Seabird abundances projected to decline in response to climate change in Britain and Ireland

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ABSTRACT: Estimating species' vulnerability to climate change is a key challenge in conservation. Many seabird species are particularly sensitive to the negative effects of warming and are thus threatened by climate change. We projected seabird abundance in 2050 in Britain and Ireland, an internationally important region for seabirds, under climate change scenario RCP8.5. Our projections were based on fitted relationships between abundance and both climatic (air temperature, precipitation) and oceanographic (sea surface temperature, potential energy anomaly) variables, estimated using a Bayesian hurdle model with spatial random effects. The most consistent responses to environmental variables were negative relationships between species presence or abundance and breeding season maximum terrestrial air temperature. Although data and modelling issues meant that future projections could be made for only 15 of the 25 species and with low predictive power for spatial abundance, predictive power was high for spatial presence and moderate for temporal abundance change. Projections suggest that seabirds will generally fare poorly under climate change in Britain and Ireland, with 10 species projected to decline in abundance by 2050. Variable model fit and projection uncertainty limited confidence, which was generally greater for declines than for increases. Fulmar, puffin and Arctic tern were each projected to decline by over 70 % with higher confidence. For a few species, colonisation of new areas may reduce projected losses, but this is potentially limited by low availability of suitable habitat. Projected abundance change was more negative for marine specialists than for generalists. Our findings highlight the vulnerability and conservation needs of seabirds in a changing climate.

KEY WORDS: Population declines · Conservation planning · Climate change vulnerability · Oceanographic variables · Bayesian model

1. INTRODUCTION

Globally, climate change is one of the 3 main threats to seabirds (Dias et al. 2019). A number of long-term studies have already documented significant climate change impacts on seabird species that breed in Britain and Ireland (Frederiksen et al. 2004, Harris et al. 2013, Perkins et al. 2018), a region which supported nearly 8 million breeding seabirds from 25 species at the start of the 21st century (Mitchell et al. 2004). Seabird species can differ greatly in their sensitivity to climate change, and so the risk of extinction from climate change is expected to contribute importantly to species' over-

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all extinction risk, adding to and interacting with other threats (e.g. invasive alien species and by-catch; Dias et al. 2019). Consequently, it is important to predict species' responses to future climate change in order to identify those that are most at risk and inform conservation planning (Foden et al. 2019, Bateman et al. 2020).

Climate change impacts on seabirds occur through a wide range of mechanisms, but for many species, oceanographic changes are key, particularly processes relating to warming of the water column. Such warming, mediated both by consequent changes in sea surface temperature (SST) and stratification, can affect primary productivity, altering the strength, timing and composition of the spring phytoplankton bloom (Scott et al. 2006, Bedford et al. 2020). This, in turn, can impact the abundance, size and availability of key fish prey species, such as lesser sandeels *Ammodytes marinus* (Johnston et al. 2021), reducing seabird breeding success (Carroll et al. 2015, Searle et al. 2022), survival rates (Harris et al. 2013) or both (Piatt et al. 2020). Additionally, seabirds typically exhibit limited capacity to respond to phenological changes (mediated by SST) in their prey (Keogan et al. 2018).

In addition to oceanography, seabirds are vulnerable to change in atmospheric climate. The effects of air temperature on seabirds are best known from the breeding season, with air temperature influencing productivity and/or adult survival through direct or indirect mechanisms (Bukaciński & Bukacińska 2000, Oswald et al. 2008, Gaston & Elliott 2013, Indykiewicz 2015). The effects of rainfall and storminess on seabird demographic rates can operate both on productivity (Thompson & Furness 1991, Newell et al. 2015) and adult survival (Frederiksen et al. 2008, Morley et al. 2016).

Several studies have forecasted that climate change will drive changes in seabird abundance or distribution in Europe. Although focussed solely on Special Protection Areas (SPAs) within the UK, Johnston et al. (2013) found that generally negative associations between both summer temperature/ rainfall and seabird abundance at colonies are projected to result in an overall seabird abundance decline of approximately 50% by 2080 under a high (A1F1) climate change scenario, with declines of more than 50% projected for 7 out of 17 species. Russell et al. (2015) projected that the range extent of 65% of seabird species that breed in Britain would decline across Europe, with Leach's storm-petrel *Oceanodroma leucorhoa*, great skua *Stercorarius skua*, Arctic skua *S. parasiticus*, black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'), Arctic tern *Sterna paradisaea* and auks being particularly vulnerable. Häkkinen et al. (2023) projected that for all but one of the 48 seabirds assessed, a greater proportion of the current European breeding area will decline than increase in climatic and oceanographic suitability by 2070–2100. These studies support the climate envelope modelling of Huntley et al. (2007) across Europe which suggested that the breeding ranges of many seabird species in Britain and Ireland would shift northwards by the end of the 21st century, resulting in the potential extirpation of a number of species in Britain and Ireland. Although much of the impact of climate change on seabirds is expected to be mediated through oceanography (e.g. Searle et al. 2022; see Johnston et al. 2021 for an overview), future projections of seabird abundance or distribution in the NE Atlantic (except for Russell et al. 2015 and Häkkinen et al. 2023, which respectively predicted distribution and climate/oceanography suitability alone; Häkkinen et al. 2021 did not make future projections) have been based solely on atmospheric climate. For the 3 seabird species studied (Atlantic puffin *Fratercula arctica*, hereafter 'puffin', northern gannet *Morus bassanus*, hereafter 'gannet', and roseate tern *Sterna dougallii*), Häkkinen et al. (2021) found that the best-performing species distribution models used both atmospheric and oceanographic information.

In this study, we use a Bayesian hurdle model to estimate the relationship between spatial and temporal variation in seabird abundance in Britain and Ireland and oceanographic and climate variables. Using the fitted relationships, we then predict future changes in abundance to 2050 as a result of projected changes in both climate and oceanography. By specifically projecting the impacts of climate change on abundance, we produce outputs directly relevant to modelling future extinction risk and species' conservation assessments (Thomas et al. 2011, Massimino et al. 2017). Species' relationships with climate may result from a combination of their physiology, ecology and behaviour (Mitchell et al. 2020); for example, surface-feeding species may be more vulnerable to impacts on food availability due to their reduced foraging flexibility (Furness & Tasker 2000). In order to help understand species' relationships with climate and oceanography, we also examine species' fitted relationships with climate and oceanography and assess whether they vary according to species' feeding ecology and habitat specialism.

2. MATERIALS AND METHODS

2.1. Seabird abundance data

Seabird breeding populations around Britain and Ireland have been counted through periodic censuses, of which Seabird Colony Register for 1985–1988 (hereafter 'SCR Census'; Lloyd et al. 1991) and Seabird 2000 for 1998–2002 (Mitchell et al. 2004) were included in the analysis. Data from the most recent census, Seabirds Count (2015–2022) are not yet available for analysis. Although neither the SCR Census nor Seabird 2000 achieved complete coverage of all seabird breeding sites and there were differences in coverage (e.g. inland sites were more completely covered in the latter; Mitchell et al. 2004), collectively they provide robust data on spatial and temporal variation (albeit only 2 temporal replicates) in seabird abundance during the second half of the 20th century. The Seabird Monitoring Programme provides annual monitoring data from a subset of colonies extending back to 1986 (JNCC 2020), but due to the incomplete nature of these data (only a small non-random subset of colonies is counted) and the fact that they generally do not provide full colony counts, they were not used.

Data were included for all census-sites in Britain, Ireland, Channel Islands and Isle of Man (hereafter 'Britain and Ireland'): 5657 in the SCR Census and 1968 in Seabird 2000 (many 'sites' in the SCR Census became 'sub-sites' in Seabird 2000), and for all species with a minimum of 10 breeding pairs in total (25 species; Section S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m725p121_supp.pdf). Counts for Manx shearwater *Puffinus puffinus*, Leach's storm-petrel and European storm-petrel *Hydrobates pelagicus* (hereafter storm-petrel) in the SCR Census were based on expert assessment rather than surveys due to the high level of uncertainty in the count methods at that time (Mitchell et al. 2004), and so the SCR Census data were omitted from the present study for these species.

The spatial resolution of all data sets was aligned to that of the UKCP18 atmospheric climate data (12 × 12 km cells). Seabird abundance for each census period was taken as the summed abundance for each species within each cell. When a census-site spanned more than one cell (affecting 282 counts in SCR Census and 1667 counts in Seabird 2000), the count for that census-site was divided among those cells in proportion to the length or area of the site spanning those individual cells and rounded to the nearest integer.

There is likely to be some unknowable location error in the seabird abundance data because in each of the censuses, the breeding locations of individual seabirds were allocated into census-sites of variable spatial extent. Some census-sites were also differently defined between the censuses. As a result, it is possible that some apparent abundance change at the site level between censuses was due to differing spatial definitions of sites (e.g. if a site in a given cell in the SCR Census was subsumed into a larger site in Seabird 2000, and the central coordinates of the Seabird 2000 site fell in a different cell). These issues introduce unavoidable error into the spatial and temporal seabird–abundance–environment relationships. However, we consider these issues to be quite minor because (1) most counts came from relatively small census-sites (79.6 and 83.9% of counts came from census-sites with a length of <2 km in SCR Census and Seabird 2000, respectively) and (2) few counts came from sites that spanned multiple cells (2.1 and 6.8% in SCR Census and Seabird 2000, respectively).

All data preparation and analysis were carried out in R version 4.2.1 (R Core Team 2022).

2.2. Seasonal delineation of environmental data

Climate can influence seabird population growth rate through either productivity or survival or through both (Sandvik et al. 2012). In selecting climatic and oceanographic variables, we chose variables which might influence seabird abundance through productivity and mortality (Johnston et al. 2021), focussing on environmental variables operating at or near the breeding colony. Climate change in the wintering areas is likely to influence seabird abundance, but there is limited information available on the precise areas where Britain and Ireland seabirds winter and how wintering areas differ between individual breeding colonies or census-sites (Buckingham et al. 2022). However, although many species of seabird are only present at the colony during the breeding season, wintering conditions around the breeding sites are still likely to influence seabird demography; for example, through changes in local prey (Frederiksen et al. 2007, Ramos et al. 2013) or by influencing the availability of breeding sites (e.g. winter rainfall damaging burrows). Therefore, we incorporated atmospheric climate and oceanographic data from both the breeding season and non-breeding season, but only at the sites where breeding takes place.

Seabird species differ in the timing of their breeding seasons and, thus, in the time period over which

environmental variables can affect productivity or potentially affect mortality after the breeding season (e.g. mediated by post-breeding condition). In order to account for this variation, breeding-season environmental variables were summarized for each species (Table S1). Species-specific breeding seasons were defined as the months during which eggs or chicks can be present, as described by Campbell & Ferguson-Lees (1972). No data were available from this source for the breeding season for the Mediterranean gull *Ichthyaetus melanocephalus* in Britain and Ireland, so the breeding season for the closely related black-headed gull *Chroicocephalus ridibundus* was used for this species.

2.3. Climate variables

In common with other studies (Johnston et al. 2013, Russell et al. 2015), we used air temperature and precipitation as proxies of relevant variation in atmospheric climate; both variables can influence seabird population growth rate through productivity and survival (Johnston et al. 2021). Observed maximum monthly temperature, minimum monthly temperature and total monthly precipitation data were derived from Had-UK (Met Office et al. 2019) and Met Éireann (Met Éireann 2020) interpolated data sets at 1 km resolution and aggregated to the cell scale. Modelled atmospheric climate variables for 1980–2080 for the same variables were derived from Met Office UKCP18 data (Met Office Hadley Centre 2018b). For the UKCP18 data, projections were available from 12 different global and regional models; there was no *a priori* reason to select any one of these runs, so the median was taken for each of the 3 monthly variables across the 12 projections.

Given that seabirds are long-lived species, we assume that climate influences abundance through its effects on several consecutive years of productivity and survival, rather than instantaneously influencing abundance solely in the census year. Therefore, atmospheric climate data were averaged over the 5 yr up to the median year of each census (1986 and 2000 respectively). A small number of counts (one Arctic skua count in the SCR Census; one Manx shearwater count and 5 storm-petrel counts in Seabird 2000) took place more than 5 yr before the median year of each census. Although these counts are therefore technically related to future climate, given strong temporal autocorrelation in both abundance and climate, the counts were left in the data set.

From these data, 4 climate variables were derived, summarizing winter and breeding season temperature and precipitation, respectively (see Table 1). Given that there is evidence that changes in the extremes of climate are more influential than climate means on the trajectory of bird populations (Pearce-Higgins et al. 2015), atmospheric climate variables were designed to encapsulate the minimum or maximum possible values to identify summer heat, winter cold and extremes of precipitation.

2.4. Oceanographic variables

The relative importance of different oceanographic variables in driving seabird abundance, distribution and demographic parameters is still not fully understood; however, the most commonly included variables in such analyses are bathymetry and SST (Nur et al. 2011, Satterthwaite et al. 2012, Carroll et al. 2015). Many studies also include an index of stratification — either its strength, phenology or both (Bertrand et al. 2014, Trevail et al. 2019). Potential energy anomaly (PEA) is a proxy measure of ocean stratification, describing the energy required to fully mix a column of water: more intensively stratified water columns have higher PEA values.

SST and PEA were derived from the Scottish Shelf Model (SSM) (De Dominicis et al. 2018, 2019), which covers much of Britain and Ireland waters at variable spatial resolution, with the highest resolution in inshore waters (as low as 1 km node spacing at the coastline). These were the only oceanographic data available that have the same timestep and greenhouse gas concentration scenario as the UKCP18 projections, allowing seabird abundance projections that incorporate both oceanographic and climate variables. However, unlike the climate data, the historical SSM data are modelled rather than directly observed (see De Dominicis et al. 2018, 2019 for more details). The variables were averaged (weekly mean) over the periods 1990–2014 and 2038–2062. The original data, being of variable spatial resolution on an unstructured grid, were aggregated (by mean) to the same cell size used as the seabird abundance and atmospheric climate data. Historical SSM data were only available from 1990 to 2014 and therefore did not overlap with the SCR Census time period (1985–1988), so were left blank for the SCR Census counts. These data also span beyond the period of the Seabird 2000 census, but we regard them as likely to be indicative of the spatial variation present across the study area given

strong temporal and spatial covariation. This means that the oceanographic variables only relate to spatial variation in presence and abundance from Seabird 2000, rather than (as for the climate variables) also accounting for temporal variation between the 2 censuses.

In our study area, the PEA of waters on and off the Scottish continental shelf differs by several orders of magnitude because the deeper waters off the continental shelf require more energy to become fully mixed, by definition. To avoid bathymetry dominating PEA values, PEA values were omitted for deeper (>200 m deep) waters (see Section S2, Fig. S1). The foraging range for some species/colonies overlapped the continental margin and abyssal plain: for these species/colonies, therefore, the value of the PEA variable only summarises the PEA of the area of that foraging range overlying the continental shelf. SSM data were not available for some distant locations beyond the continental margin, and so there were additionally missing values for SST for those locations.

The area of ocean used by individuals at a given colony varies considerably between different seabird species (Table S1), and so the 12 km cell scale was not necessarily the scale at which oceanographic variables are relevant to seabirds: for example, species may forage far beyond the cell extent. Each oceanographic variable was thus averaged over species-specific foraging ranges, derived from the review by Woodward et al. (2019). Mean maximum foraging ranges were available for all species other than Arctic skua and Leach's storm petrel; for these species, we used the estimates from the earlier review by Thaxter et al. (2012), which were based upon observed distance from shore rather than distance from colony (Table S1). For a given cell and species or oceanographic variable, the mean was taken of all values for that oceanographic variable over the species' mean maximum foraging range, weighted by the reciprocal of distance (distance + 0.1 km to avoid dividing by zero) of the oceanographic variable points from the midpoint of the cell.

2.5. Other environmental data

Bathymetry data (depth of water column in m) were derived from UKCP09 marine projections data (Hadley Centre for Climate Prediction and Research 2017). Although projections are available for sea level rise, this is predicted to be of the order of tens of cm within the study area over the 21st century (Met Office Hadley Centre 2018a), while the bathymetry data are in metres. Therefore, the same bathymetry data were used for the historical and future periods. Bathymetry data were averaged over a species' foraging range (as in Section 2.4).

Although climate is known to affect seabird distribution and abundance, fine-scale spatial variation in seabird abundance is caused by many other processes. Most simply, whilst many of our study species solely or mostly breed at the coast or on small islands, some also breed extensively inland. Therefore, we include 3 nuisance environment variables to account for spatial variation in seabird abundance: 'coastal', whether a cell was entirely more than 5 km from the coast; 'islands', whether a cell contained any islands that were less than 15 km^2 in area; and 'coastline length', the length of coastline within a cell (calculated using function 'gLength' in the R package 'rgeos' version 0.5-9; Bivand & Rundel 2021). It is worth noting that these nuisance variables will be poor descriptors of the physical variables likely to influence seabird abundance at this scale, particularly features of cliff height and length that cannot easily be derived from large-scale data sets in a way that is relevant for each species. This means that we expect our models to be relatively weak predictors of spatial variation in seabird abundance for species where such features are important, but that this does not necessarily mean that they will not be good predictors of the overall climatic component of such distributions (Johnston et al. 2013).

2.6. Modelling approach

Seabird abundance was related to environmental variables for each species individually. The fitted model was then used to project future seabird abundance in 2050, using projected atmospheric climate and oceanographic data for 2050 under the greenhouse gas concentration scenario Representative Concentration Pathway (RCP) 8.5. The RCP scenario framework was used rather than the Shared Socioeconomic Pathway framework because at the time of analysis, more relevant climate and oceanography data sets were available that used RCP scenarios. RCP8.5 represents the most aggressive future greenhouse gas concentration scenario, being equivalent to approximately 2°C global warming by 2050 compared to 1986−2005 levels (IPCC 2014), and is the scenario most consistent with the current global trajectory (Schwalm et al. 2020). Predictions were then made from these models at the Britain and Ireland scale.

Seabird abundance should be subject to both intrinsic and extrinsic causes of spatial autocorrelation (Beale et al. 2010). To infer the relationship between climate, oceanography and seabird abundance while properly accounting for spatial autocorrelation, we fitted spatial models using integrated nested Laplace approximation (INLA) (Rue et al. 2009). INLA fits models in a Bayesian framework; but by estimating (rather than sampling from) the posterior distribution, INLA provides major gains in computational efficiency compared to traditional Markov chain Monte Carlo (MCMC; a class of algorithm that generates samples from the posterior distribution) methods for fitting spatial models to large data sets. In order to account for spatial autocorrelation, we modelled seabird abundance as a function of both fixed effects (environmental variables) and a spatial random effect (see Section S3 in the Supplement).

Zero counts were inconsistently recorded in the seabird censuses. Actual zeros were rarely recorded: they represent 2.6% of all recorded counts (representing 1.9% of cells) in the SCR Census, and 11.2% of all recorded counts (representing 5.6% of cells) in Seabird 2000. The proportion of counts recorded as zero varied considerably between species. It is unclear how surveyors would decide between recording an absence as a zero or as a blank (information is not provided on this in Mitchell et al. 2004). Following Johnston et al. (2013), we assumed that in general, given that the periodic seabird censuses aim to count all seabirds at all sites present, species were not present at census-sites at which they were not recorded. We consider this assumption to be relatively inconsequential for our inference, being least valid for the few species which moved colonies between years or which could only be surveyed by tape-playback.

The available data set for a given species in a given census therefore consisted of count data (mostly positive but some zeros) for some cells and non-count data (i.e. zeros) for all remaining cells containing seabird census-sites; for all species, the non-count data constituted a larger proportion (sometimes >99%) of the total available data set than the count data. A hurdle model was therefore used (Sadykova et al. 2020); this separately models presence–absence (with a binomial likelihood) and abundance-given-presence.

Preliminary data exploration revealed that the count data were over-dispersed, presumably due to aggregation effects from colonial breeding. The negative binomial distribution, which includes a parameter for over-dispersion, was considered more appropriate than the Poisson distribution. Therefore, a zero-truncated negative binomial likelihood was used for the abundance-given-presence component of the hurdle model. Presence and abundance-given-presence were assumed to be driven by slightly different processes, and so parameters for the explanatory variables and spatial random effect were estimated separately for the 2 model components. To account for potential non-linear relationships (Hansen et al. 2021), both linear and quadratic terms were included in the full model for all continuous variables. The full model therefore comprised 9 environmental covariates, 9 quadratic terms for the environmental covariates and 3 nuisance variables (Table 1).

Default priors (as per the R-INLA package version 22.5.07) were specified for the fixed effects in the model. The priors for the Matérn covariance function of the spatial random effect were specified according to its empirical range r and marginal standard deviation σ (Bakka et al. 2018). Reasonably vague prior parameters were given: $P(r > 0.3) = 0.5$; $P(\sigma > 10) = 0.01$. Coordinates and environmental covariates were scaled to mean 0 and standard deviation 1 before inclusion in the model, to avoid numerical issues. Models were fitted in R-INLA (Rue et al. 2009), accessed through R.

Abundance data were used from both censuses, and so there were repeated measures at census-sites that were surveyed in both censuses. However, there was not enough repeated sampling (only 2 census periods) to estimate the parameters of an additional random effect for cell. Although this is unlikely to affect the estimates of the coefficients, it may result in their precision being over-estimated.

2.7. Model diagnostics and validation

Success of model convergence was assessed using the Kullback-Leibler distance (KLD) of each parameter. KLD measures the ability for the normal distribution to approximate the posterior probability distribution for a given parameter and should be close to zero if successful.

By way of validation, the ability of the model to predict withheld data was assessed for each species using presence and abundance data from just 70% (randomly selected) of the census-sites (the 'spatial fine-scale predictive ability assessment'). Using the fitted model, the species' presence and abundance was then predicted at the remaining 30% of the census-sites. The predictive performance of the model

Table 1. Environmental variables included in models of seabird abundance. For a given cell, all oceanographic variables were left blank if no ocean-containing cells were within the foraging area. SST: sea surface temperature; PEA: potential energy anomaly

Variable category	Shorthand	Calculation
Climate	Winter minimum temperature	Five year December–February mean minimum monthly temperature
	Breeding season maximum temperature	Five year mean maximum temperature of (yearly) warmest month in species-specific breeding season
	Winter precipitation	Five year mean total December–February precipitation
	Breeding season precipitation	Five year mean total precipitation of (yearly) wettest month in species-specific breeding season
Oceanography	Winter SST	Distance-weighted-mean 24 yr mean December–February SST within species-specific foraging area
	Breeding season SST	Distance-weighted-mean 24 yr mean SST over species-specific breeding season within species-specific foraging area
	Winter PEA	Distance-weighted-mean 24 yr mean December–February PEA within species-specific foraging area
	Breeding season PEA	Distance-weighted-mean 24 yr mean PEA over species-specific breeding season within species-specific foraging area
Other	Bathymetry	Distance-weighted-mean depth of water within foraging area
	Coastal	Whether cell was entirely (0) >5 km from the coast or not (1)
	Islands	Whether cell contains any islands of <15 km^2 area (1) or not (0)
	Coastline length	Length of coastline (km) within cell

was assessed by (1) the area under the curve (AUC; the discrimination ability of a classifier) of the receiver operating characteristic for the predicted and observed presences and (2) the R^2 of the relationship between the predicted and observed abundances. These statistics varied depending on the random sample of census-sites withheld, so the median of each statistic was taken over 20 model runs (enough iterations for the median to converge in preliminary analyses). We define 3 discriminatory ability categories for AUC: moderate (0.7–0.8), good (0.8–0.9) and excellent (>0.9). Following Pearce-Higgins et al. (2011), we define 4 predictive ability categories for R^2: very poor (<0.01), poor (0.01–0.06), moderate (0.06–0.25) and good (>0.25). Model fit as assessed in this way is not necessarily an estimate of the proportion of variation in the response variables explained by the fixed effects alone because some of the variation in the response variables is explained by the spatial random effect. Our estimates of predictive ability may be underestimates because oceanographic data were not available for the SCR Census timestep, and so predictions for this timestep were made solely on the basis of the terrestrial and nuisance variables.

2.8. Prediction

Predictions were made using the full model (using all data, rather than the validation model) for each species. Models typically mis-predicted known species abundance (assessed by conditional predictive ordinate, equivalent to probability density) in a given cell. For some species, there was overprediction at low population sizes. This overprediction probably arose because seabird abundance is likely to be spatially autocorrelated in multiple different ways: seabirds can form dense aggregations at very local scales (for example, there may be tens of thousands of a species within a few hundred metres at one census-site, but few or none at any other census-site for tens of km around), while dispersal between colonies and/or associations with autocorrelated environmental variables (not all of which are necessarily accounted for in our explanatory variables) can smooth abundance at larger spatial scales. For some species, the single spatial random effect we used in the abundance model may be insufficient to account for all of these sources of aggregation; the dominant effect could be of excessive smoothing, meaning that the modal expected value is too high, causing overpre-

diction at low population sizes. Similarly, given that we aggregated by 12 km cell, thus smoothing some of the local aggregation effects, this could be viewed as an overdispersion issue, and the negative binomial error structure we used is not necessarily flexible enough to generate the extreme variation of seabird abundance data. In preliminary analyses, we attempted to address these issues using multiple spatial random effects or an independent and identically distributed random effect, but these potential solutions were not successful.

Because of these issues, we estimated future abundance by multiplying observed abundance at Seabird 2000 by the predicted change in abundance (i.e. predicted abundance in 2050 / predicted abundance in 2000). To further improve comparability, UKCP18 modelled data were used for predicting abundance in both 2000 and 2050 (rather than using observed HadUK and Met Éireann data for predicting abundance in 2000), thus ensuring all the projected changes in seabird abundance were due to projected changes in climatic and oceanographic variables rather than potential differences between observed and projected values.

To predict abundance and associated uncertainty at individual sites, a frequency distribution of predicted change in abundance was generated for each cell. This was done by sampling 1 random draw x and y from the posterior distributions of the predicted abundance in 2000 and 2050, respectively, and then by dividing y by x. This calculation was repeated 10 000 times for each cell to derive a frequency distribution of predicted change in abundance for that cell. The observed abundance in 2000 was multiplied by the 2.5th, 50th and 97.5th percentile of this frequency distribution to give the median abundance (with confidence interval) for each cell. This abundance (and confidence interval) was apportioned among the constituent census-sites in the cell proportionally according to the relative size of their counts during Seabird 2000. Where a given census-site spanned more than one cell, the predicted abundance (and confidence interval) for that census-site was summed across the cells it spanned.

Our approach — using environmental variables to explain largely spatial variation in seabird abundance and then forecasting future abundance changes based on likely future climate scenarios — assumes that drivers of spatial change are also drivers of temporal change. As this assumption is not self-evident, given the issues with predicting fine-scale spatial variation in seabird abundance, and given that the aim of the work was to project overall temporal population change, we assessed the ability of the model to predict temporal population change. We carried this out by, for each species, summing predicted and observed abundance across all withheld cells (for a different random sample of withheld cells for each species), for SCR Census and Seabird 2000, respectively. This then gave predicted and observed (one value for each) proportional change in aggregated abundance. These values were then correlated across species. Our assessment may underestimate our models' ability to predict temporal change because oceanographic data were not available for the SCR Census timestep, and so predictions for temporal population change between SCR Census and Seabird 2000 (but not predictions of future temporal population change) were made solely on the basis of terrestrial climate variables. This assessment is hereafter called the 'temporal large-scale predictive ability assessment', to contrast with the 'spatial fine-scale predictive ability assessment' described in Section 2.7.

Focussing on abundance change solely at sites where a species was present during Seabird 2000 ignores the capacity for colonisation, which can compensate for declines or enhance increases in abundance. As a metric of the capacity for colonisation of new sites, we also present the median predicted change in presence probability across cells unoccupied during Seabird 2000. This metric should only be considered a maximum capacity for colonisation because not all of the unoccupied area is potentially colonisable by all species; for example, due to variation in breeding habitat suitability (presence of cliffs, shorelines of suitable substrate etc. which are not mappable across the study area).

2.9. Variation in climate–seabird relationships with feeding ecology and habitat specialism

We assessed whether species' fitted relationships with climate and oceanography varied with feeding ecology and habitat specialism. We defined 2 categories of feeding ecology, capturing whether species feed in the water column or benthos: 'diving species', species that mainly do so; and 'surface-feeding species', species that rarely or never do so (OSPAR Commission 2016). We defined 2 categories of habitat specialism, capturing whether species feed in terrestrial or freshwater habitats: 'marine specialists', species that never do so; and 'habitat generalists', species that sometimes do so.

For each climate or oceanographic variable, for each hurdle model sub-component (presence–

absence or abundance), a *t*-test was carried out with the parameter estimate as the response variable and feeding group or habitat specialism as the explanatory variable. Because some species were more closely related than others, and thus were potentially not independent in their relationships with climate and oceanography, a phylogenetic covariance structure was used in the linear model. A phylogenetic tree was averaged from 1000 Ericson backbone trees (trees downloaded from www.birdtree.org, accessed 8 March 2021; Jetz et al. 2012). The model was fitted using 'MCMCglmm' (Hadfield 2010).

3. RESULTS

3.1. Model performance and fit

Model results are not presented for species for which there was fewer than one occupied grid-cell per parameter (gannet, Leach's storm-petrel, Manx shearwater, roseate tern and Mediterranean gull) or for great skua, for which the model did not run successfully (deviance information criterion was negative infinite). For the remaining 19 species, KLD (approximately a measure of parameter convergence; see Section 2.7) was less than 0.1 for all parameters for all models, indicating that the models converged.

For 4 further species with the fewest data (<4 grid-cells of presence and abundance per parameter; Arctic skua, little tern *Sternula albifrons*, Sandwich tern *Thalasseus sandvicensis* and storm-petrel), model behaviour differed to that of more data-rich species. These species had the 4 highest median parameter estimates (range: 0.34–1.23; range of remaining 11 species: 0.12–0.29), and the 4 highest absolute estimates of Seabird 2000 population size, some of which were extremely high (predicted–observed Seabird 2000 population size: range: $9.87–1.35 \times 10^{57}$; range of remaining 15 species: 0.83–4.21). We considered these unusual statistics to be indicative of much lower reliability, particularly given the lack of data for these 4 species; therefore, projections for these 4 species are provided only in Section S4 in the Supplement. Results (projections, and subsequent analysis of projections and parameter estimates) are presented here solely for the remaining 15 seabird species.

For 2 species, the projected median change in presence probability across cells occupied in 2000 has an absolute value of greater than 5% and is of the opposite sign to the projected Britain and Ireland abundance change. For black-headed gull, presence

probability in occupied cells is projected to decline while abundance is projected to increase; for cormorant *Phalacrocorax carbo*, presence probability in occupied cells is projected to increase while abundance is projected to decline. It is difficult to conceive of a plausible ecological scenario consistent with these opposing projections; therefore, for these 2 species, the poorer model fit of the abundance component may mean that the opposite projected trend in presence probability is more likely.

In the spatial fine-scale predictive ability assessment, presence–absence was predicted with good or excellent accuracy, with AUC (classification ability; see Section 2.7) values from 0.745 (cormorant) to 0.943 (black guillemot *Cepphus grylle*) (Table 2). This suggested that overfitting was not an issue, despite the relatively large number of explanatory variables. Spatial fine-scale abundance was predicted with much lower accuracy, with R^2 values from 0.002 (guillemot *Uria aalge* and razorbill *Alca torda*) to 0.446 (black guillemot *Cepphus grylle*). Following the criteria of Pearce-Higgins et al. (2011), abundance prediction accuracy was good for 2 species, moderate for 5 species, poor for 6 species and very poor for 2 species. For 9 species, abundance was overpredicted at low observed population sizes.

We considered the following 3 criteria to be indicators of poorer model fit: predicted abundance trend in occupied area opposite to that of presence probability trend; poor or very poor R^2; and overprediction at low observed abundances. One species (common gull *Larus canus*) had no indicators of poor model fit, 9 species had one indicator and 5 species had 2 indi-

Table 2. Model fit. Median area under the curve (AUC) (presence–absence component) and R^2 (abundance component) from 20 iterations of the model

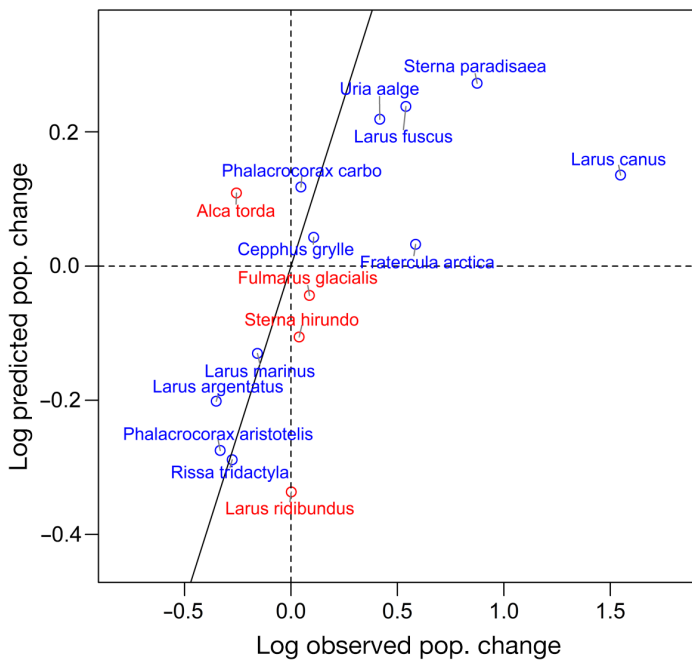| Species	AUC	R^2
Fulmar	0.916	0.231
Cormorant	0.745	0.013
Shag	0.900	0.055
Black-headed gull	0.847	0.028
Common gull	0.898	0.351
Great black-backed gull	0.883	0.206
Herring gull	0.857	0.041
Kittiwake	0.870	0.045
Lesser black-backed gull	0.780	0.010
Arctic tern	0.906	0.243
Common tern	0.816	0.060
Black guillemot	0.943	0.446
Guillemot	0.876	0.002
Puffin	0.897	0.140
Razorbill	0.892	0.002

Fig. 1. Observed and predicted population change, by species. Each point is the log observed and log predicted change in abundance between Seabird Colony Register and Seabird 2000, where abundance is summed across all cells for which data were withheld from the model. Colour shows whether species were correctly attributed to overall increase or decline: blue: correctly attributed; red: incorrectly attributed. Solid line: $y = x$; dashed lines: $x = 0$ and $y = 0$

cators (Section S5, Table S4). We defined model fit as 'better' for the 7 species that either had no indicators of poor model fit or for which the only indicator of poor model fit was overprediction at low abundances; for the remaining 8 species, we defined the model fit as 'poorer'.

In the temporal large-scale predictive ability assessment, the model had a moderate ability to predict species' overall changes in population size across all withheld cells (linear model, slope = 0.099, $R^2 = 0.211$, p = 0.0418; Fig. 1). The direction of change was correctly predicted for 11 of the 15 species.

Uncertainty was generally high: for all species, the 95% confidence intervals of the projected future abundance overlap with current abundance (Table 3). The confidence intervals of the projected future abundance do not overlap with current abundance for 7 species at the 50% level and 3 species at the 75% level (Table 3).

Three categories of relative confidence in the future projections were defined, based on a combination of model fit (Table S2) and the overlap of projected future abundance with current abundance (Table 3): (1) 'higher', better model fit and no overlap of future abundance 50% CI with current abundance; (2) 'intermediate', either better model fit and overlap of future abundance 50% CI with current abundance or poorer model fit and non-overlap of

Table 3. Projected future abundance and presence change for 19 seabird species under climate change. GB&I: Great Britain and Ireland

Species	Seabird 2000 total count (GB&I)	Predicted GB&I population size, 2050 (median and 95% CI)	Predicted abundance change (median %, GB&I)	Predicted presence probability change for unoccupied cells (median %, GB&I)
Fulmar	537988	144559 (33473–551158)[a,b]	−73.1	−72.7
Cormorant[c]	13586	12138 (2045–64585)	−10.7	+243.6
Shag[c]	32202	44600 (7123–226533)	+38.5	+8.5
Black-headed gull[c]	141871	220934 (45232–1612457)	+55.7	−63.5
Common gull	49728	50591 (14613–183392)	+1.7	−15.6
Great black-backed gull	19610	16417 (3943–70231)	−16.3	−51.0
Herring gull[c]	148849	105568 (30444–351803)	−29.1	+31.4
Kittiwake[c]	415994	192333 (35828–968980)[b]	−53.8	−81.6
Lesser black-backed gull[c]	116640	126622 (15219–1001976)	+8.6	+20.4
Arctic tern	48469	12170 (2444–69229)[a,b]	−74.9	+17.3
Common tern	13859	14404 (3183–76857)	+3.9	+24.3
Black guillemot	42701	26454 (7316–88746)[b]	−38.0	+1.8
Puffin	600751	68588 (3726–1042735)[a,b]	−88.6	−80.7
Razorbill[c]	216060	107029 (19592–523769)[b]	−50.5	−96.1
Guillemot[c]	1559484	784397 (102574–5352779)[b]	−49.7	−91.8

[a]75% CI does not overlap with Seabird 2000 total count
[b]50% CI does not overlap with Seabird 2000 total count
[c]Poorer model fit

future abundance 50% CI with current abundance; (3) 'lower', poorer model fit and overlap of future abundance 50% CI with current abundance. Under this categorization, 4 projections could be made with higher confidence, 6 with intermediate confidence and 5 with lower confidence.

3.2. Projected future abundance and presence

Under RCP8.5, 10 out of 15 seabird species are projected to decline in abundance in Britain and Ireland by 2050 (Table 3; 4 with higher confidence, 4 with intermediate confidence and 2 with lower confidence). Fulmar *Fulmarus glacialis*, Arctic tern and puffin (higher confidence) and kittiwake and razorbill (intermediate confidence) are all projected to decline by more than 50%, with a greater than 80% decline projected for puffin. Conversely, European shag *Gulosus aristotelis* (hereafter 'shag') and black-headed gull are projected to increase by more than 30%, albeit with lower confidence.

For 4 (cormorant and herring gull *Larus argentatus* with lower confidence; Arctic tern and black guillemot with higher confidence) of the 10 species for which abundance declines are projected, presence probability is projected to increase on average in cells unoccupied in 2000. This suggests that colonisation of new areas may to some extent compensate for abundance declines within the range occupied in 2000; however, this depends on the proportion of the unoccupied area that actually represents suitable habitat for these species. Projected presence probability increases are on average low for black guillemot relative to projected abundance declines, suggesting limited capacity for colonisation of new areas to compensate for abundance declines for this species.

For 3 (shag and lesser black-backed gull *L. fuscus* with lower confidence; common tern *Sterna hirundo* with intermediate confidence) of the 5 species for which abundance increases are projected, presence probability is also projected to increase on average in cells unoccupied in 2000, meaning that colonisation of new areas may contribute to further abundance gains beyond those within the cells occupied in 2000 alone.

For many seabird species, projected abundance change is highly spatially variable (Section S6, Figs. S2–S20). Generally, seabird abundance declines are expected to be more pronounced in the south and east of Britain and Ireland (Fig. 2a). For Laridae and Phalacrocoracidae (Fig. 2c,d), some

abundance increases are projected in the north of Britain and Ireland. Fulmar is projected to increase in abundance in the south of Britain (Fig. 2e).

No significant difference in projected population change was found between surface-feeding and diving species (linear model, coefficient for diving species relative to intercept: -13.47, $F_{1,13} = 0.35$, $p = 0.562$). Declines in surface-feeding and diving species are projected to be more pronounced in the SE and SW of Britain and Ireland respectively (Section S6, Figs. S21 & S22). Marine specialists are predicted to have significantly more negative population change than habitat generalists (linear model, coefficient for marine specialists relative to intercept: -50.75, $F_{1,13} = 8.33$, $p = 0.013$). There is no clear spatial pattern in projected change in marine specialists (Section S6, Fig. S23), but projected change for habitat generalist species is more negative in the SE of Britain and Ireland (Section S6, Fig. S24).

3.3. Parameter estimates

All parameter estimates for the relationship between seabird presence or abundance with climate and oceanographic variables are given in Section S7, Table S5. Only linear terms are presented in the following section because linear terms were considered to be of greater importance, being of greater absolute magnitude than quadratic terms (mean absolute linear term was $3.07\times$ the mean absolute quadratic term; linear model, $F_{1,628} = 53.93$, $p < 0.001$). The analysis of parameter estimates was only carried out for the 15 species for which projections are included in the main text.

Although estimated independently, parameter estimates for presence and abundance components for a given climate or oceanographic variable were moderately strongly positively correlated (linear model, effect size = 0.27, $F_{1,313} = 166.2$, $p < 0.001$, $R^2 = 0.345$). Overall, parameter estimates for environment–presence or environment–abundance relationships were highly variable across species. The only variables for which the 95% credible interval of the mean parameter estimate (across species, after accounting for phylogeny) did not overlap with zero were breeding season maximum temperature negative relationships with both presence (effect size = -1.49; 95% CI = -1.94, -1.06) and abundance (effect size = -0.72; 95% CI = -1.17, -0.29); winter minimum temperature positive relationship with presence (effect size = 0.81; 95% CI = 0.36, 1.24); distance from coast negative relationships with both presence (effect size = -2.00;
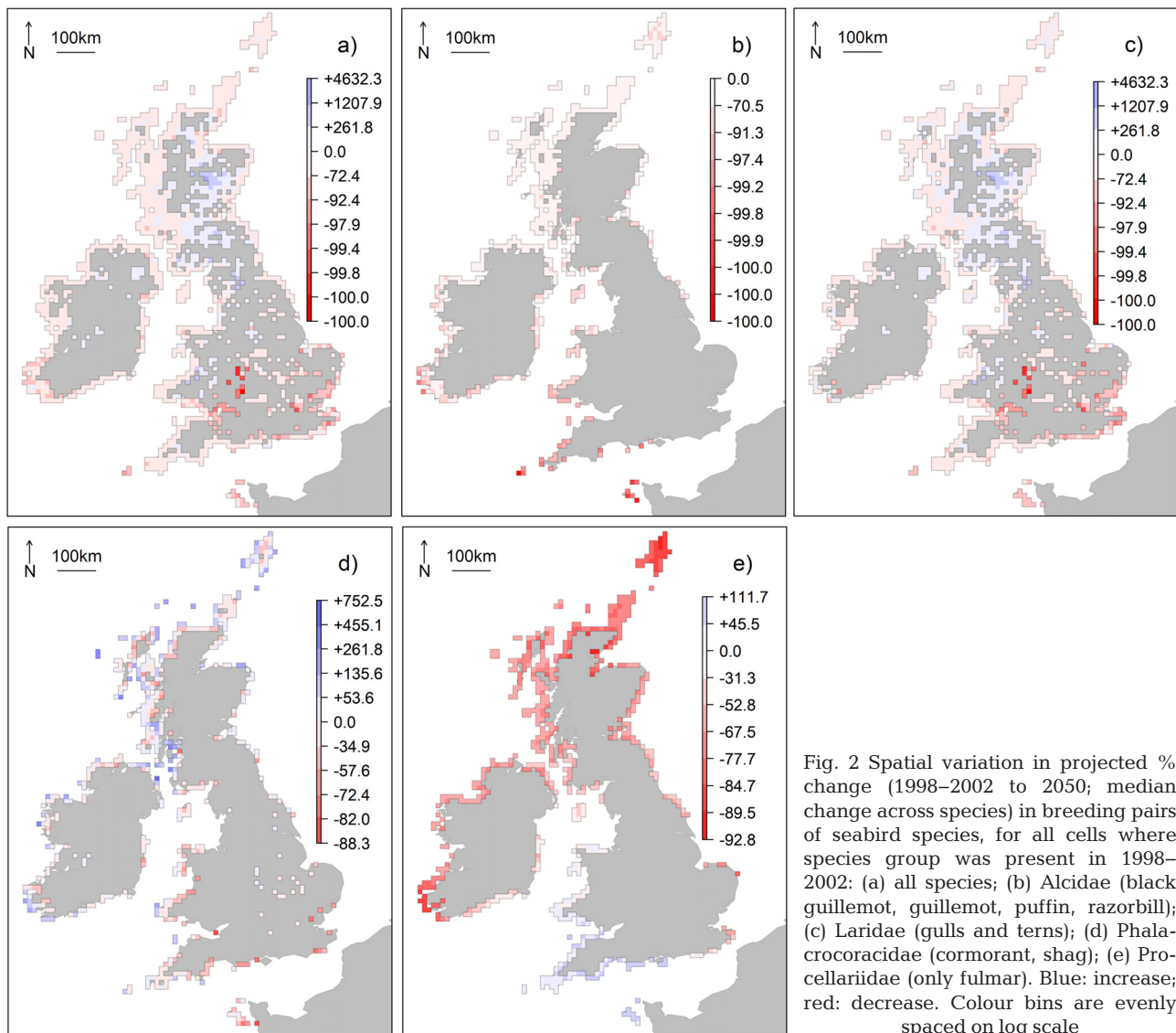
Fig. 2 Spatial variation in projected % change (1998–2002 to 2050; median change across species) in breeding pairs of seabird species, for all cells where species group was present in 1998–2002: (a) all species; (b) Alcidae (black guillemot, guillemot, puffin, razorbill); (c) Laridae (gulls and terns); (d) Phalacrocoracidae (cormorant, shag); (e) Procellariidae (only fulmar). Blue: increase; red: decrease. Colour bins are evenly spaced on log scale

95% CI = −2.46, −1.57) and abundance (effect size = −0.82; 95% CI = −1.27, −0.39). Parameter estimates for breeding season climate variables were slightly greater in absolute magnitude than for winter climate variables (paired *t*-test; mean difference = 0.27, t = 2.34, df = 59, p = 0.023).

The abundance of diving species had a more negative relationship with breeding season SST than did the abundance of surface-feeding species (Fig. 3). Relationships of both presence and abundance with breeding season maximum temperature were more negative for marine specialists than for habitat generalists (Fig. 4). For presence, marine specialists had more positive relationships with breeding season PEA and more negative relationships with winter PEA than did habitat generalists.

4. DISCUSSION

4.1. Projected changes

Our study is the first to project future abundance for seabird species in the north-east Atlantic on the basis of multiple climate and oceanographic variables. Using a model that was able to predict recent population changes across withheld data, we predict that the majority of breeding seabird species for which predictions were made (10 out of 15) will decline in abundance in Britain and Ireland during the 21st century, based on the fitted relationships with climate and oceanography (with higher, intermediate and lower confidence for 4, 4 and 2 species, respectively). Steep declines of greater than 50% of abundance between
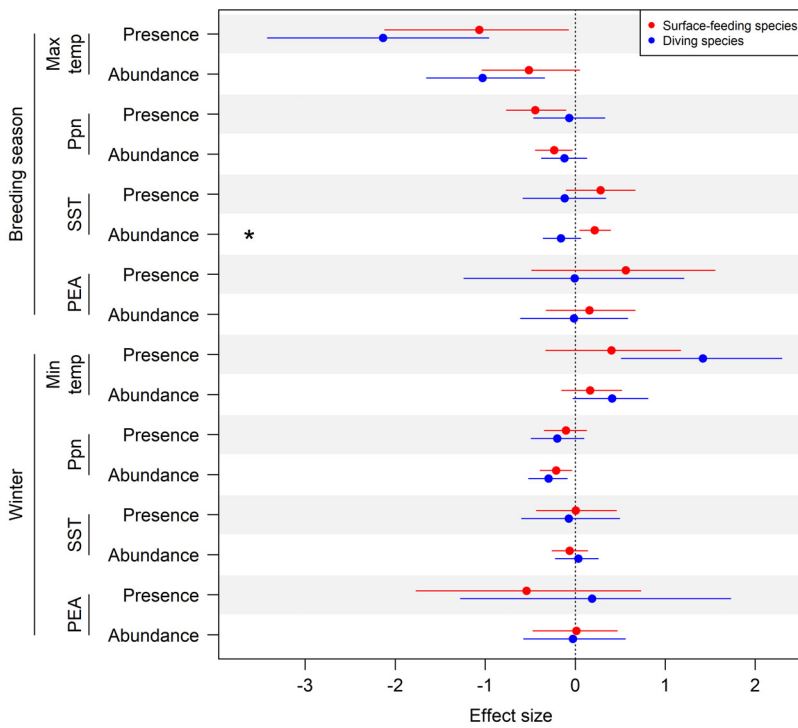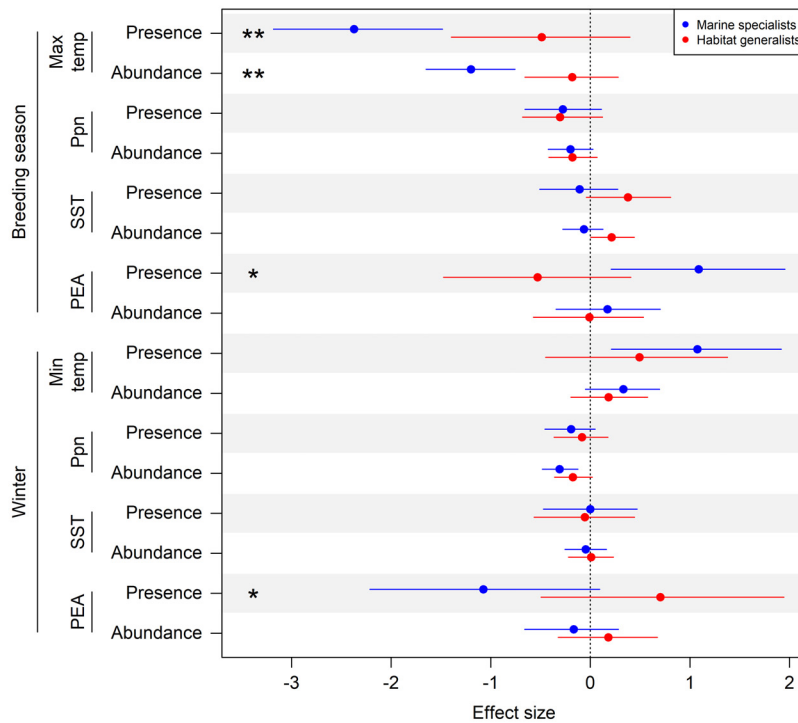
Fig. 3. Estimated mean (±95% CI) parameter estimate of species' relationship with climatic and oceanographic variables, by feeding ecology. Only estimates for linear terms are shown. Presented parameter estimates and credible intervals are from model with no intercept; significance of difference between ecological groups assessed with model with an intercept. (*) significant at $0.01 \leq \alpha < 0.05$. PEA: potential energy anomaly; SST: sea surface temperature; Ppn: precipitation. Dashed line: parameter estimate of zero

Fig. 4. Estimated mean (±95% CI) parameter estimate of species' relationship with climatic and oceanographic variables, by foraging habitat specialism. Only estimates for linear terms are shown. Presented parameter estimates and credible intervals are from model with no intercept; significance of difference between ecological groups assessed with model with an intercept. (*) significant at $0.01 \leq \alpha < 0.05$; (**) significant at $\alpha < 0.01$. Dashed line: parameter estimate of zero

1998–2002 and 2050 are predicted with higher confidence for fulmar, puffin and Arctic tern, and with intermediate confidence for razorbill and kittiwake. Abundance increases between 1998–2002 and 2050 are predicted with intermediate confidence for common gull and common tern, and with lower confidence for black-headed gull, lesser black-backed gull and shag. Of these 5 species, 2 (black-headed gull and shag) are predicted with lower confidence to increase in abundance by more than 30%.

Abundance increases at newly colonised locations (suggested by projected presence probability increases outside of the area occupied during Seabird 2000) may to some extent compensate for predicted abundance declines for cormorant, herring gull, Arctic tern and black guillemot, and may enhance predicted abundance increases for shag, lesser black-backed gull and common tern. However, this apparent capacity for colonisation should be viewed as a maximum because not all breeding habitat unoccupied in Seabird 2000 is potentially colonisable by these species. Furthermore, of the 10 species projected to decline in abundance, colonisation is projected to potentially compensate for these declines for only 4 species; additionally, for one of these species (black guillemot), the projected increase in presence probability outside the occupied area is projected to be of much lower magnitude than the projected abundance decline. Therefore, in general, we expect there to be only limited potential for colonisation of new areas to compensate for seabird population declines in Britain and Ireland.

Our projections accord with 4 similar studies in the UK or Europe which project that climate change will cause declines for the majority of seabird species in the UK. Our projections were typically in the same direction: 10 out of 15 shared species in Huntley et al. (2007); 10 out of 13 shared species in Johnston et al. (2013); 8 out of 13 shared species in Russell et al. (2015); 9 out of 11 shared species in Häkkinen et al. (2023). The only species for which our projections differed from those for all 3 other studies is lesser black-backed gull, for which we project an abundance increase under climate change. There are 3 potential causes of the differences in projections between studies. Firstly, the climate variables included in the projections differed: only Russell et al. (2015) and Häkkinen et al. (2023) also used oceanographic variables. Secondly, the metrics projected differed: the present study and Johnston et al. (2013) projected abundance, while the other 3 studies projected range. Thirdly, the geographical area differed: Johnston et al. (2013) covered UK SPAs only; the other 3 studies covered Europe. A recent study of the effects of climate variables on temporal variation in seabird breeding success was able to detect links with climate for 5 species (Searle et al. 2022), of which 4 overlap with the present study. All 4 of these species were predicted to decline in breeding success by Searle et al. (2022) and to decline in abundance by the present study. The general agreement of these (albeit not wholly independent) studies on the projected negative trend across seabird species emphasizes the climate vulnerability of Britain and Ireland's internationally important breeding seabird populations.

Even though the current study area of Britain and Ireland is relatively small compared to the ranges of the study species, considerable spatial variation in abundance trend is projected for many species. Although species' spatial responses are expected to be highly idiosyncratic, projected seabird abundance declines are typically steeper in the south and east of Britain and Ireland (particularly for surface feeders and habitat generalists) than in the north and west, where there may be increases for some species. It is notable that the south and east of Britain and Ireland is where the steepest projected increases in breeding season maximum temperature are; however, we did not assess the relative importance of different variables in projected abundance changes, and so it is not clear whether greater exposure to projected warming explains the steeper projected declines there.

The lack of a difference in projected abundance trend for surface-feeding and diving species suggests that diving species may not continue to be buffered against climate change impacts, as they are currently assessed to be (Mitchell et al. 2020). Marine specialists are projected to have more negative abundance trends than habitat generalists. This may compound the vulnerability to climate change already arising from this group's narrow ecological breadth.

In this study, we solely considered seabird species that bred in Britain and Ireland in considerable numbers at the last 2 censuses. However, redistribution of species under climate change may mean that other seabird species with a more southerly current European distribution may constitute a more important proportion of the British and Irish seabird community in the future. For example, Mediterranean gull has increased in abundance since the last seabird censuses by >6000 % (Eaton & Rare Breeding Birds Panel 2022). Projections similar to ours could be carried out for seabird species that do not currently breed in Britain and Ireland, to assess the prospects of colonisation by those species and the associated conservation implications.

4.2. Fitted presence–abundance relationships with climate/oceanography

Although other studies have modelled future changes in seabird abundance and distribution under projected environmental conditions, ours is the first study to explore the underlying fitted relationships. We found relationships with climate and oceano-

graphy to be highly variable across seabird species; however, in general, seabird presence and abundance was typically negatively related to breeding season maximum temperature. Multiple studies have found that some seabird species can be directly negatively impacted by warmer breeding season air temperatures (Gaston et al. 2002, Oswald et al. 2008), but it is unclear whether the relationships we found are due to such direct effects or due to other factors which are correlated with breeding season maximum temperature. Given that few effects of winter minimum temperature on seabirds have been documented, it is likely that the overall positive relationship we found between this variable and seabird presence is indirect, perhaps being mediated through impacts on prey abundance or storminess.

Parameter estimates for the relationship between climate/oceanography variables at the colony and seabird presence–abundance were generally lower in magnitude for winter than for breeding season climate/oceanography variables. This may be because our winter climate/oceanography variables only captured conditions close to the colony: other studies have found that although seabirds are influenced by conditions in the non-breeding season, non-breeding season conditions over the wintering range are more influential than those at the colony while the birds are elsewhere (Reed et al. 2015).

The relationship between abundance and breeding season SST was typically more positive for surface-feeding species than for diving species (for which the credible interval of the estimate overlapped with zero). Positive relationships with SST are not uncommon among marine predators (Orgeret et al. 2022); however, the mechanism behind this difference is unclear but could potentially arise from differences in typical prey between the 2 functional groups, if the prey of surface feeders typically have a more positive relationship with breeding season SST. For example, the slope of the relationship between breeding season SST and abundance for lesser black-backed gull (categorized as a surface feeder in the present study) was positive (although the 95% CI overlapped 0: slope = +0.47; 95% CI = −0.25, +1.20; Table S5). There is a prey-mediated pathway underlying such a relationship for lesser black-backed gull: Luczak et al. (2012) found evidence of a pathway of successive positive relationships between SST, decapod larvae abundance, adult swimming crab abundance and abundance of lesser black-backed gull at nearby colonies around the North Sea. Ultimately, because the effects of climate change are borne out through many variables, species that have a positive relation-

ship with breeding season SST may not necessarily be predicted to increase under climate change. For example, the relationship between herring gull abundance and breeding season SST is positive (Table S5) but herring gull is predicted to decline in abundance under climate change, perhaps because of (amongst other relationships) the negative relationship between herring gull abundance and breeding season maximum temperatures.

Some relationships require more investigation to explain their underlying mechanisms: relationships of both presence and abundance with breeding season maximum temperature were more negative for marine specialists than for habitat generalists, although this is similar to other studies on terrestrial species which have found more negative impacts of temperature on habitat specialists than generalists (Pearce-Higgins et al. 2015). For presence, marine specialists had more positive relationships with breeding season PEA and more negative relationships with winter PEA than did habitat generalists. For the latter finding, it is not clear if this is a true ecological difference or due to the potential relative difficulty of estimating relationships with PEA for habitat generalists, which may have a considerable proportion of inland colonies with no nearby PEA values. This could be elucidated by repeating the analysis using only coastal colonies and assessing whether the difference remains.

Future studies could examine our estimated seabird–climate relationships in more detail and assess whether they match observed relationships between seabird variables and weather/oceanography from field studies (Grosbois et al. 2009). If these relationships do match for a given variable, it suggests that the effect of that variable is particularly important, scaling up to drive species abundance and distribution. Additionally, if an estimated seabird–climate/oceanography relationship exists for which there is no known mechanism, field studies to identify the underlying mechanism could be valuable to help identify conservation interventions for climate change mitigation.

4.3. Limitations

It was difficult to find a strong climate/oceanography–abundance relationship for the majority of species, as evidenced by the high uncertainty in our projections and in the generally weak spatial predictive power of our models (although this is not unusual in such models; e.g. Johnston et al. 2013), even

though they performed well when projecting changes in abundance. Whilst this might suggest that the true effect of climate/oceanography on seabird abundance is weak, it could also be that the analytical framework and data used were not adequate to detect a truly strong effect of climate/oceanography on seabird abundance, for 2 main reasons. Firstly, the high spatial aggregation of seabird abundance may not have been adequately characterized even with the spatial random effect, hurdle model structure and error distribution we employed. We consider the extreme variation inherent in seabird abundance data to present an enduring challenge to its analysis. This issue could potentially be resolved by using an extremely fine-scale spatial random effect (with nodes spaced at the scale of 10s of m) to account for very local aggregative effects, but such an approach was beyond the computing resources available for the present study. Secondly, the data we used may not have adequately described the climatic and oceanographic conditions experienced by seabirds: for example, there is considerable uncertainty in the species-specific foraging ranges we used to subset the oceanographic data (Woodward et al. 2019). Also, the oceanographic data were only available for one timestep, and so we could not use temporal covariation in oceanography and seabird abundance to inform the oceanography−abundance relationship. Additionally, the data on stratification beyond the continental shelf had to be omitted. The limited nature of the oceanographic data means that the apparent greater effect sizes for terrestrial climate than oceanographic variables (Table S5) in models of seabird presence and abundance (in accord with Häkkinen et al. 2021) may be spurious.

There are 2 aspects of the ecological processes by which seabirds experience effects of climate and oceanography that make it difficult to estimate the true climate/oceanography−abundance relationship: lags and contingency. Firstly, seabird species may lag in their response to climate change (especially if relationships with climate/oceanography are indirect and only gradually cascade up through trophic levels; e.g. Suttle et al. 2007). This means that seabird abundance may not have been at equilibrium with climate/oceanography during the SCR Census and Seabird 2000. The climate/oceanography−abundance relationship might be more easily teased apart by investigating the effects of climate and oceanography on productivity and survival individually. Secondly, seabirds' abundance relationships with climate/oceanography often arise indirectly through relationships with other factors, such as prey species (John-

ston et al. 2021). If prey species (for example) differ in relationships with climate/oceanography (Wright et al. 2020) then seabird species' relationships with climate/oceanography will be contingent on other factors and be location-specific (Frederiksen et al. 2007, Carroll et al. 2015). Similarly, seabirds' demographic relationships with climate/oceanography can change over time (Hansen et al. 2021) through plasticity (e.g. due to switching between prey species) or evolution. Future work could incorporate such spatial and temporal variation in climate/oceanography−abundance relationships into projections, or update such relationships using recent Seabirds Count data.

Two challenges to interpreting our projections arise from model performance. Firstly, there were indicators of poor model fit for all but one species. Secondly, uncertainty is high, so there is relatively low support for the median projected abundance change presented, and 95 % credible intervals for all species encompass zero abundance change. Of the 15 species modelled, there were only 4 species for which both (1) model fit was better and (2) there was no overlap of the future abundance 50 % CI with current abundance. However, we are more confident of projected declines (2 lower, 4 intermediate, 4 higher confidence) than projected increases (3 lower, 2 intermediate). Uncertainty is a key feature of many species-specific estimates of vulnerability to climate change (Pearce-Higgins et al. 2017) that needs factoring into decision-making (Foden et al. 2019). The generally negative fitted relationships with temperature and propensity for projected declines generally match seabird species' current observed responses to warming in Britain and Ireland, and therefore likely at least indicate the high future vulnerability of breeding seabirds as a species group to climate change, even if there is uncertainty over species-specific projections. As noted earlier, the moderately strong positive relationship between observed and predicted temporal population change — even without including change in oceanographic variables in the projections — suggests that despite these uncertainties, our projections have value for forecasting seabird abundance change.

Further additional challenges to interpreting our projections arise from our overall approach. Firstly, as with all correlative studies, our projections will only manifest if the relationships we estimated are causal. Climate/oceanography−abundance relationships can arise spuriously if abundance and climate/oceanography also covary with another unidentified variable (Beale et al. 2008). Future work could compare the results from 2 climate/oceanography models fitted in turn: one using spatial variation alone and

one using temporal variation alone; accord between the parameter estimates in the 2 models would lend support to our projections. However, there is support in the ecological literature for at least some of the fitted relationships we found, suggesting at least some are causal. For example, field studies have found that due to impacts on foraging efficiency, some tern species are particularly sensitive to precipitation and adverse weather in the breeding season (Dunn 1973, Taylor 1983). Our finding that relationships between breeding season precipitation and presence were generally more negative for terns than for other species (Table S5) accords with this observation, suggesting that the effects of weather on foraging efficiency may scale up to drive tern distribution.

There are at least 4 components of climate change that we omitted from our models that are likely to impact seabird abundance: variability, sea level rise, storminess and winter climate change away from the colony. Firstly, we focused on likely effects on seabird abundance of temporal changes in average environmental conditions. However, under climate change, environmental conditions are expected to change over time in not only their average but also their temporal variation (Fischer & Knutti 2015); change in temporal variation in conditions may have a different effect on seabird abundance than change in average conditions. Next, sea level rise is likely to reduce colony size for many seabird species (Ivajnšič et al. 2017). Given the relatively low precision (relative to projected sea level rise) of currently available digital elevation model data, it was not possible to estimate the potential reduction in colony size arising from projected sea level rise, and so our abundance projections may be positively biased for species that nest close to the sea. Some species are particularly sensitive to storms, finding it difficult to feed (Taylor 1983), losing the ability to thermoregulate after wetting (Frederiksen et al. 2008) or having nests washed into the sea (Newell et al. 2015). Although we included precipitation in our models, we were not able to estimate a relationship between storminess and seabird abundance. If storminess rises in the study area, then we may have positively biased our abundance projections for species that are sensitive to storms. Some species segregate by colony during the non-breeding season (Buckingham et al. 2022). We did not have colony-specific data on the wintering locations of our study species, and it is uncertain the extent to which these are fixed, and so we could not relate seabird abundance to winter climate/oceanography away from the colony. Climate change is highly spatially variable across the globe, and so the effects of winter climate change away from

the colony may drive abundance in a different direction from our current projections.

4.4. Conclusions

Our analyses suggest that the majority of seabird species in Britain and Ireland are likely to decline in response to climate change. Although these projected trends are associated with significant uncertainty which varies between species, our projections can contribute to climate change vulnerability assessment (while taking account of uncertainty appropriately) and inform conservation effort appropriately among species according to urgency. Continuing and expanding annual coverage of the Seabird Monitoring Programme to include a wider spread of sites and species will help assess whether seabirds are responding to climate change according to our projections, reduce the uncertainty of future projections and inform conservation responses to climate change (Bowgen et al. 2022, Häkkinen et al. 2023) and to pressures arising from climate change mitigation (Cook et al. 2019).

In this study, we were not able to evaluate the relative importance of climate and oceanography in driving seabird abundance and distribution; however, we found that seabird presence in Britain and Ireland is generally negatively related to breeding season maximum temperature. Other relationships with climate/oceanography varied between species, with important differences in sensitivity between functional groups. Future work can explore these relationships in more depth to help identify aspects of seabird ecology on which to focus conservation efforts for climate change mitigation.

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