

Climate-driven changes in winter abundance of a migratory waterbird in relation to EU protected areas

Diego Pavón-Jordán^{1,2}*, Anthony D. Fox³, Preben Clausen³, Mindaugas Dagys⁴, Bernard Deceuninck⁵, Koen Devos⁶, Richard D. Hearn⁷, Chas A. Holt⁸, Menno Hornman⁹, Verena Keller¹⁰, Tom Langendoen¹¹, Łukasz Ławicki¹², Svein H. Lorentsen¹³, Leho Luigujõe¹⁴, Włodzimierz Meissner¹⁵, Petr Musil¹⁶, Leif Nilsson¹⁷, Jean-Yves Paquet¹⁸, Antra Stipniece¹⁹, David A. Stroud²⁰, Johannes Wahl²¹, Marco Zenatello²² and Aleksi Lehikoinen¹

¹The Helsinki Lab of Ornithology, Finnish Museum of Natural History, P.O. Box 17, Helsinki, Finland, ²Department of Biosciences, University of Helsinki, 00014 Helsinki, Finland, ³Department of Biosciences, Aarhus University, Kalø, Grenåvej 14, DK-8410 Rønde, Denmark, ⁴Nature Research Centre, Akademijos 2, Vilnius LT-08412, Lithuania, ⁵LPO-BirdLife France, Fonderies Royales, 8 rue du Dr Pujos, BP 90263, Rochefort Cedex F-17305, France, ⁶Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussel, Belgium, ⁷Wildfowl & Wetlands Trust (WWT), Slimbridge, Glos GL2 7BT, UK, ⁸British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK, ⁹Sovon Dutch Centre for Field Ornithology, P.O. Box 6521, Nijmegen 6503 GA, The Netherlands, ¹⁰Swiss Ornithological Institute, Sempach, CH-6204, Switzerland, ¹¹Wetlands International, Horapark 9, Ede 6717 LZ, The Netherlands, ¹²West-Pomeranian Nature Society, Pionierow 1/1, 74-100 Gryfino, Poland, ¹³Norwegian Institute for Nature Research, 7485 Trondheim, Norway, ¹⁴Department of Zoology, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia, ¹⁵Avian Ecophysiology Unit, Department of Vertebrate Ecology & Zoology, University of Gdańsk, Wita Stwosza 59, 80-309 Gdańsk, Poland, 16 Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences, Kamycka 1176, Praha 6 - Suchdol CZ - 165 21, Czech Republic, ¹⁷Department of Biology, University of Lund, Ecology Building, Lund, S-223 62, Sweden, ¹⁸Département Études, Aves-Natagora, Rue Nanon 98, B-5000

ABSTRACT

Aim Species are responding to climate change by changing their distributions, creating debate about the effectiveness of existing networks of protected areas. As a contribution to this debate, we assess whether regional winter abundances and distribution of the Smew *Mergellus albellus*, a migratory waterbird species listed on Annex I (EU Birds Directive) that overwinters exclusively in European wetlands, changed during 1990–2011, the role of global warming in driving distributional changes and the effectiveness of the network of Special Protection Areas (SPAs, EU Birds Directive) in the context of climate change.

Location Europe.

Methods We used site-specific counts (6,883 sites) from 16 countries covering the entire flyway to estimate annual abundance indices and trends at country, region (north-eastern, central and south-western) and flyway scales, inside and outside SPAs. We fitted autoregressive models to assess the effect of winter temperature on the annual abundance indices whilst accounting for autocorrelation.

Results The Smew wintering distribution shifted north-eastwards in Europe in accordance with the predictions of global warming, with increasing numbers in the north-eastern region and declines in the central region. Trends in wintering numbers were more positive in SPAs on the north-eastern and south-western part of the flyway. However, a large proportion of the wintering population remains unprotected in north-eastern areas outside of the existing SPA network.

Main conclusions SPAs accommodated climate-driven abundance changes in the north-eastern region of the wintering distribution by supporting increasing numbers of Smew in traditional and newly colonized areas. However, we highlight gaps in the current network, suggesting that urgent policy responses are needed. Given rapid changes in species distributions, we urge regular national and international assessments of the adequacy of the EU Natura 2000 network to ensure coherence in site-safeguard networks for this and other species.

Keywords

Climate change adaptation, conservation policy, global warming, population trends, range shift, spatio-temporal analysis.

Diversity and Distributions

Namur, Belgium, ¹⁹Institute of Biology, University of Latvia, Miera Street 3, LV-2169 Salaspils, Latvia, ²⁰Joint Nature Conservation Committee (JNCC), Monkstone House, City Road, Peterborough, Cambridgeshire PE11JY, UK, ²¹Dachverband Deutscher Avifaunisten e.V. (DDA), Federation of German Avifaunists, An den Speichern 6, Münster D-48157, Germany, ²²Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Sede ex INFS, Via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia (BO), Italy

*Correspondence: Diego Pavón-Jordán, The Helsinki Lab of Ornithology, Finnish Museum of Natural History, P.O. Box 17, Helsinki, Finland. E-mail: diego.pavon-jordan@helsinki.fi

INTRODUCTION

Accumulating evidence shows that species are responding to climate change by changing their distributions (Parmesan, 2006; Shoo et al., 2006; Brommer & Møller, 2010), creating concern about the effectiveness of existing networks of protected areas (PAs) (Araújo et al., 2011; Mawdsley, 2011; Thomas et al., 2012). Recently, efforts to understand and predict the impacts of climate change on ecosystems and biodiversity have resulted in a range of suggested adaptive management actions to accommodate such effects, including the designation of new PAs (Mawdsley, 2011). There is a general tendency for the range of many species to move polewards as climate change creates access to novel habitats in previously unavailable areas. As a result, the effectiveness of PA networks may be undermined because climate change may ultimately draw species of conservation concern away from existing PAs (Araújo et al., 2011; Mawdsley, 2011), to newly colonized areas that may lack protection. Thus, targeted (adaptive) management of individual PAs and the development and maintenance of a comprehensive network that accounts for changes in species distributions will play a key role in enabling species to cope with climate change (Mawdsley, 2011). Studies comparing changes in species distributions and abundances inside and outside PAs in recent decades are, therefore, important to appraise the effectiveness of current conservation policy (Donald et al., 2007; Mawdsley, 2011; Thomas et al., 2012; Johnston et al., 2013); yet, they are hitherto very scarce (Donald et al., 2007; Fouque et al., 2009; Johnston et al., 2013). Presence/absence data suggest that existing PAs may facilitate shifts on the northern edge of range (Thomas et al., 2012), presumably because they protect the most valuable areas, but flyway scale comparisons of changes in abundance of entire populations inside and outside of PAs are lacking. This is despite the fact that changes at the core of a species distribution are considered better indicators of redistributions than changes at range margins (Shoo *et al.*, 2005, 2006). Hence, little is known about changes in species spatial abundance patterns in relation to changes in climate throughout their entire range (Shoo *et al.*, 2005, 2006; Johnston *et al.*, 2013).

Waterbirds are especially responsive to climate change (Švažas *et al.*, 2001; Zipkin *et al.*, 2010; Gunnarsson *et al.*, 2012; Lehikoinen *et al.*, 2013) compared with many other groups (Brommer, 2008). Declines in numbers of wintering waterbirds in central Europe coupled with increases in the north suggest a northward redistribution of wintering populations (van Roomen *et al.*, 2012; Dalby *et al.*, 2013a; Lehikoinen *et al.*, 2013), as individuals adopt new suitable wintering grounds closer to the breeding areas in response to more favourable winter conditions (Ridgill & Fox, 1990; Austin & Rehfisch, 2005; Maclean *et al.*, 2008).

Although European conservation policies specifically require protection of wintering populations and grounds, most studies assessing climate change effects on species distributions relate to spring/summer populations (Brommer & Møller, 2010), whereas changes in wintering distributions are understudied (see Dalby *et al.*, 2013b). Winter conditions can limit local population size of migratory species (Newton, 1998) confirmed by the few existing studies addressing changes in wintering distributions (Ridgill & Fox, 1990; Austin & Rehfisch, 2005; Lehikoinen *et al.*, 2013). Winter temperatures are forecast to increase faster than summer temperatures during this century (European Environment Agency, 2012); hence, substantial changes in species wintering distributions are expected (Brommer & Møller, 2010; Johnston *et al.*, 2013).

Protecting migratory species requires international cooperation to safeguard them throughout the annual cycle (Donald *et al.*, 2007). The *Council Directive 2009/147/EC on the conservation of wild birds* (EU Birds Directive) aims to protect all wild European bird species and conserve their habitat through, *inter alia* the classification of Special Protection Areas for birds (SPAs), which has been shown to benefit the conservation status of some species (Donald *et al.*, 2007). However, although there are few studies evaluating the effectiveness of the SPA network in the context of the escalating effects of climate change at a relatively large scale (Johnston *et al.*, 2013), to our knowledge, it has never been evaluated throughout the entire species ranges.

Here, we provide comprehensive analysis of population changes across the entire wintering range of a protected waterbird species, the Smew *Mergellus albellus*, over 22 years (1990– 2011). We use abundance data from 16 countries covering the whole north-west and central European flyway to (1) estimate the trend of the entire wintering population, (2) assess whether the wintering population has shifted northwards, (3) analyse whether annual abundance in the north-eastern, central and south-western part of the range are related to increasing winter temperatures on the north-eastern edge (Lehikoinen *et al.*, 2013), (4) compare trends inside and outside SPAs to evaluate the effectiveness of both Smew-specific SPAs (sSPA) and the overall SPA (oSPA, see Methods) network to facilitate (climate-driven) distribution changes and (5) pinpoint potential gaps in the network for the species.

To our knowledge, this is the first study to have assessed the effect of climate change on wintering distributions using abundance data jointly with the performance of the SPA network at the flyway scale. Such studies are crucial to forecast the effects of climate change on population status (Shoo *et al.*, 2005, 2006) and are essential to properly assess the effectiveness of existing SPA networks (Johnston *et al.*, 2013) and update current conservation and management strategies to recent environmental changes.

METHODS

Study species

The Smew is a Palearctic fish-eating diving duck listed on Annex I of the EU Birds Directive (i.e. species of special conservation concern). It is relatively scarce with an estimated European population of 40,000 individuals (compared with >1,000,000 individuals of Tufted Duck Aythya fuligula and Common Goldeneye Bucephala clangula, respectively, Wetlands International, 2012). It breeds at lakes in the taiga from Fennoscandia to Kamchatka (see http://www.birdlife.org/datazone/species/factsheet/22680465). Most of the European population breeds in northern Russia (BirdLife International, 2004). The breeding population of the north-eastern part of European Russia overwinters mainly in eastern Europe (within the Black Sea and East Mediterranean flyway), whereas the population breeding in Fennoscandia and north-western Russia mainly winters in large lakes, lagoons, coastal waters and estuaries in west and central Europe (north-west and central European flyway, hereafter 'flyway') (Wetlands International, 2012).

In this study, we focus on the Smew because it is the only Annex I waterbird species that exclusively overwinters in European wetlands, it is entirely confined to open water wetlands (does not use agricultural landscapes as does for example the Whooper Swan *Cygnus cygnus*). Here, we studied the wintering population along the entire flyway (van Roomen *et al.*, 2012) covering a large geographical and climatic gradient (more than 3000 km wide from the south-west to north-east).

Smew and special protection areas (SPAs)

Data used here consisted of site-specific counts which are part of the International Waterbird Census (IWC) coordinated by Wetlands International. The IWC is an Europewide census that is carried out during mid-January. The main goal of IWC is to monitor changes in the population size and trend of waterbirds, as well as to identify important wintering areas across Europe (Wetlands International, 2012). Although IWC started in the late 1960s, many countries joined the initiative later (van Roomen *et al.*, 2012), and therefore, in this study, to use information from all 16 countries within the flyway, only data from the period 1990 to 2011 have been analysed (Number of surveyed sites including missing counts in each country are shown in Table S1).

Overall, data from 6,883 sites were included in the analysis, with approximately 291,700 Smew counted along the entire flyway (average annual count = 13.258 ± 3.840 SD) during 1990-2011 (Table S1). Moreover, each country provided specific information on whether each site censused is classified as Smew-specific Special Protection Area (sSPA; i.e. where Smew is listed as one of the qualifying criteria for site designation), as SPA that may or may not include Smew as a classifying species (oSPA) or is not an SPA (Table S2). Countries outside the EU (i.e. Switzerland and Norway) are not subject to EU Birds Directive obligations and all sites in these countries were, therefore, considered as outside of the SPA network. UK and France (in the south-western part of the range) and Czech Republic (in the centre) do not have sSPA, and therefore, SPAs in these three countries were used only for the oSPA network analysis. We also considered all sites that are currently classified as SPA sites as SPAs throughout the whole study period (1990-2011) regardless when they were first designated as SPAs because those sites had high-quality habitat prior their classification as SPAs (see e.g. Thomas et al., 2012).

Statistical analysis

Data were analysed at three spatial scales: country-specific trends, regional trends and overall flyway trend over the period 1990–2011. To analyse the data at regional scales, we combined the country-specific data into three region-specific datasets (hereafter regions) defined geographically as follows: north-east (Finland, Sweden, Norway, Estonia and Latvia), central (Denmark, Lithuania, Poland, Germany, Czech Republic and Netherlands) and south-west (UK, Belgium, France, Switzerland and Italy) (Table S1). Analyses were carried out using the software TRends and Indices for

Monitoring data (TRIM, available at www.ebcc.info). TRIM estimates annual abundance indices from count data and calculates population growth rate applying a generalized estimating equation (GEE) algorithm using information from all sites (site as repeated measure) and all years (year effect). The estimates returned by TRIM are robust and reliable because GEE accounts for overdispersion and serial correlation in the data by enlarging the standard error of the indices produced. TRIM uses a Poisson log-linear model (GLM) to impute missing values (i.e. not all sites are surveyed all years) and allows us to explore possible nonlinear patterns by splitting long-term nonlinear patterns into short-term linear segments and then averaging those slopes. The main purpose here is that TRIM first estimates a model using only the observed counts and then uses that model to impute the missing counts using an iterative procedure, taking into account both site and year effects. By doing this, TRIM is able to calculate indices and trends from a 'complete' dataset (see Pannekoek & van Strien, 2004 for further details on the procedure). TRIM has been regularly used by most European bird monitoring schemes for this purpose (Gregory et al., 2005, 2009).

Winter severity and stochasticity may increase annual fluctuations in local/regional wintering numbers by causing both increasing mortality and redistribution of birds (e.g. the cold early winter in 1997 pushed birds from the central to the south-western region and potentially caused additional mortality although the drop in flyway abundance was not drastic; see Fig. 1a). Despite good coverage of the flyway during the IWC (Table S1), not all sites are surveyed every year. Even though this problem is dealt with in the analyses, the imputation of the missing site counts by TRIM causes random fluctuations to the annual estimates. However, the proportion of counts derived from imputation of missing counts is 10.09%, 15.77% and 20.98% in the north-eastern, central and south-western regions, respectively. Therefore, the error associated with that imputation is negligible (Pannekoek & van Strien, 2004). In addition, on average over 13,000 birds are counted annually, which is about one-third of the whole flyway population and thus a substantial sample size. Furthermore, since imputation has been made in the same way every year, we consider that the observed long-term



Figure 1 (a) Population indices (and the 95% confidence interval) and (b) estimated population numbers of Smew *Mergellus albellus* in the north-west, central and south-east parts of the flyway during the study period (see Methods). Population estimates trends (see Methods) are shown from 1993 onwards, because of missing data from Italy and Estonia in 1990–1992. Note the effects of very cold winter in 1997, when birds were pushed from the north-east and central region to the south-west part of the flyway. Note also the cold winter in 2003 (Fig. S2) associated with a peak in numbers in south-western countries in that winter (Fig. S2). The high peak in population estimates of the year 2009 is mainly driven by Polish data (Fig. S1), where the most important wintering site holding 70% of the wintering numbers in Poland was not surveyed in that particular year (together with relatively high numbers in the other four sites in Poland). This peak is no longer visible when pooling the larger dataset (e.g. centre of the flyway; a).

trends should not be biased. Moreover, the proportion of missing values at the beginning and at the end of the study period was similar (59% and 50% at the beginning and end of the study, respectively) which also allows for unbiased long-term trends.

In addition to the comparison of the overall trends across the three regions commented above, we also compared trends inside and outside the SPA network. A census site can be classified as sSPA, as oSPA or non-SPA. We used this information as a covariate in the models run in TRIM. This allowed us to robustly compare, first, population trends inside and outside sSPAs and, second, population trends inside and outside the overall SPA network (oSPAs). This gave us not only an idea of the performance of the SPAs specifically classified for Smew in comparison with the rest of the sites but also the performance of the overall SPA network in comparison with sites outside the network. Trends inside and outside both the sSPA and oSPA network were estimated separately at regional and flyway scales during 1990-2011. As not all countries have sufficient data to run the sSPA or oSPA analysis, we did not calculate country-specific trends inside and outside SPAs. However, we provided country-specific data on the proportion of Smew counted within sSPAs and oSPA (Table S2).

We used the annual index from TRIM and the latest national total winter population estimate to calculate the changes of the total wintering population of the flyway and three regions. The latest national wintering population estimates for each country are found in Table S1. We anchored a countrywide estimate of the total wintering population in a certain year to the annual index estimated by TRIM for that particular year (for the corresponding method, see Lehikoinen *et al.*, 2013).

Effect of temperature on population fluctuations

We used the region-specific population indices from TRIM to assess the effect of early winter temperature in northern Europe on the observed population trend across the flyway using R 3.0.1 (R Core Team, 2013). As winter temperature in southern Finland correlates over a large area in northern Europe (Lehikoinen *et al.*, 2013), we used mean temperature in southern Finland (60–64°N; 20–31°E) during early winter (first half of winter, 16 November–15 January) as a proxy of general winter conditions at the northern margin of the range.

We first explored whether there was autocorrelation in our data using autocorrelation and partial correlation functions in R (Zuur *et al.*, 2007). Then, we ran autoregressive models, which take into account autocorrelation in the data and corrects for this when estimating the effect of the covariate (Crawley, 2007; Lehikoinen *et al.*, 2013). We ran two different autoregressive models. In the first model, we tested whether the (log-transformed) annual abundance index was affected by the direct effect of temperature and the population index the year before: Climate change, abundance change and protected areas

$$LPOP_t = a_1 + b_1 LPOP_{t-1} + b_2 TEMP_t + \varepsilon$$
(1)

where LPOP_t is the log-transformed population index in year t in each region (north-east, central, south-west), a_1 is intercept of the model, b_1 and b_2 are coefficients (slope) for LPOP_{t-1} (log-transformed population index the preceding year, i.e. t-1) and TEMP_t (early winter temperature in southern Finland in year t), respectively, and ε is an error term.

In the second model, we tested whether the (log-transformed) annual abundance index was affected by the difference in temperature between two consecutive years and the population index the year before:

$$LPOP_t = a_1 + b_1 LPOP_{t-1} + b_2 \Delta TEMP_{t,t-1} + \varepsilon$$
(2)

where LPOP_t is the log-transformed population index in year t in each region (north-east, central, south-west), LPOP_{t-1} is the log-transformed population index the preceding year (i.e. t-1) and $\Delta \text{TEMP}_{t,t-1}$ is the difference in early winter temperature in southern Finland in two consecutive years and ε is an error term.

In this way, we ran two different autoregressive models for each region (n = 6 models) and compared the Akaike's information criterion (AIC) of the two models to assess which one fitted best to our data (Burnham & Anderson, 2002).

RESULTS

Population trends

During 1990-2011, the wintering population of Smew in the flyway showed a slight but significant increasing trend (0.55% year⁻¹), but also demonstrated significant regional differences (Table 1, Fig. 1a). Wintering numbers in the north-east strongly increased whilst numbers declined in the central region (Figs 1 & 2). In the 1990s, only 6% of the total flyway population wintered on the north-eastern part of the distribution, whereas in the early 2010s, 32% remained in this area (Fig. 1b). Numbers in Finland and Estonia increased by 4,483% and 1,105%, respectively. In the southwestern part of the winter range, numbers in UK, France and Belgium increased during the 1990s but then declined during the 2000s (Fig. S1, see also Table S3 showing the same analysis using only 2000-2011 data). In Italy and Switzerland, at the southernmost end of the winter distribution, numbers decreased from the early 1990s and 2011 by 60% and 34%, respectively (Fig. 2). The central region used to hold 91% of the wintering population in the early 1990s but despite still retaining the majority of the birds, wintering numbers in this region decreased to 66% of the total wintering population.

Effect of temperature

According to the best autoregressive models, the effect of temperature on the (log-transformed) annual abundance

Table 1 Flyway and regional population trends for wintering Smew *Mergellus albellus* in the north-west and central European population, inside and outside both sSPAs and oSPAs. The best fit TRIM model overall slope (Slope) and associated standard error (SE) are given as well as the Smew counts used in the analysis. (All) refers to the trend using the whole dataset for the corresponding region or flyway (i.e. no differentiation between SPA status). Results of the Wald test comparing trends inside and outside SPAs within regions are also shown. Moderate decline (M dec) = significant decline but not significantly more than 5% per year; Stable = no significant increase or decline but it is certain that trends are < 5% per year; Moderate increase (M inc) = significant increase but not significantly more than 5% per year; and Strong increase (S inc) = significant increase more than 5% per year (see Help file in TRIM for further information).

1990–2011										
Region	Slope	SE	Trend	Counts (num. individuals)	Wald Test					
Flyway										
All	0.0063	0.0016	M inc**	291,074						
Inside sSPA	0.0003	0.0028	Stable	192,356	W = 64.52; df = 1; P < 0.001					
Outside sSPA	0.0197	0.0022	M inc**	98,718						
Inside oSPA	-0.0060	0.003	M dec*	210,266	W = 66.59; df = 1; P < 0.001					
Outside oSPA	0.0220	0.003	M inc**	80,808						
North-east										
All	0.0740	0.005	S inc**	56,016						
Inside sSPA	0.1040	0.014	S inc**	13,620	W = 21.61; df = 1; P < 0.001					
Outside sSPA	0.0660	0.005	S inc**	42,396						
Inside oSPA	0.1010	0.012	S inc**	16,507	W = 17.10; df = 1; P < 0.001					
Outside oSPA	0.0650	0.005	S inc**	39,509						
Centre										
All	-0.0098	0.0023	M dec*	219,741						
Inside sSPA	-0.0050	0.0042	Stable	169,038	W = 0.498; df = 1; P = 0.4858					
Outside sSPA	-0.0162	0.0033	M dec**	50,703						
Inside oSPA	-0.0058	0.0029	M dec*	181,826	W = 0.00; df = 1; P = 0.9777					
Outside oSPA	-0.0249	0.0048	M dec**	32,644						
South-west										
All	0.0110	0.003	M inc**	15,900						
Inside sSPA	-0.0060	0.018	Stable	939	W = 2.78; df = 1; P = 0.0954					
Outside sSPA	0.0138	0.0048	M inc**	14,961						
Inside oSPA	0.0170	0.005	M inc**	7,399	W = 1.50; df = 1; P = 0.2214					
Outside oSPA	0.0110	0.005	M inc**	8,416						

*Significant trend with P < 0.05, and **significant trends with P < 0.01. The moderate increase in some south-west population could be due to the overall increase of the population. Counts refer to the total counts used in the analysis ('raw data', not imputed) to obtain the trends. The Wald test shows whether the linear trends inside and outside differ significantly in the particular case.

index differs between regions (Table 2). Temperature has a clear direct negative effect on the log-transformed abundance index of wintering Smew in the south-western part of the flyway (model (1) in Table 2). The best model for the north-eastern part of the distribution, however, shows some evidence of a positive effect of the interannual change in temperature (Δ Temperature) on the annual abundance index (model #2 in Table 2). In both the north-eastern and the south-western regions, the annual numbers were also temporally autocorrelated, suggesting site-fidelity on the wintering grounds.

Effectiveness of the special protection areas

In the north-eastern part of the winter range, the rate of increase in abundance was significantly greater and nearly twice as rapid within sSPAs and oSPAs compared with outside sSPAs and oSPAs during the whole study period (Fig. 3, Table 1). At the centre and the south-western part of the distribution, trends did not significantly differ between sSPAs and oSPAs and areas outside SPAs (Fig. 3, Table 1). At a flyway level, however, trends outside sSPAs and the oSPA network had more positive trends than inside (Fig. 3, Table 1).

Our country-specific estimates of the wintering population (Table S2) showed that a large proportion of Smew in the north-eastern part of the distribution (where wintering numbers increased), wintered outside protected areas (98%, 90% and 81% for Finland, Latvia and Sweden, respectively).

DISCUSSION

Understanding how species are responding to climate change is of paramount importance to the continuation of effective conservation measures. Here, we demonstrate a large scale redistribution of the wintering population of Smew along its flyway. We also show for the first time that the SPA network



Figure 2 Rate of change (in percentage) in winter abundance of Smew *Mergellus albellus* during 1990–2011 in the 16 countries belonging to the north-west and central European flyway (1992–2011 and 1991–2011 for Estonia and Italy, respectively). Countries belonging to the north-eastern region are shown in black bold, countries belonging to the central region are shown in light grey and countries belonging to the south-western region are shown in dark grey. The level of significance are denoted by asterisks (** <0.01; * <0.05). Statistically significant declines are shown in italics with a minus (-) sign, and uncertain trends are denoted with a question mark (?). Note that France, Latvia and Belgium have 'Stable' population (i.e. absence of a statistically significant trend; see also Table S2 and Pannekoek & van Strien (2004) for a detailed description of the trend classifications.

Table 2 Autoregressive models corresponding to formulae (1) and (2) (see methods section). The direct effect of temperature, the effect of abundance index in the preceding year (Index(t-1)) and the effect of the difference in temperature between two consecutive years (Δ Temperature) on the regional abundance indices of Smew in 1990–2011 are shown. The model with the lowest AIC in each region is highlighted in bold (AIC differences shown). Estimates of each covariates included in the models (Estimate), the standard error associated (SE) and the significance (P) are also shown in the table

		North-east			Centre			South-west		
Model	Covariates	Estimate	SE	Р	Estimate	SE	Р	Estimate	SE	Р
1*	Intercept	0.215	0.166	0.213	0.111	0.111	0.331	0.033	0.188	0.862
	Temperature	-0.021	0.026	0.439	0.022	0.023	0.348	-0.093	0.035	0.016
	Index(t-1)	0.726	0.143	<0.001	-0.207	0.232	0.383	0.447	0.167	0.016
	AIC	3.04			0.00			0.00		
2*	Intercept	0.175	0.143	0.239	-0.009	0.086	0.921	0.19825	0.187	0.303
	ΔTemperature	0.077	0.041	0.077	0.024	0.039	0.545	0.10275	0.065	0.132
	Index(t-1)	0.742	0.132	<0.001	-0.212	0.235	0.379	0.53739	0.182	0.009
	ΔΑΙC	0.00			0.62			4.26		

Significant *P*-values are shown in bold. Italics denote marginally significant *P*-values (Zuur *et al.*, 2007). *See formulae in methods.

delivers climate change adaptation, but we pinpoint a significant gap in the SPA network in newly colonized wintering areas in north-eastern Europe (<12% of birds occurred inside sSPAs and oSPAs in Finland and Sweden compared with the average of 34% and 48% that wintered in sSPAs and oSPAs for the whole flyway, respectively, during 1990– 2011).

Spatial changes in abundance

Regional abundance of Smew changed in the past two decades, partly as a response to climate change. Wintering numbers of Smew increased on the north-eastern part of the wintering range and declined in those areas situated in the core of the wintering distribution, confirming a north-eastwards shift of



the population as expected in response to climate change (Brommer & Møller, 2010; Lehikoinen et al., 2013). Contrary to expectations, we found a slightly increasing trend in the south-western part of the wintering distribution during 1990-2011. A possible explanation for this finding could be that the overall flyway wintering population increased and that this increase would also be reflected amongst the marginal southern populations. In particular, Smew numbers increased during the 1990s in countries situated in the south-western part of the range but declined during the last decade (as well as in the central region) which may reflect a more recent redistribution north-eastwards. However, although most countries situated in the south-western part of the wintering range showed declining trends in the last decade, the absolute numbers at the end of the study period are slightly larger than at the beginning of the study, due to the large increase that occurred during the 1990s (which was also true for other waterbird species, see Lehikoinen et al., 2013). Hence, the overall increasing trend in the south-western region during 1990-2011 does not reflect exactly the current situation in this region (e.g. 2000-2011), but a long-term trend driven by a few years of greater abundance in the 1990s.

Figure 3 Annual Smew Mergellus albellus winter abundance indices (and 95% confidence intervals) and population trends in the north-west and central European flyway and northeastern, central and south-western regions during 1990-2011. Population trends inside (black line and filled circles) and outside (grey line and open circles) Smew-specific SPA (sSPA, a-d) and the overall SPA (oSPA, e-h) network at flyway level (a, e), in the north-eastern (b, f), central (c, g) and south-western region (d, h) of the range. See also Table 2 for the estimates and significance of the trends.

Interestingly, annual abundance of Smew on the southwestern margin of the wintering range correlated negatively with temperature, which supports the 'climate-forced shift of the distributional centre of gravity' hypothesis (Lehikoinen et al., 2013). Moreover, we also found some evidence of the effect of temperature in the north-eastern part of the winter range. In this case, the interannual variation in temperature seems to affect the wintering numbers in the north-eastern part of the range, meaning that there are more individuals wintering in the north-east with increasing temperature in consecutive years in northern Europe. This, together with the fact that we found the temperature effect only from the edges of the population, also fits with predictions of climate change effects on bird distributions (Brommer & Møller, 2010; Thomas et al., 2012). In addition, the decline in wintering numbers in the centre of the distribution (and southwest in the last decade) and the increase in numbers in the north-east coincided with a decade of relatively mild winters, suggesting that increasing temperature can possibly be one of the main drivers of the observed change in the Smew wintering distribution, as is the case for other waterbirds (Maclean et al., 2008; Lehikoinen et al., 2013). It is also worth noting

that the important wintering numbers in Germany declined in the last two years. This decline is probably partly linked to the 2010-2011 cold winters in central Europe when we assume that a large proportion of the German population was pushed south-westwards. This finding has very important ecological and conservation implications and suggests that large numbers of individuals can respond very rapidly to stochastic harsh weather conditions and underlines the need to maintain suitable habitat throughout the flyway. Therefore, classifying new SPAs in newly available wintering sites (in the north-east) is of paramount importance, but it is equally essential to maintain SPAs in traditional and formerly occupied wintering areas that can act as a refuge network during harsh winters (Dalby et al., 2013b; Koffijberg et al., 2013). During such winters (as in 2010) large influxes can reach the south-western part of the distribution and the SPA network in this area should be comprehensive enough to hold a representative percentage of such sudden increases in wintering numbers.

Although we only investigated the role of climate in driving the changes in the wintering distribution of Smew, other factors related to feeding ecology, interspecific competition and human pressure may also play important roles in shaping waterbird distributions and should not be neglected (Clavero *et al.*, 2011; Eglington & Pearce-Higgins, 2012). Nevertheless, as abundance in the south-west was negatively correlated with temperature, and we also found some evidence of the positive effect of temperature on abundance in the north-east, the observed changes are in line with climate change predictions (Maclean *et al.*, 2008; Brommer & Møller, 2010; Lehikoinen *et al.*, 2013) and so we believe that climate is an important driver shaping the regional abundances of Smew (and probably all other migratory waterbirds) now and into the future.

Special Protection Areas

Most importantly, we found more positive trends in Smew numbers inside Special Protection Areas classified for Smew (sSPAs) than outside sSPAs in the north-eastern region, where the population strongly increased. This suggests that, in the north-eastern part of the flyway, sSPAs preferentially accommodated birds that formerly wintered within the central region, thereby delivering climate change adaptation for this species. Moreover, Smew often winter in SPAs which are classified for other species (oSPAs) along the entire wintering range and derive additional benefits from these sites. We found more positive trends in Smew numbers inside than outside the oSPA network in the north-eastern region, suggesting that the overall network can potentially ameliorate climate change effects for species other than those for which sites were classified. This should be taken into consideration when developing/updating conservation strategies in the face of current climate change (Mawdsley, 2011). Because SPAs represent, in theory, the highest quality habitats, it is perhaps not surprising that trends inside SPAs are more favourable

than elsewhere (Thomas *et al.*, 2012). Nevertheless, the classification of those good habitats as SPAs has further contributed to protecting them against human development pressures.

The apparent contradiction in trends inside and outside sSPAs (and also the oSPA network) at a flyway level when compared to the north-eastern regional trends is because the majority of Smew occurring inside sSPA winter within the central region where numbers have in general declined whereas in the north-eastern region, most Smew winter outside sSPAs. Although the rate of increase has been higher inside north-eastern sSPAs compared with outside sSPAs, the increase has not been sufficient such that the total increase in absolute numbers has been higher outside sSPAs. This is because so few sites are designated as sSPAs in this part of the flyway. In other words, a very large proportion of Smew in north-eastern countries winters outside of the sSPA network (81-98% in Finland, Latvia and Sweden) and even outside the entire (oSPA) network (95% and 79% in Finland and Sweden, respectively). At a flyway level, the proportion of wintering individuals inside sSPAs dropped from 45% in early 1990s to 36% in early 2010s and from 55% to 42% in oSPAs. This increases the vulnerability to population decline arising from other factors, such as habitat loss or disturhance

An increasing number of waterbirds (including 16 out of 47 wintering bird species) were red-listed in the latest evaluation of the Baltic Sea (HELCOM, 2014). This highlights that the status of aquatic ecosystems in the Baltic Sea for waterbirds has become less favourable in recent years. The SPA network in the northern Baltic Sea was designated based on data collected more than two decades ago, when coastal areas were usually frozen in winter and inaccessible to waterbirds, and has not been reviewed since then. Such areas are ice-free nowadays and are becoming important waterbird wintering sites, currently supporting one-third of the entire flyway population of Smew during winter. Furthermore, the UK, France and Czech Republic have no SPAs specifically classified for Smew, despite several hundred wintering Smew occurring regularly. Therefore, an immediate policy response is needed to ensure protection of a good proportion of the population throughout the flyway, through the classification of new sSPAs and adjustment of the management of existing oSPAs to current environmental changes. We also highlight the importance of investigating both growth rates and change in total numbers to properly evaluate the effectiveness of the policy of protecting species.

Diversity and abundance of waterbirds are important features of wetlands and taken into account when developing conservation policies (Wetlands International, 2012). Thus, understanding how waterbirds and other bird species respond to climate change is essential to assess the effectiveness of current conservation policy (Donald *et al.*, 2007; Thomas *et al.*, 2012; Johnston *et al.*, 2013). Comprehensive monitoring throughout the flyway should continue to improve our understanding concerning such responses and

to be able to adjust management actions to actual and anticipated changes (Donald et al., 2007; Mawdsley, 2011; Elmberg et al., 2014). Our results show that Smew do not migrate as far south and west as they used to, and consequently, the importance of wintering sites in north-eastern Europe is rapidly increasing. Because of the unprotected status of most of these north-eastern wintering sites, their habitat is more vulnerable to changes in human land-use practices. This might have detrimental population-scale consequences in the future. The current sSPA network in the north-east is insufficiently comprehensive to accommodate the rapidly increasing Smew numbers and provide protection to a good proportion of the wintering population, underlining the need for immediate (and regular) evaluation of the SPA network (Mawdsley, 2011). Given the current rapid changes in waterbird distributions and associated colonization of new wintering grounds, there is an urgent need to identify key sites that now attract internationally important numbers, to reassess their legal designation status and establish appropriate adaptive management plans and conservation regimes that maintain a coherent and comprehensive network of protected sites that are responsive to (climate-driven) distribution changes (Mawdsley, 2011). However, the behaviour of (protected) migratory species seems to be plastic and, despite the general tendency of shifting the range polewards, they return to traditional wintering sites at the (traditional) south and south-western part of the wintering range during harsh winters (e.g. Koffijberg et al., 2013). This highlights the need to maintain the legal status of existing sSPAs that are traditional (if now irregular) wintering sites, as the regular wintering area of the species moves polewards. In this sense, the objective of the EU SPA network should be to accommodate not only the regular distribution, but also the occurrence of Smew in years when extreme weather forces birds further south and west than normal. Such recognition of the (network) role of SPAs as refuges and thus supporting populations during extreme events is already explicit objective in some countries (e.g. UK) and should be more widely adopted. These tasks are fundamental to deliver the objectives of Article 4.3 of the Birds Directive, which calls for actions from Member States and the Commission 'to ensure that the areas provided for in paragraphs 1 and 2 [i.e. SPAs] form a coherent whole which meets the protection requirements of these species...'. Such activity by Member States would be a very real example of building the 'resilience' of the Natura 2000 network to climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

 Table S1 Country-specific Smew (Mergellus albellus) count

 data (summary).

Table S2 National Smew (*Mergellus albellus*) numbers and population trends inside and outside Special Protection Areas (SPAs, 1990–2011).

Table S3 Trends of wintering Smew in the three different regions and at flyway level in the period 2000 – 2011.

Figure S1 Population trends of Smew (*Mergellus albellus*) in the 16 countries belonging to the northwest and central European flyway during 1990–2011.

Figure S2 Mean early winter temperature (16 November–15 January) in southern Finland (60–64°N; 20–31°E) during 1990–2011.

Appendix S1 Supplementary acknowledgements.

BIOSKETCH

Diego Pavon-Jordan is interested in understanding how climate change affects different aspects of the ecology and population dynamics of avian species. This Europewide project was conceived by members of NOWAC (Nordic Waterbirds and Climate Network), and the focus has been on climate-driven changes in winter distributions of several waterbird species in Europe and the consequences of those changes for conservation planning. Diego belongs to the Helsinki Lab of Ornithology (Finnish Museum of Natural History) which is carrying out several projects concerning the effects of different aspects of environmental change on avian species. Diego's websites: http://www.luomus.fi/en/aleksi-lehikoinen#Diego.

Helsinki Lab of Ornithology's website: https://www.luo-mus.fi/en/helsinki-lab-ornithology.

Author Contributions: A.L. D.P.-J and A.D.F. conceived the study. D.P.-J. analysed the data. D.P.-J. and A.L. interpreted the results. D.P.-J. and A.L. wrote the article, with significant input from P.C., A.D.F., C.A.H., R.D.H and D.A.S. All other authors collected the data and also contributed to the manuscript.

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