A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

Beyond climate envelopes: bio-climate modelling accords with observed 25-year changes in seabird populations of the British Isles

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ABSTRACT

Aim Climate envelope models (CEMs) are used to assess species' vulnerability to predicted changes in climate, based on their distributions. Extinction risk, however, also depends on demographic parameters. Accordingly, we use CEMs for 18 seabird species to test three hypotheses: (i) population sizes are larger in areas where CEMs fitted using distribution data predict more suitable climate; (ii) the presence of this relationship (Hypothesis i) is related to a species' foraging ecology; and (iii) species whose distributions and population sizes conformed most closely to indices of climatic suitability in the mid-1980s experienced the largest population changes following climatic change between 1986 and 2010.

Location Europe.

Methods Climate envelope models fitted at a 50-km resolution using European climatic and distribution data were applied using local climatic data to calculate local climatic suitability indices (CSIs) for 18 species within the British Isles. We then investigated the relationship between CSI and population size at a 10-km resolution and related both the presence of this relationship and goodness-of-fit metrics from the European models to changes in population size (1986–2010).

Results Local population sizes were significantly positively related to local CSI in 50% of species, providing support for Hypothesis (i), and these 50% of species were independently considered to be most vulnerable to changes in food availability at sea in support of Hypothesis (ii). Those species whose distributions and populations most closely conformed to indices of climatic suitability showed the least favourable subsequent changes in population size, over a period in which mean climatic suitability decreased for all species, in support of Hypothesis (iii).

Main conclusions Climate influences the population sizes of multiple seabird species in the British Isles. We highlight the potential for outputs of CEMs fitted with coarse resolution occupancy data to provide information on both local abundance and sensitivity to future climate changes.

Keywords
Ecological niche modelling, global warming, long-term studies, population monitoring, space-for-time substitutions, species distribution modelling.

INTRODUCTION

There is increasing evidence that human-induced changes in climate (IPCC *et al.*, 2007) have led to alterations in the geographical ranges and abundances of many species in recent decades (Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011; Gregory *et al.*, 2009; Lehikoinen *et al.*, 2013), with even greater changes predicted in future (Thomas *et al.*, 2004; Jetz *et al.*, 2007). To understand how species are likely to respond to climatic changes, the most widely used approach is that of climate envelope modelling, in which correlative statistical models based on empirical data on species distributions are used to predict which areas will be climatically suitable for species under different climate-change scenarios (Thomas *et al.*, 2004; Huntley *et al.*, 2007; Renwick *et al.*, 2012). Despite widely acknowledged limitations of this approach (Araújo & Rahbek, 2006; Beale *et al.*, 2008; Elith *et al.*, 2010; Zurell *et al.*, 2012), climate envelope models (CEMs) provide an empirical method of assessing species' vulnerability to future climatic changes which can be widely applied (Huntley *et al.*, 2004; Jiguet *et al.*, 2007; Davey *et al.*, 2012) and may be used to identify areas where management could be targeted to improve species' conservation prospects (Thomas *et al.*, 2011; Oliver *et al.*, 2012; Guisan *et al.*, 2013), particularly if used in conjunction with stochastic population models incorporating interactions between demography and landscape dynamics (Keith *et al.*, 2008; Anderson *et al.*, 2009). However, while projected changes in the total area of suitable climatic space have been found to differ among species with contrasting recent population trends (Gregory *et al.*, 2009; Renwick *et al.*, 2012), relationships between climatic suitability and population sizes within species' geographical ranges are less well studied and results are equivocal, with only poor correlations in some cases (Nielsen *et al.*, 2005; Jiménez-Valverde *et al.*, 2009; Oliver *et al.*, 2012), potentially limiting the applicability of CEMs for predicting population viability and extinction risks under climate change.

To date, CEMs have mostly been constructed using qualitative distribution data (presence only or presence/absence) and have been used to project changes in species' distributions only in terms of occupancy. However, significant population declines may occur before any reduction in area of occupancy (Chamberlain & Fuller, 2001) and it is population sizes and trends that are most useful in assessing the conservation status of species and determining priorities for action (O'Grady *et al.*, 2004; Akçakaya *et al.*, 2006). Some recent studies have modelled species abundance in relation to climate (Shoo *et al.*, 2005; Anderson *et al.*, 2009; Huntley *et al.*, 2012; Renwick *et al.*, 2012). However, in most cases, only occupancy data are available and whether models using such data can adequately predict population sizes (Oliver *et al.*, 2012) or trends (Green *et al.*, 2008) within a species' range has rarely been tested. VanDerWal *et al.* (2009) found that there was a significant positive relationship between local abundance and estimated climatic suitability for 58 of 69 tested species of rain forest vertebrates in the Australian Wet Tropics, but they were not able to examine changes in abundance with time and emphasized the need for tests of the predictive ability of CEMs on other empirical abundance datasets to explore the generality of their findings. Furthermore, the above tests used similar spatial scales and resolutions of data for both fitting and testing of models. Occupancy data are often available only at a coarse resolution, particularly over the wide spatial extents needed to define species' climate envelopes (Thuiller *et al.*, 2004; Luoto *et al.*, 2007). Distributional data at coarse resolutions (40 km and above) are useful to fit CEMs because such resolutions minimize the importance of habitat availability (Luoto *et al.*, 2007). Yet, conservationists and population ecologists often require information at finer resolutions, and whether CEMs generated using coarse-scale data can be used to predict population sizes or trends at finer resolutions has not previously been tested (although see Hole *et al.*, 2009 for a test of the accuracy of down-scaled predictions of species presence/absence).

Assessment of temporal changes in distribution and abundance in relation to climatic conditions requires long-term, fine-scale datasets. A high-resolution data resource exists for seabirds in the British Isles (the UK and Ireland), as a result of a comprehensive national census of breeding population sizes carried out in 1985–1988 (Lloyd *et al.*, 1991) and continued monitoring of an extensive sample of sites since then as part of the Seabird Monitoring Programme (SMP; JNCC, 2011). Seabird breeding colonies are typically conspicuous, minimizing the issue of false absences at a macroscale and allowing reliable population estimates at a fine scale. The British Isles are of international importance for seabirds, supporting >50% of the world population of several species (Mitchell *et al.*, 2004; Thaxter *et al.*, 2012), and a recent review of impacts of global climate change on seabirds (Grémillet & Boulinier, 2009) highlighted the need for improved models to define and predict impacts on populations of different species, particularly in relation to differences in trophic status and foraging ecology at sea.

Here, we combine European-scale bioclimatic data and breeding distribution (presence/absence) data for the mid-1980s to construct CEMs for 18 species of seabird whose breeding distribution includes the British Isles. We then use these models to test three hypotheses concerning population sizes of each species: (i) local population sizes are larger in those parts of a species' geographical distribution where CEMs fitted using European distribution data predict the climate to be more suitable; (ii) the ability of occupancy models to predict population sizes of different species is related to their foraging ecology; and (iii) species whose distributions and population sizes conformed most closely to indices of local climatic suitability in the mid-1980s experienced the largest subsequent population changes following climatic change between 1986 and 2010.

METHODS

Constructing European-scale climate envelope models

Distribution data

The study was restricted to 18 species of seabird that have been monitored since 1986 by the SMP (Table 1). Data used to construct the CEMs were breeding distribution data on a ~50-km resolution for each species in the mid-1980s (mainly 1985–1988), provided by the European Bird Census Council (Hagemeijer & Blair, 1997). A Universal Transverse Mercator (UTM) grid comprised 4757 cells, in which survey coverage varied geographically; coverage was lowest in Eastern Europe and Russia, resulting in some cells with species' status denoted as unknown. For the purposes of this study, species were recorded as 'present', 'absent' or 'unknown', with present including all possible, probable and confirmed breeding records. Non-coastal cells (those not intersected by the coast of European land masses and islands) were excluded from the analysis because some species of Laridae breed in non-coastal cells where they are unlikely to be dependent on the marine environment for food. This resulted in a maximum coastal distribution of 1073 grid cells.

Climatic data

We used three bioclimatic variables, chosen *a priori* to reflect known effects of climate on seabirds, to characterize species' climate envelopes. These were as follows: mean air temperature of the warmest month (MTWM; Oswald *et al.*, 2008); rainfall during the breeding season (March to August inclusive; RAIN; Thompson & Furness, 1991; Gray *et al.*, 2003); and winter/spring (December to May inclusive) sea surface temperature adjacent to each focal grid square (SST; Frediksen *et al.*, 2004) for the period 1976–1985 (inclusive). In Europe, sea surface temperatures in winter and spring influence the timing and extent of spring blooms of phytoplankton and consequently affect zooplankton biomass and thus the growth and survival of forage fish (Arnott & Ruxton, 2002; Castonguay *et al.*, 2008; Burthe *et al.*, 2012). Climatic variables were interpolated onto the 50-km coastal grid using an inverse distance weighted mean technique. MTWM and RAIN were available on a 0·5° longitude × latitude grid, whereas SST data were available on a 1° grid. For SST in cases where there were missing values for any of the four surrounding grid cells (i.e. land), the interpolation window was increased to include a further 12 1° cells that surrounded the original four. The lowest SST in the dataset was −1.8 °C. Points recorded as sea ice were converted to

Table 1 Goodness-of-fit (bootstrapped AUC values and percentage deviance explained) of climate response surface models for breeding seabirds in coastal Europe, together with median latitude and prevalence in their European range, and percentage changes in breeding numbers in the British Isles between 1986 and 2010. Vernacular names of species follow the International Ornithological Congress

Species	Bootstrapped AUC		Deviance explained (%)	European prevalence*	Median latitude*	% change 1986–2010†
	Mean	SE				
Northern Fulmar, *Fulmarus glacialis*	0.97	0.001	74	198	58.38	−17
Northern Gannet, *Morus bassanus*	0.82	0.005	14	33	59.75	77
Great Cormorant, *Phalacrocorax carbo*	0.88	0.002	45	196	54.37	10
European Shag, *Phalacrocorax aristotelis*	0.88	0.002	52	280	50.77	−33
Parasitic Jaeger, *Stercorarius parasiticus*	0.97	0.001	72	230	65.14	−57
Great Skua, *Stercorarius skua*	0.95	0.002	53	65	63.80	N/A
Black-legged Kittiwake, *Rissa tridactyla*	0.94	0.001	62	225	63.35	−47
Lesser Black-backed Gull, *Larus fuscus*	0.93	0.001	58	350	58.39	−2
European Herring Gull, *Larus argentatus*	0.97	0.001	78	419	57.94	−29
Great Black-backed Gull, *Larus marinus*	0.98	0.001	74	354	59.30	−9
Little Tern, *Sternula albifrons*	0.81	0.002	31	245	53.44	−13
Sandwich Tern, *Sterna sandvicensis*	0.83	0.003	33	124	53.89	0
Common Tern, *Sterna hirundo*	0.89	0.002	52	455	55.71	17
Roseate Tern, *Sterna dougallii*	0.90	0.004	48	36	49.41	N/A
Arctic Tern, *Sterna paradisaea*	0.96	0.001	72	380	60.21	16
Common Murre, *Uria aalge*	0.87	0.003	35	145	57.94	49
Razorbill, *Alca torda*	0.90	0.002	46	182	59.29	41
Atlantic Puffin, *Fratercula arctica*	0.93	0.002	61	142	63.34	N/A

*European prevalence and median latitude refer to the number and latitude, respectively, of grid squares occupied by each species within Europe.
†From JNCC (2011). Data not available (N/A) for Great Skua or Atlantic Puffin; data for Roseate Tern excluded because of high winter mortality beyond breeding range (see Methods for further details); data for Northern Gannet obtained from Lloyd *et al.* (1991) and Davies *et al.* (2013).

−2 °C (the approximate freezing point of sea water in the North Atlantic) to enable interpolation of SST values for grid cells near or surrounded by sea ice and to minimize the number of grid cells that had missing climatic data (one cell).

During the 10 years leading up to 1985, the climate varied spatially throughout Europe with MTWM decreasing with increasing latitude. RAIN varied greatly across Europe from less than 25 mm month^{-1} in parts of the Mediterranean region and northern Russia to up to 150 mm month^{-1} on the western British and Norwegian coasts. Like MTWM, SST also decreased with increasing latitude, from a maximum temperature of 19 °C in the south of Europe to sea ice in the very north of Europe. SST also decreased from Western to Eastern Europe.

Climate response surface (CRS) models

Climate response surface models, a type of CEM, were fitted using FORTRAN programs written for the purpose (Huntley *et al.*, 1995). There are two main attributes of these models. First, they make no *a priori* assumptions about the shape of relationships between a species' distribution and particular climatic variables (Huntley *et al.*, 2004). Second, CRS models are fitted locally rather than globally. The models allow interactions between climatic variables, recognizing that the relationship between a given climatic variable and a species' probability of occurrence in a cell is dependent on the values of the other relevant climatic variables (Huntley *et al.*, 2007). Thus, the CRS technique accommodates multimodal relationships between climate and a species' distribution (Heikkinen *et al.*, 2006). Models were generated for each species separately, generating a probability of occurrence in each grid cell given the observed climatic conditions.

To reduce the impact of overfitting on the assessment of goodness-of-fit, models were bootstrapped 100 times for each species. For each bootstrap estimate, 30% of grid squares were removed at random, except that the same proportions of presences, absences and missing records in the original data were maintained. Models were then generated using the remaining 70% of the data (training cells) and used to predict probability of occurrence for test cells (30% of grid squares; Thuiller, 2003). Simulated probabilities of occurrence from each of the 100 test datasets were then compared to observed presence/absence to produce receiver operating characteristic (ROC) plots of sensitivity against one specificity (Manel *et al.*, 2001). Mean area under the curve (AUC) of ROC plots (goodness-of-fit) across all 100 bootstraps were calculated for each species reflecting how well spatial variation in bioclimatic variables depicted species' distributions (Table 1; see Appendix S1 for further details concerning our use of AUC). We also calculated the percentage deviance explained by each model, as an alternative measure of goodness-of-fit (Hosmer & Lemeshow, 1989).

Other climate envelope models

To investigate if our results were dependent on the method used to generate CEMs, we compared the results of our CRS models with those of generalized linear models (GLMs; McCullagh & Nelder, 1983) and generalized additive models (GAMs; Hastie & Tibshirani, 1986) used previously for CEMs (Thuiller, 2003; Araújo *et al.*, 2005; Oswald *et al.*, 2011). The GLMs included linear covariates and interactions while in the GAMs, covariates were modelled as smooth terms with no interactions (see Appendix S2).

Relating historical population sizes in the British Isles to local climate

Abundance data indicating breeding population sizes in 1985–1988 were available from The Seabird Colony Register (Lloyd *et al.*, 1991). For data collection, the coast of the British Isles was divided into 10-km Ordnance Survey cells and experienced observers mapped the presence/absence of seabird colonies in each cell, followed by detailed counts of most colonies (nearly 32,000 counts in total, mainly between 1985 and 1987; see Lloyd *et al.*, 1991 for further details of data collection). Although colonies of the species we considered are conspicuous, occasionally breeding pairs may have been missed; the counts should thus be considered best estimates. Over 600 volunteers contributed to the survey; any minor counting biases linked to individual observers thus would not distort the overall pattern. For our study, we used all cells which intersected land (1029 cells in total).

To characterize climate at the same spatial scale as population sizes, MTWM and RAIN data for 1976–1985 on a 10' grid (approximately 10 km by 20 km in the British Isles; Mitchell *et al.*, 2004) and SST data for the same period on a 1° grid (Rayner *et al.*, 2003) were interpolated onto the 10-km coastal grid using an inverse distance weighted mean technique. In some cases, all cells surrounding a focal cell were designated as land, resulting in a missing value for SST and exclusion of that cell from the study. In total, 960 of the 1029 cells remained for use in further analyses. The CRS models generated using the European data were then applied to these fine-scale climatic data for the British Isles, to predict CSI for each 10-km cell for each species (range of values = 0.0–1.0, equivalent to the probability of the species being present in the cell, given the climatic conditions).

To compare CSI with local population sizes, grid cells that had a population size of zero were excluded to minimize confounding effects related to habitat availability at this spatial scale (Luoto *et al.*, 2007; VanDerWal *et al.*, 2009). Hence, we conservatively examined variation in population sizes only at occupied sites. We investigated the relationship between log$_e$ breeding population sizes and CSI in a multispecies model and also separately for each species. Population size was log-transformed in each case, to ensure that residuals were normally distributed. Multispecies analysis was conducted using a linear mixed effects model (LME) with

species identity included as a random effect. A model with both a random intercept and slope was preferred by AIC_C (see model fitting below) over one including only a random intercept, indicating that the relationship between CSI and population size differed among species. Thus, we also investigated the relationship between $\log_e$ breeding population sizes and CSI separately for each species, using generalized least squares (GLS) models. For four species, visual inspection of plots of $\log_e$ population size versus CSI suggested a step function and so CSI was examined as a two-level factor with the threshold first defined using a regression tree.

Importance of species' foraging ecology

To determine whether or not the ability of our occupancy models to predict abundance was related to species' foraging ecology, we used an independent index of the vulnerability of breeding success to reduced abundance of food in the vicinity of colonies, derived from a combination of body size, energetic cost of foraging, potential foraging range, ability to dive, amount of 'spare' time in the daily budget and ability to switch diet (table 1 in Furness & Tasker, 2000; individual traits covaried and so were not considered separately here). We used a binomial GLM to examine whether the presence of a relationship between CSI and population size (inclusion of CSI in the minimum adequate model describing variation in $\log_e$ population size) was related to this index. Our GLM also included the number and median latitude of occupied grid cells of each species within Europe (Table 1) as additional explanatory variables, because analyses of species with higher prevalence may have had greater statistical power and because extreme climatic events such as violent storms that can directly affect populations occur more frequently and are more marked at higher latitudes, potentially masking difference related to foraging ecology.

Changes in breeding populations in the British Isles since 1986

We obtained information on percentage changes in breeding populations for 15 of our study species in the British Isles between 1986 and 2010 from JNCC (2011). In addition, changes in populations of Northern Gannets *Morus bassanus* over the same period were obtained using data from Lloyd *et al.* (1991) and Davies *et al.* (2013). We excluded Roseate Tern *Sterna dougallii* from further analysis because, even if sensitive to climate, changes in its population sizes over the study period were likely to be strongly affected by mortality due to deliberate trapping at their wintering grounds in western Africa (Mitchell *et al.*, 2004). This allowed further analysis of 15 species in total.

We used two separate measures to quantify how closely distributions and population sizes conformed to local climate in the mid-1980s. These were as follows: (i) goodness-of-fit (bootstrapped AUC values) of the European CRS models and (ii) inclusion of CSI in the minimum adequate model

describing variation in $\log_e$ population size (see model fitting below). We then used a GLS model to examine the relationship between each of these two explanatory variables and the percentage change in the total populations of species from 1986 to 2010. As previously, this model also included the number and median latitude of occupied grid cells within Europe as additional explanatory variables. To check whether our results were dependent on the goodness-of-fit metric or CEM used, we then re-ran the GLS model, first using percentage deviance explained in place of bootstrapped AUC and then using GAMs in place of CRS models to generate values for AUC and percentage deviance explained (three additional tests in total).

Model fitting

With the exception of fitting and testing the CRS models, analyses were carried out in R (R Core Development Team, 2012) using the following packages: mgcv (Wood, 2011); nlme (Pinheiro *et al.*, 2012); and tree (Ripley, 2012). A backwards selection approach was then taken, selecting models with the lowest Akaike's information criterion (AIC_C; Burnham & Anderson, 2002) to arrive at a minimum adequate model in each case. Linear models assume that errors have constant variance and are independent, but non-constant error variance has previously been found when relating climatic suitability to population size (VanDerWal *et al.*, 2009) and non-independence may arise from spatial autocorrelation (Dormann *et al.*, 2007). Accordingly, appropriate functions to account for non-constant error and non-independence were included in models if deemed necessary by AIC. In multispecies models, we also controlled for evolutionary non-independence using a phylogenetic correlation structure where possible (see Appendix S4).

RESULTS

Climate response surface models based on the three bioclimatic variables produced simulated distributions that fitted the observed European distributions of our 18 study species reasonably well (Table 1; mean bootstrapped AUC = 0.91, range = 0.81–0.98; see Fig. 1a for illustrative examples and Fig. S1 for plots of the relationship between these bioclimatic variables and the probability of presence for each species). Both metrics of goodness-of-fit (bootstrapped AUC values and percentage deviance explained) for CRS models were similar to those from the GAMs but significantly better than those from the GLMs (Appendix S2). In support of Hypothesis (i), there was a significant positive relationship between climate suitability index (CSI) derived from our CRS models and $\log_e$ breeding population sizes in occupied grid squares during 1985–1988 (LME: 1.81 ± 0.31, $F_{1,3800} = 34.3$, $P < 0.0001$), with the spatial autocorrelation structure being retained. The slope of this relationship differed, however, between species; examining each species separately, a relationship between CSI and population size was found in 50%
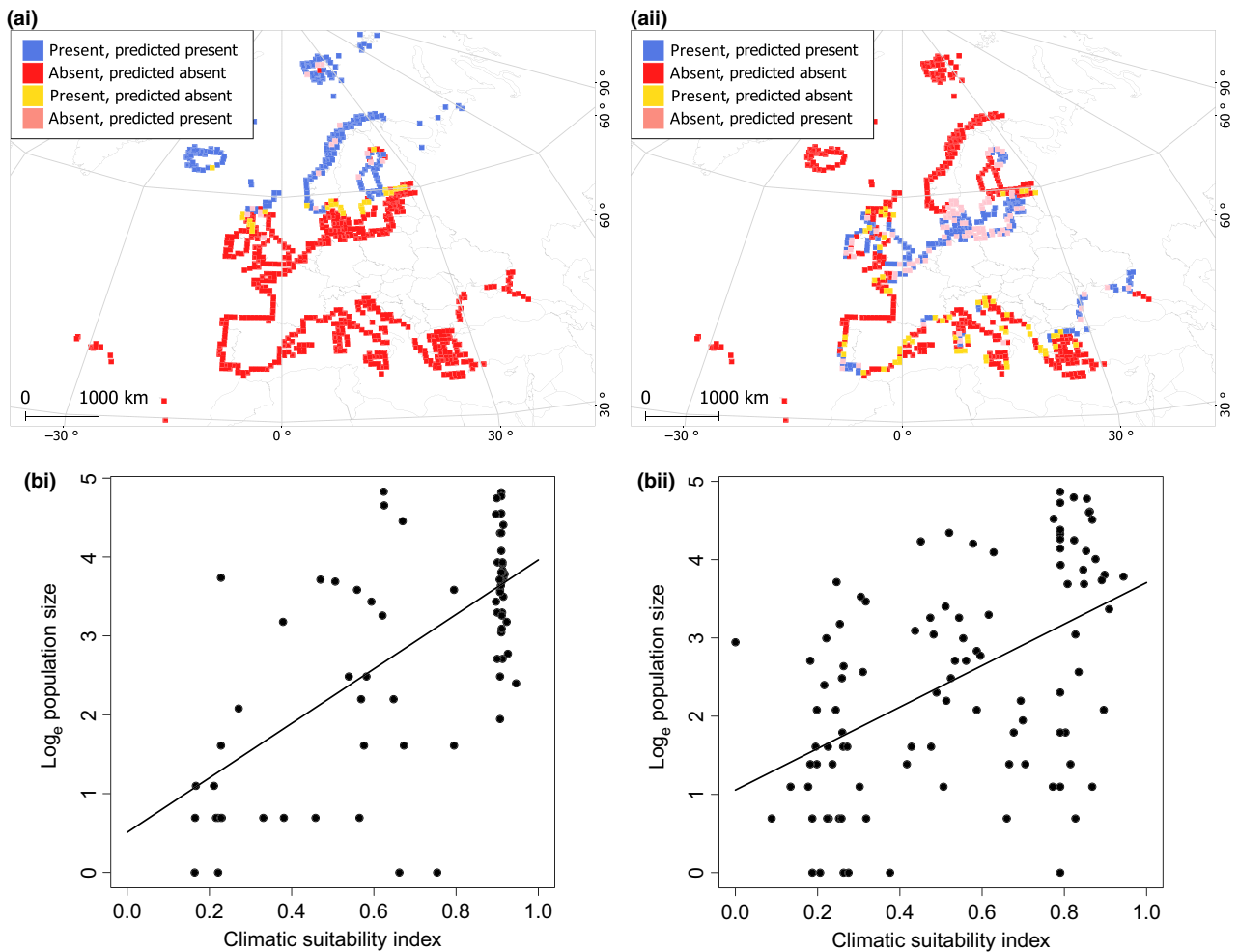
Figure 1 Example of climate response surface (CRS) for (i) Parasitic Jaeger and (ii) Little Tern: (a) match between observed and simulated distribution in 1985 based on CRS and (b) relationship between $\log_e$ population size (1985–1988) in occupied grid squares in the British Isles and local climatic suitability index obtained from CRS.

of the 18 species studied (i.e. CSI was retained by AIC_C to describe variation in $\log_e$ population size; Table 2; see Fig. 1b for illustrative examples and Fig S2 for all other species). In support of Hypothesis (ii), the species for which there was a relationship between CSI and population size were those independently considered to be most vulnerable to changes in food availability at sea as a result of their morphology and foraging ecology (Table 2; binomial GLM: $\chi^2_{1,14} = 9.12$, $P < 0.01$, $R^2 = 0.44$).

Since 1986, climatic suitability has decreased for all seabird species considered here (Appendix S3). However, there were marked differences among species in population changes between 1986 and 2010, with substantial declines (up to 57%) in several species and substantial increases (up to 77%) in others (Table 1). In support of Hypothesis (iii), the presence of a relationship between CSI and population size in 1985–1988 (Table 2) was retained to explain change in population size between 1986 and 2010 (Fig. 2; GLS; $F_{1,12} = 5.67$, $P < 0.05$). A measure of goodness-of-fit (bootstrapped AUC) of the European models was also retained in the minimum adequate

model; species with the highest AUC values have shown the least favourable population changes (Fig. 2; GLS: $F_{1,12} = 5.70$, $P < 0.05$). The overall model including both these explanatory variables explained 40% of the variation among species in the change in population size (adjusted $R^2 = 0.40$). Qualitatively similar results were found using percentage deviance explained in place of AUC (GLS $F_{1,12} = 8.98$, $P < 0.05$) with the final model explaining 50% of the variation in population trend (adjusted $R^2 = 0.50$). Using the goodness-of-fit metrics from the European-scale GAMs instead of the CRS models, both measures of conformity to climate in the mid-1980s (i.e. in terms of both distribution and abundance) were retained to explain changes in population size from 1986 to 2010. Phylogeny was not retained in any minimum adequate model and neither the frequency nor the median latitude of occupied grid squares was retained in the final models, with substantial population declines (>10%) recorded among species both with northerly distributions (e.g. Parasitic Jaeger *Stercorarius parasiticus*) and more southerly distributions (e.g. Little Tern *Sternula albifrons*; Table 1).

Table 2 The relationship between local climatic suitability index (CSI) and population sizes of seabirds in 10 × 10 km coastal grid squares in the UK and Ireland in 1985–1988, for species where visual inspection of plots indicated (a) a continuous relationship and (b) a step function. Significant relationships ($P < 0.05$) are highlighted in bold. ΔAIC_C indicates the change in AIC when CSI is included in the model. R^2 values are given only for significant relationships. Score is an index of the vulnerability of breeding success to reduced food ability in the vicinity of breeding colonies, from Furness & Tasker (2000)

(a) Species	Slope	SE	F	d.f.	P	ΔAIC_C	R^2	Score
Northern Gannet	2.14	5.68	0.14	1,5	0.72	6.8	–	5
Great Cormorant	0.92	0.98	0.88	1,155	0.35	1.29	–	7
European Shag	**3.44**	**0.94**	**13.40**	**1,365**	**<0.001**	**−9.8**	**0.04**	8
Parasitic Jaeger	**3.45**	**0.45**	**58.37**	**1,71**	**<0.0001**	**−28.7**	**0.53**	15
Great Skua	**3.94**	**0.65**	**36.16**	**1,61**	**<0.0001**	**−16.4**	**0.41**	13
Black-legged Kittiwake	**1.79**	**0.88**	**4.15**	**1,216**	**<0.05**	**−1.91**	**0.01**	16
Lesser Black-backed Gull	−1.19	2.10	0.32	1,273	0.57	1.76	–	11
European Herring Gull	−3.03	2.31	1.71	1,534	0.19	0.41	–	11
Little Tern	**2.65**	**0.46**	**33.43**	**1,98**	**<0.0001**	**−27.2**	**0.25**	21
Sandwich Tern	**5.31**	**2.29**	**5.40**	**1,51**	**<0.05**	**−2.99**	**0.09**	19
Roseate Tern	3.93	4.44	0.78	1,9	0.40	3.01	–	22
Common Murre	1.07	1.40	0.59	1,189	0.44	1.49	–	9
Razorbill	1.48	1.05	1.97	1,230	0.16	0.14	–	12
Atlantic Puffin	2.64	1.75	2.28	1,142	0.13	0.17	–	13

	Low CSI			High CSI			F	d.f.	P	ΔAIC_C	R^2	Score
(b) species	n	Mean	SE	n	Mean	SE						
Northern Fulmar	157	3.82	0.14	353	4.97	0.11	1.17	1,508	0.28	0.96	–	7
Great Black-backed Gull	**19**	**0.80**	**0.19**	**384**	**2.63**	**0.08**	**49.30**	**1,401**	**<0.0001**	**−25.76**	**0.06**	10
Arctic Tern	**183**	**3.22**	**0.14**	**80**	**5.56**	**0.23**	**8.32**	**1,261**	**<0.01**	**−4.24**	**0.24**	22
Common Tern	**10**	**0.97**	**0.22**	**195**	**3.04**	**0.12**	**69.27**	**1,203**	**<0.0001**	**−21.59**	**0.07**	20

DISCUSSION

We found a significant positive relationship between our index of local climatic suitability, generated from climate envelope models fitted to European distribution data, and local population sizes, in support of Hypothesis (i). The fact that models fitted on a 50-km resolution were positively related to population sizes at a 10-km resolution provides support for the usefulness of CEMs fitted to coarse resolution macroscale data, because population size is a key factor for persistence (Pimm *et al.*, 1988; Akçakaya *et al.*, 2006). However, climate suitability indices were not retained to explain population size for half the species we studied and the goodness-of-fit of the single species relationships we tested were not high (mean $R^2 = 0.18$, range = 0.01–0.53), as also found in recent studies of vertebrates in the Australian Wet Tropics (mean $R^2 = 0.12$; VanDerWal *et al.*, 2009) and birds and butterflies in Great Britain (mean $R^2 = 0.13$; Oliver *et al.*, 2012). Hence, while our single species CRS models predicted European presence/absence reasonably well (Table 1), we could not accurately predict population sizes in occupied grid squares with confidence. This is largely to be expected because potential abundance may not be attained at all sites (VanDerWal *et al.*, 2009), resulting in a wedge-shaped relationship between climatic suitability and population size in some cases (e.g. see Fig. 1bii). Moreover,

additional processes that can affect local population sizes, such as predation of ground-nesting species by introduced predators (Craik, 1997) and the availability of nest sites and non-marine food sources for Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* breeding in coastal towns and cities (Rock, 2005; Washburn *et al.*, 2013), were not included in our CEMs. Nonetheless, all but two species showed a positive association (Table 2), and we conclude that, on average, grid squares estimated as more suitable by CEMs supported larger local populations.

In keeping with Hypothesis (ii), we found that the ability of our occupancy models to predict local population sizes of different species was related to species' foraging ecology (Table 2). This finding suggests a tighter relationship between climate and population size among those species most affected by changes in food availability at sea, supporting a link between seabird populations and bottom-up processes affecting prey quality and availability (Wanless *et al.*, 2005; Grémillet & Boulinier, 2009).

We found that species whose distributions at a 50-km resolution within Europe conformed more closely to local climate showed less favourable subsequent changes in population size across the British Isles over a period of decreasing climatic suitability for all species, in support of Hypothesis (iii). Populations of species whose distributions and abundance in the mid-1980s conformed relatively poorly to climate increased by
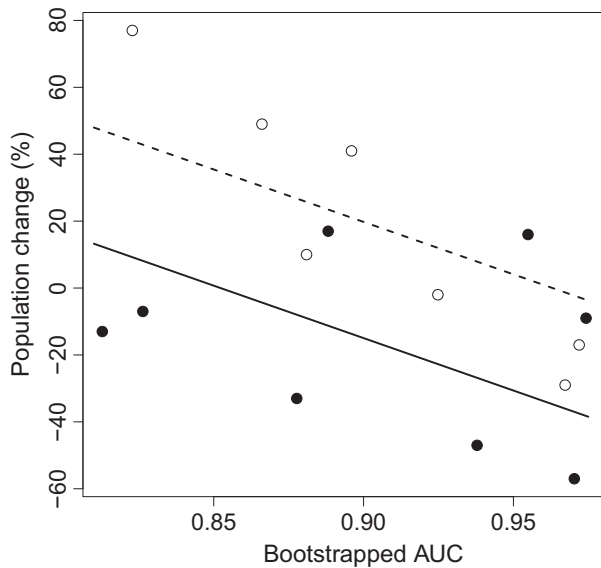
Figure 2 Relationship between the association of species' breeding distributions with climate (assessed using area under the curve of receiver operating characteristic plots (AUC) of climate response surface models) and changes in numbers of breeding seabirds in the British Isles between 1986 and 2010. Filled symbols and solid line show the relationship for species for which climate suitability index (CSI) was retained in models to explain $\log_e$ population size in 1985–1988. Open symbols and dashed line indicate the relationship for species for which CSI was not retained in the models. Data for population changes are from Table 1.

up to 77% between 1986 and 2010, continuing the long-term trend observed for most seabirds in the UK over much of the 20th century following legal protection from exploitation (Mitchell *et al.*, 2004), whereas species whose distributions and abundance conformed closely to climate reversed this trend and went into decline, by as much as 57% over 25 years. In particular, the closest relationship between climatic suitability and local population size was found in the two species of Stercorariidae studied (Parasitic Jaeger and Great Skua; R^2 values of 0.53 and 0.41, respectively; Table 2) and Parasitic Jaegers have probably declined more than any other seabird species in the UK over the last 25 years, with the population in 2012 estimated to be 81% lower than in 1986, which is likely to be in part due to decreasing climatic suitability (JNCC, 2014). Although data were not available for changes in Great Skua population size between 1986 and 2010, there is evidence that their historical increase in population sizes has slowed, with increases between 1969 and 1985 being much greater than between 1986 and 2002 and evidence of some sharp regional declines since then (Meek *et al.*, 2011). These findings further support the use of CEMs in assessing species' future vulnerability to climatic change (González-Megías *et al.*, 2008; Maclean & Wilson, 2011) and agree with studies of terrestrial birds where population sizes (Oliver *et al.*, 2012) and trends (Green *et al.*, 2008; Gregory *et al.*, 2009; Renwick *et al.*, 2012) were related to outputs from CEMs.

In our study, almost half the variation in changes in population size was explained by how closely European distributions and population sizes in the British Isles conformed to spatial variation in climate, indicating that climatic change is already having a discernible negative effect on the assemblage of seabird species in the British Isles. This finding supports the conclusions from detailed studies of annual variation in demographic parameters for some species at individual breeding sites on the west coast of the UK (Riou *et al.*, 2011), in the North Sea (Thompson & Ollason, 2001), and further afield (Irons *et al.*, 2008). However, effects may also vary regionally; for example, Frederiksen *et al.* (2007) found that the breeding productivity of Black-legged Kittiwakes *Rissa tridactyla* in Britain and Ireland was negatively correlated with winter SST but that this relationship varied geographically, reflecting regional variation in both means and trends of winter SST. Our correlative approach was unable to elucidate directly the mechanisms driving changes in populations, but for seabirds, these include both indirect effects of changes in prey quality and availability (Wanless *et al.*, 2005; Grémillet & Boulinier, 2009) and direct physiological effects on breeding adults (Oswald *et al.*, 2008, 2011), both of which were reflected in our choice of bioclimatic variables.

In conclusion, our data reveal an influence of climate on the population sizes of many seabird species across the British Isles, with broader implications for climate envelope model studies. Previous authors have tested the viability of using climate envelope models to predict changes in species' distributions by examining their ability to predict occupancy in an area different from that used to fit the models (space-for-time substitutions: e.g. Beerling *et al.*, 1995; Blois *et al.*, 2013; Lester *et al.*, 2014). Here, our tests for each species involved predictions within a subset of the overall study area, at a finer resolution and using a different demographic parameter (population size) than that used to fit the models. Our findings provide support that at least for some species, models generated using macroscale occupancy data are capable of predicting both fine-scale spatial variation in population sizes and temporal trends in abundance at national level over a period of 25 years. However, for most species, there was not a close-fitting relationship between local population sizes and climate, suggesting that while climate envelope models based on occupancy data can be very effective in identifying those species most at risk from climate change, they should be used only with caution to predict changes in local abundance. A more stringent test of these models would be whether changes with time in population sizes within individual 10-km grid squares are significantly related to changes in our index of climate suitability, and it should be possible to investigate this following the next national seabird population survey, which is scheduled for around 2016.

ACKNOWLEDGEMENTS

their data on distributions and population sizes, respectively. We thank G.McInerny for helpful discussion. DJFR was supported by NERC UKPopNet, and BJA was also supported by NERC. We thank the referees for their insightful comments, which greatly improved the manuscript. The Joint Nature Conservation Committee is the statutory advisor to the UK Government and devolved administrations on UK and international nature conservation. Its work contributes to maintaining and enriching biological diversity, conserving geological features and sustaining natural systems. JNCC delivers the UK and international responsibilities of the Council for Nature Conservation and the Countryside (CNCC), the Natural Resources Wales (NRW), Natural England (NE) and Scottish Natural Heritage (SNH). SMP data are generously contributed to the scheme by its many partners, other organizations and volunteers throughout the British Isles.

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SUPPORTING INFORMATION

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

Appendix S1 Use of AUC to assess model performance.

Appendix S2 Comparison of different methods for fitting CEMs.

Appendix S3 Temporal changes in climatic suitability.

Appendix S4 Phylogenetic relationships.

Appendix S5 The relationship between bioclimatic variables and presence.

Appendix S6 The relationship between $\log_e$ population size and climate suitability index.

Table S1 Deviance explained and bootstrapped AUC values for European models.

Table S2 Temporal changes in climatic suitability.

Figure S1 The relationship between bioclimatic variables and presence.

Figure S2 The relationship between $\log_e$ population size and climate suitability index.

BIOSKETCH

Deborah J. F. Russell is interested in using both frequentist and Bayesian techniques to model the interactions between marine predators and their changing environment. She conducted her PhD 'Modelling the Effects of Climatic Variation on British Seabirds' at the University of Leeds.

Author contributions: K.C.H., B.H., S.W., J.R. and D.J.F.R. conceived the study; D.J.F.R., Y.C.C., B.J.A. and C.B. compiled and analysed the data; and D.J.F.R., K.C.H. and S.W. wrote the paper.

Editor: Jane Elith