Journal of Applied Ecology

Journal of Applied Ecology 2016, **53,** 1862–1870 doi: 10.1111/1365-2664.12686

Spatio-temporal modelling of auk abundance after the Erika oil spill and implications for conservation

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Summary

1. Species distribution models are widely used in applied ecology and conservation. While accounting for spatial dependences is now the rule, temporal dependences have rarely been dealt with explicitly. In this study, we analyse wintering auk distribution in the Bay of Biscay and English Channel and estimate changes in abundance within and between years while accounting for space–time dependencies. We then propose a retrospective estimate of the impact of the Erika oil spill that occurred in December 1999.

2. Two series of extensive aerial surveys, repeated at intervals of 1–2 months, were carried out at a 10-year interval off the French Atlantic coast (2001–2002 and 2011–2012). Spatially and temporally explicit Bayesian models were fitted to these data to provide spatio-temporal predictions of auk abundance. These were then used to compare abundances within the area affected by the Erika oil spill two and twelve years after the catastrophe.

3. The results showed that 1·55 million auks wintered in the study area in 2011–2012. The main wintering area was the English Channel (more than one million auks) but the Bay of Biscay also became an important area in the middle of winter (470 000 auks) owing to a strong southward shift in auk distribution.

4. Two years after the catastrophe (2001–2002), the area affected by the Erika oil spill hosted a small proportion of auks of the Bay of Biscay – about 80 000 individuals. This number increased by more than three times 10 years later and reached 270 000 individuals, whereas no significant change was detected elsewhere. We suggest that it could result from a recovery after the extra-mortality induced by the Erika oil spill.

5. *Policy implications*. This study identified major auk wintering areas, with abundances much higher than previously realized. Oil spills have occurred regularly in these areas, with major delayed impacts on auk breeding populations. The worst case scenario would be if a major oil spill occurred in the English Channel in February, when abundance reaches one million auks. Although such a disaster has not so far occurred, stricter policies on the transport of hydrocarbons should be implemented to prevent such a possibility.

Key-words: aerial surveys, auks, Bay of Biscay, English Channel, Erika oil spill, species distribution models, winter

Introduction

Species distributions are temporally structured, showing seasonal or interannual changes in response to various mechanisms, but accounting for temporal autocorrelation when predicting species distribution is not yet common practice. Still, whenever possible, studies focusing on species distribution should use models that account for both spatial and temporal dependences (Fink *et al.* 2010). This is particularly relevant in conservation biology where emphasizing temporal patterns may provide an insight into the spatial stability of the distribution observed (Certain *et al.* 2007) and make it possible to compare the areas occupied by a particular species at a given time with the whole area where the species is found (Martin *et al.* 2007; Pressey *et al.* 2007). From a statistical point of view, temporal autocorrelation creates the same problem of non-independence as spatial autocorrelation and should thus be taken into account to give correct estimates (Carroll & Pearson 2000).

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Detecting temporal changes in species distribution implies collecting data from broad geographic areas over a long time period, that is at a population functioning scale (Jones 2011). This is particularly challenging for marine species such as seabirds, given their life history, overall mobility and seasonal foraging patterns which alternate between breeding and non-breeding periods. The recent development of geo-referenced loggers (Gonzalez-Solis *et al.* 2007; Frederiksen *et al.* 2012; McFarlane Tranquilla *et al.* 2013) has partly solved these problems, although loggers are usually deployed on only a few individuals and/or from a few localities (but see Block *et al.* 2011; Frederiksen *et al.* 2012). Alternatively, large-scale surveys based on counts of individuals from a ship or aircraft provide information at population level (e.g. for risk assessment, Burke, Montevecchi & Wiese 2012; Lieske, Fifield & Gjerdrum 2014; Certain *et al.* 2015). These two approaches are, in fact, complementary: large-scale surveys monitor species distribution while monitoring individuals determines the area use depending on behaviour, for example feeding, transient or resting areas (Louzao *et al.* 2009; Arcos *et al.* 2012; Camphuysen *et al.* 2012; Montevecchi *et al.* 2012).

This study analyses the spatio-temporal distribution of particularly elusive seabirds – the auks. Auks migrate during winter in areas where they are highly vulnerable to oil spills and major climatic events such as storms as they spend most of their time on the sea surface (Clarke 2009; Fort *et al.* 2013). Numbers of auks are found beached during this period which may have a significant effect on the population (Votier *et al.* 2005, 2008). Many studies have, therefore, been undertaken to determine their distribution at sea, oil spill risks and interactions with offshore wind farms (Certain *et al.* 2007, 2015; Bellier *et al.* 2010; Harris *et al.* 2010; Lorentsen & May 2012; McFarlane Tranquilla *et al.* 2013, 2014). This study uses very large-scale surveys, repeated at intervals of one or 2 months, to analyse the spatio-temporal auk distribution at sea in winter. Two survey campaigns were carried out with a 10-year interval, in 2001–2002 in the Bay of Biscay (Atlantic Ocean) and in 2011–2012 in a broader area encompassing both the Bay of Biscay and the English Channel. The study set out (i) to quantify and analyse auk distribution and abundance using spatially and temporally explicit Bayesian models, (ii) to estimate changes in distribution and abundance within years and between years and (iii) to investigate the potential effect of the Erika oil spill retrospectively by comparing data from 2011–2012 and 2001–2002 in the Bay of Biscay.

Materials and methods

SPECIES STUDIED

Auks are colonial seabirds which breed on cliffs. During the breeding period (May to July), breeders behave as central place foragers and so have a limited spatial distribution, while, in the non-breeding season, they are far more pelagic and free-ranging. Auks are wing-propelled divers, feeding mainly on small fish and some shellfish and molluscs. Flight costs are high and they consequently stay in areas with high prey concentrations to limit their foraging effort. Three species of auk were found in the study area: the Atlantic puffin *Fratercula arctica*, the common guillemot *Uria aalge* and the razorbill *Alca torda*. As it is very difficult to identify auk species from an aircraft, counts of all three species were grouped for analysis, though the common guillemot was by far the most abundant in the studied area (Cadiou, Chenesseau & Joslain 2002).

STUDY AREAS AND SURVEY METHOD

A national project to study the distribution and abundance of top marine predators throughout the entire French economic zone (635 000 km²) was conducted in 2011–2012 (the SAMM survey, *Suivi Aérien de la Mégafaune Marine*, see Fig. 1b). Aerial survey campaigns were carried out in winter 2011–2012 and summer 2012, and in each case, the survey was carried out twice. This paper focused on the winter data in the English Channel and the Atlantic Ocean (hereinafter referred to as the SAMM data). A similar, but more geographically restricted, aerial survey campaign was also carried out in 2001–2002 (see Bretagnolle *et al.* 2004; Certain & Bretagnolle 2008 for details) over 100 000 km² in the Bay of Biscay (hereinafter referred to as the ROMER data, see Fig. 1a). The ROMER campaign comprised five surveys between November 2001 and March 2002 (once per month).

Both the ROMER and SAMM surveys used the strip-transect method, in which all observations within a strip of a constant width are systematically recorded. The strip was 230 m wide in the ROMER survey and 200 m wide in the SAMM survey. ROMER flights were carried out in a Piper PA-34 Seneca fitted with flat windows, flying at a speed of 150 km h^{-1} and at an altitude of 150 m. Previous studies of bird detectability carried out using the ROMER data showed that the observed auk abundances were constant over most of the width of the strip (up to 150 m) and then decreased slightly (Certain & Bretagnolle 2008). The SAMM flights provided better observation conditions than the ROMER flights. They were carried out in a Britten-Norman Islander II fitted with bubble windows, operating at a speed of 170 km h^{-1} and at an altitude of 180 m. Two experienced observers, one on each side of the aircraft, counted the individuals in the strip and a third observer recorded the counts in a computer together with the observation conditions (glare, cloud cover and sea state). Data extraction details are given in Appendix S1 in Supporting Information.

STATISTICAL ANALYSES

Regression models were used with a random spatio-temporal structure such as:

$$Y_i \sim \mathrm{NB}(\lambda_i, \alpha) \text{ with } \log(\lambda_i) = \sum (X\beta)_i + A_i \qquad \text{eqn 1}$$

where Y is the vector of observed counts, λ the vector of conditional means, and α the dispersion parameter of the negative binomial distribution (NB) such that the variance of the count is $\lambda_i + \lambda_i^2/\alpha$. X is the fixed effect matrix, β is the vector of the regression coefficients associated with these fixed effects, and A is the spatio-temporal random effect. In this case, A is a spatio-temporal Gaussian random field such that $A \sim N(0, \sigma^2 C_{\tau,\kappa,\varsigma})$, where

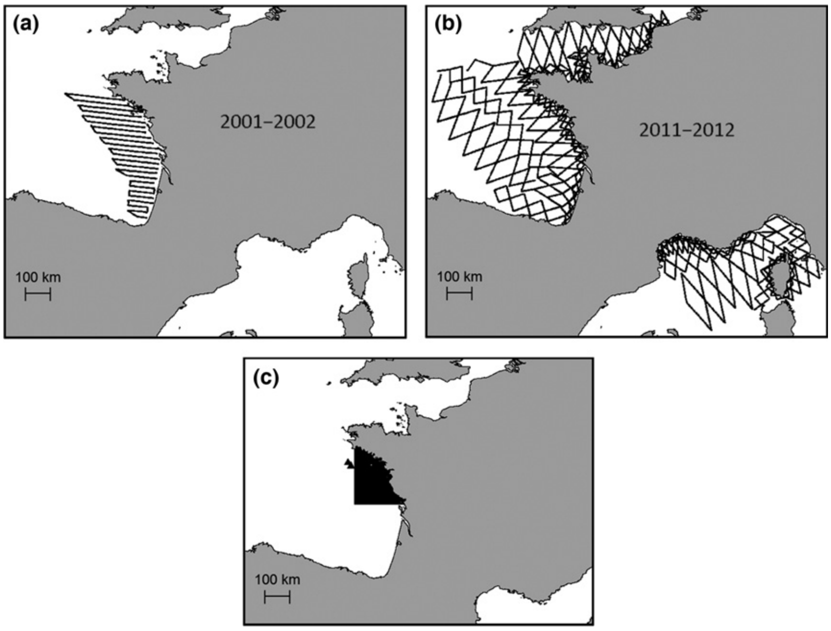

Fig. 1. Aerial transects carried out in winter 2001–2002 (five surveys from November 2001 to March 2002) and 2011–2012 (two surveys from November 2011 to February 2012). The position where the Erika oil spill sank (black triangles) and area affected (in black) are shown at the bottom (c).

σ^2 is the variance of A and C is the spatio-temporal covariance matrix with spatial parameters τ and κ (see Saas & Gosselin 2014) and temporal parameter ς.

This type of model is expensive to evaluate because Bayesian computation is required (e.g. Monte Carlo Markov chains). Integrated nested Laplace approximations allow fast computation and have been proved to be as accurate as other Bayesian tools (Rue, Martino & Chopin 2009). In case of spatially continuous structure, stochastic partial differential equations (SPDEs) with a Matérn covariance function are preconized (see Lindgren, Rue & Lindström 2011; Beguin *et al.* 2012). The Matérn smoothness parameter was set to $\nu = 1$, a value which received the most intensive testing with SPDEs. This type of approach requires a graph (constrained Delaunay triangulation) to define the relationships between the locations. A fine scale graph was chosen here so that the distance between nodes was not more than 10 km (see Appendix S2). The temporal parameter ς was computed as an autoregressive process of order 1 (Blangiardo *et al.* 2013; Cameletti *et al.* 2013). It can be interpreted as the correlation of the random field at a given location between time t and $t-1$. This produces a separable spatio-temporal model (Cressie & Huang 1999). R-code programs are given in Appendix S3 and can be adapted for other similar applications.

Non-informative priors were used for the fixed effects, $N(0,0)$ for the intercept and $N(0,0{\cdot}001)$ for other fixed effects, with notation N(mean, precision = 1/variance). Conversely, moderate *a priori* information was chosen for the spatio-temporal random terms, which helped identifying realistic values of parameters. Note, however, that the use of non-informative priors left the results almost unchanged (see sensitivity analysis in Appendix S4), likely due to the large amount of data available ($N = 4715$ and $N = 7588$ for the ROMER and SAMM data, respectively). The priors for the spatial parameters τ and κ were defined such as the *a priori* range was of 100 km (95% CI: 25–400 km), and such as the *a priori* variance was of 1 (95% CI: 0·03–30). The *a priori* range was chosen according to previous studies on auks' distribution at sea (Bellier *et al.* 2010, 2012), while the *a priori* variance was chosen to match realistic variation in auks abundance. The priors matching these information were $\log(\tau) \sim N(9{\cdot}21,\ 4)$ and $\log(\kappa) \sim N(-10{\cdot}47,\ 2)$, with spatial coordinates in metres (see Ingebrigtsen *et al.* 2014 for a similar approach). The *a priori* information chosen for the temporal parameter ς corresponded to a temporal correlation between t and $t-1$ of 0·5 (95% CI: −0·05–0·82), which suggested that auks had not disappeared suddenly from on occupied area (i.e. unlikely negative correlation). The prior matching this information was $\mathrm{logit}(\varsigma) \sim N(1{\cdot}10,\ 2{\cdot}67)$. Two modelling frameworks were then used, one for the ROMER data and one for the SAMM data to take account of possible differences in the spatio-temporal structure between these periods. Five time steps were used for the ROMER data (one per month from November to March) and two time steps for the SAMM data (17 November—12 January and 13 January—12 February).

The fixed effects part of the model included a set of variables to account for observation and environmental conditions. The variables assumed to affect the observation conditions were the glare of the sun on the sea surface within the observation window (total area affected by glare within 20° to 130° on each side of the aircraft, 0° being the front) in interaction with the glare severity (coded from 0 to 3), the cloud cover (from 0 to 8 for the SAMM data and 0 to 4 for the ROMER data, 0 for no cloud) and the sea state (from 0 to 5 on the Beaufort scale, no flights were carried out above 5). These variables were included in the model so that any reduction in auk counts attributable to changes in observation condition could be accounted for. The glare was not available for the ROMER data, and so only the side without glare was used for analysis (see Certain & Bretagnolle 2008). The environmental variable assumed to affect auk abundance was the distance from the coast because auks were found mainly in the area close to the coast (see Bellier *et al.* 2010). Linear as well as quadratic terms of these variables were included in the models in order to account for expected nonlinear effects. Moreover, the effect of the distance to the coast was allowed to vary between the English Channel and the Atlantic area by using an interaction term. Predictive power of models were evaluated by using a leave-one-out cross-validation criterion, the logarithm of the conditional predictive ordinate (LCPO, see Held, Schrödle & Rue 2010; Beguin *et al.* 2012). LCPO was computed for the null (intercept only), the non-spatio-temporal (fixed effects only) and the full (fixed effects and spatio-temporal terms) models in order to quantify the gain in using more complex models.

Model predictions were computed on a 10 × 10 km grid at each time step considered. It was assumed that all individuals above the sea surface were detected in the strip when observation conditions were optimal, that is no sun glare (0°), calm sea (0 Beaufort), moderate cloud cover (4) for the SAMM data and no cloud cover (0) for ROMER. The cloud cover had a dual effect, reducing glare, thus improving observation conditions, but also reducing the luminance. For ROMER (2001–2002), only the side without glare was used for analysis and thus the effect of cloud cover was negative (see Appendix S5). Auk abundance was predicted by setting the variables affecting observation conditions to these optimal values. The abundance of auks for each period was taken to be the total of the counts in each cell (after eliminating the area covered by lands), and the variance in the estimates was obtained by resampling the posterior distribution of the model 1000 times. The model as well as the estimates did not account for the time spent underwater. The results of studies carried out in winter suggest that at a given time, up to 25% of auks are diving below the surface water (Clarke 2009; Fort *et al.* 2013), and are, therefore, not visible to observers. Accordingly, abundance estimates provided in the text are multiplied by 1·33 to correct for diving birds. Uncorrected estimates are shown in Table 1.

Results

EFFECT OF OBSERVATIONAL CONDITIONS AND ENVIRONMENTAL VARIABLES

Observation conditions had a significant effect on auk detection. The sea state had the greatest (negative) effect as only about 50% of the auks present could be detected when sea state was above 2 on the Beaufort scale (Fig. 2; see also Appendix S5). The glare of the sun on the sea surface (only available for the SAMM data) also strongly reduced the number of auks detected (Fig. 2; Appendix S5). The cloud cover had a dual effect, reducing glare, thus improving observation conditions, but also reducing the luminance. Clear and overcast skies both reduced detection rates by about 25% (Fig. 2; Appendix S5). About the environmental component, the log-transformed distance from the coast had a quadratic effect on auk distribution, differing between oceanic areas: auks were closer to the coast in the Atlantic Ocean than in the Channel (Fig. 2; Appendix S5).

The spatio-temporal term also helped in predicting auk distribution, increasing predictive power by more than 10% (see LCPO in Appendix S5). The estimated spatial

Table 1. Auk abundance (and 95% confidence intervals) in the English Channel and the Bay of Biscay at different winter dates. Note that these abundances do not take account of the diving probability which is assumed to be 25%

	Period						
Area	November 2001	December 2001	January 2002	February 2002	March 2002	December 2011	February 2012
Erika oil spill area	17 950 (10 122–32 760)	35 310 (20 888–60 310)	47 136 (27 927–77 451)	56 078 (36 787–88 204)	58 318 (36 224–97 789)	94 245 (58 341–182 252)	205 268 (136 434–348 488)
Bay of Biscay	41 992 (27 099–65 577)	81 702 (48 801–136 075)	158 525 (101 126–251 932)	158 197 (97 130–256 482)	136 016 (89 961–226 413)	136 647 (89 676–229 439)	353 680 (243 216–547 079)
Bay of Biscay out of Erika oil spill area	23 457 (14 549–39 625)	46 207 (25 829–84 936)	109 575 (68 774–181 283)	100 355 (57 098–174 184)	77 179 (45 183–134 088)	40 901 (26 840–64 955)	140 934 (95 350–228 449)
Eastern Atlantic Ocean						179 343 (121 335–288 008)	400 343 (278 987–597 264)
English Channel						501 239 (336 708–798 571)	771 151 (544 652–1 202 326)
Total						683 340 (473 447–1 048 504)	1 172 129 (846 293–1 735 526)

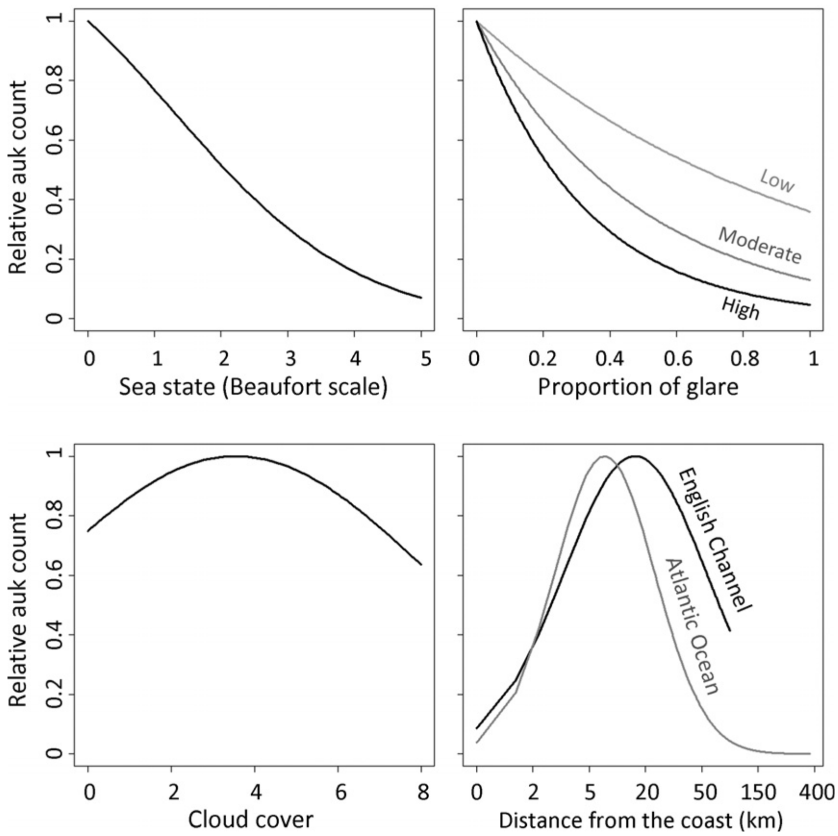

Fig. 2. Relative effect of sea state, glare, cloud cover (detection component) and distance from the coast (environmental component) on auk counts in winter 2011–2012. Details of estimated coefficients and standard errors are given in Appendix S5.

ranges were close between the two surveys (75 and 100 km for the ROMER and SAMM respectively, see Appendix S5), indicating similar distances of spatial autocorrelation. However, the overall temporal correlation between the five monthly surveys for the ROMER data was 0·34, lower than for the SAMM data (0·51), likely indicating a more dynamic distribution in the Bay of Biscay in winter 2001–2002 than in winter 2011–2012.

TEMPORAL VARIATIONS OF AUK ABUNDANCE

In winter 2011–2012, auk abundance reached 1·55 million birds in February 2012, with more than one million being estimated in the English Channel (Table 1). The highest densities were found near major river plumes and estuaries (Exe, Tamar, Seine and Somme for the Channel; Loire and Gironde for the Bay of Biscay, see also Bellier *et al.* 2010). Overall, the total abundance in February was almost twice the total abundance in December, resulting from a general southward movement (see Fig. 3 and Table 1). This southward shift was also observed between December 2001 and January 2002 in the Bay of Biscay (Fig. 3). Throughout winter 2001–2002, auk abundance in the Bay of Biscay peaked in January and February, with about 210 000 auks (Table 1). At the same time in 2011–2012, auk densities were much higher, with about 470 000 auks in the Bay of Biscay (Table 1, Fig. 3).

Within the area affected by the Erika oil spill (Fig. 1c), auk abundance was estimated at 80 000 birds in February 2002, which corresponded to 35% of the total abundance estimated in the Bay of Biscay at this period. Ten years later, auk abundance was estimated at 270 000 birds in the same area, representing 60% of the Bay of Biscay population. Therefore, from winter 2001–2002 to 2011–2012, the auk population in the Erika oil spill area increased by 190 000 birds. No such significant increase has been found outside the Erika oil spill area (see Table 1). This suggests that the 2001–2002 population wintering in the oil spill area was markedly depleted and has been replenished over the last 10 years.

Discussion

THE VALUE OF SPATIALLY AND TEMPORALLY EXPLICIT SPECIES DISTRIBUTION MODELS

The analysis of spatio-temporal species distribution is usually carried out by repeating spatial analyses at each time step (e.g. Bellier *et al.* 2010, 2012, 2013 for an in-depth spatial analysis of the auk data during ROMER survey). However, individuals are not randomly distributed through time, but respond to environmental and social constraints that are both spatially and temporally autocorrelated. Repeating independent spatial analyses across different time steps does not take into account that the distribution of individuals at one time step may affect the distribution at the next time step. Our spatio-temporal modelling approach takes account of this non-independence, considerably increasing the predictive power of the models inside the studied area (see LCPO in Appendix S5). This is

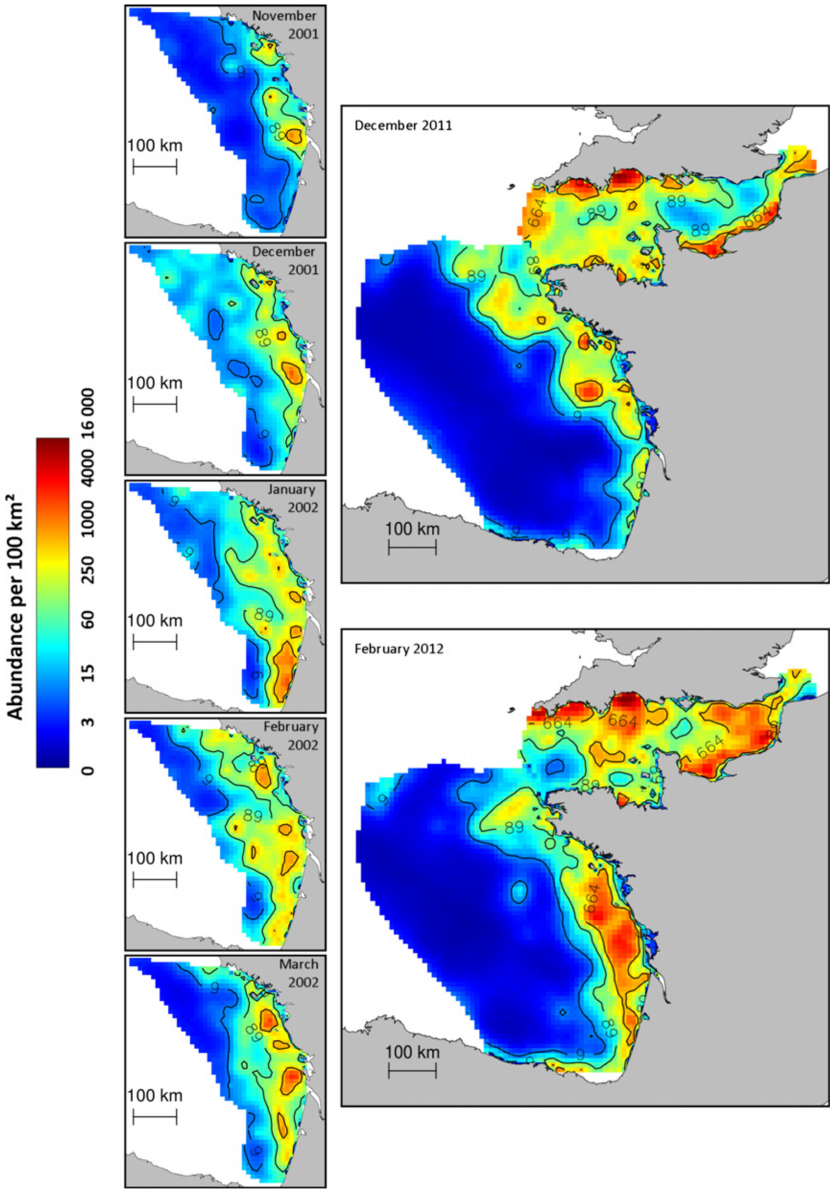

Fig. 3. Auk distribution in the Bay of Biscay (ROMER, left) and in the eastern Atlantic Ocean and English Channel (SAMM, right). Uncertainty maps (standard errors) are given in Appendix S8. Note that the abundance does not take account of the diving probability.

especially useful for predictions at locations that are not sampled (Elith & Leathwick 2009). However, priors must be chosen with care to avoid a misguided inference, especially when the amount of data is low. A sensitivity analysis to priors should always be done as an integral part of the statistical analysis framework (see Appendix S4). After checking that results have poor sensitivity to prior choice, spatially and temporally explicit models can be used more confidently to investigate the causes of latent spatial and temporal structures. More pronounced changes in the latent distribution were detected in the ROMER survey than in the SAMM survey, possibly owing to the more unstable spatio-temporal distribution of auks after the oil spill, though different temporal sampling between the two surveys does not demonstrate it.

Until now, spatially and temporally explicit species distribution models have rarely been used: Fink *et al.* (2010) proposed a framework that consists in splitting the data into several spatio-temporal blocks. A model is then fitted within each block, and spatio-temporal distribution is then averaged over all models. However, this approach does not take account of either spatial or temporal dependences within and between blocks. Hothorn *et al.* (2011) proposed an alternative framework where spatial and temporal patterns are modelled by additive nonlinear functions of space and time locations. Such structured additive regression can take account of large spatio-temporal trends but usually fails to take account of finer scale dependences (Dormann *et al.* 2007). The recently developed SPDE approach (within the R-INLA tool box) provides an easy way of using spatially and temporally explicit models with a reasonably short computation time. It should be noted, however, that this approach uses a separable spatio-temporal covariance structure, in which spatial and temporal effects are considered independently. Although being much simpler to compute and to interpret, this covariance structure does not take account of the fact that individuals move both in space and in time. The next step will therefore consist in the development of tools for fitting non-separable spatio-temporal covariance structures (Cressie & Huang 1999).

MAJOR HOT SPOTS OF WINTERING AUKS

The spatio-temporal distribution of auks at sea in the study area is highly dynamic, both between and within years. The major changes concern the southward shift of their distribution in winter, spatially detectable in the Bay of Biscay but also those found in the Channel given the trends in numbers between the two winter sessions. A total estimation of up to 1 550 000 auks in February 2012 showed that the Channel and the north-west Atlantic coast (mainly the Bay of Biscay) were clearly previously unidentified major wintering areas for auks. The number of wintering auks was actually similar to the total number of common guillemots breeding in Britain and Ireland, that is 1·6 million birds (Mitchell *et al.* 2004). The non-breeding distribution of the common guillemot is not well known, but most British birds are thought to winter fairly close to their breeding colonies. More northern populations (Barents Sea, Iceland) seem to winter in more northern latitudes (Steen, Lorentzen & Strøm 2013). Our estimated numbers clearly suggest that a major proportion of the British common guillemots winter in the Bay of Biscay (probably among the younger birds, as many auks killed by the Erika oil spillage were juveniles and immatures, Cadiou *et al.* 2004), and in the Channel. There were major hot spots close to all large river plumes (see also Bellier *et al.* 2010), where they presumably found high concentrations of prey.

A POSTERIORI STUDY OF THE EFFECT OF THE ERIKA OIL SPILL

The Erika oil spill occurred on 12 December 1999, about 60 km south of the Brittany coast in the northern part of the Bay of Biscay. The main oil slick drifted for 2 weeks before reaching the coast (Daniel *et al.* 2001) and affected over 400 km of coast from south-west Brittany to the Ile de Ré for 1 month (Fig. 1c). About 65 000 auks were found oiled in the Bay of Biscay, far more than were thought to winter in this area at that time (Cadiou, Chenesseau & Joslain 2002). This surprisingly high number raised an alert on the potential impact on breeding colonies and led to several studies being carried out in order to gain a better estimate of the number that had died (Cadiou, Chenesseau & Joslain 2002); their geographic origin (Cadiou *et al.* 2004; Riffaut *et al.* 2005); and the consequences on survival rates, breeding fecundity and population growth rates in breeding colonies in the United Kingdom (Votier *et al.* 2005). The only published estimates of the number of auks killed after the Erika oil spill were produced by totalling the number of beached birds and estimating the proportion of auks not found on the beaches. They concluded that between 70 000 and up to 130 000 auks may have been killed (Cadiou, Chenesseau & Joslain 2002). Estimating the proportion of auks not found is very difficult, as it depends on meteorological conditions (affecting the probability of reaching the beach) and survey effort (affecting the probability of finding carcasses). Studies using drift experiments showed that the number of oiled auks found might account for 10–50% of the true mortality (review in Munilla *et al.* 2011). No such drift experiment was carried out during the Erika oil spill, but based on these estimates, the number of auks killed could have reached 650 000.

The differences observed between the ROMER (2001–2002) and the SAMM (2011–2012) surveys, that is 190 000 and 260 000 auks, respectively, in the Erika oil spill area or whole Bay of Biscay, are of higher magnitude than the auk mortality estimated by Cadiou, Chenesseau & Joslain 2002. These differences could be the result of (i) an increase in population abundance, (ii) a broad-scale shift in auks' wintering distribution and/or (iii) the recovery after the mortality induced by the Erika oil spill. Estimated numbers of breeding auks in Britain and Ireland (the main geographic origin of auks wintering in the Bay of Biscay, see Cadiou *et al.* 2004), show that the population has remained stable between the two surveys (JNCC 2015). It is thus unlikely that the differences of abundance observed between the two surveys result from a general increase in population abundance. Strong changes in prey abundances may drive broad-scale shifts in auks' distribution, but the variations observed in prey abundance between the two surveys (data available from ICES, see Appendix S6) do not suggest that auks would have been more abundant in the Bay of Biscay during the SAMM survey. Auks have high wintering site fidelity (McFarlane Tranquilla *et al.* 2014), which suggests that the number of auks observed in 2001–2002 would be reminiscent of the mortality induced by the Erika oil spill (see Votier *et al.* 2005 for the effect of the Erika oil spill on breeding grounds). The third explanation that the 2001–2002 abundance corresponds to a depleted population due to the oil spill mortality thus appears likely. There is unfortunately no abundance estimate of auks before the Erika oil spill in the Bay of Biscay. However, Castège *et al.* 2004 have provided wintering distribution maps for common guillemot during this period (see Appendix S7), showing that auks were more abundant in the north of the Bay than in the south, unlike the ROMER survey which showed that auks were less abundant where the Erika oil spill happened (see Fig. 3). Moreover, it appears that auks occurred in fairly similar areas as in 2011–2012, which reinforces our hypothesis that the difference of abundance between 2001–2002 and 2011–2012 would mainly reflect the recovery after the mortality induced by the Erika oil spill. Unfortunately, without reliable abundance estimates before the oil spill, it will never be possible to prove it with certainty.

CONSERVATION IMPLICATIONS

This study showed that regular large-scale aerial surveys can help in quantifying the impact of major catastrophic events, provided that data are available before and after the event (which unfortunately was not the case for the Erika oil spill). In addition to numbers, such surveys also provide data for species distribution mapping. Such information is crucial for conservation planning: until now, no major oil spill has occurred in the Channel during the peak abundance of wintering auks (January to February). Should such a catastrophe happen, our study predicts that up to one million auks could be killed, not to mention all the other species there. The Channel is the busiest maritime thoroughfare in the world, carrying up to 20% of the world's traffic, with about 3000 ships being oil tankers. It is therefore essential that measures are taken to avoid oil spillages during late winter.

The three auk species studied here are not currently threatened in Western Europe. Breeding populations in the United Kingdom and Ireland are around 1 560 000 common guillemots (stable since 2001, but possibly increasing since 2013), 215 000 razorbills (slightly in decline since 2001) and 1 200 000 Atlantic puffins (trend unknown; Mitchell *et al.* 2004; JNCC 2015). Despite these large numbers and the apparent stability, the huge concentration of auks found wintering in the Channel and the Bay of Biscay (1·55 million wintering auks) make these areas particularly important for the conservation of these species, and especially for the common guillemot. Indeed, the English Channel and the Atlantic Ocean off the French coast likely host, in winter, more than 10% of the estimated population of the world's common guillemots.

Acknowledgements

Flight schedules and logistics were organized by Sylvie Houte and V.B. at the CEBC (ROMER) and Emeline Pettex at the CRMM (SAMM). These surveys were funded by the French Government (ROMER) and the *Agence des Aires Marines Protégées, AMP* (SAMM). We should like to thank all observers: Rodolphe Bernard and Thibault Dieuleveult; Thomas Barreau, Ariane Blanchard, Vincent Bretille, Alexis Chevalier, Cécile Dars, Nathalie Di-Méglio, Emilie Durand, Marc Duvilla, Alessio Maglio, Marie Pellé, Morgane Perri, Sandrine Serre. Thanks to Pascal Monestiez for his advice on the statistical framework. K.L.R was funded by the *AMP*.

Data accessibility

Adaptable R-script: uploaded as online supporting information (Appendix S3).

Auk count data: the data used in this paper and the data used in Appendix S6 (about small pelagic fish trends) are archived in Dryad Digital Repository http://dx.doi.org/10.5061/dryad.1hv28 (Le Rest *et al.* 2016).

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Received 7 December 2015; accepted 29 April 2016
Handling Editor: Henrik Österblom

Supporting Information

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

Appendix S1. Data extraction.

Appendix S2. Constrained refined Delaunay triangulation.

Appendix S3. Adaptable R-script.

Appendix S4. Sensitivity analysis to prior choice.

Appendix S5. Model parameter estimates.

Appendix S6. Small pelagic fish trends in and around the Bay of Biscay.

Appendix S7. Wintering distribution of common guillemot (1980−2002).

Appendix S8. Standard errors of predicted abundance.