Vol. 627: 155–170, 2019
https://doi.org/10.3354/meps13066

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 26

Winter extratropical cyclone influence on seabird survival: variation between and within common eider *Somateria mollissima* populations

L. Guéry[1,*], S. Descamps[2], K. I. Hodges[3], R. Pradel[4], B. Moe[5], S. A. Hanssen[6], K. E. Erikstad[6,7], G.W. Gabrielsen[2], H. G. Gilchrist[8], S. Jenouvrier[9,10], J. Bêty[1]

[1]Département de Biologie and Centre d'études nordiques, Université du Québec à Rimouski, Rimouski, QC G5L 3A1, Canada
[2]Norwegian Polar Institute, Fram Center, 9296 Tromsø, Norway
[3]Department of Meteorology, University of Reading, Whiteknights, PO Box 217, Reading RG6 6AH, UK
[4]CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, 34090 Montpellier, France
[5]Norwegian Institute for Nature Research, 7034 Trondheim, Norway
[6]Norwegian Institute for Nature Research, Arctic Ecology Department, FRAM – High North Research Centre for Climate and the Environment, PO Box 6606 Langnes, 9296 Tromsø, Norway
[7]Faculty of Science and Technology, UiT The Arctic University of Norway, Post box 6050 Langnes, 9037 Tromsø, Norway
[8]National Wildlife Research Centre, Environment Canada, Ottawa, ON K1S 5B6, Canada
[9]Woods Hole Oceanographic Institution, Mailstop 50, Woods Hole, MA 02543, USA
[10]Centre d'Etudes Biologiques de Chizé, UMR7372 CNRS, 79360 Villiers-en-Bois, France

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 2 arctic (northern Canada and Svalbard) and 1 subarctic (northern Norway) breeding populations of common eider *Somateria mollissima* over periods of 19, 16 and 30 yr, 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 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.

KEY WORDS: Extreme weather and climatic events · Multi-event models · Hidden states and mixture models · NAO · Arctic · Inter and intra-population heterogeneity · Migratory tactics

1. 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 identifying relevant climatic parameters that affect demographic rates (e.g. survival, recruitment or breeding success; Jenouvrier 2013) throughout the annual cycle. The winter period is one of the critical stages influencing annual survival of migratory seabirds (Barbraud et al. 2000, Sandvik et al. 2005, Frederiksen et al. 2008) through direct or

---

[*] Corresponding author: lorelei.guery@gmail.com

indirect effects of winter climatic conditions, e.g. on the availability of seabird prey or on the energetic balance of wintering seabirds (Grosbois & Thompson 2005, Harris et al. 2005).

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

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

Increased ETC activity could directly (no time lag) increase common eider foraging effort and energetic needs required to maintain body temperature (Heath et al. 2006, Heath & Gilchrist 2010) and ultimately decrease their survival. In addition, ETCs could negatively and indirectly (with time lag) affect eider survival by influencing oceanographic conditions (Visbeck et al. 2003, Sarafanov 2009) and hence eider food availability and/or food quality (Menge et al. 2008, Descamps et al. 2010). Heavy storms can indeed destroy bivalve beds at shallow depths (Brenko & Calabrese 1969, Reusch & Chapman 1995, Carrington 2002, Carrington et al. 2009) or reduce primary productivity (Fujii & Yamanaka 2008). These effects of ETCs could be modulated by coastal topography and by the presence of fjords on eider wintering grounds. Fjords, hereafter named 'climatic shelters', are defined as narrow inlets of the sea between cliffs or steep slopes, which can provide natural shelters from the wind (Howe et al. 2010). The climatic sheltering 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 2 distinct wintering grounds (e.g. more ETCs and a longer duration of extreme ETCs in southern Atlantic Canada; Table 1). We thus expect intrapopulation 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 (Fig. 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,

Table 1. Descriptive statistics of winter (December to March) extratropical cyclones (ETC) activity variables (mean ± 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 2 variables for the mean ETC activity are the total number of ETCs (No. of ETCs) and the mean of their wind speed (Mean wind) within the overlap region. The 4 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 10 m height

	Greenland	Atlantic Canada	Iceland	Northern Norway Zone 1	Northern Norway Zone 2
No. 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)
No. 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)
95th percentile (m s^{-1})	23.30	22.60	25.30	21.68	20.95

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.

2. MATERIALS AND METHODS

2.1. Study species and populations

2.1.1. 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 yr old (Hario et al. 2009) and can live an average of 15 yr (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 yr 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).

2.1.2. 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 Section 2.2) using satellite transmitters implanted in 2001 and 2003 (Mosbech et al. 2006) and in 2012 and 2013 (H. G. 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 https://nsidc.org/data/seaice_index/archives/image_select. In the Gulf of St. Lawrence, eiders preferentially feed on blue mussels *Mytilus edulis* 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).

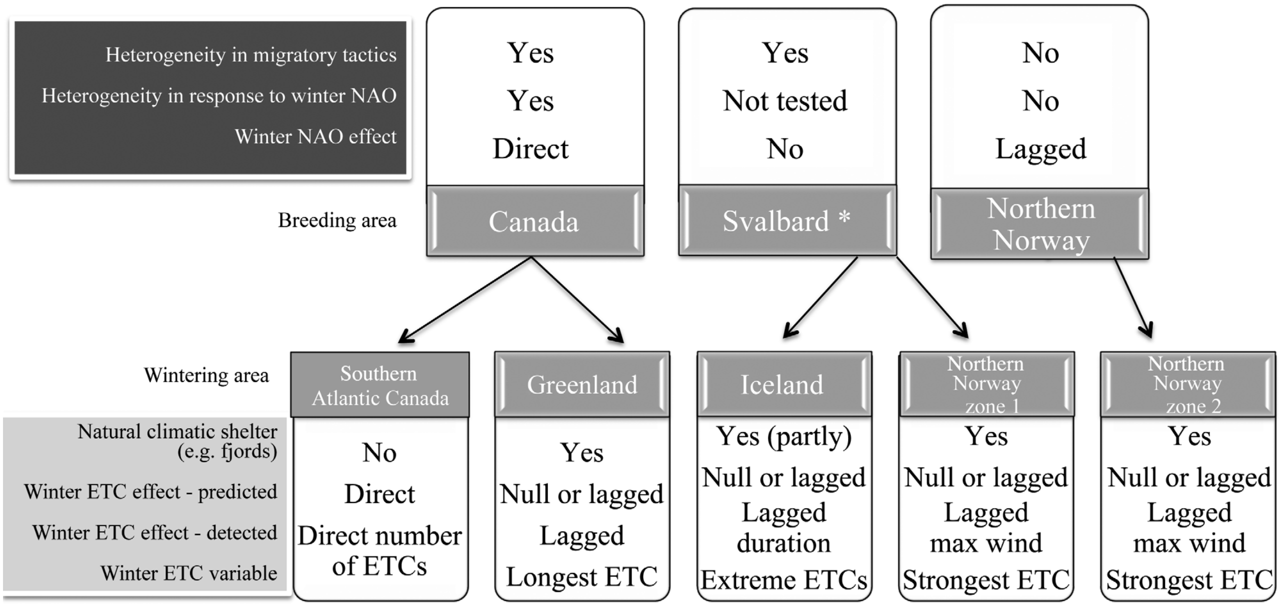

Fig. 1. Summary diagram of the winter North Atlantic Oscillation (NAO) effect (dark grey box; Guéry et al. 2017) and the local winter extratropical cyclones (ETC) effect (light grey box) on female eider *Somateria mollissima* survival, depending on their breeding population and wintering areas. For the Svalbard population, relations between survival and winter variables were given for the whole population (individual heterogeneity was not tested, see Section 2)

2.1.3. 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 Figs. 1 & 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 4 yr (2009, 2010, 2011 and 2013), while 48 females were recaptured and data were successfully retrieved from 47 geolocators. Details on capture, geolocator deployment, and the calibration, smoothing and calculations of the geolocator data are described by Hanssen et al. (2016).

2.1.4. 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 to 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 Figs. 1 & 2, all exposed to the same winter conditions.

2.2. Wintering areas

Wintering areas were defined using tracking data for the 2 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 by Mosbech et al. (2006) for the Canadian breeding population and by 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

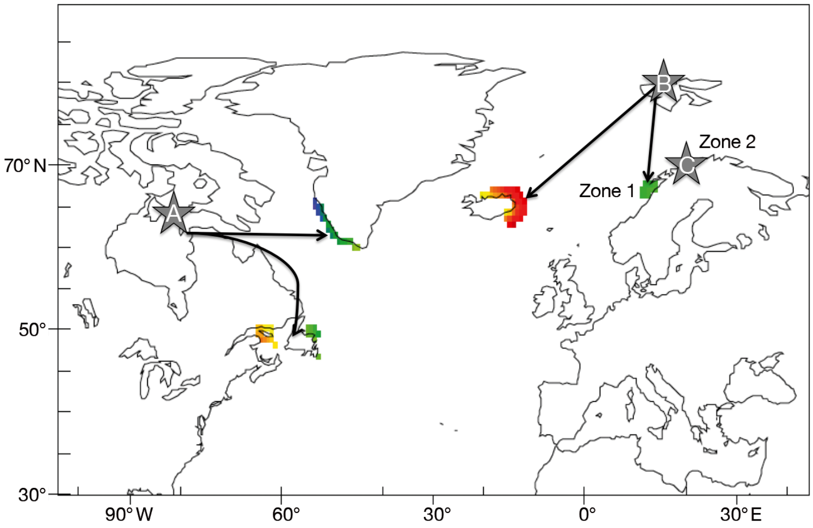

Fig. 2. Grid cells used as winter (December to March) distribution (home range Kernel core, see Section 2.2) of female common eiders (A) breeding in Canada and wintering either in west Greenland or in southern Atlantic Canada and (B) breeding in Svalbard and wintering in Iceland and northern Norway (Zone 1). (C) Resident eiders breeding near Tromsø wintered in the vicinity of the island (Zone 2). Colors show, as an example, potential differences in ETCs activity between these wintering areas

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 were 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; J. O. Bustnes and K. E. Erikstad unpubl. data) in water shallower than 10 m (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 this 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 the results did not change significantly; the length-width combination model with the lowest QAICc was selected (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m627p155_supp.pdf). 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 Fig. 2.

2.3. Variables considered

2.3.1. 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. Although 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 differ in how 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 by Roberts et al. (2014) and Hoskins & Hodges (2002), i.e. ETCs are identified and tracked using the maximum vorticity approach based on the 850 hPa relative vorticity, since it represents smaller spatial scales than pressure, and is less influenced by the background of larger spatial scales (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 >1 d and travelled >1000 km. Thus, we considered all synoptic

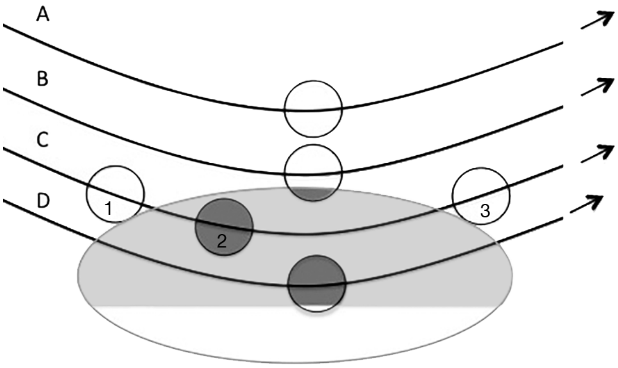

Fig. 3. Schematic of winter extratropical cyclones (ETC) variables extraction. Black lines (A, B, C and D) are examples of ETC tracks. The light grey ellipse is an example of eider wintering area with the land part masked in white, since the birds stay on the shoreline. Black circles are ETC buffer regions, 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 1 d

scale (1000 to 2500 km) ETCs in the northern hemisphere (30° to 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 to 2015 at 3 h 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° (~670 km) centred on the ETC positions (adequate for capturing the wind extremes for individual ETCs, Bengtsson et al. 2009; Fig. 3). Varying this radius between 5 and 10° 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 (Fig. 3). All the wind-related variables added to the vorticity tracks were based on the winds 10 m 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 10 m wind data to retain only data within the eider wintering areas.

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 at least once reached 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 ± 0.2 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 6 variables from mean to extreme ETC activity within the ETC regions, overlapping with the population-specific wintering area. The 2 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 4 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 Supplement (Figs. S1–S9) for each wintering area. The winter NAO was significantly correlated with at least 1 winter ETC variable, and in most cases with the number of winter ETCs in the considered area.

2.3.2. 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.

2.4. 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. The Individual Detection and Survival Heterogeneity (IDSH) mixture model developed by Guéry et al. (2017) can be used to classify female eiders from the Canadian breeding population into 2 groups, which likely represent birds using 2 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 1 of the 2 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 female survival indirectly or directly, 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 Section 2.3.1). We also compared the relationships between female eider survival and winter ETCs to the relationship between survival and winter NAO reported by Guéry et al. (2017).

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

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

where F_{cst}, F_{t} and F_{co} refer respectively to models with constant, time and covariate effects. We ranked our models with the Akaike's information criterion (Burnham & Anderson 2002) 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 northern Norwegian population.

3. RESULTS

3.1. Relationships between winter ETCs and female eider survival

In the Canadian breeding population, adult female eider *Somateria mollissima* survival was significantly linked to the number of winter ETCs in the southern Atlantic Canada with no time lag (model $1_{\mathrm{time}}\ 2_{\mathrm{Number\ of\ ETCs\ of\ sAC}}$; Table 2, Fig. 4) and the duration of the longest ETCs in southwest Greenland with a lag of 2 yr (model $1_{\mathrm{Longest\ ETC\_L2\ of\ G}}\ 2_{\mathrm{constant}}$; 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 1 of the 2 groups, which represented 24% of individual capture histories, was negatively related to the number of winter ETCs in southern Atlantic Canada (model $1_{\mathrm{time}}\ 2_{\mathrm{Number\ of\ ETCs\ of\ sAC}}$; group H2; slope on logit scale = −1.46 ± 0.38 SE; R^2_{Dev}= 0.39; Table 2, Fig. 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 2 yr (model $1_{\mathrm{Longest\ ETC\_L2\ of\ G}}\ 2_{\mathrm{constant}}$; 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 (1) the wind speed of the strongest ETC recorded on the Norwegian wintering ground Zone 1 with a lag of 2 yr (model Max wind_L2 of No1; R^2_{Dev}= 0.30;

Table 2. Effect of winter extratropical cyclones (ETC) activity with or without time lag of 1 yr (L1) or 2 yr (L2) on female adult survival of common eider *Somateria mollissima* breeding in Canada (1996–2014), Svalbard (1999–2014) and northern Norway (1985–2014). Results of analysis of deviance (ANODEV) are presented for the first 10 models. Variables from each wintering area (G: western Greenland; sAC: southern Atlantic Canada; I: Iceland; No1, No2: northern Norway Zones 1, 2 respectively) 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. Significant ANODEV results are in **bold**. n: 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, $F_{j-1,n-j}$: ANODEV test statistic following a Fisher-Snedecor distribution with *j*–1 and n–*j* degrees of freedom, p: 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)

Survival Canadian population	Deviance	Criterion QAIC	ΔCriterion ΔQAIC	$F_{j-1.n-j}$	p	R^2_{Dev}
$1_{\text{time}}\ 2_{\text{Number of ETCs of sAC}}$	**22511.14**	**8126.30**	**0.00**	**8.48**	**0.010**	**0.35**
$1_{\text{time}}\ 2_{\text{constant}}$	22525.55	8129.45	3.15	–	–	–
$1_{\text{time}}\ 2_{\text{NAO}}$	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	–	–	–
$1_{\text{Longest ETC\_L2 of G}}\ 2_{\text{Number of ETCs of sAC}}$	**22657.95**	**8146.89**	**20.47**	**8.19**	**<0.0001**	**0.43**
$1_{\text{Longest ETC\_L2 of G}}\ 2_{\text{constant}}$	**22688.83**	**8155.92**	**29.51**	**10.07**	**0.006**	**0.39**
$1_{\text{Duration extreme ETCs\_L2 of G}}\ 2_{\text{constant}}$	**22696.39**	**8158.52**	**32.21**	**8.92**	**0.009**	**0.36**
$1_{\text{Number of extreme ETCs\_L2 of G}}\ 2_{\text{constant}}$	**22700.09**	**8159.84**	**33.54**	**8.39**	**0.011**	**0.34**
$1_{\text{Number of ETCs\_L2 of G}}\ 2_{\text{constant}}$	**22710.50**	**8163.56**	**37.26**	**7.02**	**0.018**	**0.31**
Svalbard population		AICc	ΔAICc			
Max wind_L2 of No1	**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 No1	1954.02	1988.77	1.78	3.97	0.068	0.23
Number of ETCs_L1 of No1	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 1	1956.30	1991.05	4.06	2.36	0.148	0.15
Number of ETCs_L1 of No1	1957.20	1991.95	4.95	1.81	0.202	0.12
Constant	1960.67	1993.28	6.28	–	–	–
Norwegian population		QAICc	ΔQAICc			
NAO_L2+MaxWind_L1 of No2	**8471.13**	**5882.87**	**0.00**	**14.86**	**<0.0001**	**0.53**
NAO_L2+MaxWind_L2 of No2	**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 No2	**8510.29**	**5907.70**	**24.83**	**7.76**	**0.010**	**0.22**
h * Max wind_L1 of No2	**8509.98**	**5911.57**	**28.71**	**4.17**	**0.010**	**0.19**
Max wind_L2 of No2	**8517.54**	**5912.67**	**29.81**	**5.36**	**0.028**	**0.17**
h * Max wind_L2 of No2	**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	–	–	–

slope on logit scale = –0.65 ± 0.26 SE; Table 2, Fig. 5) and (2) 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).

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

3.2. Comparison between the effect of winter extra tropical cyclones and North Atlantic Oscillation

Adding year 2014 to the time series used by Guéry et al. (2017) did not change their results about the

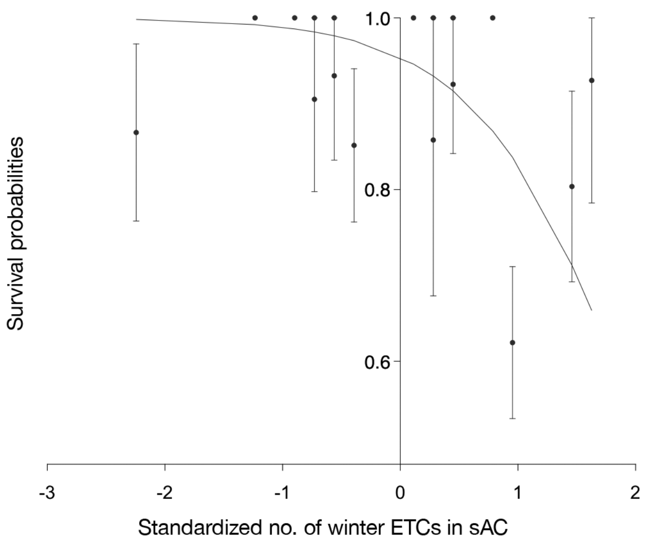

Fig. 4. Influence of the number of winter extratropical cyclones (ETCs) without time lag in southern Atlantic Canada (sAC, *x*-axis) on adult survival estimates (±1 SE; *y*-axis) of female eiders from Group H2 and breeding in the Canadian Arctic. Isolated points represent survival estimates from the 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} $2_{\text{Number of ETCs of sAC}}$; Table 2)

relationship between winter NAO and female eider survival in all 3 breeding populations, especially for the Svalbard population (i.e. winter NAO marginally explains survival fluctuations, $p = 0.073$; Table 2). We thus used this additional year in our analyses.

In the wintering areas of the Canadian population, the winter NAO was highly and significantly linked to the number of winter ETCs on the southern Atlantic Canada wintering ground ($R^2 = 0.90$; $p < 0.0001$; Fig. S1), whereas it was not linked to winter ETC activity in Greenland with a lag of 2 yr (Fig. S3). Moreover, the number of ETCs in southern Atlantic Canada performed as well as the winter NAO to explain female survival at a population level (h * NAO versus h * Number of ETCs of sAC; ΔQAIC = 1.35; $R^2_{Dev} = 0.27$ and 0.26 respectively). However, when we tested the effect of the number of winter ETCs in southern Atlantic Canada and the winter NAO on each group separately, the number of winter ETCs performed better (ΔQAIC = 3.81). It only explained ($R^2_{Dev} = 0.35$) survival variation of the group migrating in this area, and explained it better than 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 1 yr lag: $R^2 = 0.74$; $p = 0.001$; Fig. S4) but not significantly in northern Norway Zone 1 (e.g. with winter NAO with 1 yr lag: $R^2 = 0.48$; $p = 0.073$; Fig. S6). 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 yr lag) performed and explained female eider survival better than winter NAO, regardless of time lag (e.g. ΔQAIC = 2.00 between models Max wind_L2 of No1 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 1 yr time lag: $R^2 = 0.37$; $p = 0.049$; Fig. S8). Survival of female eiders breeding and wintering in northern Norway was better explained by the winter NAO with a lag of 2 yr 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 with wind speed of the strongest ETC with lags (Figs. S8 & S9), and including both variables in the same model improved its performance. Models including the effects of both winter NAO and winter

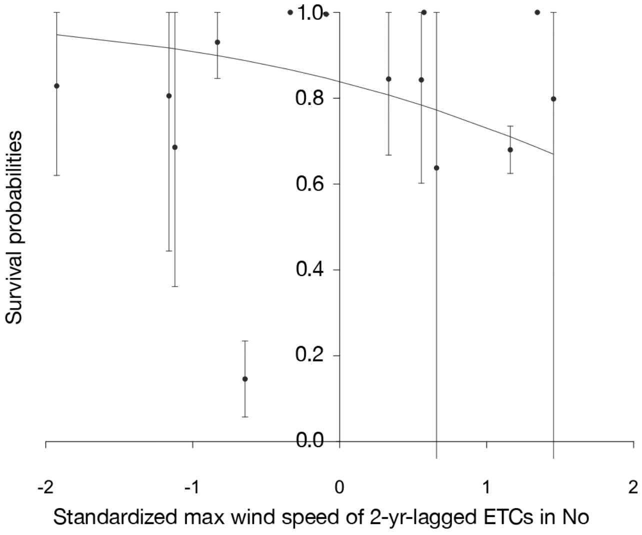

Fig. 5. Influence of the maximum (max) wind speed of winter extratropical cyclones (ETC) with a 2 yr lag (L2) in Norway zone 1 (No; *x*-axis) on adult survival estimates (±1 SE; *y*-axis) of female eiders breeding in Svalbard. Isolated points represent survival estimates from the time dependent model 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 2 yr lag (Max wind_L2 of No1; Table 2)

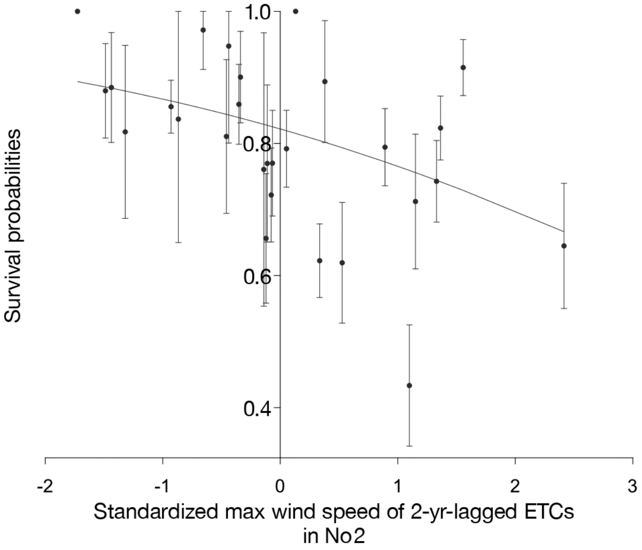

Fig. 6. Influence of the maximum (max) wind speed of the strongest winter extratropical cyclones (ETCs) with a 1 yr lag in northern Norway Zone 2 (No2, *x*-axis) on adult survival estimates (±1 SE; *y*-axis) of female eiders breeding and wintering in northern Norway. Isolated points represent survival estimates from the time-dependent model (model time; Table 2). The line represents predicted survival estimates from the model (φ(MaxWind_L1_No2); Table 2) with survival constraint by the covariate

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 2 yr combined with the maximum wind speed of ETCs with a lag of 1 yr explained 53% of female eider survival variation (model NAO_L2+Max wind_L1 of No2; Table 2).

4. 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 ETCs and their extremes on the annual adult survival of a long-lived marine duck, the common eider *Somateria mollissima*. 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.

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

The winter ETC activity seemed to have negative effects on female eider survival in all 3 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.

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

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

4.3. Contrasting effect of winter ETC activity between and within eider populations: '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 by Guéry et al. (2017). On the other hand, the wind speed of the strongest extreme winter ETCs affected — 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 by Guéry et al. (2017); indirect impacts of the same variable in Iceland were 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, a sheltering 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).

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 be directly affected by winter ETCs (Fig. 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). In contrast, 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, also facing weaker winter ETC activity than in Canada (Table 1), can feed along the shores of the fjords (J. O. Bustnes & K. E. Erikstad unpubl. 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.

4.4. 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 the survival of females breeding and wintering in northern Norway, together explaining ca. 53% of the adult female eider survival. The link between these 2 variables with oceanographic conditions in the northeast Atlantic could explain this cumulative effect. A low winter NAO with a lag of up to 3 yr 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 in turn have 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.

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

4.5. Effect of extreme events on survival

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

5. CONCLUSIONS

Even if adult survival of long-lived species is expected to 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 may directly affect only a segment of the population, depending on where birds winter. Although such intra-population heterogeneities can be generated by different factors (e.g. wintering strategy or age), they are likely to affect population trajectories and viability, and should thus be incorporated into population models (Coulson et al. 2001, Benton et al. 2006, Kendall et al. 2011).

Acknowledgements. We would like to thank all of the summer research assistants who worked at the 3 research locations over the years, Isabel Buttler and Rob Kelly for data management of the Canadian population and their valuable help at different stages of this study and Kimberly Malcolm for her essential linguistic revision. The study in the Canadian Arctic was supported by Environment Canada, Nunavut Wildlife Management Board, Greenland Institute of Natural Resources, Polar Continental Shelf Project, Fonds Québécois de la Recherche sur la Nature et les Technologies, Canadian Network of Centres of Excellence-ArcticNet, Natural Sciences and Engineering Research Council of Canada, and the Department of Indian Affairs and Northern Canada. The study in northern Norway was supported by the Norwegian Research Council, University of Tromsø, the Norwegian Institute for Nature Research, the Norwegian Directorate for Nature Management and SEAPOP program (www.seapop.no). The study in Svalbard was supported by the Norwegian Polar Institute and program MOSJ (www.mosj.no), and the eider geolocator study was supported by FRAM - High North Research Centre for Climate and the Environment. The Canadian and Norwegian Councils on Animal Care have approved this research.

LITERATURE CITED

Acevedo J, Garthe S, González A (2017) First sighting of a live hourglass dolphin (*Lagenorhynchus cruciger*) in inland waters of southern Chile. Polar Biol 40:483–486

Anker-Nilssen T, Bakken V, Strøm H, Golovkin AN, Bianki VV, Tatarinkova IP (2000) The status of marine birds breeding in the Barents Sea region. Nor Polarinst Rapp 113:137–143

Barbraud C, Weimerskirch H, Guinet C, Jouventin P (2000) Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea*. Oecologia 125:483–488

Bengtsson L, Hodges KI, Keenlyside N (2009) Will extratropical storms intensify in a warmer climate? J Clim 22: 2276–2301

Benton TG, Plaistow SJ, Coulson TN (2006) Complex population dynamics and complex causation: devils, details and demography. Proc Biol Sci 273:1173–1181

Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar Ecol Prog Ser 303:167–175

Boano G, Brichetti P, Foschi U (2010) 'La Niña'-driven Atlantic storms affect winter survival of Mediterranean Cory's Shearwaters. Ital J Zool 77:460–468

Boje J (2002) Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. Fish Bull 100: 414–422

Braby CE, Somero GN (2006) Following the heart: temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). J Exp Biol 209:2554–2566

Brenko MH, Calabrese A (1969) The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis.* Mar Biol 4:224–226

Brown ED (2002) Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. ICES J Mar Sci 59:983–996

Brown KM, Quinn JF (1988) The effect of wave action on growth in three species of intertidal gastropods. Oecologia 75:420–425

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. Monograph 5, American Fisheries Society, Bethesda, MD

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer Verlag, New York, NY

Bustnes J, Erikstad K (1988) The diets of sympatric wintering populations of Common Eider *Somateria mollissima* and King Eider *S. spectabilis* in Northern Norway. Ornis Fenn 65:163–168

Bustnes JO, Erikstad KE (1990) Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? Can J Zool 68:2280–2283

Bustnes J, Erikstad K (1993) Site fidelity in breeding common eider *Somateria molissima* females. Ornis Fenn 70:11–16

Bustnes JO, Lønne OJ (1997) Habitat partitioning among sympatric wintering common eiders *Somateria mollissima* and king eiders *Somateria spectabilis.* Ibis 139: 549–554

Buttler EI (2009) Avian cholera among arctic breeding common eiders *Somateria mollissima*: temporal dynamics and the role of handling stress in reproduction and survival. MS thesis, Carleton University, Ottawa

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Carrington E (2002) The ecomechanics of mussel attachment: from molecules to ecosystems. Integr Comp Biol 42:846–852

Carrington E, Moeser GM, Dimond J, Mello JJ, Boller ML (2009) Seasonal disturbance to mussel beds: field test of a mechanistic model predicting wave dislodgment. Limnol Oceanogr 54:978–986

Catto J (2016) Objective identification of warm seclusion cyclones and their distribution. EGU General Assembly Conf Abstr 18:10530

Chambers LE, Devney CA, Congdon BC, Dunlop N, Woehler EJ, Dann P (2011) Observed and predicted effects of climate on Australian seabirds. Emu 111:235–251

Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009a) U CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32:1071–1074

Choquet R, Rouan L, Pradel R (2009b) Program E-SURGE: a software application for fitting multievent models. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, Boston, MA, p 845–865

Cottam C (1939) Food habits of North American ducks. Tech Bull 643:1–129. US Dept Agriculture, Washington, DC

Coulson T, Catchpole E, Albon S, Morgan B and others (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531

Dee D, Balmaseda M, Balsamo G, Engelen R, Simmons A, Thépaut JN (2014) Toward a consistent reanalysis of the climate system. Bull Am Meteorol Soc 95:1235–1248

Dehnhard N, Ludynia K, Poisbleau M, Demongin L, Quillfeldt P (2013) Good days, bad days: wind as a driver of foraging success in a flightless seabird, the southern rockhopper penguin. PLOS ONE 8:e79487

Descamps S, Gilchrist HG, Bêty J, Buttler EI, Forbes MR (2009) Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. Biol Lett 5:278–281

Descamps S, Yoccoz NG, Gaillard JM, Gilchrist HG and others (2010) Detecting population heterogeneity in effects of North Atlantic Oscillations on seabird body condition: get into the rhythm. Oikos 119:1526–1536

Descamps S, Jenouvrier S, Gilchrist HG, Forbes MR (2012) Avian cholera, a threat to the viability of an Arctic seabird colony? PLOS ONE 7:e29659

Descamps S, Tarroux A, Lorentsen SH, Love OP, Varpe Ø, Yoccoz NG (2015) Large scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. Ecography 39:496–505

do Carmo Lopes (1979) Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. Sarsia 64:199–210

Dunham AE, Erhart EM, Wright PC (2011) Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. Glob Change Biol 17:219–227

Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708

Ebeling A, Laur D, Rowley R (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar Biol 84:287–294

Eriksson MO (1985) Prey detectability for fish-eating birds in relation to fish density and water transparency. Ornis Scand 16:1–7

Finney SK, Wanless S, Harris MP (1999) The effect of weather conditions on the feeding behaviour of a diving bird, the common guillemot *Uria aalge.* J Avian Biol 30: 23–30

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long lived seabird. J Anim Ecol 77:1020–1029

Frimer O (1994) The behaviour of moulting king eiders *Somateria spectabilis.* Wildfowl 45:176–187

Fujii M, Yamanaka Y (2008) Effects of storms on primary productivity and air-sea CO_2 exchange in the subarctic western North Pacific: a modeling study. Biogeosciences 5:1189–1197

Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306

Genovart M, Sanz Aguilar A, Fernández Chacón A, Igual JM, Pradel R, Forero MG, Oro D (2013) Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. J Anim Ecol 82: 121–130

Goudie R, Ankney C (1986) Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482

Grosbois V, Thompson PM (2005) North Atlantic climate variation influences survival in adult fulmars. Oikos 109: 273–290

Grosbois V, Gimenez O, Gaillard JM, Pradel R and others (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biol Rev Camb Philos Soc 83:357–399

Guéry L, Descamps S, Pradel R, Hanssen SA and others (2017) Hidden survival heterogeneity of three common eider populations in response to climate fluctuations. J Anim Ecol 86:683–693

Guillemette M, Ydenberg RC, Himmelman JH (1992) The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. J Anim Ecol 61:599–610

Hanssen SA, Gabrielsen GW, Bustnes JO, Bråthen VS and others (2016) Migration strategies of common eiders from Svalbard: implications for bilateral conservation management. Polar Biol 39:2179–2188

Hario M, Mazerolle MJ, Saurola P (2009) Survival of female common eiders *Somateria m. mollissima* in a declining population of the northern Baltic Sea. Oecologia 159: 747–756

Harris MP, Anker-Nilssen T, McCleery RH, Erikstad KE, Shaw DN, Grosbois V (2005) Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. Mar Ecol Prog Ser 297:283–296

Hawkins P, Butler P, Woakes A, Speakman J (2000) Estimation of the rate of oxygen consumption of the common eider duck (*Somateria mollissima*), with some measurements of heart rate during voluntary dives. J Exp Biol 203:2819

Heath JP, Gilchrist HG (2010) When foraging becomes unprofitable: energetics of diving in tidal currents by common eiders wintering in the Arctic. Mar Ecol Prog Ser 403:279–290

Heath JP, Gilchrist HG, Ydenberg RC (2006) Regulation of stroke pattern and swim speed across a range of current velocities: diving by common eiders wintering in polynyas in the Canadian Arctic. J Exp Biol 209: 3974–3983

Henkel LA (2006) Effect of water clarity on the distribution of marine birds in nearshore waters of Monterey Bay, California. J Field Ornithol 77:151–156

Hodges KI (1994) A general method for tracking analysis and its application to meteorological data. Mon Weather Rev 122:2573–2586

Hoskins BJ, Hodges KI (2002) New perspectives on the Northern Hemisphere winter storm tracks. J Atmos Sci 59:1041–1061

Howe JA, Austin WE, Forwick M, Paetzel M, Harland R, Cage AG (2010) Fjord systems and archives: a review. Geol Soc Lond Spec Publ 344:5–15

Høyvik Hilde C, Pélabon C, Guéry L, Gabrielsen GW, Descamps S (2016) Mind the wind: microclimate effects on incubation effort of an arctic seabird. Ecol Evol 6: 1914–1921

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) An overview of the North Atlantic oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscillation: climatic significance and environmental impact, Vol 134. American Geophysical Union, Washington, DC, p 1–36

Jenouvrier S (2013) Impacts of climate change on avian populations. Glob Change Biol 19:2036–2057

Jenouvrier S, Caswell H, Barbraud C, Holland M, Strœve J, Weimerskirch H (2009) Demographic models and IPCC climate projections predict the decline of an emperor penguin population. Proc Natl Acad Sci USA 106:1844

Jenouvrier S, Péron C, Weimerskirch H (2015) Extreme climate events and individual heterogeneity shape life history traits and population dynamics. Ecol Monogr 85: 605–624

Jones SC, Harr PA, Abraham J, Bosart LF and others (2003) The extratropical transition of tropical cyclones: forecast challenges, current understanding, and future directions. Weather Forecast 18:1052–1092

Kendall BE, Fox GA, Fujiwara M, Nogeire TM (2011) Demographic heterogeneity, cohort selection, and population growth. Ecology 92:1985–1993

Madsen FJ (1954) On the food habits of the diving ducks in Denmark. Dan Rev Game Biol 2:157–266

Menge BA, Chan F, Lubchenco J (2008) Response of a rocky intertidal ecosystem engineer and community dominant to climate change. Ecol Lett 11:151–162

Merkel FR, Jamieson SE, Falk K, Mosbech A (2007) The diet of common eiders wintering in Nuuk, Southwest Greenland. Polar Biol 30:227–234

Mosbech A, Gilchrist G, Merkel F, Sonne C, Flagstad A, Nyegaard H (2006) Year-round movements of Northern Common Eiders *Somateria mollissima borealis* breeding in Arctic Canada and West Greenland followed by satellite telemetry. Ardea 94:651–665

Pawlik JR, Butman CA (1993) Settlement of a marine tube worm as a function of current velocity: interacting effects of hydrodynamics and behavior1. Limnol Oceanogr 38: 1730–1740

Pike DA, Stiner JC (2007) Sea turtle species vary in their susceptibility to tropical cyclones. Oecologia 153:471–478

Ravn Merkel F, Mosbech A, Boertmann D, Grøndahl L (2002) Winter seabird distribution and abundance off south-western Greenland, 1999. Polar Res 21:17–36

Reusch TBH, Chapman ARO (1995) Storm effects on eelgrass (*Zostera marina L.*) and blue mussel (*Mytilus edulis L.*) beds. J Exp Mar Biol Ecol 192:257–271

Richardson LL, LeDrew EF (eds) (2006) Remote sensing of aquatic coastal ecosystem processes. Springer, Dordrecht

Rind D, Goldberg R, Ruedy R (1989) Change in climate variability in the 21st century. Clim Change 14:5–37

Roberts J, Champion A, Dawkins L, Hodges K and others (2014) The XWS open access catalogue of extreme European windstorms from 1979 to 2012. Nat Hazards Earth Syst Sci 14:2487–2501

Sæther B-E, Tufto J, Engen S, Jerstad K, Røstad O, Skåtan J (2000) Population dynamical consequences of climate change for a small temperate songbird. Science 287:854

Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. J Anim Ecol 74:817–831

Sanino GP, Van Waerebeek K (2008) A note on the southern distribution range of inshore and offshore common bottlenose dolphins *Tursiops truncatus* in the Southeast Pacific. Final report. IWC SC/60/SM18

Sarafanov A (2009) On the effect of the North Atlantic Oscillation on temperature and salinity of the subpolar North Atlantic intermediate and deep waters. ICES J Mar Sci 66:1448–1454

Sorteberg A, Kvamstø NG, Byrkjedal Ø (2005) Wintertime Nordic Seas cyclone variability and its impact on oceanic volume transports into the Nordic Seas. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds) The Nordic Seas: an integrated perspective. American Geophysical Union, Washington, DC, p 137–156

Sprung M (1984) Physiological energetics of mussel larvae (*Mytilus edulis*). I. Shell growth and biomass. Mar Ecol Prog Ser 17:283–293

Stenseth NC, Mysterud A (2005) Weather packages: finding the right scale and composition of climate in ecology. J Anim Ecol 74:1195–1198

Sukhotin AA, Abele D, Pörtner H-O (2006) Ageing and metabolism of *Mytilus edulis*: populations from various climate regimes. J Shellfish Res 25:893–899

Swennen C (1989) Gull predation upon eider *Somateria mollissima* ducklings: destruction or elimination of the unfit? Ardea 77:21–45

Systad GH, Bustnes JO, Erikstad KE (2000) Behavioral responses to decreasing day length in wintering sea ducks. Auk 117:33–40

Thomsen MS, Wernberg T, Kendrick GA (2004) The effect of thallus size, life stage, aggregation, wave exposure and substratum conditions on the forces required to break or dislodge the small kelp *Ecklonia radiata*. Bot Mar 47:454–460

Ulbrich U, Leckebusch G, Pinto JG (2009) Extra-tropical cyclones in the present and future climate: a review. Theor Appl Climatol 96:117–131

Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. Philos Trans R Soc Lond B Biol Sci 372:20160135

Vaitkus G, Bubinas A (2001) Modelling of sea duck spatial distribution in relation to food resources in Lithuanian offshore waters under the gradient of winter climatic conditions. Acta Zool Litu 11:288–302

van de Pol M, Jenouvrier S, Cornelissen JH, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Philos Trans R Soc Lond B Biol Sci 372: 20160134

Varennes E, Hanssen SA, Bonardelli JC, Guillemette M (2015) A large molluscivore bird (Common Eider, *Somateria mollissima*) is able to discriminate quality of blue mussels (*Mytilus edulis*) based on size and provenance. Can J Zool 93:655–663

Visbeck M, Chassignet EP, Curry RG, Delworth TL, Dickson RR, Krahmann G (2003) The ocean's response to North Atlantic Oscillation variability. In: Hurrell J, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscillation: climatic significance and environmental impact. Am Geophys Union, Washington, DC, p 113–145

Wakeley JS, Mendall HL (1976) Migrational homing and survival of adult female eiders in maine. J Wildl Manag 40:15–21

Wang XL, Feng Y, Compo G, Swail V, Zwiers F, Allan R, Sardeshmukh P (2013) Trends and low frequency variability of extra-tropical cyclone activity in the ensemble of twentieth century reanalysis. Clim Dyn 40:2775–2800

Wilson RP, Ducamp JJ, Rees WG, Culik BM, Nickamp K (1992) Estimation of location: global coverage using light intensity. In: Priede IG, Swift SM (eds) Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, New York, NY, p 131–134

Zammuto RM (1986) Life histories of birds: clutch size, longevity, and body mass among North American game birds. Can J Zool 64:2739–2749

Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: April 28, 2017; Accepted: July 9, 2019
Proofs received from author(s): September 11, 2019