Research

Detecting population heterogeneity in effects of North Atlantic Oscillations on seabird body condition: get into the rhythm

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Climatic influences on animal populations, mediated by changes in condition-dependent survival or reproduction, have long intrigued ecologists. We analyzed links between winter North Atlantic Oscillations (NAO), a large scale climatic phenomenon affecting weather conditions over the North Atlantic and the Arctic, and average pre-laying body mass in common eiders. Body mass is a good proxy for condition-dependent reproductive output in this species. Time series links were assessed for two eider populations breeding at high latitudes, over a 10- and a 21-year time series. Winter NAO affected body mass in both populations and these effects were easier to detect when changes in the series rhythm were assessed using a novel method based on data discretization and information theory, rather than detection based on changes in amplitude, assessed using traditional linear models. Winter conditions affected body condition of eiders in both populations. Different mechanisms, however, are likely to be involved in the two populations, one being presumably affected by direct effects of climate and the other by effects through the food chain. Therefore, the same species can respond along different pathways to the same large scale climatic pattern, an important consideration when seeking to understand or manage the response of species to present and future climate change.

The importance of climatic fluctuations in driving population dynamics is one of the oldest topics in ecology (Elton 1924), but its study has seen renewed interest in recent years. The study of climate effects has become increasingly important during this period of global climate change, but there are still numerous unresolved issues (see Grosbois et al. 2008 for a discussion in the context of survival).

Climate often does not affect populations through a single weather component but exerts influence through the co-occurrence of several dependent variables (Stenseth et al. 2003). The use of climate indices that represent a proxy of the overall climatic conditions, such as the North Atlantic Oscillation (NAO), has proven to be a remarkably robust solution to this issue. Global indices capture the complexity in the association between weather and ecological processes, whereas local climatic variables may fail to (Stenseth et al. 2003, Hallett et al. 2004). Moreover, global climate indices integrate information on several variables over several months, and can thus better reflect the complex and variable associations between local climate and ecological processes. Global indices also are generally associated with climatic conditions over large geographical areas (see Hurrell et al.

2001 for an example on the North Atlantic Oscillation). Global indices are thus suitable for assessing the effects of climate on populations whose distribution is widespread and for comparing those effects on populations living at different locations.

Climatic influences on animal populations may also be difficult to detect due to carry-over effects from energetically limiting conditions or critical periods. Indeed, effects of climate on individual traits during a particular season can be delayed (Lehikoinen et al. 2006), so that the energetically limiting conditions and their consequences are separated in time. The importance of carry-over effects of climate has been emphasized for migratory species (Norris and Taylor 2006), but is likely to affect other species. Understanding the factors that influence population dynamics thus likely requires identifying delayed effects of events happening during critical periods.

Furthermore, studies of life history trait responses to climate fluctuations have assumed there was a direct link between the amplitude of change in climate fluctuations and the amplitude of change in the response traits, often assuming the link was linear (Mysterud et al. 2001, Grosbois

et al. 2008). Changes in the rhythms (i.e. the alternance of increasing and decreasing phases) of time-series are rarely considered, except when changes are cyclic (Jenouvrier et al. 2005). Population time-series are often unpredictable and non-stationary, whereby the statistical properties of the series, such as its mean or covariance structure, depend on time (Cazelles and Hales 2006). Non-linearity, unpredictability, and non-stationarity, if present, could belie associations between different ecological time-series, when tests are based on changes in amplitudes only. Traditional linear analyses might not be appropriate to test for co-dependencies between such time-series.

Here, we analysed the association between winter NAO and body condition in two common eider *Somateria mollissima* populations (East Bay in Arctic Canada and Grindøya in northern Norway), and considered the two main components of these time-series data: their changes in amplitude and rhythm. We based our study on traditional linear models, as well as a novel approach that evaluates the degree of dynamic cohesion between time series fluctuations (the method is detailed in Cazelles 2004 and presented in Material and methods and Appendix 1).

Body condition (defined here as the amount of body reserves) is a key parameter in common eider life history and population dynamics. Female eiders are capital breeders (sensu Jönsson 1997) that do not feed and lose >40% of their body mass during incubation (Bottita et al. 2003). Pre-laying body condition is positively related to clutch size (Erikstad et al. 1993) and egg size (Hanssen et al. 2002), and consequently to duckling size (Erikstad et al. 1998). Body condition is also related to post-hatching maternal care (Bustnes and Erikstad 1991) and hence duckling survival (Erikstad et al. 1998, Öst et al. 2008). Moreover, clutch size in a given season is negatively associated with breeding propensity in the subsequent season and clutch size (Coulson 1984, Yoccoz et al. 2002). Clutch size investment even has an influence on female survival under certain (but rare) circumstances such as disease epidemics (Descamps et al. 2009). Thus, female body condition, mediated by clutch size investment in a given breeding season, can have long-term consequences on their breeding strategies.

All common eiders from the East Bay population do not winter in the same area (about 60% winter in southwest Greenland and 40% in Labrador; Mosbech et al. 2006). Consequently, the use of local climatic variables is not relevant to assess the effect of climatic fluctuations on eider body condition in this population and global indices, such as NAO, provide an ideal alternative tool. NAO reflects climate variability from eastern North America to Siberia and from the Arctic to the subtropical Atlantic (Hurrell et al. 2001), and is associated with many ecological phenomena (Ottersen et al. 2001). Winter NAO is linked to winter weather conditions in Greenland, Labrador and Norway (Banfield and Jacobs 1998, Chylek et al. 2004). Most eiders breeding at East Bay or Grindøya spend their winters at high latitudes (Bustnes and Erikstad 1993, Mosbech et al. 2006) and have to cope with harsh climatic conditions (details in Material and methods). As a consequence, winter is likely an energetically limiting period for those eiders residing in northern environments, and fluctuations in

weather conditions and food availability during this period could generate carry-over effects.

We thus expected that harsh winter conditions would negatively affect eider body condition during the subsequent breeding seasons. We tested the specific prediction that winter NAO (which is negatively correlated to temperature and positively to storminess in west Greenland and eastern Canada, Hurrell 1995, Banfield and Jacobs 1998) would be negatively related to eider body condition at East Bay. In northwest Europe, NAO is positively correlated to both temperature and storminess (Hurrell 1995, Matulla et al. 2008). Consequently, a positive or negative effect of winter NAO is expected at Grindøya if temperature or storminess, respectively, represents the main environmental component affecting eider condition. We further predicted that the association between winter NAO and eider body condition should be more pronounced at East Bay than at Grindøya. Indeed, East Bay eiders have to cope with a harsher environment during the winter (i.e. lower temperatures; Material and methods) and also have to migrate 1500–2000 km to reach their breeding grounds. Any carry-over effect of winter climate on body condition might be exacerbated by the energetic costs of migration. We tested for associations between NAO and body condition with and without time lags. An association between winter NAO and body condition involving no time-lag would suggest a direct link between winter weather and endogenous stores (e.g. via energetic expenses), whereas a delayed association (≥ 1 year) would suggest an indirect relation involving food resources (Sandvik et al. 2005).

The originality of this study is that it combines analyses of amplitude and rhythms to assess the effects of climatic fluctuations on seabird condition, and that it compares those effects in two populations living at high latitudes. Taken together, our results aid our understandings of how temporal variations in climatic conditions affect arctic vertebrates by proposing a new statistical approach to study these effects, and by emphasizing the importance of heterogeneity in the responses of populations to climate fluctuations.

Material and methods

Study populations

Canadian Arctic
This study was conducted on a small rocky island (Mitivik Island; 0.24 km²) within the East Bay Migratory Bird Sanctuary, Southampton Island, Nunavut, Canada (64°02'N, 81°47'W) from 1999 to 2008. This eider colony has between 4000 and 8000 pairs per year and is the largest colony reported in the Canadian Arctic. About 60% of the eiders from East Bay migrate ~1500 km to southwest Greenland to winter (Mosbech et al. 2006), where December to March temperatures average –7.4°C (Danish Meteorol. Inst.; Nuuk weather station 1961–1990; <www.dmi.dk/dmi/index/gronland/klimanormaler-gl.htm>). The other 40% migrate ~2000 km to Labrador and Newfoundland where December to March temperatures average –9.5°C (source: Environ. Canada, Natl Climate Data and Inf. Arch.; St-Anthony's weather station 1971–2000; <http://climate.weatheroffice.

ec.gc.ca/climate_normals/index_f.html>). An average of 280 female eiders were annually captured in large flight nets on arrival (range 75–524 females captured in June) and weighed using a Pesola scale (± 2.5 g). Most eiders at East Bay start laying during the end of June to early July; our sample of females caught in June essentially represent pre-laying females, although it may include some non-breeders.

Northern Norway
This study was conducted from 1987 to 2007 near Tromsø, northern Norway (69°49'N, 18°15'E). Grindøya is an island of 0.65 km², where between 200 and 500 pairs of eiders breed annually. Eiders from Grindøya do not migrate and spend the winter in the vicinity of their breeding location, where average December to March temperature is –3.7°C (source: Statistics Norway; Tromsø weather station 1961–1990; <www.ssb.no/english/yearbook/tab/tab-021.html>). Colony visits started at the beginning of egg-laying in mid-May and females were caught on their nest using a fishing rod with a nylon snare, after they laid their final egg. Females were weighed as above. Several experiments (e.g. clutch size manipulation, immune challenges, Hanssen et al. 2005, Hanssen 2006) took place in this eider colony. To avoid potential bias caused by these manipulations, we used the annual weight measurements taken before the start of female manipulations and only considered females that were not manipulated in the previous year (as body condition might have been influenced by delayed experimental effects).

Variables considered

Winter NAO
Winter NAO values are based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Fig. 1). Data were from <www.cgd.ucar.edu/cas/jhurrell/indices.html>. In our study, we considered NAO of the winter immediately preceding that year's breeding season (winter NAO averaged over the months of December through March), as well as winter NAOs with a time lag of one to three years. Winter NAO without any time-lag was expected to represent meteorological conditions during winter and early spring both in southwest Greenland and eastern Canada (where East Bay eiders migrate during the winter, Mosbech et al. 2006), and in northern Norway (where Grindøya eiders over-winter, Bustnes and Erikstad 1993).

Pre-laying body mass
At East Bay, data were available for 1633 females, averaging 2098 g ± 5 SE (range 1230–2900 g; Fig. 1a). At Grindøya, females were caught after laying and data were available for 1028 females, whose mass averaged 1875 g ± 5 SE (range of the body mass of females at capture: 1220–2630 g; range of the number of days between laying and capture: 1–24; Fig. 1b). Post-laying body mass is not a function of clutch size (Erikstad and Tveraa 1995), which indicates that female eiders adjust the size of their clutch to their pre-laying body mass. We estimated pre-laying body mass of Grindøya females as body mass at capture + clutch size (number of eggs) × 102 g + number of days of incubation at the time of capture × 22 g; 102 g represents the average mass of one egg
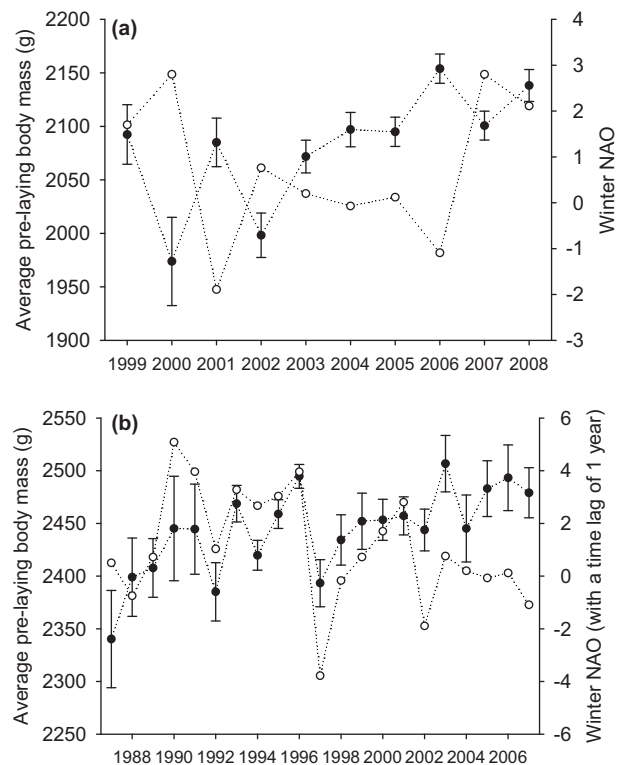

Figure 1. Relationship between average female pre-laying body mass and winter NAO in two common eider colonies; the East Bay colony (Southampton Island, Nunavut, Canada; (a)) and the Grindøya colony (Tromsø, Norway; (b)). Black symbols represent pre-laying body mass (± SE) and white symbols winter NAO (without a time lag, (a); with a one year time lag, (b)).

at Grindøya (Hanssen et al. 2002), and 22 g the average mass loss per day during incubation (Erikstad unpubl.).

Statistical analyses

Body mass, body size and body condition
The use of an adequate index of body condition is crucial to our study. Recently, it has been shown in several duck species that body mass adjusted for structural size is less correlated to body condition than body mass alone (Schamber et al. 2009). Therefore, as a first step, we compared the efficiency of mass adjusted for body size versus just mass of pre-laying female eiders in predicting body condition. We first performed linear regressions for both eider populations with body mass as the dependent variable and body size (wing length or tarsus length) as the predictor (proc REG, SAS ver. 9, SAS Inst. 2004) to determine whether variation in body size was an important determinant of variation in eider body mass. At Grindøya, only wing lengths were available. Then, we compared the proportion of variation in body condition accounted for by variation in body mass versus variation in residual body mass (corrected for body size from linear regressions). Body condition was defined here as the mass of abdominal fat, which is highly correlated to the total body fat (Jamieson et al. 2006). We collected a total of 28 pre-laying females at East Bay in 2002, 2003 and 2004; these females were dissected in the field immediately after

collection and wet abdominal fat was weighed without intestinal fat following Jamieson et al. (2006).

Effect of winter NAO on average body mass: linear analyses

We found that body mass alone was a suitable index of body condition. Thus, to assess the relationships between winter NAO and average eider body condition, we first fitted linear regressions with body mass as the dependent variable and winter NAO (with and without time lags) as the predictor. Normality of residuals was assessed by Shapiro–Wilk tests (all p-values > 0.14). Linear regressions were performed with the proc AUTOREG in SAS ver. 9 (SAS Inst. 2004) which allowed us to correct for auto-correlation (and thus dependence) among the residuals (autoregressive error regression).

Phase analyses: a symbolic dynamic approach

Temporal auto-correlation is often present in time-series, so that using traditional statistical tools such as correlation tests or chi-square tests would violate the assumption of independence among the data and thus potentially lead to unreliable results. Consequently, in many cases simple statistical tests cannot be used for testing the synchrony between time-series. The method we proposed here palliates the possible dependence among the data. This method (detailed in Cazelles 2004) required three steps: (1) defining the rhythm of a time series through the partition of the series into a sequence of symbols (i.e. data discretization); (2) quantifying relationships between rhythms of two time series using information theory; (3) quantifying statistical significance of this relationships, based on a resampling method.

For step 1, we used a simple discretization by comparing each value of the time-series with its preceding value. Given a time-series {X}, if $x_{t-1} < x_t$, then x_t is replaced by symbol 'Increase'; if $x_t < x_{t-1}$, then x_t is replaced by symbol 'Decrease'. The only information contained in the symbolic series concerns the rhythm of the initial series, and this symbolic series is 'freed' from any changes in amplitude. We then quantified the association between the two discretized time series, winter NAO (with and without time lags) and body condition, using a mutual information coefficient, which measures the amount of common information between variables. To determine whether or not the resulting associations is likely to have occurred by chance, we used the 'surrogate type 2' resampling method detailed in Cazelles and Stone (2003) and Cazelles (2004). This method preserves short-term auto-correlations of the raw series. Calculation of mutual information and creation of surrogate series were computed in MATLAB (detailed in Appendix 1).

In addition to this symbolic dynamic analysis, we still presented results from G-tests (i.e. likelihood ratio tests, Sokal and Rohlf 1981) to test for synchrony between winter NAO and eider body condition (using discretized time-series). As stated above, this test violates the assumption of data independence. However, for time-series where temporal auto-correlation is negligible, such a simple approach might be useful and we thus illustrated it in this study.

We measured associations between the discretized time-series by using Cramer's V (Cramér 1946). For a 2 × 2 contingency table, Cramer's V are equivalent to the Phi coefficient and are calculated as follows: $V = \sqrt{\dfrac{\chi^2}{n}}$, where χ^2 is the calculated χ^2 from the contingency table and n the grand total number of observations. V ranges from zero to 1 and equals zero when the variables are statistically independent.

Results

Body mass, body size and body condition

Wing or tarsus length accounted for relatively little body mass variation (Table 1). Variation in body mass was

Table 1. Relationships between body mass, body size and body condition of female common eiders.

(a) Effects of tarsus and wing lengths on pre-laying body mass (n = 1633 for the East Bay colony, Canada; and n = 1028 for the Grindøya colony, Norway). Body mass and body size (tarsus or wing lengths) have been log-transformed.

Dependent variable	Predictor	Slope ± SE	p-value	R^2
Pre-laying body mass / East Bay	wing	1.54 ± 0.092	<0.0001	0.14
	tarsus	0.29 ± 0.071	<0.0001	0.01
Pre-laying body mass / Grindoya	wing	0.004 ± 0.0003	<0.0001	0.14

(b) Relationships between body mass, adjusted and not adjusted for body size, and body condition (measured as the mass of abdominal fat). Data collected from 28 pre-laying females collected at the East Bay colony in 2002, 2003 and 2004 (the year effect on abdominal fat was not significant). The variable 'Fat' corresponds to the mass of abdominal fat; the variable "% fat" corresponds to the mass of abdominal fat divided by the total mass of the individual.

Dependent variable	Predictor	Slope ± SE	p-value	R^2
% fat	residuals$_{wing}$ [$]	0.065 ± 0.013	<0.0001	0.51
% fat	residuals$_{tarsus}$ [§]	0.064 ± 0.011	<0.0001	0.56
% fat	mass	0.060 ± 0.011	<0.0001	0.53
Fat	residuals$_{wing}$ [$]	150.5 ± 25.9	<0.0001	0.56
Fat	residuals$_{tarsus}$ [§]	147.5 ± 22.5	<0.0001	0.63
Fat	mass	139.2 ± 22.2	<0.0001	0.60

[$]: residuals from a linear regression with body mass as dependent variable and wing length as predictor
[§]: residuals from a linear regression with body mass as dependent variable and tarsus length as predictor

mainly a consequence of variation in endogenous reserves rather than in structural body size. Our results indicate that body mass alone is a good proxy of body reserves, and performs even better than body mass adjusted for wing chord (Table 1). We thus used body mass as an index of body condition in subsequent analyses and to enable comparisons between populations.

Effect of winter NAO on average body mass: linear analyses

At East Bay, the effect of winter NAO with no time lag on average body mass tended to be negative (p = 0.091; R^2 = 0.32; Table 2, Fig. 1). None of the relationships between winter NAO with a time lag of one to three years and body mass were statistically significant (all p-values $\geq$ 0.15; Table 2). At Grindøya, winter NAO with a time lag of 1 year positively affected the average annual body mass of eiders (p = 0.036; R^2 = 0.26; Table 2, Fig. 1). Effects of winter NAO with no time lag or with a time lag of two or three years were not statistically significant (all p-values $\geq$ 0.36; Table 2).

Results of phase analyses: rhythm coherence between NAO and average body mass

The analysis of symbolic dynamics indicated marked associations between winter NAO and average body mass in both eider populations. At East Bay, average pre-laying body mass was negatively associated (p = 0.024) with the winter NAO with no time lag. Both time series rise and fall together with an exact opposite rhythm (Fig. 2a). Body mass at East Bay was not associated with winter NAO of the preceding 1–3 years (all p-values > 0.2; Appendix 2). At Grindøya, pre-laying body mass was positively associated (p < 0.001) with winter NAO with a time lag of one year (Fig. 2). A delay of one year occurred between an increase (or decrease) in the winter NAO and an increase (or decrease) in the average pre-laying body mass. Winter NAO with no time lag or with a time lag of two or three years were not associated with body mass (all p-values > 0.16; Appendix 2).

Results from G-tests are similar (Appendix 2), and indicate clear associations between rhythm in body condition and winter NAO with no time lag at East Bay (Table 3; G-statistic = 12.37, DF = 1, p = 0.0004; V = 1) and with a time-lag of one year at Grindøya (Table 3; G-statistic = 16.36, DF = 1, p < 0.0001; V = 0.81).

Discussion

Mass, size and condition in eiders

Mass adjusted for structural size appears a good index of body condition in some systems (Schulte-Hostedde et al. 2005) but not all (Green 2001, Schamber et al. 2009). In several waterfowl species, body mass alone is a reliable predictor of body condition that often outperforms mass adjusted for size (Schamber et al. 2009). In East Bay eiders, a similar relation holds: the mass of abdominal fat (which is highly correlated to the mass of total body fat, Jamieson et al. 2006) is explained better by individual mass than by mass adjusted for wing length (Table 1). Furthermore, the weak mass-size relations in pre-laying female eiders from both populations (Table 1) indicated that changes in body mass were due mainly to changes in body condition (or body reserves), than to changes in structural body size. Using body mass alone as an index of body condition is thus appropriate for our study system.

Winter NAO and breeding body condition

Body mass (or condition) was linked to winter NAO in both eider populations, but the apparent mechanisms linking these variables differed between the two populations. In the Canadian Arctic, pre-laying body mass of female eiders varied in perfect synchrony with the opposite of the winter NAO of the current year (Fig. 2). Winter NAO is positively correlated to storm activity and negatively to air temperature in southwest Greenland and eastern Canada (Hurrell and Dickson 2004), so that high winter NAO values are associated with unfavourable weather conditions in those areas. Our results thus support the hypothesis that increasing storm activity and/or decreasing temperature leads to a decrease in average body condition perhaps through higher energetic costs to maintain body temperature, through lower foraging efficiency, or through a decrease in mussel abundance (an important food resource for eiders) as storms can destroy mussel beds (Reush and Chapman 1995). Lehikoinen et al. (2006) reported a similar finding between winter NAO and body condition of common eiders in the Baltic Sea. There, a positive winter NAO is indicative of early ice-break-up and warmer air temperature (Hurrell and Dickson 2004) and winter NAO was positively associated with female condition at hatching (Lehikoinen et al. 2006).

Table 2. Effect of winter NAO (with and without time lags) on average common eider pre-laying body mass from two colonies; East Bay (1999 to 2008) and Grindøya (1987 to 2007). Winter NAO corresponds to NAO averaged over December through March.

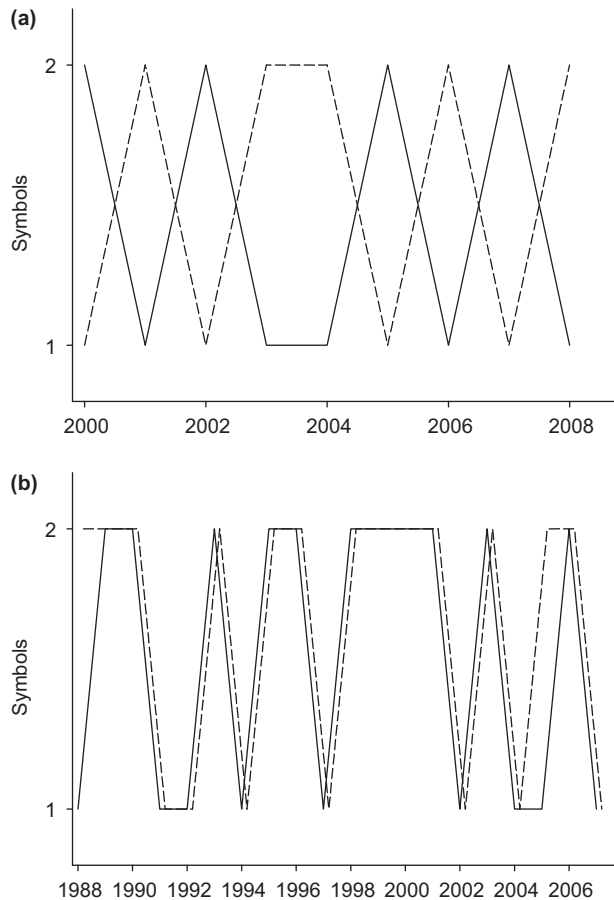|			NAO / no lag	NAO / lag of 1 year	NAO / lag of 2 years	NAO / lag of 3 years
	East Bay					
Body mass		Regression coefficients ± SE	−19.6 ± 10.0	12.3 ± 12.0	−22.6 ± 13.8	−6.8 ± 11.2
		p-values	0.091	0.34	0.15	0.56
		R^2	0.32	0.12	0.26	0.06
	Grindøya					
Body mass		Regression coefficients ± SE	−3.8 ± 4.3	8.8 ± 3.9	−4.1 ± 4.4	−1.5 ± 4.5
		p-values	0.39	0.036	0.36	0.74
		R^2	0.09	0.26	0.10	0.05

Figure 2. Symbolic time series for the winter NAO (with no time lag for the East Bay population, (a), and with a time lag of one year for the Grindøya population, (b); dashed lines) and average pre-laying body mass (solid lines) of female common eiders from two colonies; the East Bay colony (Southampton Island, Nunavut, Canada; (a)) and the Grindøya colony (Tromsø, Norway; (b)). The discretization of the time-series was based on 2 states: 1 (decrease from t – 1 to t), 2 (increase from t – 1 to t).

Table 3. Contingency tables used to test for synchrony between body condition and winter NAO (i.e. to test for associations between ups and downs of the two time-series) in two common eider colonies; East Bay (1999 to 2008) and Grindøya (1987 to 2007). Winter NAO was NAO averaged over December through March and corresponds to winter NAO of the current year (i.e. no time-lag) for the East Bay population, and to winter NAO one year before (time-lag of one year) for the Grindøya population.

(a) East Bay

	Increase phase in NAO	Decrease phase in NAO
Increase phase in body condition	0	5
Decrease phase in body condition	4	0

(a) Grindøya

	Increase phase in NAO	Decrease phase in NAO
Increase phase in body condition	11	2
Decrease phase in body condition	0	7

the next year and thus lower eider food resources. Alternatively, independent of any effect on mussel spawning, winter conditions could influence mussel growth affecting the availability of optimally sized mussels for eiders in the following winter. These mechanisms are speculative, but a lagged effect of winter climate on eider food availability remains a very realistic scenario to explain the lagged relationship between NAO and body condition at Grindøya.

Eiders breeding in northern Norway do not have to cope with extremely low temperatures during the winter as compared to eiders wintering in southwest Greenland or Labradort-Newfoundland where temperatures can fall below –30°C. Furthermore, as eiders breeding at Grindøya do not migrate they might be able to recover from harsh winter conditions before the subsequent reproductive season, if food is available. Therefore, weather conditions during winter may not represent such an important constraint for Norwegian wintering and breeding eiders, or at least may represent a less important constraint than food availability.

Our prediction that eider body condition in the breeding season is affected by weather conditions the previous winter, and that winter is a critical period in their life cycle was supported. Our results were also consistent with the prediction that winter conditions have a greater effect on eider condition at East Bay than at Grindøya when considering the direct effects of winter NAO (i.e. pronounced and significant effect at East Bay but not detectable at Grindøya: association between ups and downs of body condition and winter NAO with no time lag: Cramér's V = 1.00 at East Bay and 0.17 at Grindøya). However, the strength of the relationships between winter NAO and local climatic parameters affecting eider condition would have to be assessed before firmly concluding that winter weather had a greater direct influence on eider condition in the Canadian population than in the Norwegian. Clutch size, breeding success and offspring survival are tightly linked to eider body condition, so that body condition is likely an important component of eider population dynamics. Consequently, winter weather is expected to be a key period affecting eider populations either through

No relationship was found between body mass of female eiders breeding at Grindøya and winter NAO of the same year. However, a positive link occurred between winter NAO one year before and female body mass. A similar time-lag of one year has been found in other seabird populations breeding in northern Europe (Sandvik et al. 2005). These results suggest that weather conditions principally affect bird condition the following year through effects on the food chain. Winter temperature or storminess could affect the productivity of molluscs (the main food resources of eiders during winter, Bustnes 1998, Merkel et al. 2007) through changes in growth (Menge et al. 2008), reproduction, survival (Thieltges et al. 2004) or shell thickness, and thus digestibility (Bustnes 1998, Witbaard et al. 2005). More specifically, eiders at Grindøya are very selective in terms of prey size and feed primarily on small mussels (<20 mm, Bustnes and Eriksad 1990, Bustnes 1998), which might correspond to 1-year old mussels (Thompson 1984, Mills and Côté 2003). As a consequence, cold water temperature during the winter could have negatively affected mussel spawning around Grindøya, leading to a reduced number of small mussels

direct effects on thermoregulation and/or indirect effects via the food chain. Such effects of winter weather are unlikely to be entirely explained by average temperature. At Grindøya, where local temperature can be used because these eiders' winter location is well known (i.e. eiders remain close to their breeding area during the winter), average winter temperature explained a lower amount of variation in body condition than winter NAO (Appendix 3). Consequently, other climatic parameters were very likely to affect eider condition. Our results add to the growing evidence that global indices can outperform local climatic factors in explaining the complex associations between climate and ecological processes.

Symbolic dynamics versus linear models

Based on a simple graphical inspection, one can easily see that winter NAO and average body mass varied in a perfect opposite synchrony over the 10 years of monitoring at East Bay (Fig. 1a, 2a), and in close synchrony over the 21 years of monitoring at Grindøya (Fig. 1b, 2b). This association between winter NAO and body mass of female eider was supported by both of our approaches. However, when we considered the changes in rhythm in winter NAO and in body mass through a symbolic dynamic approach, we found that the effects of winter NAO on eider body mass were more easily detected (lower p-values). Non-linear effects of winter NAO and/or non-stationarity in the NAO or body condition time series could be advocated to explain why considering the rhythms rather that the amplitudes led to a stronger statistical association between NAO and body condition. Non-linearity was likely not of primary importance as a linear effect of NAO on eider body mass was adequate to describe the relationship (based on generalized additive models; unpubl.). Conversely, non-stationarity in the time-series might be important. Indeed, body mass in both populations exhibited a significant positive trend ($p < 0.05$), indicating that the mean of these time-series was non-stationary. De-trending the Norwegian time-series led to similar results as those based on symbolic dynamics (when a linear trend was added to the model, the effect of winter NAO with a lag of 1 year became highly significant; Appendix 4). However, for the Canadian time-series, adding a linear trend did not change the results (i.e. when a linear trend was added to the model, the effect of NAO remains not significant; Appendix 4). Non-stationarity can occur in different ways and does not always correspond to a linear or smooth trend in the mean. For example, an abrupt change in some environmental conditions, such as associated with regime shifts (deYoung et al. 2008), could lead to an abrupt change in the mean of a time-series and thus to non-stationarity. As a consequence, detrending a time-series is not always sufficient to take non-stationarity into account. The symbolic dynamic approach as proposed here and detailed in Cazelles (2004) provides a very efficient and relatively simple tool to study the synchrony between time-series, even in the presence of non-stationarity, and when the form of non-stationarity is unknown.

Variation in the response of populations to climatic fluctuations

One of the main challenges facing ecologists is to predict the effects of climate change on wildlife dynamics, abundance and distribution. Most studies concerning the relationships between climate and animal characteristics are based on a single population (but see Forchhammer et al. 2002 and Tveraa et al. 2007 for examples). However, the response to climate variations may vary between populations. We found that two eider populations living at similar latitudes, but experiencing different density, life history and environmental constraints, were affected by winter NAO index, but that mechanisms linking NAO (and therefore climate) to eiders were different.

Individuals were captured at a different period (before laying for East Bay eiders and after laying for Grindøya eiders); such population heterogeneity might be due to methodological differences rather than differences in the response to climatic fluctuations. Indeed, post-laying body mass of females at Grindøya was dependent on the mass of their eggs (post-laying mass = pre-laying mass – mass of the eggs). Therefore, winter NAO could have affected body condition of females, who have in turn adjusted the mass of their eggs accordingly. In such a situation, the effect of winter NAO on post-laying mass could have been undetected. However, egg size did not vary with year in this population (Erikstad et al. 1998), so this previous explanation seems unrealistic.

Consequently, even if we cannot reject with certainty some alternative hypotheses (as is the case in every descriptive study), heterogeneity among populations in the response to climatic fluctuations remains the most likely explanation to the observed patterns between NAO and body condition.

Conclusion

Two main conclusions arose from our study. First, our results indicate that using changes in only amplitude to assess the effects of climatic fluctuations on ecological processes may not be enough. Indeed, such effects may be more apparent when considering changes in rhythm, in particular when time-series are non-stationary. We propose that such rhythm analyses should be routinely performed when investigating the effects of climate on animal populations. The symbolic dynamic approach of Cazelles (2004) appears to be a very useful method for such 'rhythm synchrony' analyses, and has the advantage of being applicable even on short time series.

Subsequently, our study emphasizes that different mechanisms may be involved in population responses to climatic fluctuations. Such population-level heterogeneity may contribute to the complexity of conservation or management issues in the context of climate warming. The Arctic is the place on Earth where climate is warming the most rapidly (Anisimov et al. 2007). Research in the Artic is logistically challenging and expensive, and relatively few animal populations have been monitored over decades (but see Gaston et al. 2005 on Brünnich's guillemots, Dickey et al. 2008 on snow geese for some examples). However, it seems crucial to develop monitoring programmes in the near future that can differentiate among plausible mechanisms behind the impact of arctic warming on populations (Yoccoz et al. 2001, Nichols and Williams 2006). Furthermore, this variation should be integrated in predictive models to assess their robustness (Morin and Thuiller 2009).

References

Anisimov, O. A. et al. 2007. Polar regions (Arctic and Antarctic). – In: Parry, M. L. et al. (eds), Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the 4th Assessment Rep. of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, pp. 653–685.

Banfield, C. E. and Jacobs, J. D. 1998. Regional patterns of temperature and precipitation for Newfoundland and Labrador during the past century. – Can. Geogr. 42: 354–364.

Bottita, G. E. et al. 2003. Effects of experimental manipulation of incubation length on behavior and body mass of common eiders in the Canadian Arctic. – Waterbirds 26: 100–107.

Bustnes, J. O. 1998. Selection of blue mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*, by size in relation to shell content. – Can. J. Zool. 76: 1787–1790.

Bustnes, J. O. and Erikstad, K. E. 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. O. and Erikstad, K. E. 1991. Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. – Can. J. Zool. 69: 1538–1545.

Bustnes, J. O. and Erikstad, K. E. 1993. Site fidelity in breeding common eider *Somateria mollissima* females. – Ornis Fenn. 70: 11–16.

Cazelles, B. 2004. Symbolic dynamics for identifying similarity between rhythms of ecological time series. – Ecol. Lett. 7: 755–763.

Cazelles, B. and Stone, L. 2003. Detection of imperfect population synchrony in an uncertain world. – J. Anim. Ecol. 72: 953–968.

Cazelles, B. and Hales, S. 2006. Infectious diseases, climate influences and nonstationarity. – PLoS Med. e328: doi: 10.1371/journal.pmed.0030328.

Chylek, P. et al. 2004. Global warming and the Greenland ice sheet. – Climate Change 63: 201–221.

Coulson, J. C. 1984. The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. – Ibis 126: 525–543.

Cramér, H. 1946. Mathematical methods of statistics. – Princeton Univ. Press.

Descamps, S. et al. 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.

deYoung, B. et al. 2008. Regime shifts in marine ecosystems: detection, prediction and management. – Trends Ecol. Evol. 23: 402–409.

Dickey, M.-H. et al. 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. – Global Change Biol. 14: 1973–1985.

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. – J. Exp. Biol. 2: 119–163.

Erikstad, K. E. and Tveraa, T. 1995. Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*. – Oecologia 103: 270–274.

Erikstad, K. E. et al. 1993. Clutch-size determination in precocial birds: a study of the common eider. – Auk 110: 623–628.

Erikstad, K. E. et al. 1998. Significance of intraclutch egg-size variation in common eider: the role of egg size and quality of ducklings. – J. Avian Biol. 29: 3–9.

Forchhammer, M. C. et al. 2002. North Atlantic Oscillation timing of long- and short-distance migration. – J. Anim. Ecol. 71: 1002–1014.

Gaston, A. J. et al. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). – J. Anim. Ecol. 74: 832–841.

Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? – Ecology 82: 1473–1483.

Grosbois, V. et al. 2008. Assessing the impact of climate variation on survival in vertebrate populations. – Biol. Rev. 83: 357–399.

Hallett, T. B. et al. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. – Nature 430: 71–75.

Hanssen, S. A. 2006. Costs of an immune challenge and terminal investment in a long-lived bird. – Ecology 87: 2440–2446.

Hanssen, S. A. et al. 2002. Incubation start and egg size in relation to body reserves in the common eider. – Behav. Ecol. Sociobiol. 52: 282–288.

Hanssen, S. A. et al. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. – Proc. R. Soc. Lond. B 272: 1039–1046.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. – Science 269: 676–679.

Hurrell, J. W. and Dickson, R. R. 2004. Climate variability over the North Atlantic. – In: Stenseth, N. C. et al. (eds), Marine ecosystems and climate variation. Oxford Univ. Press, pp. 15–31.

Hurrell, J. W. et al. 2001. The North Atlantic Oscillation. – Science 291: 603–605.

Jamieson, S. E. et al. 2006. An evaluation of methods used to estimate carcass composition of common eiders *Somateria mollissima*. – Wildlife Biol. 12: 219–226.

Jenouvrier, S. et al. 2005. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. – Proc. R. Soc. Lond. B 272: 887–895.

Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. – Oikos 78: 57–66.

Lehikoinen, A. et al. 2006. Winter climate affects subsequent breeding success of common eiders. – Global Change Biol. 12: 1355–1365.

Matulla, C. et al. 2008. European storminess: late nineteenth century to present. – Clim. Dynam. 31: 125–130.

Menge, B. A. et al. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. – Ecol. Lett. 11: 151–162.

Merkel, F. R. et al. 2007. The diet of common eiders wintering in Nuuk, southwest Greenland. – Polar Biol. 30: 227–234.

Mills, S. C. and Côté, I. 2003. Sex-related differences in growth and morphology of blue mussels. – J. Mar. Biol. Ass. UK 83: 1053–1057.

Morin, X. and Thuiller, W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in

species range shifts under climate change. – Ecology 90: 1301–1313.

Mosbech, A. et al. 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.

Mysterud, A. et al. 2001. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. – Nature 410: 1096–1099.

Nichols, J. D. and Williams, B. K. 2006. Monitoring for conservation. – Trends Ecol. Evol. 21: 668–673.

Norris, D. R. and Taylor, C. M. 2006. Predicting the consequences of carry-over effects for migratory populations. – Biol. Lett. 2: 148–151.

Öst, M. et al. 2008. Social and maternal factors affecting duckling survival in eiders *Somateria mollissima*. – J. Anim. Ecol. 77: 315–325.

Ottersen, G. et al. 2001. Ecological effects of the North Atlantic Oscillation. – Oecologia 128: 1–14.

Reusch, T. B. H. and Chapman, A. R. O. 1995. Storm effects on eelgrass (*Zostera marina L.*) and blue mussel (*Mytilus edults L.*) beds. – J. Exp. Mar. Biol. Ecol. 192: 257–271.

Sandvik, H. et al. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. – J. Anim. Ecol. 74: 817–831.

Schamber, J. L. et al. 2009. Evaluating the validity of using unverified indices of body condition. – J. Avian Biol. 40: 49–56.

Schulte-Hostedde, A. I. et al. 2005. Restitution of mass/size residuals: validating body condition indices. – Ecology 86: 155–163.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – W. H. Freeman and Co.

Stenseth, N. C. et al. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. – Proc. R. Soc. Lond. B 270: 2087–2096.

Thieltges, D. W. et al. 2004. Too cold to prosper – winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. – J. Exp. Mar. Biol. Ecol. 311: 375–391.

Thompson, R. J. 1984. Production, reproductive effort, reproductive value and reproductive cost in a population of the blue mussel *Mytilus edulis* from a subarctic environment. – Mar. Ecol. Prog. Ser. 16: 249–257.

Tveraa, T. et al. 2007. What regulates and limit reindeer populations in Norway. – Oikos 116: 706–715.

Witbaard, R. et al. 2005. Growth trends in three bivalve species indicate climate forcing on the benthic ecosystem in the southeastern North Sea. – Climate Res. 30: 29–38.

Yoccoz, N. G. et al. 2001. Monitoring of biological diversity in space and time. – Trends Ecol. Evol. 16: 446–453.

Yoccoz, N. G. et al. 2002. Costs of reproduction in common eiders (*Somateria mollissima*): an assessment of relationships between reproductive effort and future survival and reproduction based on observational and experimental studies. – J. Appl. Stat. 29: 57–64.

Appendix 1

Phase analyses: a symbolic dynamic approach

The method (detailed in Cazelles 2004) consisted of three steps: (1) defining the rhythm of a time series through the partition of the series into a sequence of symbols; (2) quantifying the relationships between the rhythms of two time series through the use of information theory; (3) quantifying the statistical significance of these relationships based on a resampling method.

For the step 1, we used a simple discretization based on two symbols. Discretization is done by comparing each value of the time-series with its preceding value. Given a time-series $\{X\}$, if $x_{t-1} < x_t$, then x_t is replaced by symbol 'Increase'; if $x_t < x_{t-1}$, then x_t is replaced by symbol 'Decrease'. Note that considering four symbols (increase, decrease, peak, trough) as in Cazelles (2004) led to the same results.
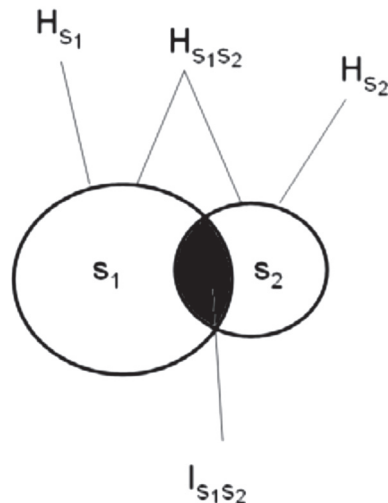
We then quantified the association between the two discretized time series, winter NAO (with and without time lags as for the classical cross-correlation function) and body condition, using information theory. This leads to the determination of entropy (that measures the disorder contained in a given time series) and then of a mutual information coefficient. Mutual information measures the amount of common information between variables. Mutual information between series $\{S1\}$ and $\{S2\}$ (noted $I_{S1,S2}$) can be calculated as follows (from Cazelles 2004):

$I_{S1,S2} = H_{S1} + H_{S2} - H_{S1,S2}$, where H_{S1} and H_{S2} are the entropy of the symbolic series S1 and S2, and $H_{S1,S2}$ is their joint entropy. The entropy of a time-series $\{S\}$ is defined as:

$$H_S = -\sum_{i=1}^{k} p(s_i) \log_2[p(s_i)]$$, where $p(s_i)$ is the probability

that $\{S\}$ takes the value s_i, and is simply estimated as the fraction of s_i in the series.

And the joint entropy between two series $\{S1\}$ and $\{S2\}$ is defined as:

$$H_{S1S2} = -\sum_{i=1}^{k}\sum_{j=1}^{k} p(s1_i, s2_j)\log_2[p(s1_i, s2_j)]$$, where $p(s1_i,$

$s2_j)$ is the probability of observing simultaneously $s1_i$ and $s2_j$ in the series, and is simply estimated as the fraction of the pair $(s1_i, s2_j)$ observed in the series.

Finally, the last step quantifies the statistical significance of this association. To do this, we used the "surrogate type 2" resampling method detailed in Cazelles and Stone (2003) and Cazelles (2004), which preserves the short-term auto-correlations of the raw series (i.e. we created resampled time-series, called surrogate series, that had the same auto-correlation as the raw series). In our study, we created surrogates for the body condition series only, and calculated the mutual information between this surrogate body condition series and the raw NAO series. These mutual information values define the mutual information distribution used to test the null-hypothesis of random association between series. Briefly, the surrogate series is computed in the following way:

1. A frequency histogram with n equal intervals is created from the values in the original series (n = 4 and 5 for the East Bay and Grindøya data, respectively). In other words, we split the range of the values of the raw series into n equal (but arbitrary) intervals.
2. A transition matrix describing the time-evolution of the series is created based on observed frequencies of the data in the raw series. This transition matrix gives the probability of moving from values that are within interval i to values that are within interval j (with i and j being some intervals of the frequency distribution of the raw data). To illustrate this, consider the following time-series $\{5\ 10\ 20\ 14\ 1\}$. Given the very short length of the series, we considered only two intervals i =]0–15] and j =]15–20]. We have four transitions in this time-series, two from i to i (transitions 5 to 10 and 14 to 1); 1 from i to j (transition 10 to 20); 1 from j to j (transition 20 to 14) and 0 from j to i. This leads to the transition matrix:

$$\begin{array}{cc} & i \qquad\qquad j \\ \begin{array}{c} i \\ j \end{array} \left[\begin{array}{cc} \dfrac{2}{2+1} & \dfrac{1}{2+1} \\ \dfrac{1}{1+0} & \dfrac{0}{1+0} \end{array} \right] \end{array} = \begin{bmatrix} 0.67 & 0.33 \\ 1 & 0 \end{bmatrix}$$

3. An initial value s_0 is randomly chosen from the raw data (s_0 is one point of the raw series)
4. s_1 is determined using the transition matrix: 1) the interval i which s_1 belongs to is determined based on the transition matrix, and 2) the value of s_1 is randomly chosen among all the elements of interval i.
5. The previous step is iterated to obtain a surrogate series of the same length as the raw series.
6. Steps 1 to 5 are iterated k times to obtain k surrogate series (k = 1000 in our study)
7. From these k surrogate series, the distribution of mutual information is constructed based on the null hypothesis of random association between the raw time-series.
8. We then compare the mutual information of the raw series with this distribution and extract the 95th percentiles of this distribution.

Appendix 2

Results (p-values) from different methods testing for an association between winter NAO and average body mass in two colonies of common eiders, East Bay (1999 to 2008) and Grindøya (1987 to 2007). Winter NAO corresponds to NAO averaged over the months of December through March. Significant values in bold.

		NAO	NAO-lag of 1 year	NAO-lag of 2 year	NAO-lag of 3 year
East Bay	Symbolic dynamics	**0.024**	0.27	0.50	0.86
	G-tests (DF = 1)	**0.004**	0.091	0.29	0.63
Grindøya	Symbolic dynamics	0.76	**<0.001**	0.17	0.95
	G-tests (DF = 1)	0.44	**<0.001**	0.072	0.89

Appendix 3

Effect of winter NAO and average winter temperature (with a time lag of one year) on average pre-laying body mass at the Grindøya colony of common eiders (data from 1987 to 2007). Winter NAO and winter temperature corresponds, respectively, to NAO or mean monthly temperature averaged over the months of December through March. A continuous variable Year has been included to de-trend the time-series (Appendix 3).

	NAO / lag of 1 year	Winter temperature / lag of 1 year	Year	R^2
Regression coefficients ± SE (p-value)	10.00 ± 2.70 (p = 0.002)	–0.062 ± 4.03 (p = 0.99)	5.62 ± 0.64 (p<0.0001)	0.79
Regression coefficients ± SE (p-value)	9.96 ± 2.12 (p = 0.002)		5.62 ± 0.64 (p<0.0001)	0.79
Regression coefficients ± SE (p-value)		8.57 ± 4.21 (p = 0.058)	3.95 ± 0.79 (p<0.0001)	0.61

Appendix 4

Effect of winter NAO (with a time lag of one year for the Grindøya colony) on average pre-laying body mass in two common eider colonies: East Bay (1999 to 2008) and Grindøya (1987 to 2007). Winter NAO corresponds to NAO averaged over the months of December through March. A continuous variable Year has been included to de-trend the time-series (Appendix 3).

			Regression coefficients ± SE	p-values	R^2
	East Bay				
Body mass		NAO	–7.82 ± 9.10	0.42	0.60
		Year	12.91 ± 4.15	0.021	
	Grindøya				
Body mass		NAO / lag of 1 year	9.96 ± 2.12	0.0002	0.79
		Year	5.62 ± 0.64	<0.0001	