

# Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre

Sébastien Descamps · Hallvard Strøm · Harald Steen

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**Abstract** Analysis of synchrony in population fluctuations is a central topic in ecology. It can help identify factors that regulate populations, and also the scales at which these factors exert their influence. Using long-term data from seven Brünnich's guillemot colonies in Svalbard, Norway, we determined that year to year population fluctuations were synchronized in six of the seven colonies. The seventh colony was located farther away and in a different oceanographic system. Moreover, all seven colonies have declined significantly since the late 1990s following a very similar pattern. If the rate of population decline does not change, Brünnich's guillemots in Svalbard have a high probability of becoming quasi-extinct within the next 50 years. The high synchrony between the different colonies could further increase this risk of extinction. Our results indicate that environmental forcing plays a role in the colony size fluctuation of Brünnich's guillemot (i.e., a Moran effect). These fluctuations are well explained by changes in the subpolar gyre in the region where Brünnich's guillemots overwinter. This subpolar gyre weakened in the mid-1990s, leading to a warming of the North Atlantic. Our study indicates that this basin-scale shift in the subpolar gyre is closely related to the decline in Brünnich's guillemot in Svalbard. Our results suggest that the causal mechanism linking changes in oceanographic conditions in the North Atlantic and Brünnich's guillemot

population dynamics are likely mediated, at least partly, by changes in recruitment.

**Keywords** Moran effect · Regime shift · Svalbard · Subpolar gyre · Synchrony · *Uria lomvia*

## Introduction

The study of population synchrony (i.e., the positive covariation in population size fluctuations) is a major topic in ecology. Examining synchrony in population fluctuations, either over the short term (inter-annual variation) or long term (trend) can help identify both the factors that regulate populations and the scales at which these factors operate. Synchrony analyses also have management or conservation applications; the risk of extinction, at the meta-population or species levels, is positively related to synchrony between sub-populations (Earn et al. 2000; Engen et al. 2005; Heino et al. 1997; Palmqvist and Lundberg 1998) because drastic population declines have a greater probability of occurring simultaneously when population synchrony is high. The previous studies document synchrony of inter-annual population size variations, but the same conclusion obviously applies for synchrony in the long-term trend when this trend is negative.

Many empirical studies show clear evidence of population synchrony at different spatial scales, and the presence of spatial synchrony (spatial autocorrelation of variation through time) in population dynamics is often observed (Liebhold et al. 2004). For example, synchrony between populations of gypsy moth (*Lymantria dispar*) was significant for populations separated by up to 1200 km (Johnson et al. 2005). Similarly, the dynamics of caribou (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) in

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S. Descamps (✉) · H. Strøm · H. Steen  
Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway  
e-mail: sebastien.descamps@npolar.no

Greenland are synchronized over distances ranging from 1000 to 1700 km (Post and Forchhammer 2002). Such population synchrony can be explained by three, non-exclusive, ecological mechanisms (Bjørnstad et al. 1999): (i) dispersal of individuals between populations (Ranta et al. 1998), (ii) trophic interactions where, for example, a mobile parasite or predator impacts several host or prey populations (Ims and Steen 1990) and (iii) the Moran effect, which refers to the common effect of environmental factors, like climate, on geographically separated populations sharing a common structure of density dependence (Moran 1953). All three mechanisms have the potential to synchronize the dynamics of populations at various spatial scales, yet disentangling between these three mechanisms is challenging.

Here, we focused on synchrony in short- and long-term colony size fluctuations between colonies of an arctic top predator, the Brünnich's guillemot (*Uria lomvia*). Our study was based on data from seven colonies in the Svalbard archipelago, Norway, that were monitored for 23 years (1988–2010; Fig. 1). Oceanographic conditions vary from the south to the north of Svalbard (Svendsen et al. 2002), and we expected that colonies close to each other should exhibit a higher degree of synchrony (i.e., neighbouring colonies should experience similar spring and summer feeding conditions and thus have similar breeding probability and success). Despite a relatively limited effect on population growth rate, breeding parameters are often a key determinant of long-lived species population dynamics because of large inter-annual fluctuations (Gaillard et al. 2000; Sæther and Bakke 2000). Therefore, similar spring and summer environmental conditions and consequently similar breeding probability and breeding success between colonies could lead to higher synchrony between neighbouring colonies.

The Brünnich's guillemot was red-listed in Norway in 2010 due to population decline (Kålås et al. 2010). Consequently, quantifying the degree of synchrony between Brünnich's guillemot colonies and understanding the environmental drivers of colony size fluctuations is needed to understand and assess extinction risk of the Norwegian population (Heino et al. 1997; Palmqvist and Lundberg 1998).

To assess population synchrony and the effect of distance between colonies, we first considered the short-term (year to year) fluctuations by analysing the detrended time series. Second, we considered raw data and focused on the long-term fluctuations (i.e., trend). We compared both the slope of this long-term trend and also the onset of decline in each population. Third, we tested for the effects of two large-scale climatic and oceanographic drivers, the winter North Atlantic Oscillation (wNAO) and the subpolar gyre index (SPG). These two parameters are tightly linked to



**Fig. 1** Map of the seven Brünnich's guillemot colonies studied in the Svalbard archipelago (Norway). One of these colonies is located on Bjørnøya (Bear Island) and six are on Spitsbergen; among the six Spitsbergen colonies, four are within the same fjord (Isfjorden)

oceanographic and climatic conditions in the North Atlantic (Hatun et al. 2005; Hurrell and Dickson 2004; Hurrell et al. 2001) where Svalbard Brünnich's guillemot overwinter (Fort et al. 2013; Steen et al. 2013). There have been a substantial number of studies relating wNAO to seabird life history (for a few examples, see Descamps et al. 2010; Frederiksen et al. 2004; Sandvik et al. 2005; Votier et al. 2005). However, to our knowledge none have yet considered the potential relationships between seabird life history or population dynamics and the subpolar gyre, despite the considerable importance of this parameter in the North Atlantic marine ecosystem (Hatun et al. 2009). The SPG is linked to the NAO (Lohmann et al. 2009) but is likely more closely related to oceanographic conditions and thus to seabird food availability and distribution. The SPG weakened noticeably in the mid-1990s, leading to a shift in the marine ecosystem (Hatun et al. 2009). Here, we tested the effects of these two parameters on Brünnich's guillemot colony size fluctuations with and without a time-lag of

1–5 years. Because Brünnich's guillemots recruit at about 5 years of age (Gaston et al. 1994) an effect of the environment on juvenile survival and thus recruitment might only be detected 5 years later at the colony level.

Finally, we quantified the risk of pseudo-extinction for each colony (i.e., probability that the colony will decline by more than 90 % at least once in the next 50 years) and also for the whole set of colonies, using simple stochastic models under the assumption that the trend and variation observed in the last decade remain unchanged.

## Methods

### Study system

The Brünnich's guillemot has a circumpolar distribution from 46 to 82°N, and is one of the most numerous seabirds at northern latitudes and in Svalbard (Strøm 2006a). In total, 142 colonies are known in Svalbard, the largest of which are situated on the west coast and in the southeast (including Hopen and Bjørnøya Islands). Brünnich's guillemot is a cliff-nesting bird breeding in dense colonies ranging from a few hundred to >100,000 individuals. Outside the breeding season, Brünnich's guillemots spend most of their time at sea. They start egg laying at the end of May/early June, incubate a single egg for about a month and then feed their chick at the nest for approximately 3 weeks until their chick jumps into the sea (end of July/early August). Adult(s) stay with their chicks at sea for an additional four to eight weeks, until chick independence.

In each of the seven Brünnich's guillemots colonies, one to 11 plots were chosen (in 1988), and since then the

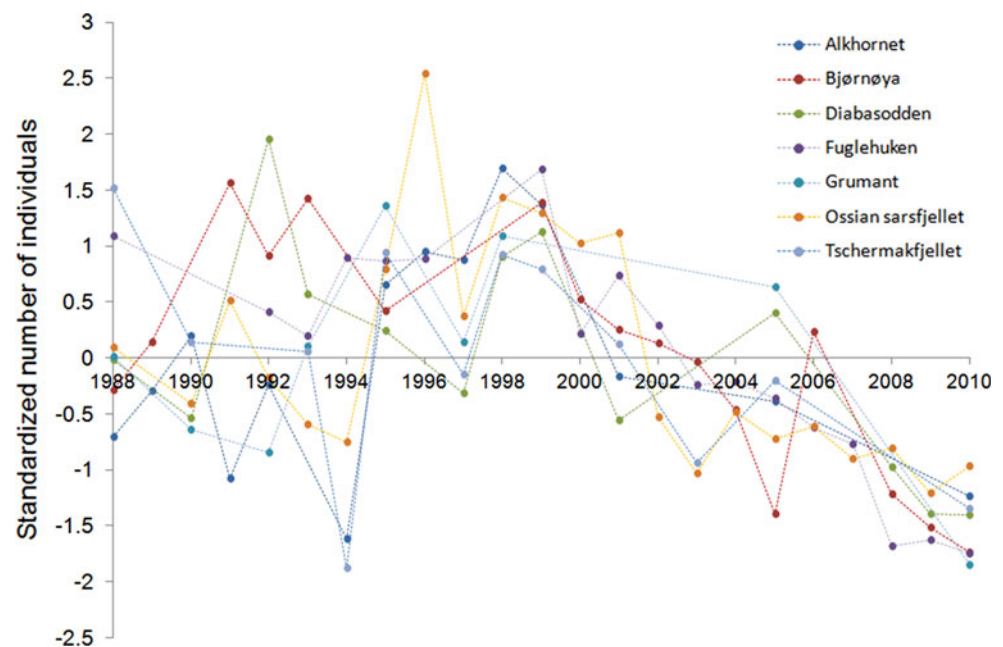
number of birds breeding in those plots has been counted almost annually (on average plots have been counted 15 times between 1988 and 2010, range: 9–22). Following standardized international procedures to monitor guillemot colonies (Walsh et al. 1995), we counted the total number of individuals present in each plot with binoculars (10×). Distinguishing between breeding and non-breeding (transient) individuals from a distance is not possible in guillemots, so all individuals present in each plot are counted. Our results thus report colony attendance rather than number of breeding individuals per se.

The standard procedure was to visit each colony and plot several times per season (up to eight times) during late incubation/early rearing period, but due to logistical constraints some plots or colonies were visited only once per season. At each visit, the number of guillemots present in each plot was counted two to three times. For each year, we averaged the number of guillemots counted in each plot at each visit and for every count. Then, we summed the numbers of guillemots to get one estimate of colony size per year and per colony. Our dataset consisted then in 106 colony size estimates for period 1988–2010 (Fig. 2).

### Environmental parameters

The North Atlantic Oscillation represents the difference of normalized sea level pressure between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland. Data were extracted from [www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html). We considered the winter NAO, that is, monthly NAO values averaged over the months of December through March. The winter NAO is associated with climatic conditions (temperature, storminess) in the North Atlantic (Hurrell

**Fig. 2** Temporal trends of Brünnich's guillemots breeding on the Svalbard archipelago. Figure is based on  $n = 106$  observations on seven colonies from 1988 to 2010 and shows standardized data (deviation from mean divided by standard deviation)



and Dickson 2004; Hurrell et al. 2001), which is the main overwintering area of Svalbard Brünnich's guillemots (Fort et al. 2013; Steen et al. 2013).

The North Atlantic subpolar gyre is a large counter-clockwise rotating body of cold and low-saline subarctic water in the central northern North Atlantic Ocean which dominates the physical oceanography of the region (Hatun et al. 2005). Indexes of this subpolar gyre can be calculated from sea surface heights, which reflect both the composition of water masses and the associated currents. Data used in this study are from Hatun et al. (2009) and H. Drange (Norwegian Institute for Marine Research, pers. comm.). Two indices were available: one based on simulated sea surface height anomalies in the North Atlantic subpolar gyre from 1988 to 2007, and one based on observed satellite observations from 1993 to 2010. To obtain a series covering our entire study period (1988–2010), we extrapolated the first index by using a regression equation linking both indices during the period 1993–2007 (this regression indicates that both SPG indexes were highly correlated,  $r = 0.79$ ).

#### Statistical analyses

In a first step, we quantified the synchrony in short-term colony size fluctuations between colonies of Brünnich's guillemots. We used cross-correlation functions which measure the strength of association between two variables. We calculated the mean cross-correlation and associated bootstrap confidence intervals using the *mSynch* function (*ncf* package) in R (R Development Core Team 2010). The method is described in detail in Bjørnstad et al. (1999) and Paradis et al. (2000). We considered first the (log-transformed) count data and then, in a second step, those count data adjusted for the long-term quadratic trend (i.e., residuals of a quadratic regression). Cross-correlation based on abundances can reflect the long-term temporal trends and not the short-term fluctuations; cross-correlation functions between the residuals should reflect those short-term fluctuations. To assess whether or not synchrony between colonies varies with the spatial scale considered, we compared the synchrony between all colonies (Spitsbergen plus Bjørnøya) first, then between all Spitsbergen colonies (i.e., we excluded Bjørnøya) and finally between only Isfjorden colonies (four colonies: Alkhorneret, Bjørndalen, Diabasodden, Tschermakfjellet; Fig. 1). Assuming that synchrony decreases with distance between colonies, synchrony between Isfjorden colonies should be higher than synchrony between Spitsbergen ones, which should in turn be higher than synchrony between all colonies (i.e., including Bjørnøya should decrease the synchrony). To assess the effect of spatial distance between colonies, we also used the spline correlogram approach developed by

Bjørnstad et al. (1999). This method provides an estimate of the spatial covariance function (i.e., the function describing the relationship between geographic distance between colonies and their synchrony).

In a second step, we considered the variation between colonies in their long-term trends. We used a mixed model approach where colonies were defined as random factors. This allowed us to take into account non-independence in our data and to quantify the between-colony heterogeneity in the long-term trend. This is the same statistical approach as in studies of variation in individual reaction norms (e.g., Nussey et al. 2007). In our case, the sample unit was the colony and not the individual, and we focused on trends in abundance and not reaction norm (i.e., we focused on the effect of time on abundance and not on the effect of environment on phenotype). We used the *lmer* function (*lme4* package) in R (R Development Core Team 2010), with a *Poisson* distribution and *log* link function. To test for a negative trend and for variation in this trend between colonies, we compared different models (see Table 1 and “Results”) using QAIC. We followed the same approach as the one detailed in Bolker et al. (2009; supplementary material). We considered linear and quadratic models as well as piecewise regressions. An increase in colony size followed by a plateau could lead to the selection of a quadratic effect of the year, which could wrongly suggest a decrease in colony size in the latest years. Therefore, to determine if colony size significantly decreased in more recent years, we also considered piecewise regressions (Toms and Lesperance 2003). We defined a breakpoint in year 1999, because after 1999 all colonies were decreasing (see “Results” and Table 1b, c). Auto-correlation analyses indicated that the (detrended) number of individuals in year  $t$  was independent of the (detrended) number of individuals in years  $t-1$  to  $t-3$ , except for one colony (Ossian Sarsfjellet), where correlation with a lag of 2 years was significant (Online Resource 1). This showed that density-dependence was not a major driver of colony size in our system and that temporal auto-correlation in our data did not affect our results.

To assess the effect of environmental covariates, we used the same approach and included those covariates as both a fixed effect and a random one, in interaction with the colony. This allowed us to identify whether or not those covariates significantly affected colony size fluctuations and whether or not their effect was similar in all colonies.

We also compared the onset of population decline for the different guillemot colonies. The onset of decline in a given colony was defined as the inflection point of its quadratic trend (i.e., the year when the first derivative of the quadratic regression is null, or in other words, the year when colony size reached its maximum). For each colony,

**Table 1** Modelling of the temporal population size trends of Brünnich’s guillemot colonies in the Svalbard archipelago

Model number ≠	Model description	np	QAIC	ΔQAIC
1	Year + year <sup>2</sup> + (year + year <sup>2</sup>  colony)	9	114.000	0.000
2	Year <sub>88–99</sub> + year <sub>00–10</sub> + (year <sub>00–10</sub>  colony)	6	116.243	2.243
3	Year <sub>88–99</sub> + year <sub>00–10</sub> + (year <sub>88–99</sub> + year <sub>00–10</sub>  colony)	9	118.834	4.834
4	Year <sub>88–99</sub> + year <sub>00–10</sub> + (year <sub>88–99</sub>  colony)	6	132.683	18.683
5	Year + year <sup>2</sup> + (1 colony)	4	133.167	19.167
6	Year <sub>88–99</sub> + year <sub>00–10</sub> + (1 colony)	4	136.018	22.018
7	Year <sub>98–10</sub> + (1 colony)	3	141.710	27.710
8	Year <sub>88–99</sub> + (1 colony)	3	186.210	72.210
9	Year + (1 colony)	3	206.167	92.167
10	1 + (1 colony)	2	275.010	161.010

Analyses are based on  $n = 106$  counts in seven colonies from 1988 to 2010. Models were fitted using a Poisson error distribution and a log-link function. Model selection was based on QAIC;  $np$  represents the number of parameters for each model, and  $\Delta QAIC$  the difference in QAIC between the model considered and the model with lowest QAIC. QAIC were calculated using an overdispersion ( $\hat{\sigma}$ ) of 19.22, estimated from model 1

we calculated this onset of decline  $D$  as:  $D = \frac{-b}{2c}$ , where  $b$  and  $c$  are the linear and quadratic coefficients, respectively, of the regression of the number of individuals over 1 year. To calculate confidence intervals around those estimates of  $D$ , we used the “empirical approach” described in Kosmelj et al. (2005). This method is based on probability theory related to bivariate normal distribution. To generate 95 % CI around the estimate of  $D$ , we generated 1000 samples from the bivariate normal distribution  $N[-b, 2c, s(-b), s(2c), cov(-b, 2c)]$ . All terms defining this distribution came from the output of models:  $\log(\text{colony size}) = a + b \times \text{year} + c \times \text{year}^2$ , run for each colony separately. For each colony, the 95 % CI was defined as the interval encompassing 95 % of these samples (for details, see Kosmelj et al. 2005).

**Risk of quasi-extinction**

With the assumption that density dependence does not play a significant role in the population trend of Brünnich’s guillemot in Svalbard (see Online Resource 1), we can write the following density-independent stochastic model:

$$N_{t+1} = [\bar{\lambda} + \varepsilon(t)] \times N_t, \text{ where } \varepsilon(t) \text{ has a mean of 0 and a variance of } \sigma_\varepsilon^2.$$

This is equivalent to Formula 5.2a in Lande et al. (2003), where  $\frac{\Delta N}{N} = \bar{\lambda} - 1 + \varepsilon(t)$ . Using this model, we simulated 1000 population size trajectories for each colony over the next 50 years. At each time step and for each colony, we randomly chose an annual growth rate that follows the distribution  $N(\bar{\lambda}, \sigma_\varepsilon^2)$  where  $\bar{\lambda}$  and  $\sigma_\varepsilon^2$  have been estimated for each colony using colony counts from 1999 to 2010 (i.e.,  $\bar{\lambda}$  and  $\sigma_\varepsilon^2$  represent, respectively, the average

and standard error of the annual growth rate from 1999 to 2010). The risk of quasi-extinction at the colony level is defined as the percentage of these 1000 trajectories that went below (at least once in the next 50 years) the threshold of 10 % of initial colony size. The initial colony size was defined here as the colony size in 1999, which corresponds approximately to the year before the decline started.

Then, to estimate the risk of quasi-extinction at the population level, we ran the same stochastic models for each colony as the ones described above and we summed the number of estimated individuals in every colony at each time step. We gave different weights to each colony based on their absolute size. Indeed, at the population level, the loss of a colony with 1000 individuals does not have the same impact as the loss of a colony with >100 000 individuals. Those weights were calculated as the ratio of the total size of the entire colony (the total number of individuals in each colony has been counted once between 2005 and 2011) divided by the sum of individuals over all colonies. The fact that colony sizes have not been counted at the same period and that colony sizes varied with time does not affect our weights. Indeed, a small colony in 2011 was still a small colony in 1999, so that regardless of the colony count, the weight of the small colonies (e.g., Ossian Sarsfjellet or Diabasodden) would still remain small compared to the weight of the large ones (Bjørnøya and Fuglehuken). Similarly, the risk of quasi-extinction at the population level was then calculated as the percentage of the 1000 trajectories that went below (at least once) the threshold of 10 % of initial population size. Those models ignored demographic stochasticity, which is likely negligible as those colonies are >1000 individuals.

## Results

### Synchrony in colony size fluctuations

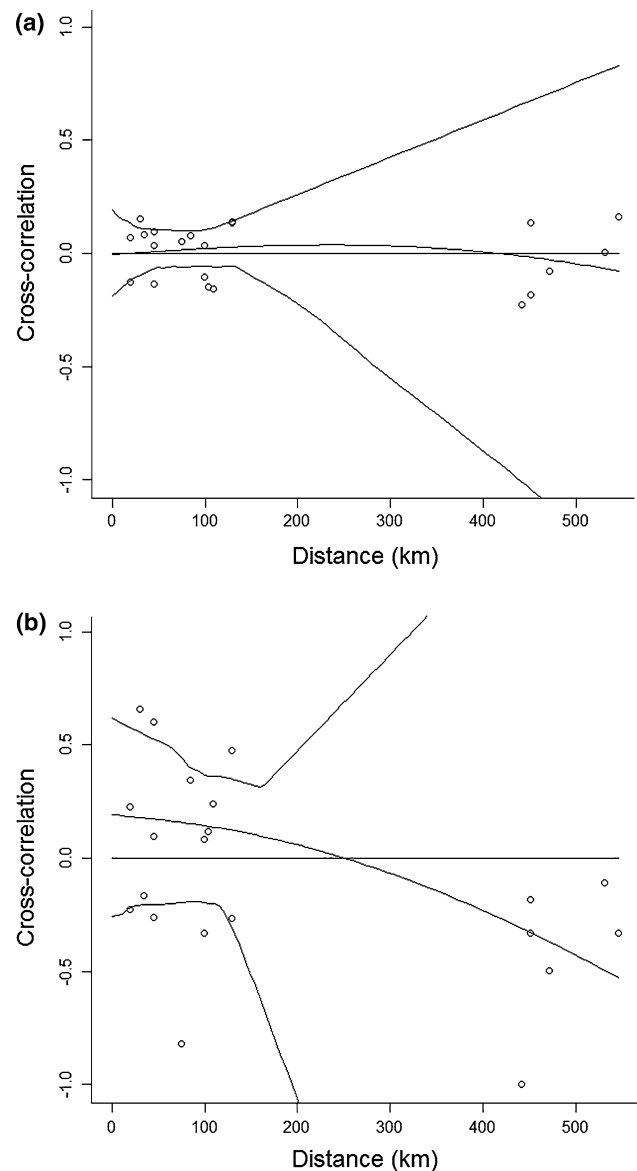
Cross-correlation analyses demonstrated significant positive synchrony between Brünnich's guillemot colonies (cross-correlation coefficient: 0.65; 95 % CI: [0.57, 0.72]). Synchrony was similar when considering only Spitsbergen colonies (cross-correlation coefficient: 0.66; 95 % confidence interval: [0.57, 0.74]) or Isfjorden colonies (cross-correlation coefficient: 0.67; 95 % confidence interval: [0.51, 0.80]). This is consistent with results from the spline correlogram, which shows no effect of the distance between colonies on their synchrony (Fig. 3a). The large confidence interval around the cross-correlation function was a consequence of small sample size ( $n = 7$  colonies).

When considering the detrended counts (residuals from a quadratic regression), we found a lower, not significant, synchrony between colonies (cross-correlation coefficient: 0.18; 95 % CI: [−0.11, 0.56]). Therefore, the observed synchrony between guillemot colonies in Svalbard was mainly due to a common long-term quadratic trend. However, when considering only the Spitsbergen colonies (i.e., when removing Bjørnøya), we found a significant positive synchrony (cross-correlation coefficient: 0.36; 95 % CI: [0.02, 0.68]). Results were similar when considering only the four Isfjorden colonies (cross-correlation coefficient: 0.40; 95 % CI: [−0.04, 0.88]). These results are supported by the spline correlogram (Fig. 3b), which indicated a (non-significant) decrease in the cross-correlation function with increasing distance between colonies. This decrease is driven by the low correlations between the Bjørnøya colony and the Spitsbergen ones (Fig. 3b; average correlation between the Bjørnøya colony and the Spitsbergen ones:  $-0.19 \pm 0.30$  SE; average correlation between the Spitsbergen colonies:  $0.36 \pm 0.09$  SE). As before, the large confidence interval of the cross-correlogram function was due to a relatively small sample size ( $n = 7$  colonies).

Overall, our results showed significant synchrony in the long-term trend, indicating that all colonies declined. The synchrony in short-term fluctuations is lower and only significant when Bjørnøya is excluded. Brünnich's guillemot colonies on Spitsbergen fluctuated partly synchronously, but year to year fluctuations on Bjørnøya were independent of fluctuations on Spitsbergen.

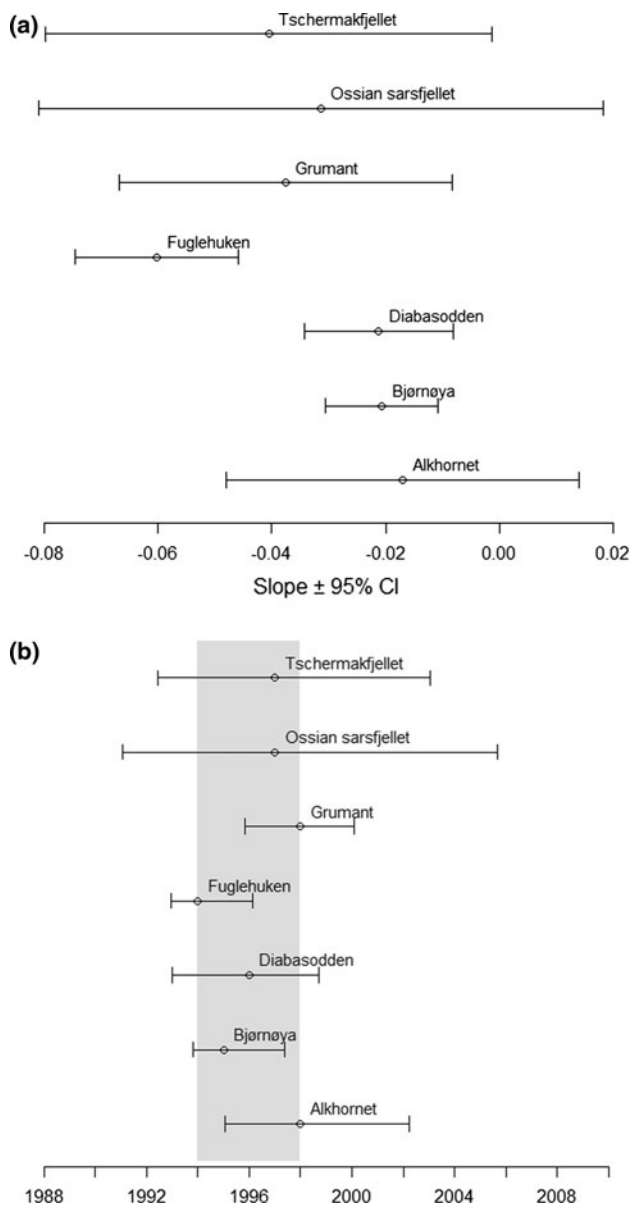
### Variation in the long-term trend and in the onset of decline

The number of individuals in Brünnich's guillemot colonies exhibited a clear quadratic pattern between 1988 and 2010 (Fig. 2; Table 1; e.g., model 5 vs models 9 or 10).



**Fig. 3** Relationship between synchrony in colony size fluctuations and distance between colonies. **a** Cross-correlation coefficients from the raw data. **b** Correlation coefficients from the detrended data (i.e., residual from a quadratic regression). The lines represent the spline correlogram and 95 % bootstrap confidence intervals. The zero-correlation reference line corresponds to the region-wide correlation (i.e., cross-correlation coefficients have been centered around the mean region-wide correlation)

Colony size increased until the mid- or late-1990s and then clearly dropped. This pattern is confirmed by piecewise regressions, which indicated a significant increase until 1999, followed by a significant decrease (Fig. 2; Table 1; e.g., model 6 vs models 7 or 8). Temporal trends varied between colonies (Table 1; model 1 vs 5), during both the increasing and decreasing phase (Table 1; model 6 vs 7 and model 6 vs 8; Fig. 4a represents the estimated slope during



**Fig. 4** Comparison of the rate (a) and onset (b) of colony size decline in Brünnich’s guillemot colonies in the Svalbard archipelago. The rate of decline (a) is calculated from model 2 in Table 1b and represents the slopes of linear regressions on a log scale ( $\pm 95\%$  CI). Those confidence intervals take into account the overdispersion  $\sigma$  ( $\hat{\sigma} = 19.22$ ; see legend of Table 1) and have been calculated as  $SE \times 1.96 \times \sqrt{\hat{\sigma}}$ . The onset of decline (b) represents the inflection points ( $\pm 95\%$  bootstrap CI) of quadratic trends using all data (1988–2010). The grey bar (b) indicates the period 1994–1998

the decreasing phase); this inter-colony difference was due to only one colony, Fuglehuken (see Online Resource 2).

The estimated onset of decline (i.e., inflection point of the quadratic regressions) for the guillemot colonies ranged from 1985 (Tschermakfjellet colony) to 1999 (Alkhornet). However, the onset of decline for the Tschermakfjellet colony is driven by the count in 1988 which showed a large

number of birds compared to successive years. Removing this count, and thus considering only period 1989–2010, showed that the decline in colony size began in 1997 for this colony. Confidence intervals around those estimates indicated a strong overlap (Fig. 4b), which suggests that the decline started around the same period (1994–1998) for all colonies.

#### Effects of the winter NAO and subpolar gyre index

None of the winter NAO parameter considered (without and with a time lag) explained a significant proportion of Brünnich’s guillemot colony size variation (see Online Resource 3). The same results were obtained for the subpolar gyre index when no lag or a lag of 1–4 years were considered (see Online Resource 3). However, the subpolar gyre index with a lag of 5 years was closely related to variation in guillemot colony size (Table 2) and a simple model with this single covariate explained a large proportion in this variation ( $R^2$  varied from 0.27 to 0.79; Fig. 5). This 5 year delayed effect of the subpolar gyre index was not only due to a common trend with colony size; indeed, this effect remained significant when a quadratic trend was included in the model (Table 2; model 1).

The best model among the ones we tested showed that colonies exhibited a variable quadratic trend and a variable influence of the subpolar gyre. As before, this variation in the subpolar gyre effect was due to only one colony, Fuglehuken (Fig. 2). This gyre effect was stronger in that colony (Fig. 5).

#### Risk of extinction

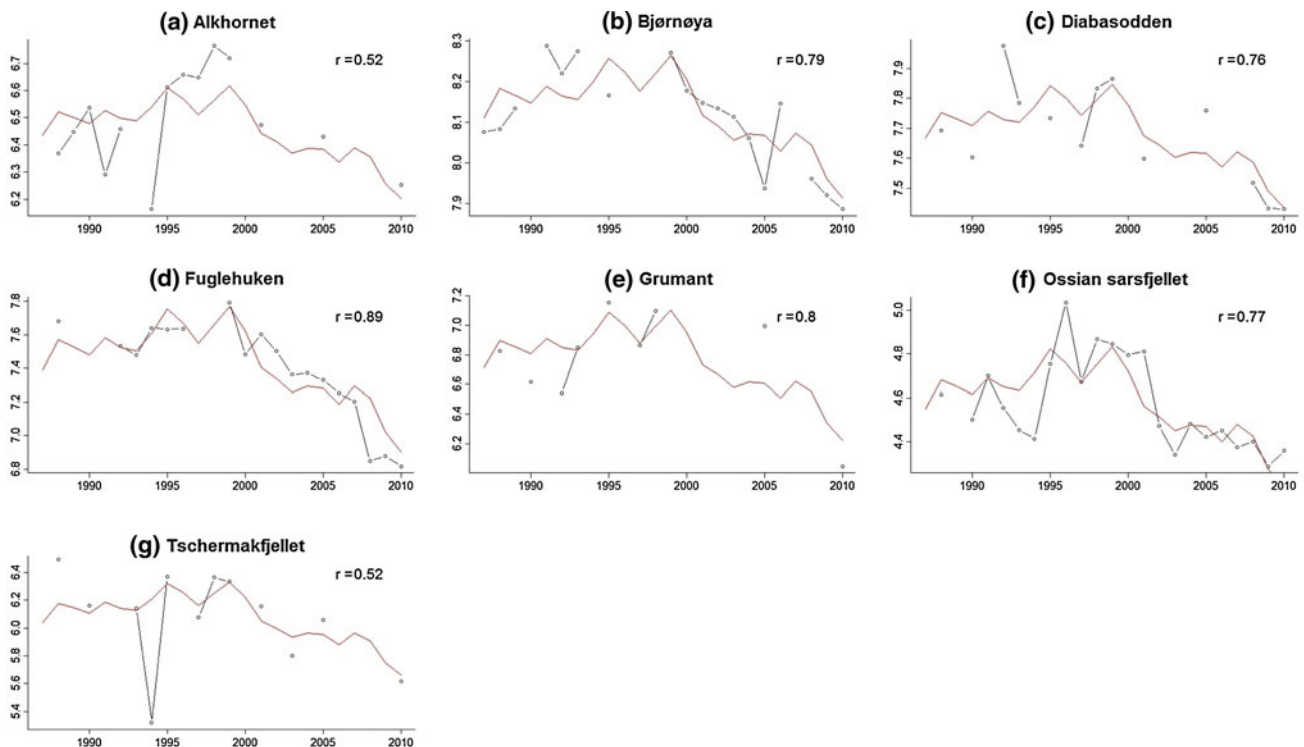
Our stochastic models indicated that, if the current trend observed in each colony over the last decade does not change, the risk of quasi-extinction will vary between 33 and 100 % in the next 50 years, depending on the colony considered (Fig. 6). All colonies but Bjørnøya have a risk of pseudo-extinction  $>93\%$ . The lower risk for Bjørnøya is the consequence of a higher average annual growth rate ( $\bar{\lambda}$ ) in the period 1988–2010, primarily due to one year (2005–2006) where population counts showed a large increase (Fig. 2). Removing this single year for the calculation of  $\bar{\lambda}$  and  $\sigma_e^2$  led to a risk of quasi-extinction risk of 100 % for Bjørnøya.

The risk of quasi-extinction at the population level (i.e., risk that the total number of individuals in the seven colonies dropped below 10 % of its 1999 level) is 43 % in the next 50 years (Fig. 6h). It increased to 93 % when considering 100 years (Fig. 6i). This is based on the assumption that the trend will remain the same in the next 50 or 100 years as it was during 1999–2010.

**Table 2** Effects of the sub-polar gyre (SPG) on variation in Brünnich's guillemot colony size in the Svalbard archipelago

Model number $\neq$	Model description	np	QAIC	$\Delta$ QAIC
1	Year + year <sup>2</sup> + SPG-Lag 5 + (year + year <sup>2</sup> + SPG-Lag 5 colony)	14	107.723	0.000
2	Year + year <sup>2</sup> + SPG-Lag 5 + (year + year <sup>2</sup>  colony)	10	109.822	2.099
3	Year + year <sup>2</sup> + (Year + year <sup>2</sup>  colony)	9	114.000	6.277
4	SPG-Lag 5 + (SPG-Lag 5 colony)	5	115.904	8.181

Models were fitted using a Poisson error distribution, and a log-link function. Model selection was based on QAIC; *np* represents the number of parameters for each model, and  $\Delta$ QAIC the difference in QAIC between the model considered and the model with lowest QAIC. QAIC were calculated using an overdispersion ( $\hat{c}$ ) of 19.22, estimated from model 3. Only models including the effect of the subpolar gyre with a 5 year time lag were shown; other environmental parameters did not affect colony size fluctuations (for details, see “Results”)



**Fig. 5** Observed (black line and symbols) and simulated (red line) colony size for Brünnich's guillemots in the Svalbard archipelago. Simulated values are based on a single environmental covariate, the subpolar gyre index (for details, see “Methods” section), and are

extracted from model 4 in Table 2. The Pearson correlation coefficients between observed and simulated values are indicated in the top right corner within each panel (colour figure online)

## Discussion

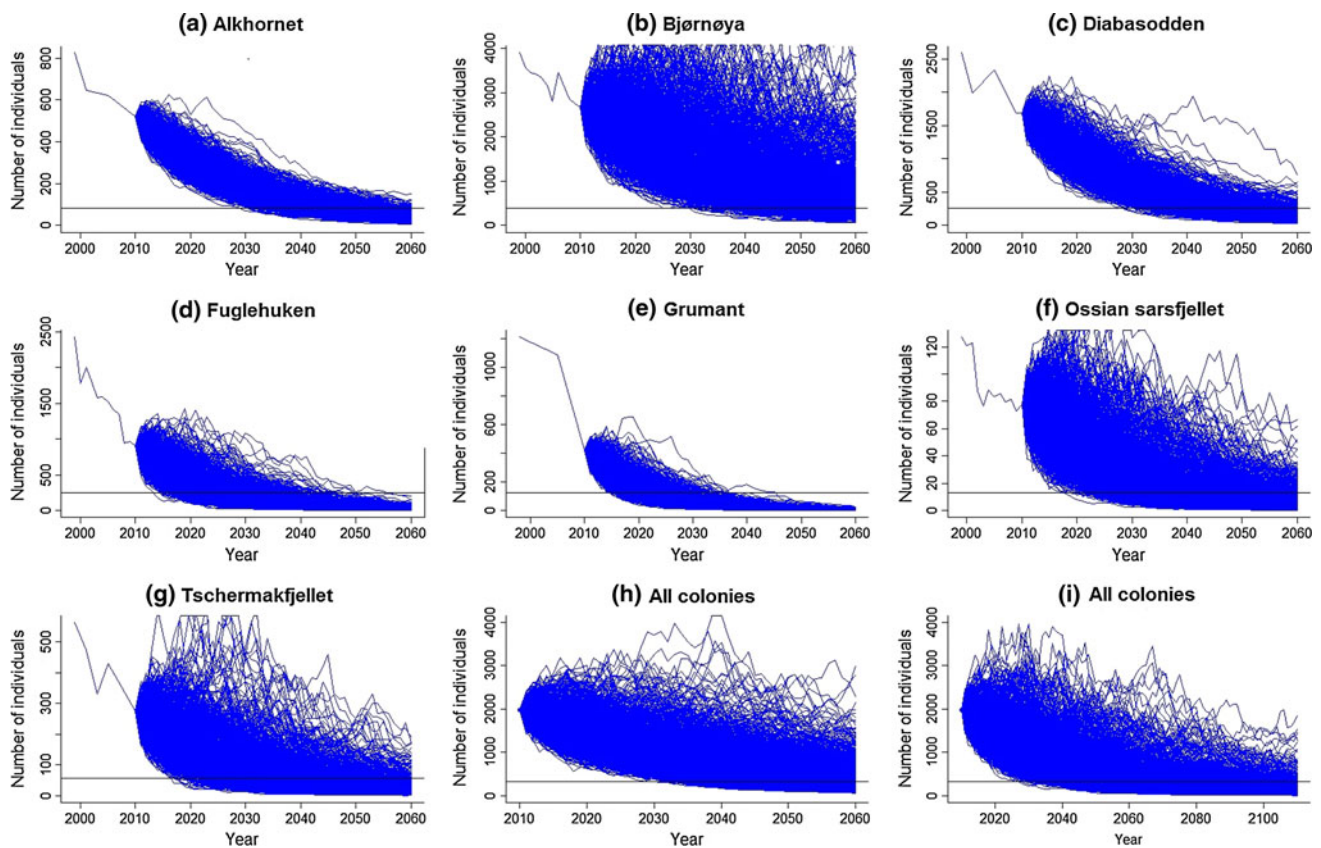
### Decline of Brünnich's guillemot in Svalbard

Brünnich's guillemots in Svalbard are clearly and rapidly declining. Our results show a strong similarity in the pattern of decline between colonies. All but one colony considered here declined at a similar rate (Fuglehuken declined more rapidly), and all colonies started to decline during the same period (between 1994 and 1998). The rate of decline varied from 2 to 5 % per year since the mid- or late-1990s, and during the last decade guillemot colonies have decreased in size by about 15–45 %. If the trend continues

at the same rate, the Svalbard population of Brünnich's guillemots has almost one chance out of two (43 %) of becoming (quasi-) extinct within the next 50 years and would be extinct in the next 100 years. Moreover, the relatively high synchrony in year to year fluctuations between Spitsbergen colonies also increases the risk of extinction because all those colonies may crash concurrently (Heino et al. 1997).

Of course, these predictions are based on the assumption that the environmental conditions and guillemot demographic parameters during the next 50 or 100 years will remain unchanged. This is highly speculative and somewhat unrealistic. Guillemots may also show some





**Fig. 6** Risk of pseudo-extinction in the next 50 (a–h) or 100 years (i) for Brünnich’s guillemot in the Svalbard archipelago. a–g Trajectories for seven distinct colonies. h and i Trajectories of the population (i.e., the sum of individuals from all seven colonies)

behavioural plasticity (e.g., diet switching) that may allow them to cope with poor environmental conditions (Gremillet and Charmantier 2010).

All colonies included here are located in the southern and western parts of Svalbard, and all colonies except Bjørnøya are strongly influenced by warm, Atlantic water masses (Loeng 1991). The eastern part of Svalbard is exposed to different oceanographic conditions due to colder Arctic water masses (Svendsen et al. 2002). If the decline in Brünnich’s guillemot is driven by summer oceanographic conditions, trends might differ in the east or north-east colonies (i.e., if changes in the environment in the East differ from changes in the West). The only available data from East Svalbard are from the Koval’skifjellet colony (77°3’46’’N, 17°10’38’’E). Counts were conducted in 1988, 1992 and 2002 (using the same plots). These counts (4915, 4124 and 3488 individuals, respectively) suggest the population may be declining. However, such results should be considered with great caution because the long-term trend cannot be assessed with certainty using only three data points.

#### Environmental forcing and the Moran effect

Attributing spatial synchrony in animal population dynamics to environmental forcing and the Moran effect is difficult (but see Grenfell et al. 1998; Post and Forchhammer 2002). To attribute synchronous fluctuations of populations to large-scale environmental parameters may be confounded by the synchronizing influences of dispersal or trophic interactions (Bjørnstad et al. 1999).

In Brünnich’s guillemot, spatial coupling by dispersal or trophic interaction (predation) can be ruled out as potential drivers of population synchrony. Indeed, the main predators of Brünnich’s guillemots in Svalbard are the glaucous gull (*Larus hyperboreus*) and Arctic fox (*Vulpes lagopus*). Both predators mainly take chicks, and the arctic fox mainly in the periphery of the colonies. The Arctic fox population in Svalbard increased between 1990 and 1995 and then decreased until 1998 (Fuglei et al. 2003), whereas glaucous gulls were generally decreasing, at least in Bjørnøya (Strøm 2006b). Moreover, considering the average distance between the colonies considered here

(190 km) and the fact that most of these colonies are separated either by a fjord or the open sea, it seems very unlikely that those predators had the potential to impact and synchronize guillemot colony population dynamics.

Breeding site fidelity is generally high in seabirds, and in Brünnich's guillemot in particular (Gaston et al. 1994). Moreover, juvenile dispersal in Brünnich's guillemot is also very low (Steiner and Gaston 2005). Consequently, the dispersal of individuals between colonies is expected to be very limited and thus cannot synchronize their fluctuations. Therefore, as the monitored colonies shared some density-independent population dynamics (for details, see "Results"), our study should provide a reliable test of the Moran effect as a potential mechanism leading to population synchrony, a common density-dependence structure being a pre-requisite of the Moran theorem.

Our results show that, when considering the synchrony in short-term (or year to year) fluctuations (i.e., detrended time series), Spitsbergen guillemot colonies varied synchronously but that fluctuations in Bjørnøya were independent, even if the long-term trend was the same. This tells us about those environmental drivers and the scale at which they exert their influence. Bjørnøya is exposed to a different oceanographic regime. Cold, arctic water occupies the shelf areas around Bjørnøya whereas west Spitsbergen is more influenced by warmer, Atlantic water (Loeng 1991). Variations in sea-surface temperature (SST) around Bjørnøya are weakly related to those in SST around Isfjorden (where the Alkhornt, Diabasodden, Grumant and Tschermakfjellet colonies are located) or Kongsfjorden/Prins Karl Forland (close to the Fuglehuken and Ossians Sarsfjellet colonies; Online Resource 3). Therefore, fluctuations in food availability in spring and summer are likely different in Spitsbergen and Bjørnøya, which could thus lead to different fluctuations in breeding propensity and breeding success, for example, and consequently population size (Jenouvrier et al. 2005).

Despite the absence of synchrony between Spitsbergen and Bjørnøya, all colonies in Svalbard showed similar declines. Such a similar trend indicates that some important changes or environmental shifts have occurred at a large spatial scale.

Importance of the bio-geographical shift in the north-eastern Atlantic ocean?

Marine ecosystems can show sudden and dramatic changes in their bio-physical properties over periods of decades or longer, even spanning entire ocean basins (deYoung et al. 2008). Such changes in the state of an ecosystem have been called "regime shifts" (deYoung et al. 2008).

In the North Atlantic, such a regime shift occurred in the mid-1990s, when the circulation of the subpolar gyre

declined substantially after 1995 (Hatun et al. 2005, 2009). This gyre corresponds to rotating cold and low-saline subarctic water in the central northern Atlantic, and a decrease in this subpolar gyre has led to warming and salinification of the region south of Iceland (Hatun et al. 2005). The shift in this subpolar gyre has been associated with pronounced changes in the physical environment (e.g., SST, salinity) and fauna (from plankton to whales), from the English channel to the south of the Barents Sea. For example, the copepod *Calanus finmarchicus*, a subarctic zooplankton species, decreased in abundance south of Iceland after the shift in the gyre (Hatun et al. 2009).

This shift in the North-East Atlantic occurred over the same period, or just prior to, declines in Brünnich's guillemots breeding in Svalbard. Considering the dramatic influence this shift had on both the ocean's physical parameters and fauna, it clearly had the potential to affect top predators such as guillemots. The effects of the subpolar gyre shift were pronounced in the south and west of Iceland and the south of Greenland (Hatun et al. 2005, 2009), which are areas used by guillemots during the winter and/or during migration.

Our results strongly support a causal relationship between changes in the subpolar gyre and changes in Brünnich's guillemot colony sizes. We showed that the subpolar gyre index explained a large proportion of the variation in guillemot colony size fluctuation, independently of a common long-term trend. This effect is similar in all colonies but one, Fuglehuken. Further investigation is needed to understand why this colony showed a different response to variation in the subpolar gyre. In particular, we would need to identify the wintering area and migration routes of guillemots breeding at the Fuglehuken colony.

The 5 year lag we observed suggests that this causal pathway is mediated by recruitment and thus juvenile survival. It has previously been shown that Brünnich's guillemots are sensitive to shifts in SST and that the magnitude of SST shift is more important than its direction in determining the subsequent rate of population change. More specifically, Brünnich's guillemots showed negative colony size trends with large temperature shifts, whatever the direction of those shifts (Irons et al. 2008). This supports the hypothesis that the shift in subpolar gyre, which is highly correlated with changes in SST (Hatun et al. 2005, 2009), has played an important role in the decline of Brünnich's guillemots in Svalbard.

The shift in the subpolar gyre could also explain why all colonies, including Bjørnøya, declined in a similar way, despite differences in short-term fluctuations. A large-scale shift in the mid-1990s could have caused the decline at the population level (Irons et al. 2008), but then year to year fluctuations at the colony scale could have been mainly driven by more local variables; this could further explain

why Bjørnøya fluctuates independently of Spitsbergen colonies. A potential mechanism could be that deterioration of the feeding conditions in the winter affected bird survival (Gaston 2003), particularly juvenile survival, and that local variations in spring and summer conditions affected breeding propensity and breeding success of guillemots. A linear decline in survival interacting with stochastic fluctuations in breeding parameters could lead to a similar rate of decline between populations, yet with different short-term fluctuations as observed in our study. However, proper retrospective analyses (Caswell 2000) would be needed to conclude about the respective role of survival and reproductive parameters in Brünnich's guillemot population fluctuations.

## Conclusion

Our study clearly indicated that colony sizes of Brünnich's guillemots in Svalbard have declined rapidly in the last decade. The decline is very similar, and was initiated over the same time period across all monitored colonies (between 1994 and 1998) coinciding with a major shift in oceanographic conditions. Considering the large distances between colonies (up to 550 km) and the fact that birds from those colonies winter from Iceland to South-West Greenland, such a generalized decline between Svalbard guillemots suggests that a large-scale deterioration in the environment has occurred. The 1995 shift in the subpolar gyre and consequent changes in the subarctic waters of the North Atlantic have very likely played an important role in the population decline of Brünnich's guillemots in Svalbard.

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## References

- Bjørnstad ON, Ims RA, Lambin X (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol Evol* 14:427–432
- Bolker BM et al (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Caswell H (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627
- Descamps S et al (2010) Detecting population heterogeneity in effects of North Atlantic Oscillations on seabird body condition: get into the rhythm. *Oikos* 119:1526–1536
- deYoung B et al (2008) Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol Evol* 23:402–409
- Earn DJD, Levin SA, Rohani P (2000) Coherence and conservation. *Science* 290:1360–1364
- Engen S, Lande R, Saether BE, Bregnballe T (2005) Estimating the pattern of synchrony in fluctuating populations. *J Anim Ecol* 74:601–611
- Fort J et al (2013) Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. *J Avian Biol* 44:001–008
- Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob Change Biol* 10:1214–1221
- Fuglei E, Oritsland NA, Prestrud P (2003) Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biol* 26:93–98
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Ann Rev Ecol Syst* 31:367–393
- Gaston AJ (2003) Synchronous fluctuations of thick-billed murre (*Uria lomvia*) colonies in the eastern Canadian arctic suggest population regulation in winter. *Auk* 120:362–370
- Gaston AJ, Deforest LN, Donaldson G, Noble DG (1994) Population parameters of thick-billed Murres at Coats Island, Northwest-Territories, Canada. *Condor* 96:935–948
- Gremillet D, Charmantier A (2010) Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecol Appl* 20:1498–1503
- Grenfell BT et al (1998) Noise and determinism in synchronized sheep dynamics. *Nature* 394:674–677
- Hatun H, Sando AB, Drange H, Hansen B, Valdimarsson H (2005) Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science* 309:1841–1844
- Hatun H et al (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. *Prog Oceanogr* 80:149–162
- Heino M, Kaitala V, Ranta E, Lindstrom J (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264:481–486
- Hurrell JW, Dickson RR (2004) Climate variability over the North Atlantic. In: Stenseth NC, Ottersen G, Hurrell JW, Belgrano A (eds) *Marine ecosystems and climate variation*. Oxford University Press, Oxford, pp 15–31
- Hurrell JW, Kushnir Y, Visbeck M (2001) The North Atlantic Oscillation. *Science* 291:603–605
- Ims RA, Steen H (1990) Geographical synchrony in microtine population-cycles—A theoretical evaluation of the role of nomadic avian predators. *Oikos* 57:381–387
- Irons DB et al (2008) Fluctuations in circumpolar seabird populations linked to climate oscillations. *Glob Change Biol* 14:1455–1463
- Jenouvrier S, Barbraud C, Cazelles B, Weimerskirch H (2005) Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions. *Oikos* 108:511–522
- Johnson DM, Liebhold AM, Bjornstad ON, McManus ML (2005) Circumpolar variation in periodicity and synchrony among gypsy moth populations. *J Anim Ecol* 74:882–892
- Kosmelj K, Blejec A, Cedilnik A (2005) Interval estimate for specific points in polynomial regression. *J Comput Informat Theory* 4:287–291
- Kålås JA et al. (2010) Norwegian Red List for Species
- Lande R, Engen S, Sæther B-E (2003) *Stochastic population dynamics in ecology and conservation*. Oxford University press, Oxford
- Liebhold A, Koenig WD, Bjornstad ON (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Syst* 35:467–490

- Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. *Polar Res* 10:5–18
- Lohmann K, Drange H, Bentsen M (2009) A possible mechanism for the strong weakening of the North Atlantic subpolar gyre in the mid-1990s. *Geophys Res Lett* 36:L15602
- Moran PAP (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Aust J Zool* 1:291–298
- Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. *J Evol Biol* 20:831–844
- Palmqvist E, Lundberg P (1998) Population extinctions in correlated environments. *Oikos* 83:359–367
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (2000) Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. *Ecology* 81:2112–2125
- Post E, Forchhammer MC (2002) Synchronization of animal population dynamics by large-scale climate. *Nature* 420:168–171
- R Foundation for Statistical Computing. R Development Core Team (2010) R: a language and environment for statistical computing (<http://www.R-project.org>), Vienna, Austria
- Ranta E, Kaitala V, Lundberg P (1998) Population variability in space and time: the dynamics of synchronous population fluctuations. *Oikos* 83:376–382
- Sæther B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653
- 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
- Steen H, Lorentzen E, Strøm H (2013) Winter distribution of guillemots (*Uria spp.*) in the Barents Sea. Norwegian Polar Institute Report Series, 141
- Steiner UK, Gaston AJ (2005) Reproductive consequences of natal dispersal in a highly philopatric seabird. *Behav Ecol* 16:634–639
- Strøm H (2006a) Brünnich's guillemot. In: Kovacs KM, Lydersen C (eds) Birds and mammals of svalbard. Norwegian Polar Institute, Tromsø
- Strøm H (2006b) Glaucous gull. In: Kovacs KM, Lydersen C (eds) Birds and mammals of svalbard. Norwegian Polar Institute, Tromsø
- Svendsen H et al (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133–166
- Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84:2034–2041
- Votier SC et al (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecol Lett* 8:1157–1164
- Walsh PM, Halley DJ, Harris MP, del Nevo A, Sim IMW, Tasker ML (1995) Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds. Joint Nature Conservation Committee, Royal Society of the Protection of Birds, Institute of terrestrial Ecology, Seabird Group, Peterborough