FEATURE ARTICLE

Weakening of the subpolar gyre as a key driver of North Atlantic seabird demography: a case study with Brünnich's guillemots in Svalbard

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ABSTRACT: The Arctic is experiencing environmental changes at unprecedented rates. These changes are spreading throughout the entire food web, affecting apex predators such as seabirds. Brünnich's guillemot *Uria lomvia* populations in Svalbard archipelago have significantly declined since the mid-1990s. For long-lived species such as seabirds, population growth rate is highly sensitive to changes in adult survival rates, and slight changes in survival may have large consequences at the population level. Adult survival rates, were estimated for Brünnich's guillemots individually marked and monitored from 1986 to 2011 at Bjørnøya, Svalbard. While survival appeared to be repeatedly high (mean ± SE; 95 ± 1%) from 1986 to 1995–98 (transitional years, when Svalbard guillemot colonies started to decline), it dropped by 9–12% over the period 1995–98 to 2011. This decline coincided with the occurrence of an abrupt ecosystem shift in the North Atlantic Ocean in the mid-1990s and the weakening of the Atlantic subpolar gyre. Variations in the subpolar gyre index (SGI) were significantly associated with inter-annual variation in guillemot annual survival, and a strong gyre (i.e. cold waters on guillemot wintering grounds) was associated with high adult survival. Our results, combined with other studies, suggest that the SGI may be an important global proxy to assess oceanographic conditions and changes in marine ecosystems in the North Atlantic.

KEY WORDS: Climate change · Regime shift · Seabirds · Adult survival · Subpolar Gyre Index · Winter North Atlantic Oscillation · Sea surface temperature · *Uria lomvia* · Arctic
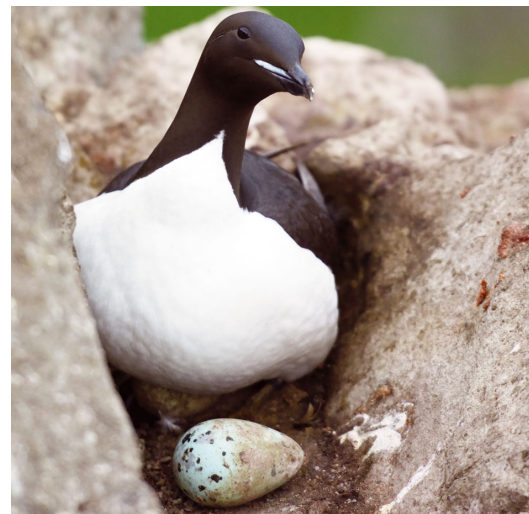
Decline of adult Brünnich's guillemot (*Uria lomvia*) in Svalbard is associated with the weakening of the North Atlantic subpolar gyre.

Photo: Julie Fluhr

INTRODUCTION

Evidence of the effects of global warming on vertebrate population dynamics is unequivocal (Parmesan & Yohe 2003, Jenouvrier 2013), notably in the Arctic where ecosystems are already experiencing rapid changes (Wassmann et al. 2011, Hansen et al. 2013, Field et al. 2014). Identifying the underlying demographic responses and their environmental drivers is critically needed in the context of climate change. In

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long-lived species, population growth rate is highly sensitive to changes in adult survival rates and a slight change in adult survival can dramatically affect the overall population dynamics (Gaillard et al. 2000, Saether & Bakke 2000). Even if adult survival is expected to be canalised against environmental variability in such long-lived organisms (Wagner et al. 1997, Gaillard & Yoccoz 2003), it may still be affected by environmental fluctuations (see Durant et al. 2003, Lavers et al. 2008, Oro et al. 2010, Hovinen et al. 2014, for a few examples on seabirds). To assess the effects of climate variation on adult survival in long-lived organisms, it is therefore important to understand their population dynamics.

Explaining climate-driven ecological processes in free-living populations remains a difficult task, as individuals move over space and time, and are affected by complex and multiple climatic features (Stenseth & Mysterud 2005). Identifying the relevant environmental parameters involves locating areas used by individuals at each life stage. Since the effects of environmental fluctuations on adult survival may operate outside the breeding period, such a task may be very arduous, especially for migratory seabirds, which spend the winter at sea.

Among arctic seabirds, Brünnich's guillemot *Uria lomvia* is an example of a long-lived species highly sensitive to recent environmental changes (Gaston et al. 2005, Descamps et al. 2013). In particular, colonies in Svalbard (Norway) have significantly declined (between 15 and 45%) since the mid-1990s and are under threat of extinction within the next 50 yr if the current rate of decline continues (Descamps et al. 2013). An abrupt ecosystem shift, which took place in the north-east Atlantic in 1995 (Häkkinen & Rhines 2004, Hátún et al. 2009), has probably affected colony sizes of Svalbard Brünnich's guillemots (Descamps et al. 2013). This shift was the consequence of a weakening of the subpolar gyre (SPG) after 1995 associated with an abrupt weakening of the North Atlantic Oscillation (NAO) (Häkkinen & Rhines 2004), and an increase in sea-surface temperature (SST) and salinity in the North Atlantic Ocean (Hátún et al. 2005, Hátún 2009). Such a shift has affected many marine organisms, from plankton to fish, seabirds and marine mammals (Hátún et al. 2005, Hátún 2009), through trophic cascades or amplification (Irons et al. 2008, Kirby & Beaugrand 2009). Furthermore, the synchronization of population declines in Brünnich's guillemots breeding in Iceland and southern Greenland suggests that population changes may have been driven by events at their common wintering grounds (Frederiksen et al. 2016).

Here, using long-term monitoring data of Brünnich's guillemots breeding at Bjørnøya, Svalbard, we estimated adult annual survival through capture-mark-recapture (CMR) modeling (Lebreton et al. 1992). We first tested the hypothesis that survival declined after the mid-1990s in relation with the decrease in population size observed at Bjørnøya (Descamps et al. 2013). Second, we predicted that large-scale fluctuations in oceanographic conditions reflected by changes in the North Atlantic SPG would explain temporal variation in adult guillemot survival. Finally, the migration routes and the distribution at-sea during the non-breeding season of Svalbard guillemots have recently been identified (Fort et al. 2009, Steen et al. 2013), allowing us to investigate how adult survival is affected by local environmental conditions, such as SST, outside the breeding season. We thus tested the hypothesis that the shift in the SPG affected guillemot survival, mostly through changes in sea temperature (via bottom-up effects and changes in the food chain). Finally, we discuss the value of the subpolar gyre index (SGI) as a global proxy to assess oceanographic conditions and changes in marine (and even terrestrial) ecosystems in the North Atlantic, in comparison with the winter North Atlantic Oscillation (wNAO) index, a global proxy widely used in ecology over the past decades (e.g. Mysterud et al. 2003, Sandvik et al. 2012). Since the NAO is computed as a difference in atmospheric pressure, whereas variations in the SPG are known to reflect measurable changes in ocean conditions (e.g. SST and salinity; see Hátún et al. 2005, Hátún 2009), we supposed that the wNAO would drive marine organism traits and demography to a lesser extent and/or less directly than the SPG. Moreover, while numerous investigations have emphasized the role of the wNAO on the ecology of marine organisms in the North Atlantic (Drinkwater et al. 2003), we are among the first to investigate the influence of the SPG.

METHODS

Species and study site

Brünnich's guillemot *Uria lomvia* is a circumpolar species breeding in the Arctic and Subarctic (from 46° 00′ N to 82° 00′ N). It is one of the most numerous seabird species in the Svalbard Archipelago, with a total breeding population estimated at 850 000 pairs (Strøm 2006). The study site was located on Bjørnøya, the southernmost island of the Svalbard Archipelago,

in the Barents Sea (74° 25′ N, 19° 00′ E), hosting a colony of about 150 000 guillemots. Adults first breed at 3 to 5 yr old (Gaston et al. 1994), laying a single egg in June, and can live >30 yr (Elliott et al. 2015). Both parents share incubation for about a month and chick-feeding duties until the chick, less than half grown and unable to fly, jumps to the sea about 3 wk later. At the end of July or early August, the male parent undertakes a migration by swimming towards the wintering grounds in the company of its chick (Gaston & Jones 1998, Strøm 2006). The chick-rearing period at-sea lasts 4 to 8 wk (Strøm 2006).

Capture-mark-recapture data

CMRs of breeding adults were carried out annually during the breeding period (June–July) from 1986 to 2011 (except in 1987 and 1994). During incubation or brooding periods, individuals were caught with a nylon loop attached to the end of a telescopic pole. Once captured, they were marked with a numbered metal ring (from the Stavanger Museum, Norway) and an individually coded colour ring for identification at distance. Recapture data correspond to both live recaptures and resightings of marked individuals. In this study, we used 332 capture-recapture histories of adult guillemots from 1986 to 2011 (see details in Supplement 1 at www.int-res.com/articles/suppl/m563p001_supp.pdf).

Environmental data

Subpolar gyre index

We used the North Atlantic SGI as a proxy of the variability of the marine environment in the North Atlantic region. The SGI 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 Hátún et al. (2009) and H. Drange (University of Bergen, pers. comm.). Two indices were available: one index based on simulated sea surface height anomalies from 1983 to 2007, and another index based on satellite observations from 1993 to 2010. To obtain a series covering our entire study period (1983–2011) (see Supplement 2), we extrapolated the first index by using a regression equation linking both indices during the overlapping period 1993–2007 (this regression indicates that both SGIs were highly correlated, r = 0.79) (see details in Descamps et al. 2013).

wNAO index

The NAO is the most prominent source of atmospheric variability in the Northern Hemisphere, identified in all months of the years. This oscillation represents a basin-scale alternation of atmospheric masses over the North Atlantic between the subtropical and Subarctic regions (Hurrell et al. 2001). The NAO has a strong influence on the hydro-dynamics of the North Atlantic Ocean (Dickson & Brander 1993, Dickson et al. 1996, Flatau et al. 2003), e.g. it has an effect on the SPG (Flatau et al. 2003, Beaugrand et al. 2009, Lohmann et al. 2009). The NAO has different regional effects on SST, implicating contrasting ecosystem responses. When the NAO is in its positive phase, it has a negative influence on the SST over the SPG (Marshall et al. 2001). As a result, the number of warm-water species diminishes in the southwestern part of the gyre (Beaugrand 2009). In the north-east Atlantic (including the North Sea), the NAO influence is opposite and the number of warm-water species increases during a positive NAO phase. We used the wNAO index (December–March) as a proxy of winter conditions in the North Atlantic. The wNAO station-based index values were retrieved from Hurrell (2016) (see Supplement 2).

Sea surface temperature

SST data were used to reflect the local environmental conditions outside the breeding season. For the monthly SST values that corresponded to the areas used by wintering birds, we used distribution maps of adult guillemots monitored with geolocation sensor (GLS) tags from September to March for 3 yr (2007−2010). In mid-September, the equipped individuals performed southward migration to overwinter off the coasts from northeast Iceland to southeast Greenland (see details in Supplement 3 and in Fort et al. 2013). Mean SST values were computed for the areas included in the 85% contour kernel, over 3 periods, outward and inward migration (September to October and February to March, respectively), and winter (November to January) (see Supplements 2 & 3). Monthly SST data with a resolution of 1° longitude by 1° latitude were downloaded from http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.sst/ (Reynolds et al. 2002).

Adult survival modeling

Goodness-of-fit tests

The first step in the CMR modelling consisted of testing the assumption of independence of fates and identity of rates among individuals by implementing goodness-of-fit (GOF) tests on a biologically plausible general model (Lebreton et al. 1992). In a single-state approach, the reference model for fit assessment is the Cormack-Jolly-Seber (CJS) model, in which survival (Φ) and recapture (p) probabilities are fully time-dependent (Φ_t, p_t). To test whether this general model fitted the data, we used the program U-CARE 2.3.2 (Choquet et al. 2009). The overall GOF test of the CJS model indicated lack of fit (Pearson chi-squared statistic, $\chi^2 = 141.21$, df = 78, p < 0.001; Table 1) mostly caused by a positive correlation between successive events of capture, known as trap-happiness (test 2.CT: $\chi^2 = 75.61$, df = 20, p < 0.001; Table 1). The generalization of the CJS model accounting for this feature correctly fitted the data (Table 1) and was used to start the model selection (Pradel et al. 2005). The remaining heterogeneity was accounted for by scaling model deviances using a variance inflation factor ($\hat{c}$) calculated, after discarding the 2.CT component, by dividing χ^2 by its df, i.e. $\hat{c} = 65.59/58 = 1.13$ (Choquet et al. 2009).

A recent approach, set in a multi-event framework, was used to take into account immediate trap-dependence (see details in Pradel & Sanz-Aguilar 2012). We considered models with a constant increase in capture probability following a capture event. The increase was either on the logit scale (TP structure in Table 2; Pradel 1993), or on the log scale, i.e. a multiplicative coefficient (CTP structure in Table 2; see details in Appendix 4 and Crespin et al. 2008). We

Table 1. Goodness-of-fit (GOF) tests using the Cormak-Jolly-Seber (CJS) model for Brünnich's guillemots breeding on Bjørnøya, Svalbard (data from 1986 to 2011, n = 332 capture histories). χ^2: Pearson statistic (that tests the null hypothesis that data are homogeneous), $\hat{c}$: variance inflation factor

Test	χ^2	df	p	$\hat{c}$
TEST 2.CT	75.6113	20	<0.001	
TEST 2.CL	45.9437	26	<0.05	
TEST 3.SR	8.3082	17	0.96	
TEST 3.SM	11.3373	15	0.73	
Overall test	141.2055	78	<0.001	1.81
Model with immediate trap-dependence[a]	65.5892	58	0.23	1.13

[a]Reduced GOF test: Test 2.CL + Test 3.SR + Test 3.SM

Table 2. Modeling capture and survival probabilities of adult Brünnich's guillemots breeding on Bjørnøya, Svalbard (data from 1986 to 2011, n = 332). Survival parameters were set to be constant over a time period ($cst_{[years]}$) or time-dependent over a time period ($t_{[years]}$). np: number of estimable parameters; DEV: deviance; QAICc: Akaike information criterion corrected for small sample and overdispersion; ΔQAICc: difference between the QAICc of the current model and the minimum QAICc; t: time-dependent effect; cst: constant effect; LT: linear trend effect; [ ] time period on which a given effect is tested; CHC: coefficient of heterogeneity of catchability; CTP: coefficient of trap-dependence; HC: heterogeneity of catchability effect; TP: trap-dependent effect

Effect on survival	Effect on capture	np	DEV	QAICc	ΔQAICc
Capture					
$t_{[86-11]}$	CHC	49	3276.93	3001.78	0.00
$t_{[86-11]}$	CTP	47	3394.07	3101.14	99.36
$t_{[86-11]}$	t	45	3539.59	3137.12	135.34
$t_{[86-11]}$	HC	28	4048.77	3640.23	638.45
$t_{[86-11]}$	TP	27	4071.04	3657.86	656.08
$t_{[86-11]}$	cst	25	4263.96	3824.41	822.63
Survival					
$cst_{[86-97]}, t_{[97-11]}$	CHC	40	3283.54	2988.34	0.00
$cst_{[86-96]}, t_{[96-11]}$	CHC	41	3282.25	2989.33	0.99
$cst_{[86-95]}, t_{[95-11]}$	CHC	42	3281.89	2991.14	2.80
$LT_{[86-11]}$	CHC	28	3315.64	2991.45	3.11
$cst_{[86-98]}, LT_{[98-11]}$	CHC	29	3316.97	2994.71	6.37
$cst_{[86-98]}, t_{[98-11]}$	CHC	39	3293.26	2994.82	6.48
$cst_{[86-97]}, cst_{[97-11]}$	CHC	28	3322.70	2997.70	9.36
$cst_{[86-98]}, cst_{[98-11]}$	CHC	28	3323.15	2998.09	9.75
$cst_{[86-96]}, LT_{[96-11]}$	CHC	29	3321.16	2998.42	10.08
$t_{[86-11]}$	CHC	49	3276.93	3001.78	13.44
$cst_{[86-96]}, cst_{[96-11]}$	CHC	28	3003.01	3004.26	15.92
$cst_{[86-95]}, cst_{[95-11]}$	CHC	28	3007.19	3008.45	20.11
$cst_{[86-95]}, LT_{[95-11]}$	CHC	29	3340.32	3015.38	27.04
$cst_{[86-97]}, LT_{[97-11]}$	CHC	29	3352.18	3025.88	37.54
$cst_{[86-11]}$	CHC	27	3384.71	3050.48	62.14

alternatively considered the possibility that the positive correlation between successive captures was due to intrinsic heterogeneity where some individuals are intrinsically more catchable. There, we assumed 2 classes of individuals with distinct probabilities of capture with a constant increase in one class as compared to the other. Again, the increase was either on the logit (HC structure in Table 2) or on the log scale (CHC structure in Table 2; see details in Supplement 4 and Crespin et al. 2008). We found that intrinsic inter-individual differences in the susceptibility to being captured were more likely than heterogeneity induced by the capture event itself (see Table 2). According to the best-supported model, highly catchable individuals ($p_1 = 0.54$, 95% CI = 0.44–0.61) were 2.8 times more likely to be recaptured than the less-catchable ones ($p_2 = \beta.p_1$ with $\beta = 0.36$, 95% CI = 0.20–0.56).

Model selection procedure

CMR statistical modeling was performed with the software E-SURGE 1.8.5 (Choquet & Gimenez 2012). Model selection was based on the Akaike's information criterion adjusted for overdispersion and small sample size (QAICc; see details in Burnham & Anderson 2002). The lower the QAICc, the better the trade-off between prediction bias and parsimony. If the difference in QAICc values between 2 models is <2, the models are deemed to have equal statistical support and in case of nested models, the simplest was preferred.

Using a step-down approach (Lebreton et al. 1992), we modeled the recapture probabilities (p) first and then the survival probabilities (ϕ). Recaptures were fixed at 0 in 1987 and 1994 (i.e. years with no field work). To test the hypothesis of a decline in survival, models including time-dependent or constant survival (ϕ_t and ϕ_i, respectively) were compared with models where survival followed a linear trend (ϕ_{LT}) over the whole study period. Then, an additional set of models was fitted to the data to test the hypothesis of a decline in survival since the transitional years 1995–1998 (when Svalbard guillemot colonies started to decline, Descamps et al. 2013). Such a change in the temporal pattern of adult survival was modeled by setting constant survival rates over the hypothesized pre-declined period, and testing either a constant, time-dependent or linear effect on survival over the remaining period.

Modeling environmental effects on adult survival

Brünnich's guillemots mainly prey on fish ≤3 yr old (Gaston & Noble 1985) so we tested whether the SGI and SST would affect annual survival rates by considering time-lags up to 3 yr. Moreover, since adult survival showed a linear trend over the study period (see 'Results: Decline in Brünnich's guillemot survival'), and to ensure that any relationship between survival and an environmental variable was not solely due to the co-occurrence of a common trend, we considered both the effects of the standardized environmental parameters as well as their detrended values (i.e. residuals from a linear regression).

Analysis of deviance (ANODEV) tests were performed to assess whether the environmental parameters explained a significant proportion of the temporal variation in adult survival (Grosbois et al. 2008). We calculated the statistic $F_{cst/co/t}$:

$$F_{cst/co/t} = \frac{\frac{Dev_{cst} - Dev_{co}}{f-1}}{\hat{c}} \quad \text{with } \hat{c} = \frac{Dev_{co} - Dev_t}{n-f} \quad (1)$$

where Dev_{cst}, Dev_{co} and Dev_t represent the deviances among the constant, the covariate and the time-dependent models, respectively; n is the number of survival estimates obtained from time-dependent models and f is the number of parameters required to describe the relationship between survival and the focal environmental covariate (Grosbois et al. 2008). The statistic $F_{cst/co/t}$ follows a Fisher-Snedecor distribution with $(f-1)$ and $(n-f)$df, under the null hypothesis, H_0, that the covariate in F_{co} has no effect on survival. The temporal variation in survival accounted for by a given covariate was computed using the statistic $R^2\_DEV = \frac{Dev_{cst} - Dev_{co}}{Dev_{cst} - Dev_t}$ (Grosbois et al. 2008). ANODEV tests were also performed to assess the statistical support for a linear trend in adult survival over the study periods.

To test for the effects of environmental covariates independently of any linear trend effect, we considered the same formulas as above but with Dev_{LT} (deviance of the model including a linear trend) and Dev_{co+LT} (deviance of the model including a linear trend and a covariate) instead of models Dev_{cst} and Dev_{co}, respectively.

RESULTS

Decline in Brünnich's guillemot survival

Adult survival of Brünnich's guillemots *Uria lomvia* showed large and significant inter-annual variation and dropped significantly from 1995–98 onwards (Fig. 1 and Table 3). Models with constant survival over the hypothesized pre- and post-decline period received much more support than models with constant survival over the entire period (ΔQAICc > 42; Table 2, Supplement 5). These models estimated a mean survival probability of 0.95 (±0.01 SE) from 1986 to 1995–98, followed by survival estimates ranging from 0.83 to 0.86 (±0.01 SE) over the post-decline period, i.e. a drop in survival varying between 9 and 12% (Table 3). The best supported model ($\phi_{cst[86-97],t[97-11]}$) showed a constant survival of 0.95 (±0.01 SE) from 1986 to 1997, followed by inter-annual variations over the remaining period (1997–2011). Survival was particularly low in 2006–2007. However, the difference in survival during 1986–1997 and 1997–2011 was not driven by this single year. Indeed, a model with 3 modalities (survival in 1986–1997, survival in 1997–2006 and 2007–2010, and survival in 2006–2007) still indicated that survival after 1997 (0.85 ± 0.01 SE) was significantly lower than survival
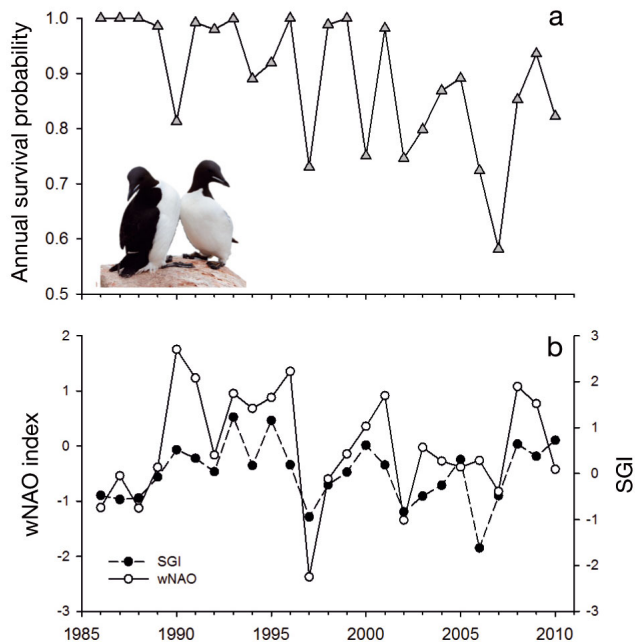
Fig. 1. (a) Annual survival of Brünnich's guillemot breeding on Bjørnøya, Svalbard and (b) inter-annual variation in the subpolar gyre index (SGI) and the winter North Atlantic Oscillation (wNAO) index in 1986–2011. (a) Survival estimates from the fully time-dependent model. (b) Detrended SGI index values (with no lag) and wNAO index values (with 2 yr lag)

before 1997 (0.95 ± 0.01 SE) independent of the low survival in 2006–2007 (0.57 ± 0.08 SE).

Environmental effects

The SGI, the wNAO index and winter SST (Nov–Jan) with and without lags explained a significant amount of temporal variation in Brünnich's guillemot survival (Supplement 6). In particular, the SGI without a time lag explained 69% of the variation in survival (Supplement 6). Once detrended, only the SGI (without lag) and the wNAO (with a lag of 2 yr) had a significant effect on survival ($R^2\_DEV = 0.27$, $p < 0.05$ and $R^2\_DEV = 0.26$, $p < 0.05$, respectively; Table 4; Fig. 1). As predicted, both slopes of the SGI and the wNAO index effects were positive (Table 4) indicating that a strong SGI and wNAO were associated with high survival (Fig. 2). Even though the SGI (no lag) and wNAO (2 yr lag) are significantly correlated (Spearman correlation: rho = 0.58, $p < 0.05$; see Supplement 7), when combined into the same model, they explained a higher proportion of the variation in guillemot survival ($R^2\_Dev = 0.36$) than each variable considered separately (Table 4). We found no signifi-

Table 3. Decline in survival (means of estimates) in adult Brünnich's guillemot over the hypothesized post-decline period 1995–98 to 2011. CI– and CI+ represent the lower and upper limits of the 95% confidence interval, respectively

Period	Adult survival estimate	Decline in survival	CI–	CI+
1986–1995	0.95		0.93	0.97
1995–2011	0.86	−9%	0.84	0.88
1986–1996	0.95		0.93	0.97
1996–2011	0.85	−10%	0.83	0.87
1986–1997	0.95		0.93	0.97
1997–2011	0.84	−11%	0.82	0.86
1986–1998	0.95		0.93	0.96
1998–2011	0.83	−12%	0.81	0.86

cant effect of detrendred SSTs (Table 4) indicating that their previous effects (using standardized SSTs; see Supplement 6) were mostly due to a common long-term trend and not year-to-year variability.

DISCUSSION

Our study clearly supports the hypothesis of a decline in adult Brünnich's guillemot *Uria lomvia* survival at Bjørnøya, Svalbard, since the mid-1990s. Survival was repeatedly high (0.95 ± 0.01 SE) from 1986 to 1995–98. Such a survival rate is higher than previous estimations in other Brünnich's guillemot populations (e.g. 0.89 in Gaston et al. 1994, and 0.93 in Sandvik et al. 2005). However, survival dropped by 9–12% over the remaining period (from 1995–98 onwards), reaching a minimum of 0.56 ± 0.08 SE in 2006–2007. This decline in adult survival corroborates recent observations of a general decline in Brünnich's guillemot colony sizes in Svalbard archipelago since the mid-1990s (Descamps et al. 2013). While Descamps et al. (2013) suggested that this decline in population size might have been driven by changes in juvenile survival and recruitment, our study shows that an alteration in adult survival was also likely involved. Demographic modeling based on a simple life cycle (Supplement 8) supports the hypothesis that the observed decline in adult survival rate was unsustainable and thus drove, at least partly, the decline in population size. Changes in breeding propensity or breeding success may have also played a role in the guillemot population decline but unfortunately no long-term data on guillemot reproduction were available to test this hypothesis.

Adult survival of Brünnich's guillemots in Bjørnøya was clearly associated with changes in the state of the North Atlantic SPG circulation (Häkkinen & Rhines

Table 4. Relationships between detrended environmental covariates and survival rates of adult Brünnich's guillemots. Recapture probabilities were set as time-dependent with a coefficient of heterogeneity for all models (p_{CHC}). np: number of estimable parameters; DEV: deviance; F: Fisher-Snedecor test statistic; β-slope: estimate of the environmental covariate effect on survival ± SE; R^2_DEV: temporal variation in survival accounted for by the focal environmental covariate; Φ: estimated probability of survival; SGI: subpolar gyre index; wNAO index: winter North Atlantic Oscillation index; SSB: spawning stock biomass; SST: sea surface temperature. $\Phi_{LT[86-11]}$ represents the model where the probability of survival Φ is set to follow a linear trend from 1986 to 2011. $\Phi_{t[86-11]}$ represents the model where the probability of survival Φ is set to be time-dependent from 1986 to 2011. Recapture probabilities were time-dependent with a coefficient of heterogeneity for all models. **Bold** covariates indicate that the variations of the focal covariate explain variations in guillemots' survival significantly

Model	np	DEV	QAICc	F	p	β-slope ± SE	R^2_DEV
$\Phi_{LT[86-11]}$	28	3315.64	2991.45				
$\Phi_{t[86-11]}$	49	3276.93	3001.78				
SGI no lag							
+ wNAO 2 yr lag	**30**	**3301.56**	**2983.17**	**6.29**	**<0.05**	**+0.37 ± 0.19**	**0.36**
SGI							
No lag	**29**	**3305.02**	**2984.14**	**4.16**	**<0.05**	**+0.54 ± 0.19**	**0.27**
1 yr lag	29	3308.36	2985.01	2.54	0.10	+0.47 ± 0.19	0.19
2 yr lag	29	3310.94	2987.29	1.52	0.24	−0.38 ± 0.18	0.12
3 yr lag	29	3314.37	2990.33	0.37	0.69	−0.18 ± 0.17	0.03
wNAO index							
No lag	29	3309.70	2990.04	1.99	0.16	−0.28 ± 0.15	0.15
1 yr lag	29	3311.92	2991.82	1.17	0.33	−0.21 ± 0.16	0.09
2 yr lag	**29**	**3305.63**	**2984.68**	**3.84**	**<0.05**	**+0.47 ± 0.14**	**0.26**
3 yr lag	29	3311.24	2990.97	1.41	0.27	+0.27 ± 0.16	0.11
SST Sept−Oct							
No lag	29	3313.23	2992.84	0.73	0.49	+0.14 ± 0.17	0.06
1 yr lag	29	3313.97	2993.44	0.50	0.62	−0.05 ± 0.17	0.04
2 yr lag	29	3311.65	2991.22	1.26	0.30	−0.18 ± 0.12	0.10
3 yr lag	29	3313.98	2993.54	0.49	0.62	−0.01 ± 0.13	0.04
SST Nov−Jan							
No lag	29	3313.25	2992.85	0.72	0.50	−0.09 ± 0.10	0.06
1 yr lag	29	3313.69	2993.22	0.58	0.57	+0.07 ± 0.12	0.05
2 yr lag	29	3313.70	2993.21	0.58	0.57	+0.06 ± 0.10	0.05
3 yr lag	29	3313.80	2993.39	0.55	0.58	−0.05 ± 0.11	0.04
SST Feb−Mar							
No lag	29	3313.83	2993.36	0.54	0.59	+0.05 ± 0.12	0.04
1 yr lag	29	3314.00	2993.52	0.49	0.62	+0.01 ± 0.12	0.04
2 yr lag	29	3313.33	2992.90	0.70	0.51	−0.09 ± 0.12	0.05
3 yr lag	29	3313.98	2993.47	0.49	0.62	+0.03 ± 0.11	0.04

2004, Hátún et al. 2005). Concomitant changes observed in the SGI, the wNAO index, SST on the wintering grounds and guillemot survival provide evidence that environmental conditions in the wintering grounds have shift in the last decades. The SGI— without any time-lag—explained 69% of the interannual fluctuations in survival (or 27% when the linear trend was removed) and its positive link with guillemot survival suggests that a strong gyre (i.e. cold waters on the wintering grounds) was associated with higher survival probabilities. By modifying the North Atlantic thermohaline circulation, the shift in the SPG substantially impacted the whole food web, from phytoplankton to top-predators, in the Northeast Atlantic (Hátún et al. 2009). An increase in SST and

an abrupt decline in phytoplankton abundance associated with a change in the entire plankton communities were notably reported in 1995 in the vicinity of Iceland, close to the wintering range of Brünnich's guillemots from Bjørnøya (Fort et al. 2013, Steen et al. 2013). The decline in adult survival since the mid-1990s could therefore be related to changes in food availability—through bottom-up trophic cascades—on the wintering grounds. A study carried out on Brünnich's guillemot colonies distributed throughout the circumpolar Arctic and sub-Arctic regions (Irons et al. 2008) corroborates our hypothesis of negative consequences, mediated through the food web, of such large abrupt ecosystem shifts for this species. Moreover, climatic conditions have been found to af-
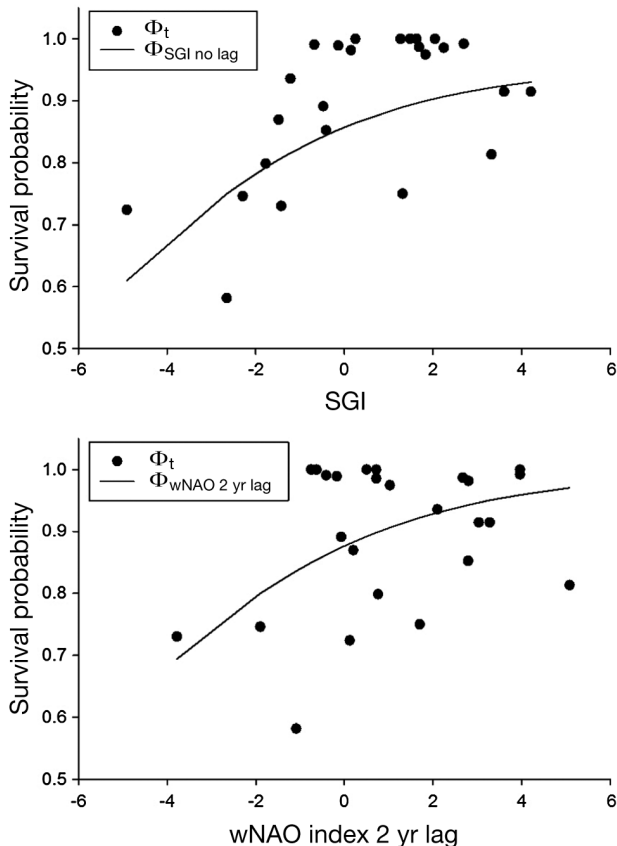
Fig. 2. Relationship between survival of Brünnich's guillemots and (a) the subpolar gyre index (SGI) and (b) the winter North Atlantic Oscillation (wNAO) index. Φ_t: survival probability as a function of detrended index (a) SGI with no lag and (b) wNAO index with 2 yr lag. Curves represent the survival modeled with detrended indices — (a): $\Phi_{SGI\,no\,lag}$ and (b) $\Phi_{wNAO\,2\,yr\,lag}$

fect the distribution and abundance of North Atlantic fish communities on which Brünnich's guillemots prey (e.g. Atlantic herring *Clupea harengus* or capelin *Mallotus villosus*; Alheit & Hagen 1997, Ottersen et al. 2001). Marked changes have notably been observed during the recent warming, since the mid-1990s in the waters north of Iceland (Astthorsson & Gislason 1998, Astthorsson et al. 2007, Valdimarsson et al. 2012). Our analyses on *Calanus finmarchicus* (see Supplement 9) suggest that intermediate pathways by which the SPG may affect guillemots may not take place through this copepod (see Supplement 10), which is considered to be a keystone species in the North Atlantic (Fort et al. 2012, Frederiksen et al. 2013). Other copepods (e.g. *C. glacialis*, *C. hyperboreus*) may be more indicative of biological shifts that may propagate until seabird level. Future studies should focus on the direct trophic resource of Brünnich's guillemots, although biological data in ge-

ographically defined areas are currently difficult to find and trophic relationships very difficult to assess. While Atlantic herring and capelin may constitute an important part of the diet of Brünnich's guillemots (Barrett et al. 1997), we could not show that survival of guillemots were primarily driven by changes in the availability of these preys in their wintering grounds (see Supplements 9 & 10). Further investigations on the diet of Brünnich's guillemots through the seasons and across their geographical range are needed to find factors more likely to drive adult survival. Moreover, Hipfner (2008) highlighted that prey timing, rather than prey biomass, may be a key factor to explain changes in survival in Cassin's auklets *Ptychoramphus aleuticus*. Such prey–predator match–mismatch mechanisms, driven by an increase in SST, could explain the decline in guillemot survival in the Arctic.

Contrary to our expectations, no apparent link was found between guillemot adult survival and (detrended) sea temperatures. We found concomitant long-term changes in both guillemot adult survival and sea temperatures on the wintering ground but these relationships did not hold at a year-to-year scale, perhaps because the guillemot wintering area considered in our study was exclusively based on 3 winters (2007–2010). Guillemots may have spent the winter in different areas in other years. Frederiksen et al. (2016) estimated that millions of breeding-age guillemots from Svalbard colonies winter in the western Atlantic, including similar areas used by guillemots breeding at Bjørnøya (i.e. around Iceland and northeast Greenland), but also different ones (i.e. from north Newfoundland to central-west Greenland). Our local winter SST time series may therefore not be fully representative of the local conditions experienced by guillemots since 1986. Further studies are needed to determine inter-annual repeatability in guillemot wintering areas. Moreover, it is an empirical fact that large-scale climatic indices often explain more variation than single weather components (Stenseth 1985, Hallett et al. 2004). At the wintering grounds, preys of Brünnich's guillemots are most likely not only affected by sea temperature but also by a combination of oceanographic features that vary in time and space. Consequently, local SST may convey less information than the SPG, which could explain why no significant relationship was detected between local SST and guillemot survival. Moreover, being top predators of marine ecosystems, seabirds are potential competitors with commercial fisheries. It is possible that fisheries in the wintering grounds have increased guillemot mortality directly

through entanglement in fishing nets (Tasker et al. 2000, Žydelis et al. 2013) and/or indirectly through prey depletion (Montevecchi 2002). Many other anthropogenic (e.g. hunting, pollution) and biological (e.g. energetic content of prey, new diseases or parasites; Descamps 2013) factors, likely to affect the survival of seabirds, remain elusive. Future studies should therefore concentrate on ecosystem processes by which hydrodynamic shifts alter the structure and trophodynamics of pelagic ecosystems.

To our knowledge, this study is among the first to highlight a strong relationship between the SPG and vertebrate population dynamics, or more specifically vertebrate survival. One previous study (Hersteinsson et al. 2009) reported that the SPG has an effect on the abundance and mass of a terrestrial vertebrate, the Icelandic Arctic fox *Vulpes lagopus*. The mechanism was unclear but may have taken place through changes in prey abundance (Hersteinsson et al. 2009). So far, many studies on seabirds breeding around the North Atlantic have demonstrated the influence of the NAO on life history traits and population dynamics (e.g. Wanless et al. 2009, Descamps et al. 2010, Sandvik et al. 2012, Smith & Gaston 2012). As a 'weather package' (Stenseth et al. 2003), the NAO index is assumed to be a reliable proxy for North Atlantic climate, catching most of the variation in several atmospheric and oceanographic parameters (e.g. precipitation regimes, sea ice cover; see Hurrell 1995). The SGI is also a promising proxy for assessing changes in environmental conditions in the North Atlantic, especially within marine ecosystems. Our study indicates that both environmental variables (the SGI and wNAO index) explained a significant amount of the inter-annual variation in Brünnich's guillemot survival. Combined together, these 2 variables explained 36% of the variation in guillemot survival compared to ca. 26% when treated separately. This suggests that, even if both variables are significantly correlated (see Supplement 7; Böning et al. 2006), they may represent different mechanisms and processes driving guillemot survival. Although the NAO index and the SGI are correlated to each other, they do not have the same SST signature (Beaugrand et al. 2009) and both should be used in synergy. The SGI reflects oceanographic conditions experienced by marine organisms more directly than the NAO index. By affecting the temperature and the salinity of water masses in the north-east Atlantic Ocean, changes in the SPG strongly impact the phytoplankton and zooplankton communities (Hátún et al. 2009), which are at the basis of the food chain. Our results support these findings by linking the SPG

with ecological processes—here, the decline in seabird survival. While we did not identify intermediate pathways by which changes in oceanic conditions affect the decline in Brünnich's guillemots' survival, the SGI seems to adequately reflect changes in the environment of guillemots, explaining 36% of the inter-annual variations in survival and up to 69% of variation over the whole period of the study. Our results, combined with other studies, suggest that the SGI may be an important and promising large-scale environmental index for understanding changes in both marine and terrestrial ecosystems in the North Atlantic. Further investigations should be conducted to identify the mechanisms through which the SPG affects the ecosystems more precisely.

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