



Projected future vulnerability of seabirds within the INTERREG VA area to climate change

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Executive summary

In this study we projected seabird abundance in 2050 under climate change in western Scotland, Northern Ireland and the border counties of the Republic of Ireland (the INTERREG VA area). This was carried out to inform analysis of the vulnerability of each species to climate change.

Projections were made based on a fitted relationship between terrestrial and marine climate and seabird occurrence and abundance combined. Air temperature and precipitation were used to summarise terrestrial climate, while sea surface temperature and potential energy anomaly were used to summarise marine climate. Seabird abundance data were derived from the most recent two national seabird censuses for Britain and Ireland. The relationship was fitted using a Bayesian hurdle model with a spatial random effect. Future projections were made under climate change scenario RCP8.5.

Models could be produced for 19 out of the 25 species breeding in the area. The majority of species are projected to decline in abundance in the INTERREG VA area, although there is considerable uncertainty in this for all species. Furthermore, for most species the trend is expected to vary spatially within the INTERREG VA area. In general, the INTERREG VA area is projected to hold a greater proportion of species' British and Irish populations by 2050 than at present. For some species with few data the model results are less reliable. Models and projections are summarized in this report with more detailed information provided in the species (Appendix B) and management region (Appendix E) accounts whilst projections are also provided in shapefile format.

Overall, the projected trends in abundance accord with recent observed trends, suggesting that species may already be responding to climate change. Interestingly, the effect size was greater for terrestrial than marine climate variables; however, the interpretation of this is not straightforward.

The climate change vulnerability for each species was estimated by combining the projected abundances with: i) information from the literature review of mechanisms by which climate change affects seabirds; and ii) recent observed trends in abundance. The majority of species are expected to be vulnerable to climate change; however, climate change will likely present four species with opportunity. The results of the climate change vulnerability analysis, as well as the spatially detailed projections, can be used to inform conservation of seabird populations to mitigate their risk under climate change.

1. Introduction

The impacts of climate change on natural systems are growing (Scheffers et al. 2016), and are projected to become more important through time (e.g. Warren et al., 2018). In response, it is important to identify the species that are likely to be most vulnerable to future climate change impacts, in order to inform conservation planning (Foden et al. 2019). Whilst a wide range of approaches have been developed to inform climate change vulnerability assessment (see Foden et al. 2019 for an overview), it appears that the most robust approaches use historical trend information to parameterise models of projected future impact (Wheatley et al. 2017), and there is building evidence that models that project future climate change impacts do have some predictive power in explaining recent population trends (Green et al. 2008; Stephens et al. 2016). Such approaches have already been applied to European birds (Huntley et al. 2007), British birds (Johnston et al. 2013; Massimino et al. 2017) and biodiversity in Britain across a range of taxa (Pearce-Higgins et al. 2017). Collectively, these tend to show that cold-associated northern and upland species, and species of conservation concern, are amongst the most vulnerable to climate change (Massimino et al. 2017, Pearce-Higgins et al. 2017).

Britain and Ireland support approximately one quarter of Europe's breeding seabird populations, many of which are sufficiently abundant to achieve international importance (Stroud et al. 2001). A total of nearly 8 million seabirds from 25 seabird species were estimated to breed in Britain and Ireland at the start of the 21st century (Mitchell et al. 2004) – including the majority of the world's population of Manx shearwaters *Puffinus puffinus* (90%), northern gannets *Morus bassanus* (68%; hereafter 'gannet') and great skuas *Stercorarius skua* (60%). Bespoke modelling has suggested that many seabird species are particularly sensitive to climate change (Johnston et al. 2013). In line with this, a number of long-term studies have already documented significant impacts on British seabird populations, particularly affecting black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'), Arctic skua *Stercorarius parasiticus*, and Atlantic puffins *Fratercula arctica* (hereafter 'puffin') (Frederiksen et al. 2004a; 2004b; 2006; 2007a; 2007b; Burthe et al. 2012; Harris et al. 2013; Carroll et al. 2015; Perkins et al. 2018). Such changes have also been noted elsewhere across their breeding range, with kittiwake and puffin now being classified as vulnerable on the International Union for Conservation of Nature Red List of Threatened Species (Birdlife International 2020a; 2020b).

These impacts occur through a wide range of mechanisms, but key appears to be the impact of rising ocean temperatures, which through bottom-up processes affect primary productivity, altering the strength, timing and composition of the spring phytoplankton bloom (Scott et al. 2006; Bedford et al. 2020), and in-turn impacting the abundance, size and availability of key fish prey species, such as lesser sandeels *Ammodytes marinus* (Johnston et al. 2021). This can reduce seabird breeding success (e.g. Frederiksen et al. 2006; Burthe et al. 2012; Carroll et al. 2015) and survival rates (Frederiksen, Wanless, et al. 2004; Harris et al.

2013), impacting populations, a number of which are in long-term decline (JNCC 2020). At the same time, climatic changes may also have more direct impacts on seabirds, with warmer air temperatures associated with heat-stress in some species during the breeding season (Oswald et al. 2008), whilst others can be particularly vulnerable to heavy rainfall and storm events causing direct adult mortality resulting in seabird wrecks or destroying breeding attempts (Frederiksen et al. 2008; Newell et al. 2015; Morley et al. 2016). There is also strong evidence for the impacts of oceanography-mediated changes in seabird distribution at sea with modelling scenarios indicating significant changes by 2050 (Sadykova et al. 2020). It is also becoming apparent that migratory flyways of seabirds are likely to shift in response to climate change, most notably in the Arctic (Clairbaux et al. 2019).

The potential vulnerability of seabirds to climate change may result from a combination of their physiology, ecology and behaviour (Mitchell et al. 2020). It has been suggested that surface-feeding species may be more vulnerable to impacts on food availability due to their reduced foraging flexibility (Furness and Tasker 2000), as may those with more restricted diets (Howells et al. 2018). Breeding ecology is likely to have a big impact on the vulnerability of nest sites to detrimental climatic events such as storm surges, strong winds or heavy precipitation (Newell et al. 2015), whilst their migratory behaviour will affect the geographic scale over which species are impacted by climate change (Pearce-Higgins & Green 2014).

Previous modelling has suggested that British seabirds are particularly vulnerable to climate change when considering the influence of terrestrial climatic variables on the range/distribution and abundance of breeding populations. Generally negative associations between both summer temperature/rainfall and seabird abundance at colonies are projected to result in an overall decline in the seabird assemblage across UK Special Protection Areas (SPAs) of approximately 50% by 2080 under a high (A1F1) climate change scenario, with declines of more than 50% projected for 7/17 species (Johnston et al. 2013). Russell et al. (2015) projected that the range extent of 65% of British breeding seabirds would decline across Europe, with Leach's storm-petrel *Oceanodroma leucorhoa*, great skua, Arctic skua, kittiwake, Arctic tern *Sterna paradisaea* and auks being particularly vulnerable. These studies support the climate envelope modelling of Huntley et al. (2007) across Europe which also 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 extinction of a number of species in Britain and Ireland. Except for Russell et al. (2015), these existing studies have been based only on terrestrial climate variables, omitting changes to oceanographic variables, which are likely to provide the main mechanism by which climate change will affect seabird species (see Johnston et al. 2021 for an overview).

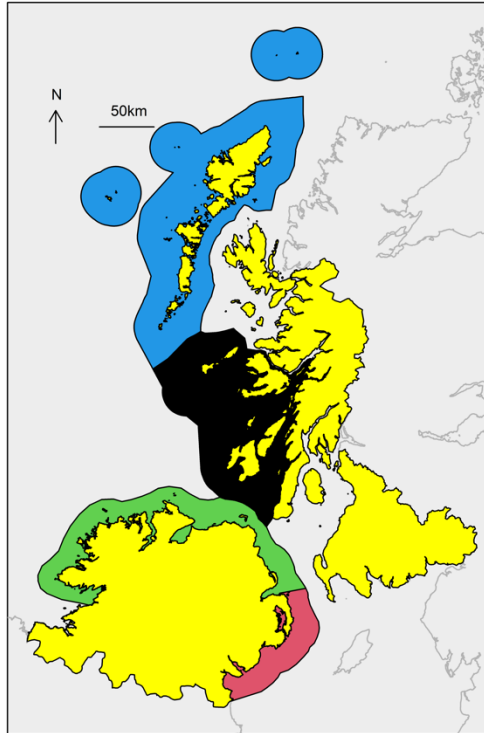


Figure 1. INTERREG VA area (yellow) and MarPAMM management regions (blue, Outer Hebrides; black, Argyll; red, Co. Down – Co. Louth; green, North Coast Ireland – North Channel).

In this study, we incorporate both projected changes in a range of oceanographic and terrestrial climatic variables, in order to produce new projections on abundance as well presence/absence patterns, both for Britain and Ireland as a whole, and specifically for the INTERREG VA area that is the focus of the MarPAMM project (Figure 1). Within this region there are four MarPAMM management regions: Outer Hebrides; Argyll; Co. Down – Co. Louth; and North Coast Ireland – North Channel. This area encompasses the West of Scotland, including the Outer and Inner Hebrides; and the entire coast of Northern Ireland. Within the Republic of Ireland (Ireland hereafter), the north-west and north-east (border) counties are encompassed. Incorporating both the North Atlantic and the Irish Sea is important since oceanographic conditions vary temporally and spatially, with the north-west of Scotland, Ireland, and Northern Ireland being more exposed and experiencing higher wave heights and energies than coasts within the Irish Sea (Baxter et al., 2011; Masselink et al., 2016), which may impact seabird vulnerability to climate change.

Seabirds around Britain and Ireland have been monitored through periodic censuses: Operation Seafarer provided a first, but incomplete assessment from 1969-70 (Cramp et al. 1974), the Seabird Colony Register (hereafter 'SCR Census' 1985-88; Lloyd et al. 1991) and Seabird 2000 (Mitchell et al. 2004) which included data from 1998-2002. Together, these provide good data on spatial and temporal variation in abundance during the second half of the 20th Century. Data from the current census, Seabirds Count (2015-2020+), are still being

collected, collated and analysed, and therefore are not available for inclusion in this analysis, but in the future would provide an opportunity for further analysis and to validate the models presented. At the same time, the Seabird Monitoring Programme (SMP) provides annual monitoring data from a non-random subset of specific colonies extending back to 1986 (JNCC 2020). Due to the incomplete nature of these data, and the fact they focus on temporal changes in specific colonies rather than a comprehensive snapshot, we use the census data from SCR Census and Seabird 2000.

Using these seabird data we model spatio-temporal variation in the abundance of seabirds from across Britain and Ireland as a function of both climatic and oceanographic variables, as well as a number of fixed topographical and bathymetric variables. Then we project future changes in abundance to 2050 as a result of projected changes in both climate (UKCP18, Met Office Hadley Centre 2018) and oceanography (Scottish Shelf Model, De Dominicis et al. 2018, 2019) variables under a RCP8.5 (business-as-usual) climate change scenario equivalent to approximately 2°C global warming by 2050 compared to 1986-2005 levels (IPCC 2014). Whilst national projections are used to indicate overall vulnerability of each species to climate change, we specifically focus on projections within the INTERREG VA area as the main output from this analysis. In addition to the results presented in this report, the detailed projections by site (see under methods for how defined) and species are provided as shapefiles and spreadsheets, and summarised in species-specific factsheets that also draw on information from the supporting review of climate change mechanisms affecting seabirds (Johnston et al. 2021). These site-specific projected abundances are also inputs to the at-sea modelling undertaken in Task 2.2 (Cleasby et al. 2021).

2. Methods

2.1 Seabird abundance data

All seabird species that breed in Britain and Ireland, except yellow-legged gull *Larus michahellis*, were initially included within the analysis (25 species; see Table 1), because they all breed within the INTERREG VA region (Figure 1). Seabird abundance data were derived from the two most recent seabird censuses of Britain, Ireland, Channel Islands and Isle of Man (SCR Census, 1985-88; Seabird 2000, 1998-2002). Counts for Manx shearwater, Leach's storm-petrel *Oceanodroma leucorhoa* and European storm-petrel *Hydrobates pelagicus* (hereafter 'storm-petrel') in SCR Census were based on best guesses rather than surveys due to the high level of uncertainty in the count methods at that time (P. I. Mitchell et al. 2004), and so these data were omitted from the present study for these species. Although neither census achieved complete coverage of all seabird breeding sites, inland sites were more completely covered in Seabird 2000 than in SCR Census (Figure 2; Mitchell et al. 2004). Data were included

from all census-sites in Britain, Ireland, Channel Islands and Isle of Man (hereafter 'Britain & Ireland').



Figure 2. Census-site locations: a) SCR; b) Seabird 2000.

Key environmental data used in the analysis (see 2.2, 2.3) were available at the 12 km x 12 km square (hereafter 'cell') level, based on the British National Grid. Seabird abundance for each census period was therefore likewise derived by simply taking the summed abundance for each species within each cell. Data were included from all census-sites (Figure 2): 5,657 in SCR Census and 1,968 in Seabird 2000 (many 'sites' in SCR Census became 'sub-sites' in Seabird 2000). When a census-site spanned more than one cell (affecting 282 counts in SCR Census, and 1,667 counts in Seabird 2000), the count for that census-site was divided among those cells in proportion to the length / area of the site spanning those individual cells, and rounded to the nearest integer.

2.2 General approach to environmental and seabird ecology data

In selecting terrestrial climate and oceanographic variables, we chose variables which might influence seabird abundance through productivity and mortality (Johnston et al. 2021), focusing on environmental variables operating at or near the breeding colony (rather than in the wintering grounds). 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. Seabird abundance is expected to be influenced by terrestrial climate both

directly (by conditions experienced during the breeding season) and indirectly (by effects of non-breeding season conditions, such as by heavy winter rainfall damaging burrows – Johnston et al. 2021). Likewise, seabird abundance is expected to be influenced by oceanographic variables both directly (such as through storm-related mortality) and indirectly: for example, in Portugal, winter SST is negatively related to the proportion of sand smelt (*Atherina* spp.) in little tern *Sternula albifrons* breeding season diet, which itself is positively related to little tern clutch size (Ramos et al. 2013; Correia, 2016). Therefore we incorporate terrestrial climate and oceanographic data from both the breeding season and non-breeding season, but only at the sites where breeding takes place.

Table 1. Species-specific breeding seasons and foraging ranges, after Campbell and Ferguson-Lees (1972) and Woodward et al. (2019). * seabird foraging range from Thaxter et al. (2012) instead (see 2.4).

Common name (BTO Species code)	Scientific name	Breeding season	Foraging range (km)
Fulmar (F.)	<i>Fulmarus glacialis</i>	May-Sep	542.3
Manx shearwater (MX)	<i>Puffinus puffinus</i>	May-Oct	1346.8
Leach's storm-petrel (TL)	<i>Oceanodroma leucorhoa</i>	May-Oct	91.7*
Storm-petrel (TM)	<i>Hydrobates pelagicus</i>	May-Oct	336.0
Gannet (GX)	<i>Morus bassanus</i>	Apr-Oct	315.2
Cormorant (CA)	<i>Phalacrocorax carbo</i>	Mar-Sep	25.6
Shag (SA)	<i>Phalacrocorax aristotelis</i>	Jan-Oct	13.2
Arctic skua (AC)	<i>Stercorarius parasiticus</i>	May-Aug	62.5*
Great skua (NX)	<i>Stercorarius skua</i>	May-Sep	443.3
Black-headed gull (BH)	<i>Chroicocephalus ridibundus</i>	Apr-Sep	18.5
Common gull (CM)	<i>Larus canus</i>	Apr-Aug	50.0
Great black-backed gull (GB)	<i>Larus marinus</i>	Apr-Aug	73.0
Herring gull (HG)	<i>Larus argentatus</i>	Apr-Aug	58.8
Kittiwake (KI)	<i>Rissa tridactyla</i>	May-Sep	156.1
Lesser black-backed gull (LG)	<i>Larus fuscus</i>	Apr-Sep	127.0
Mediterranean gull (MU)	<i>Ichthyaeetus melanocephalus</i>	Apr-Sep ¹	20.0
Arctic tern (AE)	<i>Sterna paradisaea</i>	May-Aug	25.7
Common tern (CN)	<i>Sterna hirundo</i>	May-Sep	18.0
Little tern (AF)	<i>Sternula albifrons</i>	May-Sep	5.0
Roseate tern (RS)	<i>Sterna dougallii</i>	June-Aug	12.6
Sandwich tern (TE)	<i>Thalasseus sandvicensis</i>	Apr-Sep	34.3
Black guillemot (TY)	<i>Cephus grylle</i>	May-Sep	4.8
Guillemot (GU)	<i>Uria aalge</i>	Apr-Aug	73.2
Puffin (PU)	<i>Fratercula arctica</i>	Apr-Sep	137.1
Razorbill (RZ)	<i>Alca torda</i>	Apr-Aug	88.7

¹ breeding season for Mediterranean gull uses that of black-headed gull (see below).

Seabird species differ substantially in the timing of their breeding seasons, and thus in the time period over which environmental variables can affect productivity and carry-over mortality. In order to account for this, breeding-season environmental variables were summarized within each species' breeding season (Table 1). Species-specific breeding seasons were defined as the months during which eggs or chicks can be present, as described by Campbell and Ferguson-Lees (1972). Being based on the timing of active nests, this resource generally gave a definition of seabird breeding-seasons intermediate between the narrow- and broad-sense definitions of seabird breeding seasons (based on timing of migration) in a recent review (Furness 2015). No data were available for the breeding season for Mediterranean gull *Ichthyiaetus melanocephalus*, so the breeding season for the closely-related black-headed gull *Chroicocephalus ridibundus* was used for this species since they often breed at the same colonies.

2.3 Terrestrial climate data

In common with other studies (e.g. Johnston et al. 2013; Russell et al. 2015), we used air temperature and precipitation as proxies of relevant variation in terrestrial climate. Temperature and precipitation can both have direct or indirect effects on 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 datasets at 1km resolution and aggregated to the 12 km x 12 km cell scale. Modelled terrestrial climate variables for 1980-2080 for the same variables were derived from Met Office UKCP18 data (Met Office Hadley Centre 2018; Figure 3a, b). 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 three monthly variables across the 12 projections.

We assume that climate influences abundance through cumulative years' effects on population growth rate, rather than instantaneously influencing abundance solely in the census year. Therefore, terrestrial climate data were averaged over the five years up to the median year of each census (1986 and 2000 respectively). A small number of counts (one Arctic skua count in SCR Census, and one Manx shearwater count and five storm-petrel counts in Seabird 2000) took place more than five years before the median year of each census. Although these counts are unavoidably related to future climate, given strong spatial variation in both abundance and climate, are likely to also reflect associations between later counts of those species and climate: these counts were therefore left in the dataset.

From these data, four terrestrial climate variables were derived, summarizing winter and breeding season temperature and precipitation respectively (Table 2). These variables were designed to capture extremes (rather than central tendency) of climate, because there is

evidence that the extremes of climate are more influential on the trajectory of bird populations (Pearce-Higgins et al. 2015a).

Table 2. 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.

Variable name	Calculation
<i>w_tasmin</i>	Five-year December-February mean minimum monthly temperature
<i>br_tasmax</i>	Five-year mean maximum temperature of (yearly) warmest month in species-specific breeding season
<i>w_pr</i>	Five-year mean total December-February precipitation
<i>br_pr</i>	Five-year mean total precipitation of (yearly) wettest month in species-specific breeding season
<i>w_sst</i>	Distance-weighted-mean 24-year mean December-February SST within species-specific foraging area
<i>br_sst</i>	Distance-weighted-mean 24-year mean SST over species-specific breeding season within species-specific foraging area
<i>w_pea</i>	Distance-weighted-mean 24-year mean December-February PEA within species-specific foraging area
<i>br_pea</i>	Distance-weighted-mean 24-year mean PEA over species-specific breeding season within species-specific foraging area
<i>bathymetry</i>	Distance-weighted-mean depth of water within foraging area
<i>coastal</i>	Whether cell was entirely (0) more than 5 km from the coast or not (1)
<i>islands</i>	Whether cell contains any islands of less than <15 km ² area (1) or not (0)
<i>coastline_length</i>	Length of coastline (km) within cell

2.4 Oceanographic variables

The relative importance of different oceanographic variables in driving seabird abundance, distribution and demographic parameters are poorly known; however, the most commonly included variables in such analyses are bathymetry and Sea Surface Temperature (SST) (e.g. Carroll et al., 2015; Nur et al., 2011; Satterthwaite et al., 2012). Many studies also include an index of stratification – either its strength, phenology, or both (Bertrand et al. 2014; Trevail et al. 2019). We therefore use three oceanographic variables to characterize relevant variation in the marine environment for seabirds: SST, potential energy anomaly (PEA, the energy required to fully mix a column of water) and bathymetry.

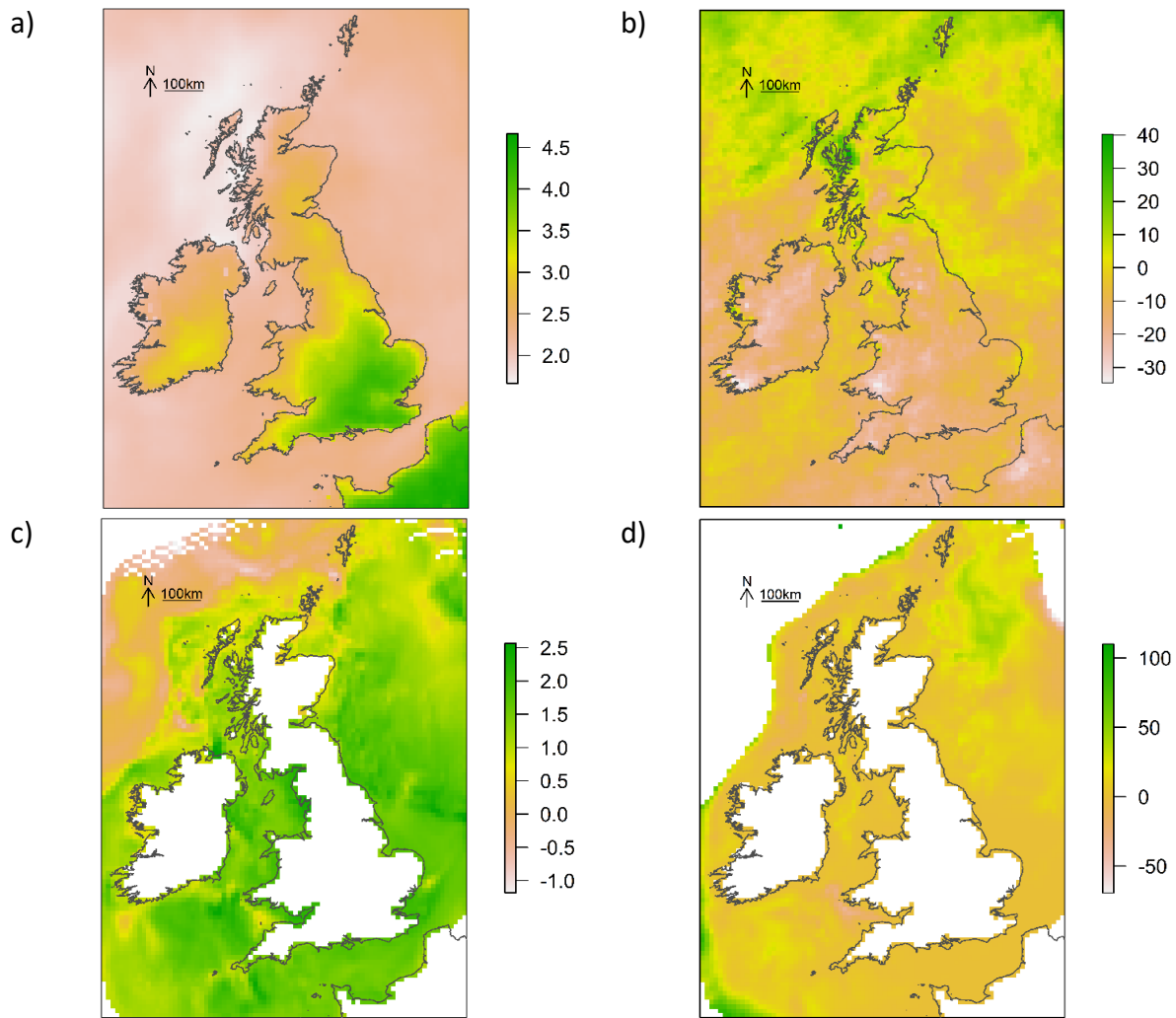


Figure 3. a-d) Example change surfaces for environmental variables (see Table 1) used in modelling (black polygons = INTERREG VA area). a) Change in five-year mean maximum temperature of (yearly) warmest month in Northern fulmar *Fulmarus glacialis* (hereafter ‘fulmar’) breeding season (*br_tasmax*, 1996-2000 to 2046-2050); b) Change in five-year mean total precipitation (mm) of (yearly) wettest month in fulmar breeding season (*br_pr*, 1996-2000 to 2046-2050); c) June SST change (1990-2014 to 2038-2062); d) June PEA change (1990-2014 to 2038-2062, masked to <200m ocean depth).

We include PEA as a measure of ocean stratification: more intensively stratified water columns have higher PEA values. In our study area, the PEA of waters on and off the 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. The dominance of bathymetry in variation in PEA therefore overwhelms local spatial patterns in PEA on the continental shelf. As bathymetry was already used in the model, PEA values were therefore omitted for deeper (>200m deep) waters.

SST and PEA were derived from Scottish Shelf Model (SSM; De Dominicis et al. 2018, 2019) data. Therefore, unlike the terrestrial climate data used to fit the model in this study, the oceanographic data we use are modelled rather than observed data. The SSM covers much

of Britain and Ireland waters (Figure 3c, d) at variable spatial resolution, with highest resolution (as low as 1 km node spacing at the coastline) in Britain and Ireland waters. The variables retrieved were SST and PEA averaged (weekly mean) over the periods 1990-2014 and 2038-62. The original data, being of variable spatial resolution on an unstructured grid, were aggregated to the same 12 km x 12 km grid as the seabird abundance and terrestrial climate data. Data from the historical time period only covered the years 1990 to 2014, and therefore did not overlap with the SCR Census time period (1985-1988); SST and PEA values for the SCR Census counts were left blank. Although the SSM data span significantly beyond the period of the Seabird 2000 census, they were the only oceanographic data available linked to the UKCP18 projections, and we therefore regard them as likely to be indicative of the spatial variation present across the MARPAMM area. However, if species' responses to variation in marine climate differ according to whether that variation is temporal or spatial, then our projections based purely on spatial variation in marine climate may be less reliable.

Bathymetry data were derived from UKCP09 marine projections data (Hadley Centre for Climate Prediction and Research 2017). These consist of the depth of the water column in m on a 12 km x 12 km grid. 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 m. Therefore the same bathymetry data were used for the historical and future periods.

Due to variation in seabird species foraging distances (Table 1), the area of ocean available (and thus the area over which oceanographic variables are relevant) from a given colony varies considerably between species. Each oceanographic variable was thus averaged over species-specific foraging ranges, derived from Woodward et al. (2019), which provides updated seabird foraging range estimates to those of Thaxter et al. (2012). We used mean maximum foraging range from Woodward et al. (2019) for all species other than Arctic skua and Leach's storm petrel. For these two species no mean maximum foraging range from colonies was available, and so we used the estimates from Thaxter et al. (2012) which were based upon observed distance from shore rather than distance from colony (Table 1). For a given cell and species / oceanographic variable, the mean was taken of all values for that variable over the species' mean maximum foraging range, weighted by the reciprocal of distance (distance + 0.1km to avoid dividing by zero) of the oceanographic variable points from the midpoint of the cell (Table 2).

2.5 Environmental data - other

Spatial variation in seabird abundance is caused by many processes. Most simply, many of our study species solely or mostly breed at the coast or on small islands, whilst some also breed extensively inland. We therefore include three 'nuisance' variables (i.e. non-target environmental variables, used to absorb some variation in seabird abundance) to account for

spatial variation in seabird abundance: *coastal* – whether a cell was entirely more than 5km from the coast; *islands* – whether a cell contained any islands less than 15km² in area; *coastline_length* – the length of coastline within a cell. It is worth noting that these 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 datasets 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 climatic component of such distributions (e.g. Johnston et al. 2013). To test this, future validation of these models using the completed Seabirds Count data, when available, would be recommended, to test how well observed changes in seabird populations from 2000 to 2020 match model predictions based on observed changes in climatic and oceanographic variables over that period.

All data preparation was carried out in R (R Core Team 2018).

2.6 Modelling approach

Seabird abundance at the two most recent censuses was related to environmental variables for each species individually, using data from across Britain and Ireland. The fitted model was then used to project future seabird abundance in 2050, using projected terrestrial and oceanographic data for 2050 under the greenhouse gas concentration scenario RCP8.5. RCP8.5 represents the most aggressive future greenhouse gas concentration scenario, but also 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, before being subset to the INTERREG VA region.

Seabird abundance should be subject to both intrinsic and extrinsic causes of spatial autocorrelation (Beale et al. 2010). To make inferences about the relationship between climate, oceanography and seabird abundance, while properly accounting for spatial autocorrelation, we fit 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 presents major gains in computational efficiency compared to traditional MCMC methods for fitting spatial models to large datasets.

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. The spatial random effect (here, a Gaussian random field) with Matérn spatial covariance structure was approximated using the SPDE approach (Lindgren et al. 2011; Bakka et al. 2018). This approach makes a simplified representation of a continuous Gaussian random field in terms of a number of linear basis functions. For this approach, a two-dimensional mesh must be

specified in order to define the basis functions. The mesh was defined according to the geographical locations of the data-contributing cells (Figure 4). The coordinates of these locations were transformed to a projected coordinate reference system (WGS84 / UTM 30N) so that the scale was the same for both dimensions, and these transformed coordinates were scaled to mean 0 and standard deviation 1 to avoid numerical issues. The parameters of the mesh were defined in such a way that: the inner portion of the mesh included all of the census points for that species; the inner portion of the mesh was covered by regular small triangles (but not too small that model runtime was unacceptably high); and a large buffer was left outside the inner portion in order to avoid boundary effects in the spatial random field within the area of interest. Once the mesh had been created, a projector matrix was then specified to link the spatial random effect to the locations of the observed data.

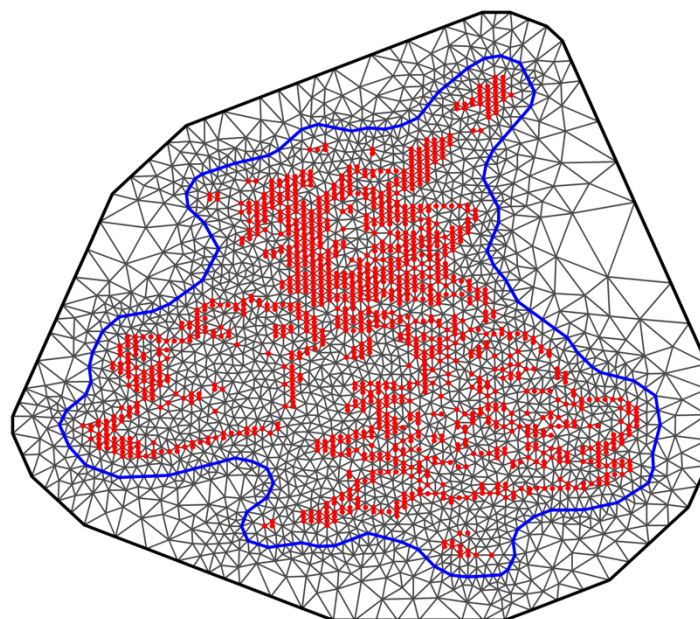


Figure 4. INLA model mesh (see 4.2): red points = contributing census-sites, blue and black lines define inner and outer portions of mesh, grey lines link mesh nodes.

Counts (zero or positive) were not recorded for all species at all census-sites. For census-sites at which no count for a given species was recorded, it was assumed that the species was not present. Therefore the available dataset for a given species in a given census 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 dataset than the count data. A hurdle model was therefore used (e.g. Sadykova et al. 2020); this separately models presence/absence (with a binomial likelihood) and abundance-given-presence.

Given that the seabird abundance data are counts, the distribution family used for the abundance-given-presence likelihood needed support over the set of positive integers, and so needed to be a zero-truncated distribution. Preliminary data exploration also revealed that

the non-zero seabird abundance data were over-dispersed, presumably due to aggregation effects from colonial breeding. The negative binomial distribution, which includes a parameter for over-dispersion, was therefore considered more appropriate than the Poisson distribution. The more flexible Tweedie distribution sometimes used for seabird abundance (e.g. Johnston et al. 2013) is not currently available for INLA. 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 two model components.

Seabirds are expected to have hump-shaped relationships with environmental variables. Therefore both linear and quadratic terms were included in the full model for all continuous variables. The full model comprised nine environmental covariates, nine quadratic terms for the environmental covariates, and three nuisance variables (Table 2).

Default priors were given for the fixed effects in the model. The priors for the Matérn covariance function of the random effect were specified according to its range r and standard deviation σ . Reasonably vague prior parameters were given: $P(r > 0.3) = 0.5$; $P(\sigma > 10) = 0.01$. All environmental covariates were scaled to mean 0 and standard deviation 1 before inclusion in the model. 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. Although this is unlikely to affect the estimates of the coefficients, it may overestimate the precision of the estimates. Although there is repeated sampling (i.e. two census periods) at the same cells, there is not *enough* repeated sampling (only two census periods) to estimate the parameters of an additional random effect for cell.

2.8 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.

The ability of the model to predict withheld data was assessed for each species. For each species, a validation model was fitted using presence and abundance data from just 70% (randomly selected) of the census-sites. 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 was assessed by: a) the area under the curve (AUC; the discrimination ability of a classifier) of the receiver operating characteristic for the predicted and observed presences; b) R^2 of the relationship between the predicted and the observed

abundances; c) root mean-square error (RMSE) of the predicted 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).

Some seabird species (e.g. Leach's storm-petrel, gannet and Manx shearwater) are abundant but only have a small number of colonies in Britain and Ireland. These species therefore have relatively few data from which to model the relationship between climate and abundance. Results are not presented for species with fewer than one data per parameter.

2.9 Prediction

Prediction was made using the full model (using all data, rather than the validation model) for each species. Predictions of a response variable under given conditions are easily made in Bayesian models, by simply supplying the model with the covariate values of interest and leaving the response variable blank for those values. Therefore, when given future values for the environmental covariates, the model can be used to predict future species abundance. Models typically mis-predicted known species abundance (assessed by Conditional Predictive Ordinate, equivalent to probability density) in a given cell, particularly at low observed population sizes. Therefore future predicted abundance was adjusted by multiplying predicted *change* in abundance (i.e. predicted abundance in 2050 / predicted abundance in 2000) by the observed abundance at Seabird 2000. For comparability, UKCP18 modelled data were used for predicting abundance in both 2000 and 2050 (rather than using HadUK/Met Éireann data for predicting abundance in 2000). Strictly speaking, as these predictions are for one future climate change pathway, they are really projections of a potential future based on the assumptions of climatic and oceanographic change associated with that pathway, and the model assumptions linking climatic and oceanographic data to seabird abundance.

Multiplying predicted change in abundance by observed abundance at Seabird 2000 means that census-sites not occupied at Seabird 2000 will also not be predicted to be occupied in 2050, and therefore assumes there will be no colonisation of new locations. Therefore an additional cell-level index of overall predicted change in relative presence probability (from the presence/absence component of the hurdle model) was produced for all land cells in the study area.

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 2050 and 2000 respectively, and then by dividing x by y . 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.

Projections were made over the entirety of Britain and Ireland, and then subset to the INTERREG VA area. As defined here, the INTERREG VA area contains: EU NUTS (nomenclatures d'unités territoriales statistiques) regions Arran & Cumbrae, Argyll & Bute, Dumfries & Galloway, East Ayrshire and North Ayrshire mainland, Lochaber, Na h-Eileanan Siar (Western Isles), South Ayrshire, and Skye & Lochalsh in Great Britain; Northern Ireland; and Cavan, Donegal, Leitrim, Louth, Monaghan and Sligo in Ireland (Figure 1). For each species, adjusted predicted future abundance (with confidence intervals) is presented for all census-sites, and summed within a) the INTERREG VA region and b) Britain and Ireland. We also present equivalent projections for each of four MPA regions separately (Appendix E).

2.10. Vulnerability assessments

We used the projected changes in seabird abundance, information from the literature review (Johnston et al. 2021), and recent observed trends (between census or from the SMP monitoring scheme), as inputs to an assessment of the vulnerability of each species to climate change. We followed the Thomas et al. (2011) methodology that compares the extent to which projected trends match those currently observed. This method has been shown to produce projections that correlate with observed trends (Wheatley et al. 2017). This framework also makes use of evidence that the observed changes can be linked to climate change, and considers the extent to which populations and distributions may have additional vulnerabilities (e.g. see Burthe et al 2014 for overview) or constraints, such as being limited by other factors such as fisheries pressure and predation.

Thomas et al. (2011) use two separate projections to inform climate change vulnerability assessment: projected range trend within the existing range, and projected range trend outside of the existing range. Because we model abundance rather than changes in distribution, our approach differed from the exact approach of Thomas et al. Firstly, we followed Pearce-Higgins et al. (2014) to use projections of changes in abundance rather than range extent. Secondly, we did not make abundance projections outside the existing range, and so we used the species' projected abundance change value to represent projected change in both Stage II (recent range) and Stage IV (future range) of the Thomas et al. (2011) framework, and the same observed population change value in Stages I (recent range) and III (future range). This is summarized in Figure 5 and means that the final vulnerability scores are a function of both observed and projected future population trajectories (Table 3). Where these differ in direction and there is evidence of a climate link to the observed changes as

well as the projected changes, then the outcome may indicate that species have both a risk of decline and potential opportunity for increase, depending upon the strength of evidence.

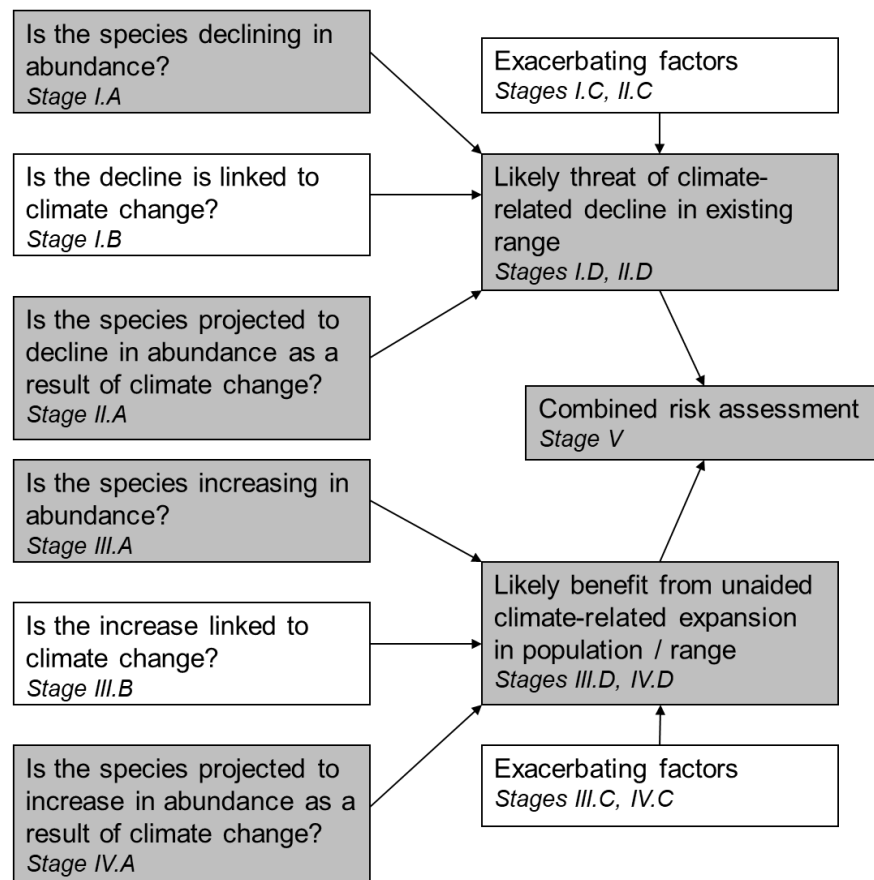


Figure 5. Summary of the processes involved in the application of the full Thomas et al. (2011) framework, and how those are represented by the various stages of the process. Grey boxes require data on observed and projected population changes, and white boxes use additional literature.

Table 3. Cross-tabulation of the risks and opportunities associated with climate change for each species, in order to produce the overall vulnerability assessment. Dark orange cells are indicative of high vulnerability, medium orange, moderate vulnerability; light orange, vulnerability and opportunity; light blue, low impact; medium blue, moderate opportunity and dark blue, high opportunity.

Opportunity/Risk	VERY HIGH	HIGH	MEDIUM	LOW
LOW	HIGH RISK	HIGH RISK	MEDIUM RISK	LIMITED IMPACT
MEDIUM	HIGH RISK	MEDIUM RISK	RISKS & OPPORTUNITY	MEDIUM OPPORTUNITY
HIGH	MEDIUM RISK	RISKS & OPPORTUNITY	MEDIUM OPPORTUNITY	HIGH OPPORTUNITY
VERY HIGH	RISKS & OPPORTUNITY	MEDIUM OPPORTUNITY	HIGH OPPORTUNITY	HIGH OPPORTUNITY

For this evidence, we used the climate change mechanism review (Johnston et al. 2021), SMP population trends (JNCC 2020) and where those are lacking, changes in abundance from Seabird 2000 (Mitchell et al. 2004). The assessment has levels of confidence associated with it, depending upon the strength of evidence linking observed and projected changes, the fit of the modelled changes and the quality of the survey data to generate observed trends. We used the model fit results to identify good, moderate and poor quality models. Species with population trends reported by SMP were regarded as good, whilst trend information from Seabird 2000 was regarded as being of poor quality as being ~20 years out-of-date. Updating this with the new Seabirds Count census results when available would be sensible to do. Although we did not have specific population change data for the INTERREG VA region, we repeated the vulnerability assessment for this region based on the projected changes specific for colonies in the region to give a likely indication of any potential differences as they apply to this region.

3. Results

3.1 Model performance and fit

Table 3. Model fit. Median AUC (presence/absence component), R^2 and RMSE (abundance component) from 20 iterations of model. We define three discriminatory ability categories for AUC, colour-coded: moderate (0.7-0.8, light blue); good (0.8-0.9, medium blue); excellent (>0.9, dark blue). We define four predictive ability categories for R^2 , following Pearce-Higgins et al. 2011: very poor (<0.01, dark orange); poor (0.01-0.06, light orange); moderate (0.06-0.25, light blue); good (>0.25, medium blue).

Species	AUC	R^2	RMSE
Fulmar	0.916	0.231	2520.0
Storm-petrel	0.926	0.003	40085.3
Cormorant	0.745	0.013	78.2
Shag	0.900	0.055	162.2
Arctic skua	0.984	0.097	455.0
Black-headed gull	0.847	0.028	1480.7
Common gull	0.898	0.351	857.9
Great black-backed gull	0.883	0.206	74.5
Herring gull	0.857	0.041	513.3
Kittiwake	0.870	0.045	3743.3
Lesser black-backed gull	0.780	0.010	1035.0
Arctic tern	0.906	0.243	438.0
Common tern	0.816	0.060	90.3
Little tern	0.908	0.014	35.6
Sandwich tern	0.794	0.011	1251.7
Black guillemot	0.943	0.446	98.0
Guillemot	0.876	0.002	10044.4
Puffin	0.897	0.140	6558.8
Razorbill	0.892	0.002	1593.5

The model did not run successfully for four species (great skua, Leach's storm-petrel, roseate tern *Sterna dougallii* and Mediterranean gull), the latter three of which had fewer than one data per parameter. Model results are therefore not presented for these species, nor for the remaining two species (gannet and Manx shearwater – see 2.8) for which there were fewer than one data per parameter. Results are presented for the remaining 19 seabird species. However, for data-poor species (those with fewer than 4 data per parameter) model behaviour differed to that of more data-rich species. This was reflected as relatively extreme absolute projections for Arctic skua, little tern, Sandwich tern *Thalasseus sandvicensis* and storm-petrel (Table 4) and parameter estimates for Arctic skua, Sandwich tern and storm-

petrel (Appendix A). Although results are presented here for these four species, they may be unreliable and therefore should be treated with caution.

KLD (approximately a measure of parameter convergence; see 2.8) was less than 0.1 for all parameters for all models which did not fail, indicating that the models converged. Model fit, assessed using withheld data, varied considerably between species and between model components (Table 3). Presence/absence was predicted with high accuracy, with AUC (classification ability; see 2.8) values from 0.745 (cormorant) to 0.984 (Arctic skua). Abundance was predicted with lower accuracy, with R^2 values from 0.002 (guillemot *Uria aalge* and razorbill *Alca torda*) to 0.446 (black guillemot *Cephus grylle*). Following the criteria of Pearce-Higgins et al. (2011), none were regarded as excellent, two as good, four as moderate, ten as poor and three as very poor. Root mean-square error represents the absolute error in the models' abundance predictions and varies from 35.6 (little tern) to 40085.3 (storm-petrel). Model fit as assessed here 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.

3.2 Parameter estimates

The spread of parameter estimates across all species for each variable is presented in Figure 6. Parameter estimates often differed considerably between presence and abundance components of the model. Unsurprisingly for seabird species, both presence and abundance were generally negatively related to distance inside the coast. Typically, parameter estimates for relationships with terrestrial climate were of greater magnitude, and more consistently so across species, than for relationships with oceanographic variables. Apart from nuisance variables, the five variables with significant (credible intervals not overlapping with zero) parameter estimates for the most species (linear terms in abundance component only) were: breeding season maximum temperature (mostly negative), winter precipitation (all negative), winter minimum temperature (mostly positive), and breeding season and winter potential energy anomaly (all negative and all positive respectively).

Breeding season SST was only significant in abundance sub-models for Arctic skua (negative), black-headed gull (positive) and herring gull (positive). There was considerable variation in parameter estimates across species: these are presented in Appendix A.

3.3 Projected future abundance and presence

In general, most (14 of 19) species are predicted to decline in abundance in the INTERREG VA area (Table 4). Arctic skua and storm-petrel were projected to respectively decline to extinction or virtually to extinction within the project area, although these projections were

based respectively on poor and very poor model fits. Fulmar, Arctic tern, little tern, Sandwich tern and puffin were all projected to decline by more than 50% across the INTERREG VA area, with particularly high rates of loss exceeding 90% projected for puffin. Conversely, shags, black-headed gulls and lesser black-backed gulls were all projected to increase by more than 50% across the region. Given the incorporation of fine-scale variation in these predictions at the colony level into the uncertainty associated with these estimates, it is worth noting that the 95% confidence intervals of each of the projections overlap with current abundance, with the exception of Arctic skua. Typically, the INTERREG VA region is projected to hold an increasing proportion of species' Britain and Ireland populations; however, this varies greatly between species.

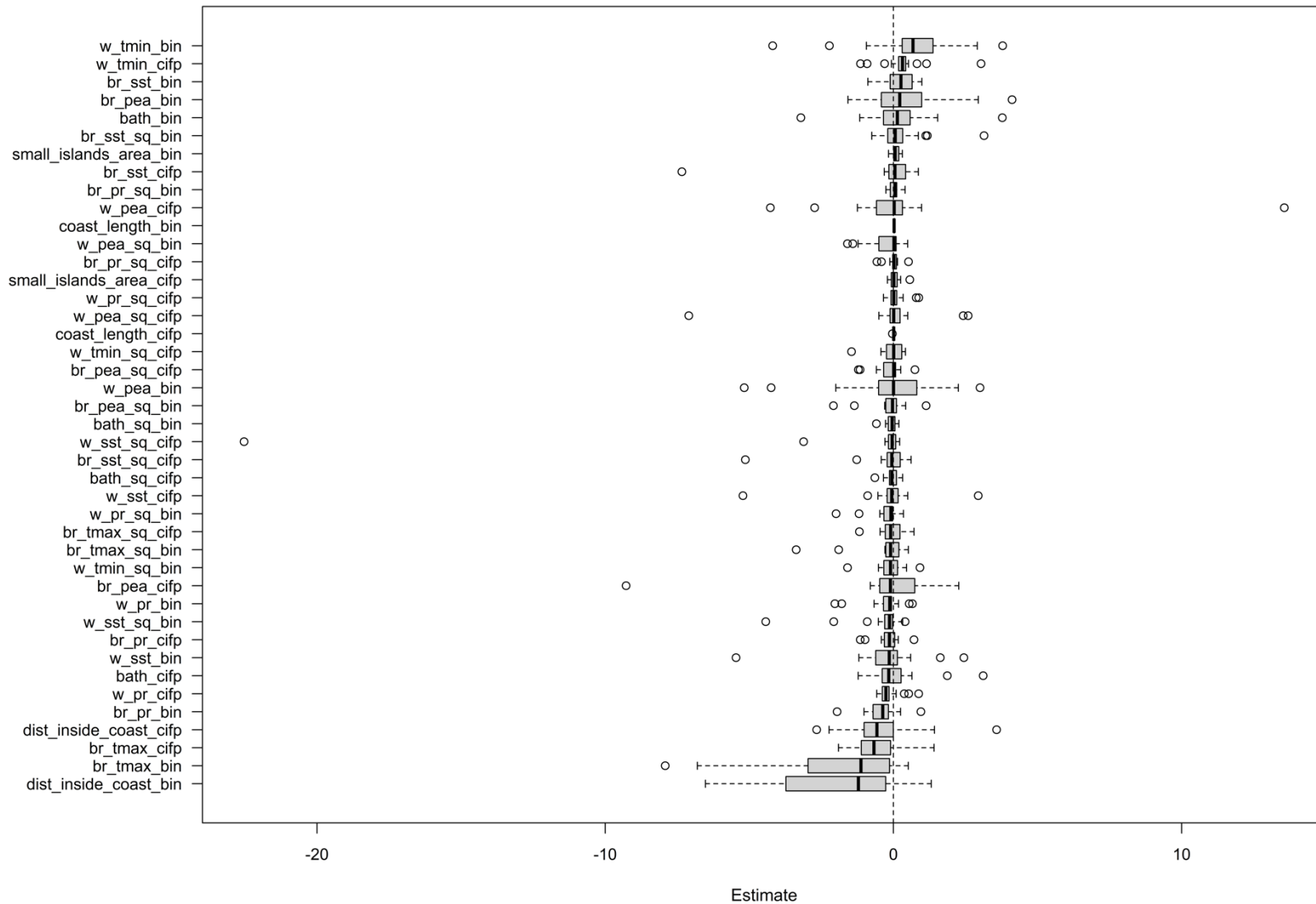


Figure 6. Forest plot of spread of parameter estimates across species, for each variable in presence/absence sub-model (“_bin”) or abundance sub-model (“_cifp”). Variable names are as in Table 2; quadratic terms are denoted by “_sq”. Variables are scaled and centred: the parameter estimates can be directly compared.

Table 4. Projected future abundance for 19 seabird species under climate change. Data-poor species with less reliable model performance (see 3.1) are asterisked. Blue text indicates increases; red text indicates declines.

Species	Seabird 2000 count (UK&I)	Predicted GB&I population size, 2050 (median and 95% CI)	Predicted change (median %, GB&I)	Seabird 2000 count (INTERREG VA area)	Predicted INTERREG VA area population size, 2050 (median and 95% CI)	Predicted change (median %, INTERREG VA area)	Proportion of population in INTERREG VA area (Seabird 2000)	Proportion of population in INTERREG VA area (median 2050 prediction)
Fulmar	537988	144559 (33473 - 551158)	-73.1	145607	50441 (11342 - 180591)	-65.4	0.271	0.349
Storm-petrel*	82818	14799 (20 - 27142284)	-82.1	7731	6 (0 - 226287)	-99.9	0.093	0
Cormorant	13586	12138 (2045 - 64585)	-10.7	3407	3300 (465 - 16899)	-3.1	0.251	0.272
Shag	32202	44600 (7123 - 226533)	38.5	9511	14422 (1994 - 74849)	51.6	0.295	0.323
Arctic skua*	2136	0 (0 - 0)	-100	177	0 (0 - 0)	-100	0.083	0
Black-headed gull	141871	220934 (45232 - 1612457)	55.7	15633	37588 (6271 - 217212)	140.4	0.110	0.170
Common gull	49728	50591 (14613 - 183392)	1.7	6161	5242 (1159 - 22057)	-15.0	0.124	0.104
Great black- backed gull	19610	16417 (3943 - 70231)	-16.3	4953	5043 (1204 - 18315)	1.8	0.253	0.307
Herring gull	148849	105568 (30444 - 351803)	-29.1	31327	26742 (7806 - 87371)	-14.6	0.210	0.253
Kittiwake	415994	192333 (35828 - 968980)	-53.8	54388	28475 (4334 - 153082)	-47.6	0.131	0.148
Lesser black- backed gull	116640	126622 (15219 - 1001976)	8.6	14080	41934 (4441 - 298649)	197.8	0.121	0.331
Arctic tern	48469	12170 (2444 - 69229)	-74.9	7131	1524 (139 - 13042)	-78.6	0.147	0.125
Common tern	13859	14404 (3183 - 76857)	3.9	3911	4629 (1023 - 24493)	18.4	0.282	0.321
Little tern*	2093	995 (38 - 26521)	-52.5	242	65 (9 - 3149)	-73	0.116	0.066
Sandwich tern*	13977	4300 (41 - 4413284)	-69.2	2282	534 (14 - 69440)	-76.6	0.163	0.124
Black guillemot	42701	26454 (7316 - 88746)	-38	14452	9077 (2103 - 31958)	-37.2	0.338	0.343
Puffin	600751	68588 (3726 - 1042735)	-88.6	241671	16731 (661 - 280381)	-93.1	0.402	0.244
Razorbill	216060	107029 (19592 - 523769)	-50.5	82617	44669 (7365 - 215660)	-45.9	0.382	0.417
Guillemot	155948 4	784397 (102574 - 5352779)	-49.7	298349	151772 (13934 - 1211377)	-49.1	0.191	0.193

Presence probability is a by-product of the modelling framework rather than a target quantity to be estimated, but it does provide some information about potential areas for colonisation where presence probability is projected to increase. Species-specific maps of projected future abundance and presence are presented in the species factsheets (Appendix B). Although abundance and presence were allowed to form different relationships with explanatory variables, abundance and presence were generally projected to change in the same direction for most species. Black-headed gull is a notable exception, where due to the different relationships with explanatory variables, presence is projected to decline while abundance is projected to increase. It is difficult to conceive of a plausible ecological scenario consistent with these opposing projections: therefore, for this species, the poorer model fit of the abundance component may mean that the (opposite) projected negative trend in presence is more likely.

The abundance trend for each species is predicted to vary spatially across the INTERREG VA area. Projected spatial abundance trends are highly idiosyncratic, but for declining species declines are generally projected to be more pronounced in the south (e.g. Arctic tern, although see fulmar). For some species, e.g. shag, there is no clear spatial pattern in projected abundance trend. By-species projection maps are presented in the species factsheets, Appendix B; detailed projections of abundance by site are provided in Appendix C.

3.4. Vulnerability assessment

It was possible to formally assess the vulnerability of 17 species to climate change (Table 4). Although we could not make a formal assessment for storm-petrel given the lack of repeat census data for this species, we have also included it in the assessment with a very high risk of decline and low likelihood of benefit based on the projected changes (Table 4). Most projected changes were associated with a poor level of confidence apart from little tern, Arctic tern, kittiwake and Arctic skua which were of moderate confidence due to the concordance between high magnitude observed and projected declines supported by additional literature about supporting climate change mechanisms (Johnston et al. 2021).

Eleven species were rated as having a high vulnerability to climate change, and four a moderate vulnerability, whilst only four were regarded as having a potential opportunity to increase from climate change (common tern, black-headed gull, common gull and lesser black-backed gull). Shags have a mixed vulnerability due to observed declines consistent with negative effects of SST upon sandeels, and also their vulnerability to storms (see Johnston et al. 2021 for more detail), whilst the modelling projects that their abundance will increase through time. Two species show reduced vulnerability to climate change in the INTERREG VA region (great black-backed gull and cormorant) where greater population increases are also projected for lesser black-backed gull. Conversely, common gull appears more vulnerable to climate change impacts in the INTERREG VA region than the rest of the country (Table 6).

Table 5. The results of the risks and opportunities for 18 seabird species under a high emissions (RCP 8.5) scenario by 2050 for Britain and Ireland. Species are listed by their BTO code (see Table 1). Those in bold are associated with moderate confidence, whilst the others have poor confidence. Dark orange cells are indicative of high vulnerability, medium orange, moderate vulnerability; light orange, vulnerability and opportunity; light blue, low impact; medium blue, moderate opportunity and dark blue, high opportunity.

		RISK				TOTALS
		VERY HIGH	HIGH	MEDIUM	LOW	
OPPORTUNITY	LOW	AF, AE, F., KI, HG, AC, TM	PU, TY, GB, CA	TE, GU, RZ		11
	MEDIUM		SA		CM	3
	HIGH				BH, LG	5
	VERY HIGH				CN	0
TOTALS		7	5	3	4	19

Table 6. The results of the risks and opportunities for 18 seabird species under a high emissions (RCP 8.5) scenario by 2050 for the INTERREG VA region. Species are listed by their BTO code (see Table 1). Those in bold are associated with moderate confidence, whilst the others have poor confidence. Those marked in red have an altered vulnerability compared to the national picture. Red cells are indicative of high vulnerability, orange, moderate vulnerability; dark green, vulnerability and opportunity; light green, low impact; blue, moderate opportunity and purple, high opportunity.

		RISK				TOTALS
		VERY HIGH	HIGH	MEDIUM	LOW	
OPPORTUNITY	LOW	AF, AE, F., KI, HG, AC, TM	PU, TY, CM	TE, GU, RZ	GB, CA	11
	MEDIUM		SA			3
	HIGH				BH	3
	VERY HIGH				CN, LG	2
TOTALS		7	4	4	4	18

4. Discussion

4.1 Overall findings

Although species' fitted relationships with terrestrial climate and oceanographic variables were highly idiosyncratic, there were some generalities. Effect sizes were typically greater and more consistent for terrestrial climate variables than for oceanographic variables. Therefore terrestrial climate may be more important than marine climate in driving spatial variation in seabird abundance in Britain and Ireland (but see 4.3).

This study is the first to project future abundance for seabird species in the north-east Atlantic on the basis of multiple terrestrial climate and multiple oceanographic variables. In common with Johnston et al. (2013), which focussed on seabird abundance in UK SPAs, we predict that the majority of seabird species will decline in abundance in the INTERREG VA area over the 21st century, based on the fitted relationships with climate. Fifteen of the nineteen species modelled were projected to decline, with eleven at the national level and ten within the INTERREG VA region having a high vulnerability to climate change. The greatest decline is predicted for Arctic skua: like Huntley et al. (2007), we predict that this species will not breed in the INTERREG VA area (or indeed Britain and Ireland) by the middle of the 21st century. Steep declines of greater than 50% of abundance are predicted for fulmar, puffin, Arctic tern, little tern, sandwich tern and storm-petrel (although the latter three species have results which are less reliable).

Some spatial variation in abundance trend is predicted even within the relatively small INTERREG VA area. This is idiosyncratic with respect to species: for example, the steepest declines in abundance are predicted to be in the south and east area for black guillemot, and the north and west of the area for fulmar (see species-specific factsheets – Appendix B). Increases are predicted for five species, of which two (black-headed gull and lesser black-backed gull *Larus fuscus*) are predicted to more than double in abundance.

Moving to a wider context for the predictions, the INTERREG VA area is predicted to become more important for seabirds in the face of the general predicted declines. The proportion of the Britain and Ireland population held in the INTERREG VA area is predicted to increase for the majority of species, because declines are generally predicted to be lesser and increases are predicted to be greater in this area.

4.2 Comparisons with annual data from the SMP and projections from other studies

Table 7. Predicted (this study, 2000-2050) and recent observed (SMP since 2000, or inter-census pre-2000) decadal changes in seabird populations. Storm-petrel is omitted because it is not monitored under SMP and accurate counts are not available for SCR Census. Blue text indicates increases; red text indicates declines.

Species	Predicted changes (% decade ⁻¹ , GB & I)	Observed changes (% decade ⁻¹ , UK or GB & I)	Source
Fulmar	-14.6	-21.1	SMP (UK, 2000-2018)
Cormorant	-2.1	-3.9	SMP (UK, 2000-2018)
Shag	+7.7	-13.3	SMP (UK, 2000-2018)
Arctic skua	≤-20.0	-38.9	SMP (UK, 2000-2018)
Black-headed gull	+11.1	+17.8	SMP (UK, 2000-2018)
Common gull	+0.3	+26.6	Census (GB & I, 1985-88 to 1998-2002)
Great black-backed gull	-3.3	-3.0	Census (GB & I, 1985-88 to 1998-2002)
Herring gull	-5.9	-9.6	Census (GB & I, 1985-88 to 1998-2002)
Kittiwake	-10.8	-27.8	SMP (UK, 2000-2018)
Lesser black-backed gull	+1.7	+29.6	Census (GB & I, 1985-88 to 1998-2002)
Arctic tern	-15.0	-7.2	SMP (UK, 2000-2018)
Common tern	+0.7	+8.3	SMP (UK, 2000-2018)
Little tern	-10.5	-23.9	SMP (UK, 2000-2018)
Sandwich tern	-13.8	+6.6	SMP (UK, 2000-2018)
Black guillemot	-7.6	+2.9	Census (GB & I, 2003-04 to 2013-2015)
Guillemot	-9.9	+0.1	SMP (UK, 2000-2018)
Puffin	-17.7	+14.0	Census (GB & I, 1985-88 to 1998-2002)
Razorbill	-10.1	+18.3	SMP (UK, 2000-2018)

Our projections are generally in accordance with recent observed trends in seabird population size taken from the SMP (JNCC 2020) or if the species is one without species trends reported by SMP, the two most recent censuses (bearing in mind that the census data were used in the projections and so are not independent). There was a moderate positive relationship ($R^2 = 15.7\%$) between observed and predicted trends (Table 7). There was a slight tendency for observed trends (11/18; 61.1%) to be more positive (i.e. true declines are less pronounced and increases are greater) than our predictions. The five species with the largest discrepancy between observed and predicted trends are shag, common gull, lesser black-backed gull, razorbill and puffin; for the latter four of these the observed changes have been more positive than our predictions. It is worth noting that for common gull, lesser black-backed gull and puffin, this may be because the observed changes were from SCR Census to Seabird 2000

(1985-88 to 1998-2002), and therefore may not reflect the likely greater impacts of climate change observed more recently during SMP (2000-2018). In addition to the differences in time-periods between observed and predicted trends, variation in the coverage by the SMP sites (only a small subset of Britain and Ireland seabird colonies) and potential lags between climate change impacts and changes in seabird abundance may also account for variation between observed and predicted trends, as well as the fact that climate change is not the only cause of variation in seabird population size.

Climate change vulnerability assessments vary considerably in projected risk for a given species, based on the geographical area, timescale and assessment framework used (Wheatley et al. 2017). Prior to this study, four others report on the vulnerability of British seabirds to climate change in comparable ways. Wheatley et al. (2017) applied a wide range of vulnerability assessment approaches. Pearce-Higgins et al. (2017) applied a simplified version of the Thomas et al. (2011) framework that failed to account for potentially exacerbating or confounding factors to bioclimate models of occurrence (Beale et al. 2014), whilst Ausden, M. unpubl. following Pearce-Higgins et al (2017) took those same bioclimate models but applied the full Thomas et al. (2011) framework. Finally, Pearce-Higgins et al. (2015b) also applied the full Thomas et al. (2011) framework to the comparison between the abundance projections of Johnston et al. (2013) and changes in abundance from Seabird 2000.

Of these climate change vulnerability studies, the most similar to the present study are therefore probably Pearce-Higgins et al. (2015b) and Ausden et al. (unpubl.) as both also used the same Thomas et al. (2011) risk assessment framework. Across these three frameworks, fulmar, kittiwake, Arctic tern, and puffin were all rated as vulnerable to climate change, whilst both Arctic skua, and black guillemot were similarly rated as vulnerable by Ausden et al. (unpubl.) and this study, but were not modelled by Pearce-Higgins et al. (2017). All three studies assessed both black-headed gull and lesser black-backed gull as likely to have an opportunity to benefit from climate change. Collectively, these are probably the most robust assessments across species, whilst for others, there is less consistency or even strong contrast, such as for cormorant, great black-backed gull, herring gull and little tern, each of which are rated as having high vulnerability by one study but high opportunity by another. A comparison table of previous climate change vulnerability assessments for seabirds in Britain and Ireland is presented in Appendix D.

4.3 Limitations and future study

As for some other studies modelling the effects of climate change on seabird abundance (Johnston et al. 2013; Pearce-Higgins et al. 2017; Wheatley et al. 2017), some species had too few data to fit the models successfully. This prevents assessment of the threat posed by

climate change for six species. Additionally, four data-poor species had enough data for the model to run, but the model behaved strangely and the results for these species must be interpreted with caution. Although the hurdle model required many parameters, preliminary analyses showed that these problems were not resolved by running the model with fewer parameters, and therefore these issues do not arise from a low ratio of data to parameters. The availability of more data on the relationship between climate and seabird abundance from the current Seabirds Count census may allow models to be fitted successfully for more species.

Sea level rise and increased storminess are potential mechanisms by which climate change may affect seabirds (Johnston et al. 2021), that we were not able to incorporate specifically in our models because the available digital elevation models (DEMs) of the coast of Britain and Ireland are at too coarse a vertical resolution. If finely-resolved DEMs become available for the study area, then the analysis could be updated to quantitatively predict loss of colony area, an issue flagged up by Johnston et al. (2021) which is of high concern for ground nesting seabirds on low-lying coastal areas in particular.

Except for a few species, predicted abundance was only weakly related to observed abundance. This could indicate that climate, or the climate variables we selected, only explains a small proportion of variation in seabird abundance. Alternatively, it could be that our model did not account adequately for the highly over-dispersed nature of seabird abundance data. For seabird species breeding in small dense colonies, aggregation may take place over a very small spatial scale (hundreds of m – low km). Our model could only detect spatial autocorrelation over a range of >12 km; a much higher resolution spatial random effect adequate to account for spatial aggregation over a very short range would have a much greater model runtime. It is worth noting that this poor performance of models to predict local variation in seabird abundance was also a feature of the models of Johnston et al. (2013) which were able to successfully predict recently observed changes, suggesting that this is not a major limitation with respect to our ability to produce meaningful projections.

Based on the outputs of our models it could be argued that terrestrial climate may be more important than marine climate in driving spatial variation in seabird abundance in Britain and Ireland. Alternatively, it could be that the oceanographic variables we used in this study less-well characterized variation in the marine environment relevant to seabirds than the terrestrial variables described the terrestrial environment. For example, there is considerable uncertainty in the species-specific foraging ranges used to subset the oceanographic data for some species (Woodward et al. 2019). Furthermore there is likely to be considerable colony specific and even annual variation in the foraging ranges of seabirds. Also, the time periods over which oceanographic data were summarized were longer than those for the terrestrial climate data. Additionally, the timing of minima or maxima in oceanographic variables may

be more relevant to seabird population growth rate than is the central tendency (e.g. Ramírez et al. 2016).

Generally, uncertainty is high in our predictions, potentially indicating that variation in seabird abundance is not explained by climate alone. This means that the scenario of no change in abundance, or even a trend opposite to that indicated by the median, falls within the spread of credible scenarios for all species except Arctic skua. This uncertainty is carried forward into our vulnerability assessment, with only four of the assessments at a national level and five for the INTERREG VA region being associated with moderate confidence. None had high confidence. Again, this is not a feature specific to these model projections, but one that generally characterizes many other climate change projections at the species level (see also Pearce-Higgins et al. 2017).

There are four key reasons why species may not match our predictions in the present study. Firstly, species (particularly for long-lived species like seabirds and when only productivity is impacted by climate change) may lag behind climate change: for example, it is thought that Arctic skua is already at considerable disequilibrium with its climate space in Europe (Huntley et al. 2007). Secondly, apparent relationships between species and climate frequently arise from unrelated processes (Beale et al. 2008); our approach of using a spatial random effect may have helped avoid estimating some, but not necessarily all, spurious relationships between seabird abundance and climate. Thirdly, the predictions for four of our data-poor species are likely to be less reliable. Finally, climate change is only one of several drivers of population change in seabirds, and may be relatively minor in importance compared to other drivers.

Although the results presented here are based on climate and oceanographic data which have only recently become available, nearly two decades have passed since the seabird census data were collected. When the seabird census data from Seabirds Count become available, the analysis can be updated to either increase the precision of future projections, or to respond to changing relationships between seabird abundance and climate. Importantly, the new data may allow projection of future abundance for species for which there were too few data in the present study. Also, the relationship between seabird abundance and oceanographic variables is parameterised solely using seabird abundance data from Seabird 2000. If oceanographic data become available for the timestep corresponding to SCR Census, the analysis can be updated accordingly.

One of the main findings of this report is that the majority of seabird species in the INTERREG VA area are at high or very high risk from climate change. Our projections and climate change vulnerability assessment can be used to apportion conservation effort appropriately among species according to its urgency. However, policymakers must remain aware of the

uncertainty in the projections, particularly when targeting conservation effort spatially. The adaptation report (Pearce-Higgins et al 2021) can be used to identify the appropriate conservation actions to be implemented for individual species. Seabird monitoring will continue to be crucial for informing and targeting conservation actions.

Although this study purely aimed to project future abundance under climate change in a specific area, more general ecological insights could be drawn through minor developments on this work: by adapting our methods or by analyzing our results. Firstly, the relative importance of terrestrial and marine climate in driving variation in seabird abundance could be assessed by comparing the predictive power of models fitted with solely terrestrial or solely oceanographic data. Next, do our projections differ in predictable ways between species? For example, we might expect species to differ in their response to climate change according to their feeding ecology (e.g. Furness and Tasker 2000; Howells et al. 2018).

Finally, some of the species studied had considerable discrepancies between observed and predicted trends under climate change. This could be due to an inaccurate fitted climate-abundance relationship, arising from data insufficiency or modelling issues. However, climate change may still be one of the more minor anthropogenic sources of current population change for some species, for example compared to ongoing breeding habitat loss, predation or overfishing. The Seabirds Count census will provide observed trends for more species and from a wider geographical area. This can be used to identify whether species are differing from their expected trend under climate change; isolating the cause of such discrepancies may help inform their conservation.

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Disclaimer

The views and opinions expressed in this report do not necessarily reflect those of the European Commission or the Special EU Programmes Body (SEUPB).

Supplementary material

Appendix A: Parameter estimates for each species

Appendix B: Species factsheets

Appendix C: Shapefiles of change in abundance by site, and text file explaining use

Appendix D: Comparison of seabird climate change vulnerability assessments for Britain and Ireland

Appendix E: Projections by MarPAMM management area

All appendices are available to download online:

https://www.mpa-management.eu/?page_id=617

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