvik et al. 2005, Frederiksen et al. 2008) through direct or indirect effects of winter climatic
5 conditions, e.g. on the availability of seabird prey or on the energetic balance of wintering
6 seabirds (Grosbois & Thompson 2005, Harris et al. 2005).

7 Extreme climatic events such as heat waves, droughts, intense precipitation and storms
8 are predicted in most future climate scenarios to increase in frequency in some regions and have
9 been identified as one of the largest threats to wildlife (Easterling et al. 2000, IPCC 2002,
10 Ummenhofer & Meehl 2017). While studies based on long-term population monitoring and
11 fluctuations of extreme events over time are needed to quantify the effect of such events on bird
12 demography (van de Pol et al. 2017), there are still very few examples of such studies
13 (Jenouvrier et al. 2009, Boano et al. 2010, Genovart et al. 2013, Descamps et al. 2015). Some of
14 them deal with the effect of tropical cyclones, defined as air masses rotating around a centre of
15 low atmospheric pressure originating in the tropics. Their associated strong winds are often
16 reported as examples of extreme events, which can drive wildlife demography (e.g. Dunham et
17 al. (2011) on a lemur species, Pike and Stiner (2007) on sea turtle species or Chambers et al.
18 (2011) on seabirds). However, the vulnerability of wildlife to cyclones occurring outside the
19 tropics, i.e. extratropical cyclones (ETCs; defined as 30–90°N or S; Wang et al. 2013), has never
20 been investigated although they are a dominant feature of mid-latitude atmospheric variability
21 and play a primary role in determining local weather. Indeed, they are often associated with
22 extreme winds and precipitation, as well as rapid changes in temperature (Hoskins & Hodges
23 2002, Ulbrich et al. 2009, Wang et al. 2013). Hence, assessing the potential effects of ETCs and

1 their extremes on species breeding, wintering or migrating outside the tropics is important to
2 understand ecological responses to changes in climatic conditions.

3 In this study, we examined the relationship between local winter ETCs and the adult
4 female survival of a long-lived sea duck, the common eider (*Somateria mollissima*) in three
5 breeding populations wintering in the North Atlantic. A previous study reported significant
6 relationships between a global climatic index, the North Atlantic Oscillation (hereafter, NAO;
7 Hurrell et al. 2003), and female eider survival (Guéry et al. 2017). The effects of the NAO on
8 eider survival could potentially be explained by the ETCs. Indeed, the NAO is correlated with
9 the mean intensity, track density and mean speed of ETCs (Sorteberg et al. 2005), especially in
10 winter (Hurrell et al. 2003). We thus expect that the frequency and intensity of winter ETCs
11 would be the main drivers behind the winter NAO-eider survival relationship.

12 Increased ETC activity could directly (no time lag) increase common eider foraging effort
13 and energetic needs required to maintain body temperature (Heath et al. 2006, Heath & Gilchrist
14 2010) and ultimately decrease their survival. In addition, ETCs could negatively and indirectly
15 (with time lag) affect eider survival by influencing oceanographic conditions (Visbeck et al.
16 2003, Sarafanov 2009) and hence eider food availability and/or food quality (Menge et al. 2008,
17 Descamps et al. 2010). Heavy storms can indeed destroy bivalves beds at shallow depths
18 (Brenko & Calabrese 1969, Reusch & Chapman 1995, Carrington 2002, Carrington et al. 2009)
19 or reduce primary productivity (Fujii & Yamanaka 2008). These effects of ETCs could be
20 modulated by coastal topography and by the presence of fjords on eider wintering grounds.
21 Fjords, hereafter named “climatic shelters”, are defined as narrow inlets of the sea between cliffs
22 or steep slopes, which can provide natural shelters from the wind (Howe et al. 2010). The
23 climatic shelter effect of fjords has already been suggested for marine wildlife (Boje 2002,

Brown 2002, Sanino & Van Waerebeek 2008, Howe et al. 2010, Acevedo et al. 2017). Hence, we expect that the effects of ETCs on birds should be lessened for eiders wintering in areas offering climatic shelters.

Most female eiders breeding in Canada winter in southwest Greenland, where there is access to climatic shelters (fjords), while the rest of the population winter in southern Atlantic Canada, with no access to fjords (Mosbech et al. 2006, Guéry et al. 2017). Winter ETC activity also varies between these two distinct wintering grounds (e.g. more ETCs and a longer duration of extreme ETCs in southern Atlantic Canada; Table 1). We thus expect intra-population heterogeneity in the response of female eider survival to ETC activity in this Canadian breeding population, and we predict that winter ETC activity would have a more pronounced negative influence on the survival of eiders wintering in southern Atlantic Canada (Figure 1). The majority of females breeding in Svalbard winter in the northeast fjords of Iceland while the others winter in fjords of northern Norway. Female eiders breeding in northern Norway are year-round residents and spend the winter in fjords close to their breeding grounds. The direct effects of winter ETC activity on survival should thus be strongly reduced in both the Svalbard and Northern Norway breeding populations. Overall, the effects of ETCs on eider survival may thus vary among and within populations, depending on the presence of climatic shelters and on the frequency and/or intensity of the ETC affecting the specific wintering grounds used by birds.

3. Materials and methods

3.1. Study species and populations

3.1.1. Common eider (*Somateria mollissima*)

Common eiders are sea ducks that mostly breed in the Arctic and whose females are typically faithful to their natal colony (Wakeley & Mendall 1976, Swennen 1989). They start breeding between 2 and 5 years old (Hario et al. 2009) and can live an average of 15 years (Zammuto 1986). Females do not feed and stay most of the time on their nest during incubation while males leave the colony soon after egg laying. Male recapture (or resighting) is very low which prevents any survival analyses based on CMR for eider males, and we thus focused our study on females. Only adult females (>2 years old as they come back to the colony to attempt breeding) were captured on their breeding grounds and included in the study, but their exact age was unknown. Eider winter diet includes several marine resource types such as bivalves, marine *polychaete* worms, gastropods, crustaceans and echinoderms (Goudie & Ankney 1986, Guillemette et al. 1992, Merkel et al. 2007).

3.1.2. Canadian Arctic, East Bay Island

Data were collected from 1996 to 2014 on East Bay Island, Nunavut, Canada. An average of 545 ringed female eiders (ranging from 209 in 1997 to 1035 in 2006) were annually resighted from observation blinds or physically captured. The wintering areas of 26 common eider females were determined (see below) using satellite transmitters implanted in 2001 and 2003 (Mosbech et al. 2006), and in 2012 and 2013 (Gilchrist unpubl. data). Female eiders from East Bay winter either in southwest Greenland (78%) or near sea ice edges of southern Atlantic Canada (22%) along southern Labrador, Newfoundland, and south of the Gulf of Saint-Lawrence (Mosbech et al. 2006). Sea ice is observed only in the southern Atlantic wintering area (http://nsidc.org/data/seaice_index/archives/image_select.html). In the Gulf of St. Lawrence, eiders preferably feed on blue mussels that they find near the shore, in kelp beds or in rocky

habitat (Guillemette et al. 1992), while they feed on gastropods in Newfoundland (Goudie & Ankney 1986) and on softshell clams *Mya eideri* and marine *polychaete* worms that they find in soft sediments in southwest Greenland (Merkel et al. 2007).

3.1.3. Svalbard, Prins Heinrich Island

An average of 65 females (ranging from 8 in 2003 to 136 in 2007, with 0 captured in 2000 and 2006) were captured every year from 1999 to 2014 on Prins Heinrich Island, on the west coast of Svalbard, one of several islands housing an eider colony with 3000 breeding females. No heterogeneity in detection occurred (Guéry et al. 2017). About 77% of eiders in this breeding population migrated to northeastern Iceland and 23% to northern Norway (Hanssen et al. 2016), called zone 1 in Figure 1 and Figure 2. Wintering locations were determined from geolocators (Global Location Sensing or GLS logging; Wilson *et al.* 1992) deployed on female common eiders breeding on Storholmen Island, located 5 km NE of Prins Heinrich Island. A total of 95 females were equipped in June or July over four years (2009, 2010, 2011 and 2013), while 48 females were recaptured and data was successfully retrieved from 47 geolocators. Details on capture, geocator deployment, and the calibration, smoothing and calculations of the geocator data are described in Hanssen et al. (2016).

3.1.4. Northern Norway, Grindøya Island

This study was conducted in an eider colony (200-500 pairs) on Grindøya, an island near Tromsø, northern Norway. During the breeding seasons of 1985-2014, nesting female eiders were captured (average of 104; ranging from 36 in 2014 to 235 in 1995) with a noose pole during the incubation period, i.e. only physical recaptures occurred (no band reading at distance).

Females from Grindøya annually breed in habitats including beach, stunted forest or bushes that induced heterogeneity in detection probability (Guéry et al. 2017). They are resident and preferably feed on blue mussels. They thus spend the winter in the vicinity of their breeding location in northern Norway (Bustnes & Erikstad 1993, Anker-Nilssen et al. 2000), called zone 2 in Figure 1 and Figure 2, all exposed to the same winter conditions.

3.2. Wintering areas

Wintering areas were defined using tracking data for the two migrating populations: from satellite transmitters for the Canadian breeding population and geolocators for the Svalbard breeding population. All tracking data were filtered to keep only reliable locations following the procedures described in Mosbech et al. (2006) for the Canadian breeding population and in Hanssen et al. (2016) for the Svalbard breeding population. Due to the lack of variation in day length with respect to latitude close to equinoxes, latitudes estimated from geolocators are unreliable for these specific periods and data were excluded close to the spring equinox (March) for Svalbard eiders. Thus, we considered winter locations from December to March for the Canadian population and from December to February for the Svalbard population. We then calculated kernel densities (90%) and kernel contours using the *adehabitatHR* package in R (Calenge 2006). Finally, as female eiders only reside at sea and along shorelines during winter, we subtracted land cover from the density core contours to get the final wintering areas.

No tracking data was available for females from northern Norway, but eiders are known to stay close to the shore in the vicinity of their breeding island (mostly within 50 km, Bustnes and Erikstad unpublished data) in water shallower than 10m (Bustnes & Lønne 1997). As eiders spread along the shoreline, we defined their wintering area as the smallest ellipse that is allowed

by the grid resolution of the data used to identify ETCs and is parallel to the shoreline and centred on the breeding island (i.e., with a major axis of 200 km and a minor axis of 160 km). Different winter ranges (50 and 100 km added on each axes) were also tested and results did not change significantly; the length-width combination model with the lowest QAICc was selected (Table S2 in the supplementary material). We also subtracted land cover to get the final wintering areas. Grid cells used to extract winter ETCs variables on each of these final wintering areas are presented in Figure 2.

3.3. Variables considered

3.3.1. Winter ETC variables

ETCs in the northern hemisphere are weather systems with an anticlockwise circulation, around a centre of low atmospheric pressure. They regulate local weather and contribute to the general circulation of the atmosphere through the transport of energy and momentum polewards (Hoskins & Hodges 2002, Ulbrich et al. 2009, Wang et al. 2013). ETCs are different from tropical cyclones since they primarily get their energy from horizontal temperature contrasts, though diabatic processes can also play an important role in their development, whereas tropical cyclones are dependent on evaporation over warm tropical waters and develop via the release of latent heat. Even if tropical cyclones can undergo extratropical transition (Jones et al. 2003) to become extratropical cyclones, no tropical cyclones reached the latitudes of the eider wintering areas during the study period.

Several methods exist to track ETCs, using either minimum pressure or maximum vorticity (in the northern hemisphere), which is a measure of the spin of the air. Because these methods are different in what and when a cyclone is defined, they often differ in how many

cyclones are detected. However, differences mainly occur for the weaker storms, and they generally agree for the strongest ones. Readers are referred to Ulbrich et al. (2009) for a comprehensive review of studies using different cyclone tracking methods. In this study, we used the approach described in Roberts et al. (2014) and Hoskins and Hodges (2002), i.e. ETCs are identified and tracked using the maximum vorticity approach based on the 850hPa relative vorticity since it represents smaller spatial scales than the pressure and is less influenced by the large-scale background (Hodges 1994, Hoskins & Hodges 2002, Roberts et al. 2014). To remove short-lived and stationary systems, tracks were retained for further analysis only when they lasted longer than 1 day and travelled further than 1000 km. Thus, we considered all synoptic scale (1000-2500 km) ETCs in the northern hemisphere (30-90°N), which cover a broad range of intensities, extreme or not. Data used for the cyclone tracking are from the European Centre for Medium-Range Weather Forecasts (ECMWF) Interim reanalysis (ERA-Interim, Dee et al. 2014) for the December-March period of 1979-2015 at 3-hour time resolution (see Roberts et al. 2014).

Properties from the female eider wintering areas were added to the tracks by defining a spherical cap sampling region of arc radius 6° (~670km) centred on the ETC positions (adequate for capturing the wind extremes for individual ETCs, Bengtsson et al. 2009; Figure 3). Varying this radius between 5-10 degrees did not change our main conclusions. To calculate the winter ETC activity experienced by female eiders, we considered all ETC regions overlapping with the population-specific wintering area defined above (Figure 3). All the wind-related variables added to the vorticity tracks were based on the 10m winds above the sea surface, available from the ERA-Interim data, as eiders generally fly just a few meters above the water. This was achieved by masking the 10m wind data to retain only data within the eider wintering areas.

4. Several classifications of extreme ETCs exist (see review of Catto (2016)), and we used the one based on wind impact, one of the major impacts of ETCs. We defined extreme ETCs as cyclones that reached at least once a wind speed above the 95th percentile threshold of the local wind speed distribution (Table 1). Wind speeds can vary substantially in our study areas. In Greenland for example, winter wind speeds associated with ETCs were an average of $11.7 \pm 0.2 \text{ m s}^{-1}$, while wind speed reached 28.5 m s^{-1} during the strongest ETC (Table 1). To describe ETC activity in each wintering area during the winter (December to March), we considered six variables from mean to extreme ETC activity within the ETC regions overlapping with the population-specific wintering area. The two variables for the mean ETC activity are the total number of ETCs (Number of ETCs), where an ETC is counted if the sampling region overlaps a wintering region, and their mean wind speed (Mean wind). The four other variables measure the number of extreme ETCs, i.e. with wind speeds above the 95th percentile threshold of the local wind speed distribution at least once in the overlap region, the number of days of extreme ETC (Duration extreme ETCs), the duration of the longest ETC (Longest ETC) and the maximum wind speed of the strongest ETC (Max wind), all relative to the overlap. Descriptive statistics of each variable on wintering area are described in Table 1. Correlations (statistical test based on Pearson's correlation coefficient with the function cor.test in the software R) between variables of winter ETC activity and winter NAO are presented in the supplementary material (Figure S1-S9) for each wintering area. The winter NAO was significantly correlated with at least one winter ETC variable and in most cases with the number of winter ETCs.

5.1.1. Winter North Atlantic Oscillation

Winter North Atlantic Oscillation (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 (Descamps et al. 2010, Guéry et al. 2017), when all the birds were on their wintering grounds.

5.2. Mark-recapture modelling procedure

We tested the effect of local winter ETCs variables extracted from wintering locations on female eider survival with and without taking into account survival heterogeneity among individuals. Individual Detection and Survival Heterogeneity (IDSH) mixture model developed in Guéry *et al.* (2017) can be used to classify female eiders from the Canadian breeding population into two groups, which likely represent birds using two geographically distinct wintering locations (southern Atlantic Canada vs. Greenland). We used this IDSH mixture model to assign each female to a specific group and then tested whether variations in winter ETC variables on each wintering location explain eider survival variation in one of the two groups. A lack of recapture data in the Svalbard breeding population prevented us from properly testing intra-population heterogeneity, so the ETC effect of each wintering ground (either Iceland or northern Norway) was tested on the whole population. To assess if ETC influences indirectly or directly female survival, we studied the influence of ETC activity with and without time lags. We considered the frequency, amplitude and duration of the winter ETCs (see details in the winter ETC variables section). We also compared the relationships between female eider

1 survival and winter ETCs to the one between survival and winter NAO reported in Guéry et al.
2 (2017).

3 We analysed 3954, 553 and 1336 individual encounter histories of female Common
4 eiders respectively from the Canadian Arctic, Svalbard and northern Norway. We first checked
5 the fit of our datasets to the single-state Cormack-Jolly-Seber (CJS) reference model (Burnham
6 1987) with goodness-of-fit tests computed using U-CARE (Choquet et al. 2009a) and presented
7 in Supporting Information S1. Avian cholera outbreaks have occurred regularly in the Canadian
8 population, which strongly affected eider survival (Descamps et al. 2009, Descamps et al. 2012).
9 To account for this cause of mortality from the analysis, we removed the individuals that died
10 because of the cholera at their last capture/recovery (right-censoring). Indeed, cholera mortality
11 only occurred on the breeding grounds (Buttler 2009) and all individuals that died from cholera
12 were collected at the end of the season and their ring reported. Models were implemented in
13 program E-SURGE (Choquet et al. 2009b). Details about the implementation of the IDSH
14 mixture models in program E-SURGE are given in Appendix S2 of Guéry et al. (2017). We then
15 performed analyses of deviance (ANODEV, Grosbois et al. 2008) to test whether or not
16 variations in the covariate were significantly associated with variation in female eider survival in
17 each population, and we calculated the proportion of deviance (Dev) explained by a given
18 covariate as:

$$R_{Dev}^2 = \frac{Dev(F_{cst}) - Dev(F_{co})}{Dev(F_{cst}) - Dev(F_t)}$$

20 where F_{cst} , F_t and F_{co} refer respectively to models with constant, time and covariate effects. We
21 ranked our models with the Akaike's information criterion (Burnham & Anderson 2002)
22 adjusted for overdispersion (Quasi-Akaike's information criterion, QAIC) for the Canadian
23 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 northern Norwegian population.

6. Results

6.1. Relationships between winter ETCs and female eider survival

In the Canadian breeding population, adult female eider survival was significantly linked to the number of winter ETCs in the southern Atlantic Canada with no time lag (model 1_{time} 2_{Number of ETCs of sAC}; **Table 2**; Figure 4) and the duration of the longest ETCs in southwest Greenland with a lag of two years (model 1_{Longest ETC_L2 of G} 2_{constant}; **Table 2**). As predicted, the most parsimonious model detected different survival responses among individuals, i.e. a significant individual heterogeneity in the survival response to winter ETC activity in this population. In this model, survival variation of one of the two groups, which represented 24% of individual capture histories, was negatively related to the number of winter ETCs in southern Atlantic Canada (model 1_{time} 2_{Number of ETCs of sAC}; group H2; slope on logit scale = -1.46 ± 0.38 SE; $R^2_{Dev} = 0.39$; **Table 2**; Figure 4). Survival of the other group (group H1, 76% of capture-histories) was significantly reduced by the duration of the longest ETC in southwest Greenland with a lag of two years (model 1_{Longest ETC_L2 of G} 2_{constant}; slope on logit scale = -0.41 ± 0.08 SE; $R^2_{Dev} = 0.39$; **Table 2**).

Survival of female eiders breeding in Svalbard and northern Norway was associated with lagged winter ETC activity (**Table 2**). Survival of females breeding in Svalbard was negatively associated with i) the wind speed of the strongest ETC recorded on the Norwegian wintering ground zone 1 with a lag of two years (model Max wind_L2 of No; $R^2_{Dev} = 0.30$; slope on logit scale = -0.65 ± 0.26 SE; **Table 2**;

Figure 5) and ii) the duration of extreme ETCs in Greenland with the same time lag (model Duration extreme ETCs_L2 of I; $R^2_{Dev} = 0.28$; slope on logit scale = -0.47 ± 0.24 SE; **Table 2**).

1 In the northern Norway breeding population, survival of female eiders was significantly
2 reduced by maximum wind speed of the strongest ETC of northern Norway zone 2 (Fig.2) with
3 time lags of one and two years ($R^2_{Dev} = 0.22$; see Table 2; Figure 6). Moreover, all individuals
4 showed the same response in survival (i.e., no significant heterogeneity was detected,
5 $\Delta QAIC_c > 3$; Table 2).

6 ***6.2. Comparison between the effect of winter extra tropical cyclones and North Atlantic*** 7 ***Oscillation***

8 Adding year 2014 to the time series used in Guéry et al. 2017 did not change their results
9 about the relationship between winter NAO and female eider survival in all three breeding
10 populations, especially for the Svalbard population (i.e., winter NAO marginally explains
11 survival fluctuations, $p = 0.073$; Table 2). We thus used this additional year in our analyses.

12 In the wintering areas of the Canadian population, the winter NAO was highly and
13 significantly linked to the number of winter ETCs on the southern Atlantic Canada wintering
14 ground ($R^2 = 0.90$; $p < 0.0001$; Fig S2.1; Supporting Information S2), whereas it was not linked to
15 winter ETC activity in Greenland with a lag of 2 years (Fig S2.3; Supporting Information S2).
16 Moreover, the number of ETCs in southern Atlantic Canada performed as well as the winter
17 NAO to explain female survival at a population level ($h \cdot NAO$ versus $h \cdot \text{Number of ETCs of sAC}$;
18 $\Delta QAIC = 1.35$; $R^2_{Dev} = 0.27$ and 0.26 respectively). However, when we tested the effect of the
19 number of winter ETCs in southern Atlantic Canada and the winter NAO on each group
20 separately, the number of winter ETCs performed better ($\Delta QAIC = 3.81$). It only explained
21 ($R^2_{Dev} = 0.35$) survival variation of the group migrating in this area and explained it better than
22 the direct winter NAO (models $1_{time} 2_{\text{Number of ETCs of sAC}}$ versus $1_{time} 2_{NAO}$; Table 2).

For the Svalbard population, the lagged winter NAO was significantly associated with the total number ETCs in Iceland (e.g. with winter NAO with one-year lag: $R^2 = 0.74$; $p = 0.001$; Fig S2.4; Supporting Information S2) but not significantly in northern Norway zone 1 (e.g. with winter NAO with one-year lag: $R^2 = 0.48$; $p = 0.073$; Fig S2.6; Supporting Information S2). However, the ETC related covariates performed better than the NAO to explain variation in survival of Svalbard eiders. No significant influence of winter NAO (lagged or not) on survival was detected, whereas the maximum wind speed of ETCs in Norwegian wintering grounds (with a 2 years-lag) performed and explained female eider survival better than winter NAO regardless of time lag (e.g. $\Delta QAIC = 2.00$ between models Max wind_L2 of No and NAO; Table 2).

For the Norwegian breeding and wintering population, the winter NAO was significantly associated with the number of extreme winter ETCs (e.g. with winter NAO with one-year time lag: $R^2 = 0.37$; $p = 0.049$; Fig S2.8; Supporting Information S2). Survival of female eiders breeding and wintering in northern Norway was better explained by the winter NAO with a lag of two years alone (model NAO_L2, $R^2_{Dev} = 0.32$; Table 2) than by any winter ETC-related covariate. The winter NAO with lags was not significantly associated to wind speed of the strongest ETC with lags (Fig S2.8; Fig S2.9; Supporting Information S2) and including both variables into the same model improved its performance. Models including the effects of both winter NAO and winter ETC activity performed better (Table 2) and explained a larger proportion of variation in survival (Table 2) than a model with winter NAO only. In particular, the winter NAO with a lag of two years combined with the maximum wind speed of ETCs with a lag of one year explained 53% of female eider survival variation (model NAO_L2+Max wind_L1 of nNo; Table 2).

7. Discussion

The marine environment in non-tropical regions is highly influenced by ETCs (Hoskins & Hodges 2002, Ulbrich et al. 2009, Wang et al. 2013). Although several marine species winter in these regions, no study has quantitatively investigated the effect of cyclones occurring outside the tropics on wildlife. By coupling long-term capture-mark-recapture data with individual tracking information to identify wintering areas, we provide the first quantitative study of the impact of winter extratropical cyclones (ETCs) and their extremes on the annual adult survival of a long-lived marine duck, the common eider. As predicted, we detected inter- and intra-population heterogeneity in the response to winter ETC activity, which could be partly driven by the presence of climatic shelters on the specific wintering grounds used by birds. Moreover, the underlying mechanisms involved in the winter ETC effects seem to differ between and within populations, as it can be with or without time lags.

7.1. Climatic fluctuations affect survival of a long-lived species

The winter ETC activity seems to have negative effects on female eider survival in all three breeding populations studied and explained between ca. 22% and 43% of the inter-annual variation in survival. These effects are similar to the effects of tropical hurricanes recorded on Mediterranean Cory's shearwaters migrating to the Central Atlantic and Southern Atlantic (Boano et al. 2010). Eiders are long-lived and their population growth rate is very sensitive to changes in adult survival (Sæther et al. 2000). Adult survival is expected to be buffered against environmental variability (Gaillard & Yoccoz 2003), but several studies also showed that climatic variation, whether extreme or not, could affect the adult survival of long-lived species (e.g. Sandvik et al. 2005). Detecting a negative influence of local (here winter ETC activity)

and/or global (e.g. winter NAO) climatic variables on survival is thus important to better understand the future viability of their populations.

7.2. Direct impact of winter ETCs versus indirect impact of their extremes on survival

Winter ETC activity can directly increase seabird mortality through different mechanisms. They can disturb their feeding behaviour, which is sensitive to the occurrence of stormy weather (e.g. Finney et al. 1999). Common eiders are mostly visual feeders (Frimer 1994), so foraging can be affected by water turbidity associated with strong winds or sea-surface conditions that reduce visual acuity (Eriksson 1985, Henkel 2006). Since ETC activity increases winds, waves and current speed, it can also increase foraging costs. While common eiders employ a variety of tactics to reduce energy costs during diving, descent duration and number of strokes during descent increase exponentially with increasing current velocity, suggesting an increase in the energetic costs of diving (Heath et al. 2006, Heath & Gilchrist 2010). During ETCs, fast currents, the strong increase in drag and energetic costs of diving can even make foraging unprofitable with net energy gain per dive cycle predicted to reach zero and become unprofitable at 1.21 m s⁻¹ at 11.3 m depth (Hawkins et al. 2000, Heath et al. 2006, Heath & Gilchrist 2010). Common eiders stop foraging and rest well below this threshold (Heath & Gilchrist 2010), which lowers their energetic gains (Dehnhard et al. 2013). Adding to the fact that the winter period reduces the feeding window of these diurnal feeders (Systad et al. 2000, Heath & Gilchrist 2010), winter ETC activity can potentially cause starvation (Chambers *et al.* 2011).

On the other hand, extreme ETCs may impact eider survival through indirect (lagged) effects via the food chain. Different mechanisms can be proposed; extreme wind events

1 associated with extreme ETCs are an important natural disturbance in coastal systems
2 (Richardson & LeDrew 2006), decreasing the food availability of common eiders' benthic prey.
3 Winter diet of common eiders includes different marine resources depending on their wintering
4 grounds. Eiders consume preferably blue mussels of smaller sizes (Bustnes & Erikstad 1990,
5 Varennes et al. 2015) found near the shore, in kelp beds or rocky habitat in the Gulf of St.
6 Lawrence (Guillemette et al. 1992) or in northern Norway (Bustnes & Erikstad 1988), softshell
7 clams *Mya eideri* and marine *polychaete* worms found in soft sediments in southwest Greenland
8 (Merkel et al. 2007), gastropods in Newfoundland (Goudie & Ankney 1986), or sometimes
9 crustaceans and echinoderms. They can also include sea urchins found in shallow water near the
10 shore (<10 m; Cottam 1939, Madsen 1954, Bustnes & Lønne 1997).

11 Extreme cyclones can remove large intertidal and subtidal areas rich in fauna and
12 macroalgae (e.g. Thomsen et al. 2004), destroy bivalve beds at shallow depths (Reusch &
13 Chapman 1995, Carrington 2002, Carrington et al. 2009) and directly decimate sea urchins and
14 drive their community structure (Ebeling et al. 1985). In addition, winter ETCs can induce strong
15 wave action, which lowers blue mussel growth rates (Sukhotin et al. 2006), reduce primary
16 productivity, lowering mussel growth rates to taking 3-5 years to reach 1-2cm (Bustnes &
17 Erikstad 1990, Varennes et al. 2015) if carried to the extreme (Fujii & Yamanaka 2008), and act
18 on intertidal gastropod populations via size-specific mortality and indirectly affect them by
19 altering their foraging behaviour, growth and life histories (Brown & Quinn 1988). Also, oceanic
20 volume fluxes are positively related to Nordic seas cyclone activity (Sorteberg et al. 2005)
21 providing transportation of blue mussel larvae over long distances (Berge et al. 2005). As larvae
22 settle when they reach a size between 0.026 - 0.035mm (Sprung 1984) and current velocity
23 drives the settlement of marine *polychaete* worms (Pawlik & Butman 1993), extreme winter ETC

activity could decrease these species' settlement with higher velocity and thus decrease food availability for eiders in subsequent years. Hence, extreme ETCs may have cascading effects on eider survival through a variety of mechanisms affecting the availability of their prey.

7.3. Contrasted effect of winter ETC activity between and within eider populations: a “climatic shelter” effect?

The strongest relation we detected was a direct and negative link (consistent with our predictions) between the total number of winter ETCs in southern Atlantic Canada and the survival of female eiders breeding in Canada. More specifically, this variable was only associated with the survival of one group of birds (group H2; 24% of individual capture histories), potentially those migrating to the southern Atlantic Canada area as suggested in Guéry et al. (2017). On the other hand, the wind speed of the strongest extreme winter ETCs impacted, with a time lag, the survival of female eiders breeding and wintering in northern Norway, and also, although less strongly, those breeding in Svalbard. Indirect effects of the duration of extreme ETC activity in southwest Greenland were also detected in one group of Canadian birds (group H1; 76% of individual capture histories), potentially those wintering on the southwest Greenland ground as suggested in Guéry et al. (2017); indirect impacts of the same variable in Iceland was observed on survival of female eiders from the Svalbard breeding population.

We propose that the detected inter- and intra-population heterogeneity, i.e. the direct versus indirect impacts of winter ETC activity on survival described above, can be partly explained by variation in the natural “climatic shelters” available on eider wintering grounds. We suggest that direct effects can occur in the absence of shelter, whereas indirect effects likely occur via the impact of ETC activity on prey availability. Shelter against wind can result in

microclimate effects and affect eider energetics during incubation (Høyvik Hilde et al. 2016). At a larger spatial scale, the shelter effect of fjords on marine wildlife has been proposed in the literature (see review by Howe et al. (2010)). Howe et al. (2010) defined fjords as “inshore sheltered deep-water bodies, which often possess a unique biogeochemistry, fauna, hydrography and sedimentation”. Fjord and channel systems in Scandinavia, Iceland and Greenland form some of the largest estuarine areas in the world and can be used by marine mammals seeking refuge from severe weather conditions (Sanino & Van Waerebeek 2008, Acevedo et al. 2017) or for spawning grounds, nursery, and recruitment areas by many marine fish with contrasting life histories, varying from mesopelagic (Lopes 1979) and pelagic (Brown 2002) to demersal fish (Boje 2002).

8. Female eiders wintering in southern Atlantic Canada feed along the sea ice edge (Goudie & Ankney 1986) with potentially few climatic shelter areas. These individuals can thus be directly exposed to harsh weather conditions and hence be directly impacted by winter ETCs (Figure 1). In addition, sea ice formation covers shallow coastal waters, so wintering sea ducks are cut off from their marine resources and lose potential feeding sources that could have compensated losses of energy caused by low air temperature and foraging in deeper and agitated waters (Vaitkus & Bubinas 2001). On the contrary, Canadian breeding female eiders that winter in southwest Greenland are likely less vulnerable to direct effects of ETC activity because they have access to fjords extending deep inland (Ravn Merkel et al. 2002), which may provide shelters that are well protected against extreme ETC winds. In addition, female eiders from Svalbard or northern Norway wintering along the Norwegian coast, although facing weaker winter ETC activity than in Canada (

Table 1), can feed along the shores of the fjords (Bustnes and Erikstad unpublished data), which may also provide good climatic shelters and reduce the direct effects of ETC activity. However, the effect of ETCs on benthic invertebrates in fjords or in exposed coastal areas deserves further investigation to better understand the role of natural climatic shelters on the food chain and on eider survival.

8.1. Effect of winter NAO and ETCs

The potential mechanisms involved in the relationships between female eider survival, winter NAO and local ETC activity seem to differ between populations. Winter ETCs appeared to be one of the main drivers explaining the observed NAO effects on female eider survival (Guéry et al. 2017) but only in the Canadian wintering population. In the Norwegian breeding population, we found evidence that NAO and ETCs can have independent and cumulative influences. For females breeding in the Canadian Arctic, the previously detected direct effect of the winter NAO might be due, at least in part, to its relation with the number of ETCs in the southern Atlantic Canada. Conversely, lagged winter NAO and lagged wind speed of the strongest ETC in northern Norway seem to have independent and cumulative influences on survival of females breeding and wintering in northern Norway, explaining together ca. 53% of the adult female eider survival. The link between these two variables with oceanographic conditions in the North East Atlantic could explain this cumulative effect. A low winter NAO with a lag of up to 3 years leads to an increase in sea temperature and salinity in the sub-polar North Atlantic (Sarafanov 2009). This increase in sea temperature and salinity may have in turn a negative impact on blue mussel larvae and adult survival (Brenko & Calabrese 1969, Braby & Somero 2006, Menge et al. 2008), adding to the negative effect of ETC activity on them.

1 Large-scale climate indices, such as the NAO, are often used as proxies of environmental
2 conditions as they integrate both temporal and spatial components of several weather variables
3 (Stenseth & Mysterud 2005). However, our study showed that local weather variables are
4 essential and complementary to sharpen our understanding of the mechanisms linking climate
5 fluctuations and wildlife responses.

6 7 ***8.2. Effect of extreme events on survival***

8 While many studies have focused on a single extreme climatic event (ECE), or one
9 characteristic of several ECEs (usually frequency), we have investigated several characteristics
10 of ECEs (frequency, duration and amplitude) over a long-term study. Interestingly, female
11 common eider survival was affected by the amplitude and duration of ECEs but not by their
12 frequency; Canadian female survival was not impacted by the number of extreme ETCs in
13 southern Atlantic Canada but the total number ETCs, whether extreme or not. We detected an
14 effect of the amplitude of ECEs in regions of relatively low ETC activity, while we found an
15 effect of the duration in areas of intense ETC activity. This pattern probably stood out because
16 the effect of ECEs occurred mostly through the food web in our study systems, where long
17 lasting or large ECEs more likely affect the benthic ecosystems. Our results are noteworthy as
18 population models focusing on the impact of ECEs usually focus on their frequency (e.g.
19 (Jenouvrier et al. 2015) rather than their duration or amplitude. Frequency, amplitude and
20 duration of extreme weather events are predicted to increase in most future climate scenarios
21 (Rind et al. 1989, Easterling et al. 2000), potentially impacting population persistence.

22 23 ***8.3. Conclusion***

Even if adult survival of long-lived species should be buffered against environmental variability (Gaillard & Yoccoz 2003), extreme weather conditions (such as extreme ETCs) significantly affect adult survival during the wintering period. This is especially important in the case of extreme weather events whose frequency, amplitude and duration are predicted to increase in most future climate scenarios (Rind et al. 1989, Easterling et al. 2000), especially at high latitudes in the northern hemisphere (Bengtsson et al. 2009, Ulbrich et al. 2009).

As previously emphasized (Guéry et al. 2017), to predict the effects of global change on wild populations, differences in individual life-history strategies (e.g. migration strategies) must be taken into account as they introduce inter- and intra-population heterogeneities in the response to climatic fluctuations. In our case, an increase in winter ETC severity or frequency could directly affect only a segment of the population depending on where birds winter. Although it can be generated by different factors (e.g.. wintering strategy or age), such intra-population heterogeneities will impact population trajectories and viability, and should thus be incorporated into population models (Coulson et al. 2001, Benton et al. 2006, Kendall et al. 2011).

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11. Tables

Table 1: Descriptive statistics of winter (December-March) extratropical cyclones (ETC) activity variables (mean \pm SE (min-max)) on each wintering ground from 1996-2014 for Greenland and Atlantic Canada, 1999-2014 for Iceland and northern Norway zone 1 and 1985-2014 for northern Norway zone 2. The two variables for the mean ETC activity are the total number of ETCs (Number of ETCs) and the mean of their wind speed (Mean wind) within the overlap region. The four other variables measure the number of extreme ETCs, i.e. with wind speed above the 95th percentile threshold of the local wind speed distribution at least once in the overlap region, the number of days of extreme ETC (Extreme ETCs (days per winter)), the duration of the longest ETC and the maximum wind speed of the strongest ETC (Max wind) all relative to the overlap. “95th percentile” is the 95th percentile threshold of local wind speed distribution (m s^{-1}). Wind speeds are at a 10-m height.

	Greenland	Atlantic Canada	Iceland	northern Norway zone 1	northern Norway zone 2
Number of ETCs	45.55 ± 2.01 (29-62)	69.33 ± 1.40 (56-79)	53.27 ± 3.11 (29-72)	32.87 ± 1.74 (25-50)	33.79 ± 1.49 (20-54)
Mean wind (m s^{-1})	11.64 ± 0.22 (9.97-13.68)	12.77 ± 0.13 (11.74-14.22)	14.14 ± 0.14 (13.18-15.16)	9.35 ± 0.19 (8.09-10.20)	9.63 ± 0.20 (8.09-12.92)
Number of extreme ETCs	1.78 ± 0.37 (0-6)	1.78 ± 0.37 (0-6)	2.27 ± 0.34 (1-5)	1.33 ± 0.27 (0-3)	1.79 ± 0.35 (0-9)
Duration extreme ETCs (days per winter)	0.44 ± 0.08 (0-1.12)	0.74 ± 0.13 (0-2.63)	0.5 ± 0.09 (0.12-1.37)	0.25 ± 0.06 (0-0.62)	0.44 ± 0.12 (0-3.25)
Longest ETC (days per winter)	3.67 ± 0.20 (2.75-5.87)	3.67 ± 0.17 (2.5-4.62)	4.05 ± 0.25 (3-6.5)	1.77 ± 0.20 (0.37-3.25)	2.20 ± 0.32 (0.12-7.25)
Max wind (m s^{-1})	24.87 ± 0.37 (21.74-27.61)	25.74 ± 0.52 (22.27-29.15)	28.68 ± 0.58 (25.54-32.67)	22.77 ± 0.70 (18.82-29.26)	22.51 ± 0.52 (17.68-29.26)
95 th percentile (m s^{-1})	23.30	22.60	25.30	21.68	20.95

Table 2: Effect of winter extratropical cyclones (ETC) activity with or without time lag of one (L1) or two (L2) years on female adult survival of common eider breeding in Canada (1996-2014), in Svalbard (1999-2014) and in northern Norway (1985-2014). Results of analysis of deviance (ANODEV) are presented for the first ten models. Variables from each wintering area (G for western Greenland, sAC for southern Atlantic Canada, I for Iceland, No for northern Norway zone 1 and nNo for northern Norway zone 2) were tested either on each class separately (In the Canadian population: 1 stands for the group H1 wintering potentially in Greenland and 2 for the group H2 potentially in sAC), on both in interaction (h) or without heterogeneity.

Survival	Deviance	Criterion	Δ Criterion	$F_{j-1,n-j}$	p	R^2_{Dev}
Canadian population		QAIC	Δ QAIC			
1_{time} 2_{Number of ETCs of sAC}	22511.14	8126.30	0.00	8.48	0.010	0.35
1 _{time} 2 _{constant}	22525.55	8129.45	3.15	-	-	-
1 _{time} 2 _{NAO}	22521.81	8130.12	3.81	1.58	0.227	0.09
Time (no heterogeneity)	22578.08	8146.23	19.92	-	-	-
h* _{time}	22483.95	8146.58	20.28	-	-	-
1_{Longest ETC_L2 of G} 2_{Number of ETCs of sAC}	22657.95	8146.89	20.47	8.19	<0.0001	0.43
1_{Longest ETC_L2 of G} 2_{constant}	22688.83	8155.92	29.51	10.07	0.006	0.39
1_{Duration extreme ETCs_L2 of G} 2_{constant}	22696.39	8158.52	32.21	8.92	0.009	0.36
1_{Number of extreme ETCs_L2 of G} 2_{constant}	22700.09	8159.84	33.54	8.39	0.011	0.34
1_{Number of ETCs_L2 of G} 2_{constant}	22710.50	8163.56	37.26	7.02	0.018	0.31
Svalbard population		AICc	Δ AICc			
Max wind_L2 of No	1952.24	1986.99	0.00	5.48	0.036	0.30
Duration extreme ETCs_L2 of I	1952.69	1987.44	0.45	5.08	0.042	0.28
Time	1932.26	1988.14	1.14	-	-	-
Number of ETCs of No	1954.02	1988.77	1.78	3.97	0.068	0.23
Number of ETCs_L1 of No	1954.15	1988.90	1.91	3.87	0.071	0.23
NAO	1954.24	1988.99	2.00	3.80	0.073	0.23
Mean wind_L1 of I	1955.53	1990.28	3.29	2.87	0.114	0.18
Mean wind of No	1956.30	1991.05	4.06	2.36	0.148	0.15
Number of ETCs_L1 of No	1957.20	1991.95	4.95	1.81	0.202	0.12
Constant	1960.67	1993.28	6.28	-	-	-
Norwegian population		QAICc	Δ QAICc			
NAO_L2+MaxWind_L1 of nNo	8471.13	5882.87	0.00	14.86	<0.0001	0.53
NAO_L2+MaxWind_L2 of nNo	8473.73	5884.65	1.78	13.68	<0.0001	0.51
Time	8412.23	5896.07	13.20	-	-	-
NAO_L2	8498.12	5899.34	16.48	12.68	0.001	0.32
Max wind_L1 of nNo	8510.29	5907.70	24.83	7.76	0.010	0.22
h* Max wind_L1 of nNo	8509.98	5911.57	28.71	4.17	0.010	0.19
Max wind_L2 of nNo	8517.54	5912.67	29.81	5.36	0.028	0.17
h* Max wind_L2 of nNo	8515.84	5915.60	32.73	3.14	0.033	0.15
NAO_L1	8525.57	5918.18	35.32	3.07	0.091	0.10
Constant	8538.47	5924.99	42.13	-	-	-

Significant ANODEV results are in bold. n is the number of survival estimates obtained from model Ft (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, $F_{j-1,n-j}$ 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 survival variation explained by the covariate (see Grosbois *et al.* 2008 for more details).

12. Figures

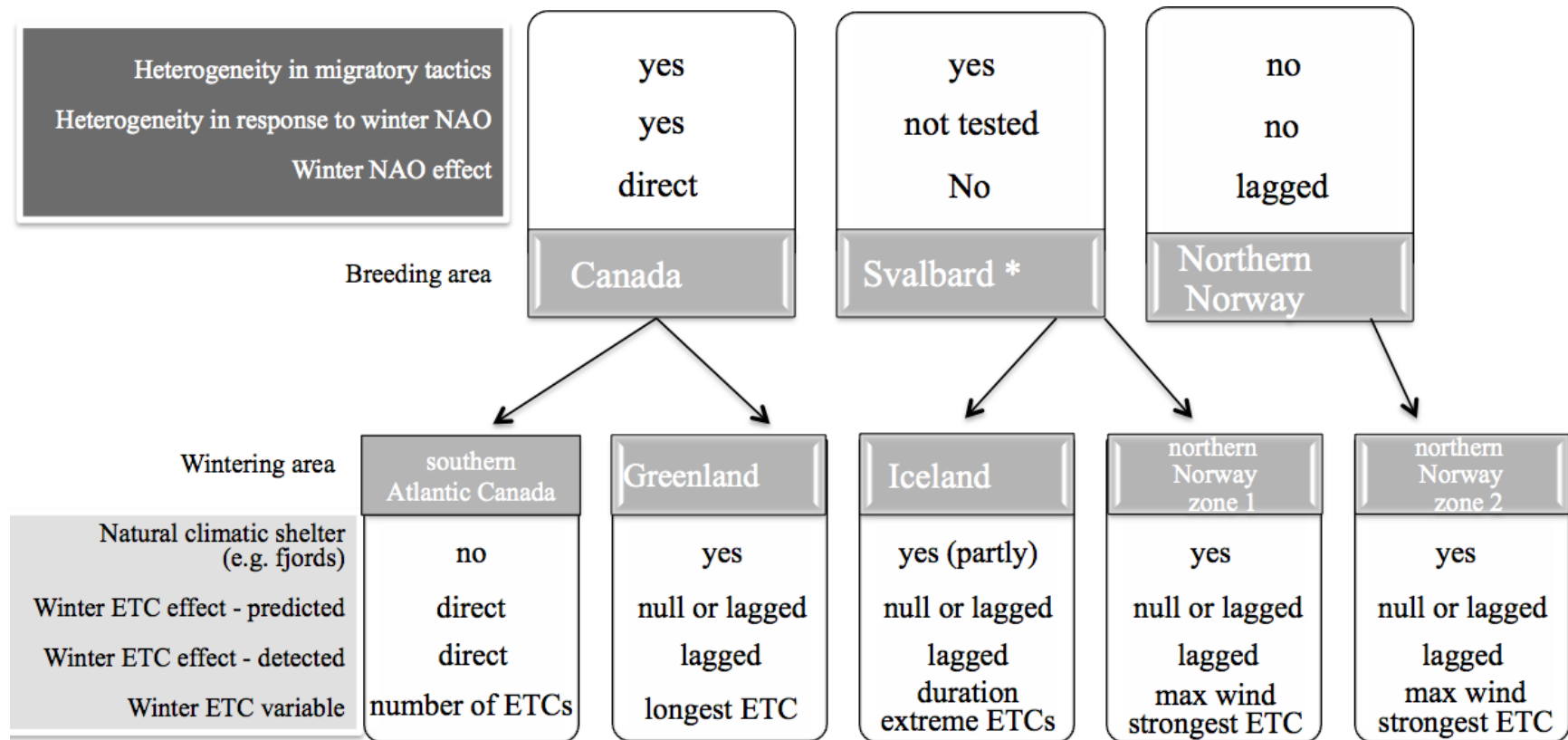


Figure 1: Summary diagram of winter North Atlantic Oscillation (NAO) effect (dark grey box; Guéry *et al.* 2017) and local winter extratropical cyclones (ETC) effect (light grey box) on female eider survival depending on their breeding population and wintering areas. For the Svalbard population, relations between survival and winter variables were given for the whole population (individual heterogeneity was not tested, see methods).

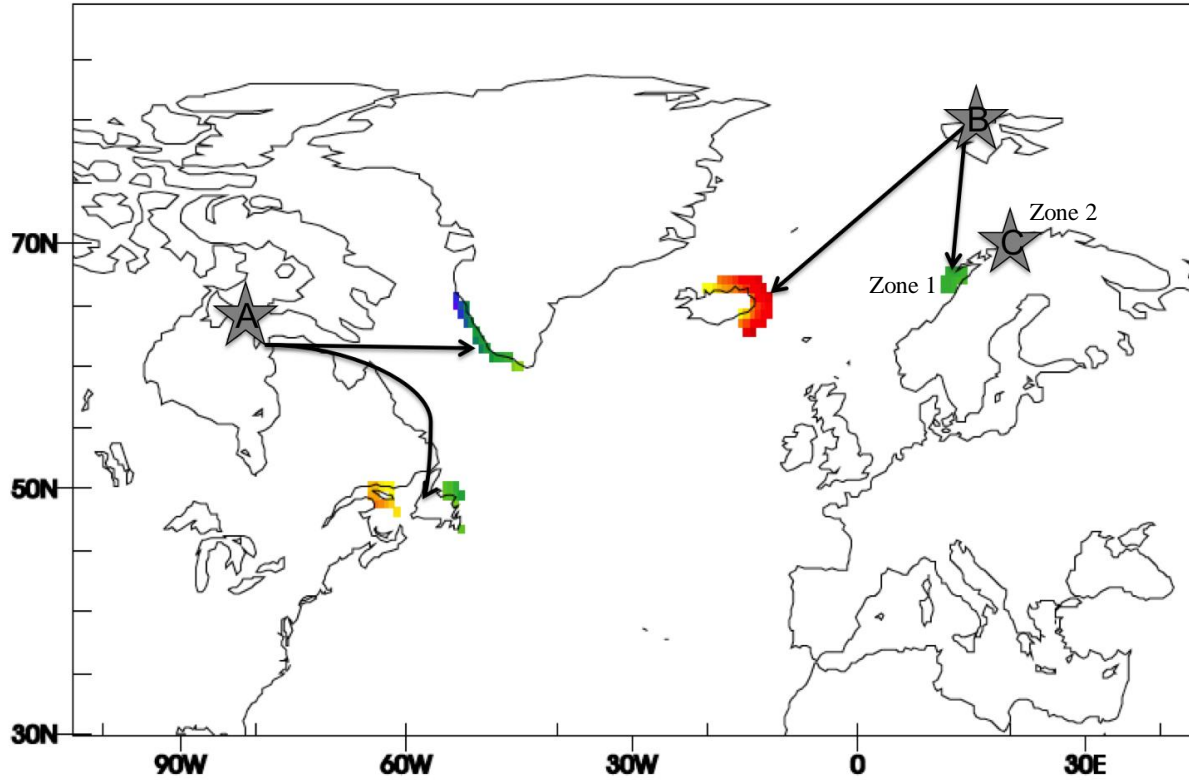


Figure 2: Grid cells used as winter (December to March) distribution (home range Kernel core, see methods) of female common eiders breeding in Canada (A) and wintering either in west Greenland or in southern Atlantic Canada, breeding in Svalbard (B) and wintering in Iceland and northern Norway (zone 1). Resident eiders breeding near Tromsø (C) wintered in the vicinity of the island (zone 2).

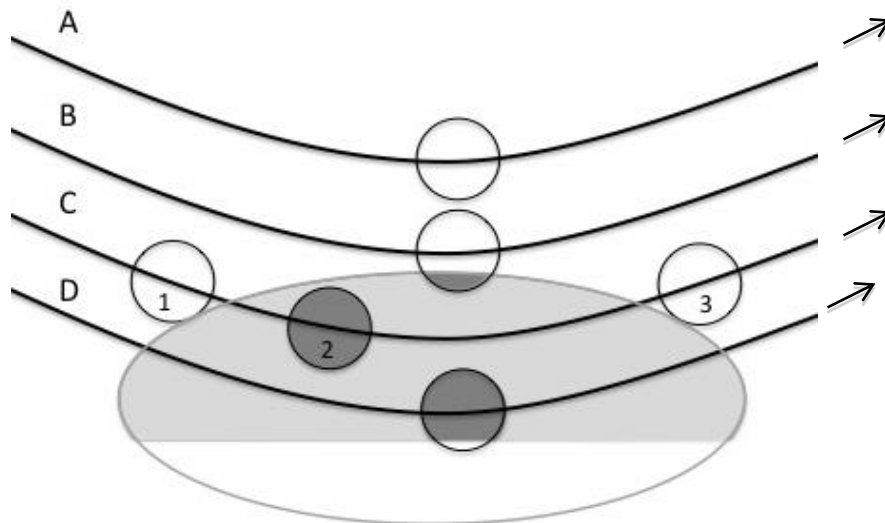


Figure 3: Schematic of winter extratropical cyclones (ETC) variables extraction. Black lines (A, B, C and D) are examples of ETC tracks. The light grey ellipse is an example of eider wintering area with the land part masked in white. Black circles are ETC buffer regions, i.e. a 6-degree geodesic radius cap centred on the ETCs, at different time (e.g. time “1” to “3” for the ETC track “C”). Parts in dark grey represent the ETC regions overlapping with the wintering area used to extract the winter ETC variables. For example, ETC corresponding to track B would be included in the number of ETC and if the numbers 1 to 3 referred to days, the duration of the ETC corresponding to track C is one day.

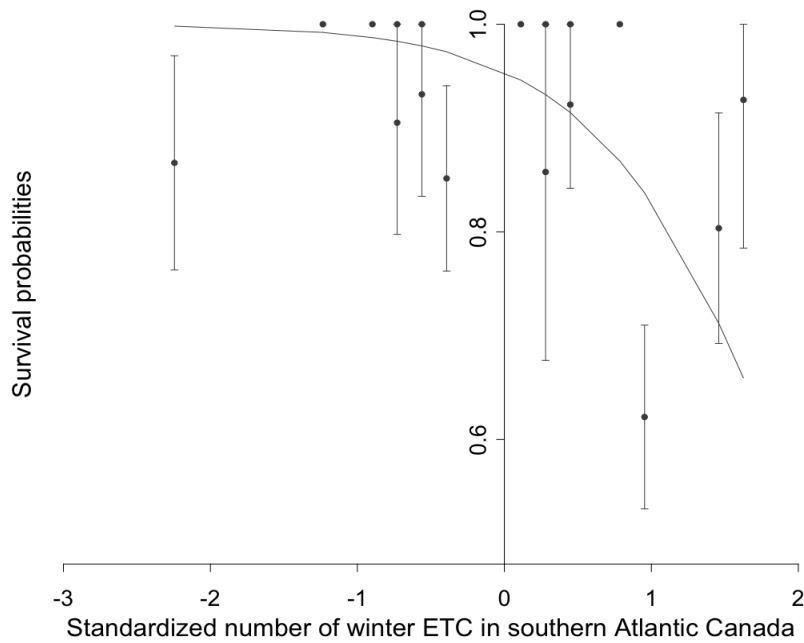


Figure 4: Influence of the number of winter extratropical cyclones (ETC) without time lag in southern Atlantic Canada (x- axis) on adult survival estimates (\pm SE; y-axis) of female eiders from group H2 and breeding in the Canadian Arctic. Isolated points represent survival estimates from the time dependent model with heterogeneity (model h*time; Table 2). The line represents predicted survival estimates constraint by the number of winter ETCs in southern Atlantic Canada (model with heterogeneity 1_{time} 2_{Number of ETCs of sAC}; Table 2).

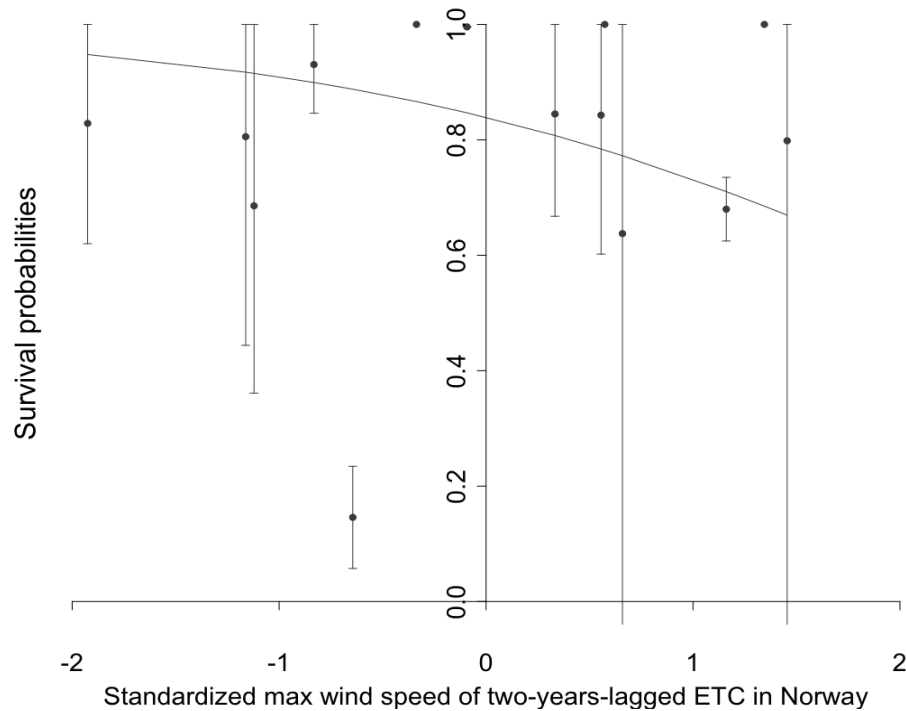
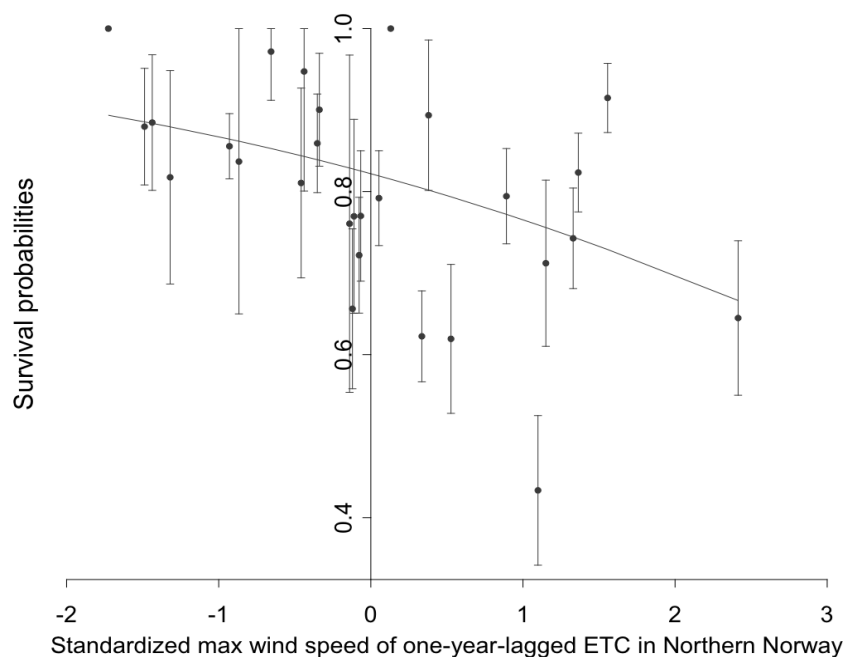


Figure 5: Influence of the maximum (max) wind speed of winter extratropical cyclones (ETC) with a two-years lag (L2) in Norway zone 1 (No; x- axis) on adult survival estimates (\pm SE; y-axis) of females eiders breeding in Svalbard. Isolated points represent survival estimates from the time dependent model with heterogeneity (model Time; Table 2). The line represents predicted survival estimates from the model with survival constraint with the maximum wind speed of the strongest ETCs with a two-year lag (Max wind_L2 of No; Table 2).

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Figure 6: Influence of the maximum (max) wind speed of the strongest winter extratropical cyclones (ETC) with a one-year lag in northern Norway zone 2 (x- axis) on adult survival estimates (\pm SE; y-axis) of female eiders breeding and wintering in northern Norway. Isolated points represent survival estimates from the time dependent model (model time; Table 2). The line represents predicted survival estimates from the model ($\phi(\text{MaxWind_L1_nNo})$; Table 2) with survival constraint by the covariate.

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64 13. Supporting Information captions:

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Table S1: Goodness-of-fit (GOF) tests results for the standard time-dependent Cormack-Jolly-Seber model (CJS-model) and the time-dependent model with individual heterogeneity of detection (IDH-model) for common eider breeding in Norway (1985-2014), Canada (1996-2014) and Svalbard (1999-2014).

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Table S2: Effect of the maximum wind speed of the strongest winter extratropical cyclones with or without time lag of one (L1) or two (L2) years on female adult survival of common eider breeding in northern Norway (1985-2014). Results of analysis of deviance (ANODEV) are presented for the four width-length combinations.

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Figure S1 to S9: Correlations between winter NAO and local winter ETCs-related variables with or without time lags in each wintering areas (Greenland (G), southern Atlantic Canada (sAC), Iceland (I), northern Norway zone 1 (No) and northern Norway zone 2 (Nno)) for the three populations breeding either in Canada (1996-2014), in Svalbard (1999-2014) or in northern Norway (1985-2014).

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