Study to examine the impact of climate change on seabird species off the east coast of Scotland and potential implications for environmental assessments

June 2022

Scottish Government
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KR Searle, J Waggitt, P Evans, M Bogdanova, F Daunt, A Butler

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Searle, K. R., Waggitt, J., Evans. P., Bogdanova, M., Daunt, F. & A. Butler

UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB

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Executive Summary

- Offshore Renewable Developments (ORDs) can make a significant contribution to the Scottish Government's target to generate 50% of overall energy consumption from renewable sources by 2030, but there is a requirement on Scottish Government to deliver them in a sustainable manner in accordance with the requirements of the Marine Strategy Framework Directive (EC/2008/56), the Habitats Directive (EC/92/43) and the Birds Directive (EC/79/409). Offshore renewable developments have the potential to affect seabirds that are protected by the EU Birds Directive, and transposed domestic legislation, notably from collisions with turbine blades and through displacement from important habitat.

- A key current concern is that Population Viability Analyses that are the standard method of forecasting future population change of seabirds as part of ORD assessments, do not account for any effects of environmental change on populations. However, many seabird species in the UK have shown marked declines in recent decades and there is widespread evidence that these are in part caused by changes in marine ecosystems as a result of climate change. Climate change can affect seabird populations indirectly via changes in food supply, or directly such as through mortality from extreme weather.

- In this project, we examined the potential impacts of climate change by quantifying the effects of climate on seabird distribution, abundance and demography. We developed future estimates for the spatial distribution and abundance at seabird foraging areas and for demographic rates, abundance, and the influence of varying foraging ranges at seabird breeding colonies on access to suitable climate conditions.

- To identify climate variables of relevance to seabird demographics we conducted a literature review in Web of Science (WoS) using the terms 'seabirds', 'climate', 'productivity', 'breeding success', 'survival' and 'demography'. This identified 20 published studies, which we summarised into two sets of climate variables (terrestrial and marine) relating to breeding success or adult survival. We focused on variables for the analysis that were sufficiently spatially or spatio-temporally resolved to be relevant to seabirds breeding on the east coast of the UK, and which were also available in projected future climate scenarios, with the exception of terrestrial wind which we included in the retrospective analyses because the literature review highlighted its important effects on demography. The list of variables included three terrestrial (minimum air temperature; max precipitation; mean wind speed) and four marine (sea surface temperature, sea surface salinity, North Atlantic Oscillation and Atlantic Multidecadal Oscillation). All predictions for future climate were made using forecasted variables from UKCP09 projections for the SRES Scenario A1B (medium). Spatiotemporal forecast variables represented an average over 30 years (2070-2099), and predictions represented a 'typical' year across this period. This was the only set of climate projections for all marine and terrestrial variables available at the onset of the project, and as such, the resulting predictions show potential changes to seabird distribution and demography under future climate conditions fifty years hence. Therefore, predictions probably represent a more extreme set of changes than is likely over the next 20-30 years of relevance to the lifetime of currently consented and planned offshore wind farms.

- We constructed statistical models to link at-sea survey data on the spatial distribution of birds and colony-based estimates of productivity and abundance to key climate-related variables in the form of a retrospective analysis of historical data. We then used modelled estimates for relationships between distribution, demographic rates and climate to forecast future projected change in at-sea distributions, productivity, adult survival (indirectly estimated from counts and breeding success) and population growth rates. At-sea distribution and abundance were modelled using a Generalised Estimated Equation – Generalised Linear Model (GEE-GLM) modelling approach, building upon previous models developed for the NERC/DEFRA MERP and ORJIP Sensitivity Mapping Tool projects. We analysed the effect of climate variables on productivity and adult survival via both frequentist generalised linear mixed models (GLMMs), which are very widely used in statistical ecology, and Bayesian approaches which offer a more flexible approach for formulating ecological processes within models. We used colony-specific and year-specific data on counts and productivity from the Seabird Monitoring Programme (SMP) for breeding colonies throughout the region of interest.

- Modelling of seabird at-sea distribution and climate showed that two species, Atlantic puffin and black-legged kittiwake, favoured the coldest waters and were therefore most likely to respond negatively to climate warming. In contrast, three species (common guillemot, razorbill and in particular northern gannet) showed an association with warmer waters, and were therefore least likely to be negatively affected by warming.

- At-sea distribution modelling resulted in widespread predicted declines under future climate projections among the majority of the species analysed. This was particularly the case for Atlantic puffin and black-legged kittiwake, in which declines were predicted to occur in both summer and winter. Common guillemot, herring gull and razorbill were predicted to decline during the summer months only, and great black-backed gull were predicted to decline during only winter months. In contrast, northern gannet were predicted to increase in both summer and winter, and notably razorbill were also expected to increase in winter months.

- Relative spatial distributional changes were only apparent in two species, common guillemot and razorbill, both of which were predicted to increase in the northern North Sea and decrease in the southern North Sea. Temporal shifts in distribution were predicted for Atlantic puffin and northern gannet, both of which were predicted to use the North Sea region more extensively in summer than winter, a pattern predicted to remain under the future climate scenario. Four species: common guillemot, razorbill, great black-backed gull and herring gull consistently showed higher numbers across the North Sea during winter. For common guillemot and razorbill these differences between winter and summer densities were predicted to become more marked under future climate conditions. These projections imply that common guillemot and razorbill may shift to have greater interactions with ORDs in the North Sea during the non-breeding period than currently, if future climate projections are manifest. Black-legged kittiwake were predicted to continue to use the North Sea throughout the year.

- These overall declines in abundance and spatial and temporal shifts in distribution are in line with previous work, suggesting that seabird habitat suitability, driven by

changes in climate, will shift northwards in the North Sea over the next century, with associated widespread declines for many species.

- Productivity models demonstrated strong links between productivity and key climate variables in five species (Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, northern gannet), particularly highlighting associations with marine climate, with terrestrial climate playing a much more minor role. In four of the five species where strong climatic effects on productivity were detected, future climate projections indicated large declines in productivity relative to current productivity rates – this was the case for: Atlantic puffin, black-legged kittiwake, common guillemot and great black-backed gull. Only one species, northern gannet, was predicted to have increased productivity under future climate projections. In all five species, modelling indicated there would be very limited or no opportunity for species to increase productivity under future conditions by expanding foraging ranges around breeding colonies to access more suitable climatic conditions.

- An important finding from the analysis of productivity and climate was that pre-breeding conditions were generally more important than conditions during the breeding season. This may result from the effect of such conditions on the quality or abundance of prey during the period of peak energy demand during breeding. Alternatively, it may represent a carry-over effect whereby conditions experienced by seabirds in one season (in this case late winter) have downstream consequences on subsequent seasons.

- These predicted declines in productivity, together with predicted declines in at-sea density and shifts in range in certain species, support past work on effects of climate warming on distribution and demography that threaten the future well-being of many breeding seabirds in the UK. Only one species, the northern gannet, showed future predictions of increased abundance and productivity, likely reflecting its more catholic diet, with less dependence on prey species that are negatively affected by warming. Our results suggest there will be profound changes to the North Sea seabird community in the coming century. This work has used a multi-colony, multi-species approach to broaden the knowledge base for understanding how seabirds breeding in the UK eastern seaboard may be affected by future climate change, demonstrating expected potential declines in a wider suite of species than previously identified.

- Our analyses on indirectly estimating adult survival from counts and breeding success data has highlighted the difficulties in robustly estimating adult survival from these data. A key area for future work is, therefore, to expand empirical observations more directly linked to survival, such as mark-recapture and mark-resighting data across a wide range of colonies and environmental conditions. Similarly, there is a nationwide lack of empirical data on juvenile survival in seabirds, which greatly inhibits current attempts to predict future population responses of seabirds to pressures.

- The results of these analyses suggest that climate change will have substantial impacts on demography and abundance of seabirds in the North Sea over the 21st century, and the impacts are likely to vary, in magnitude and form, between species. A failure to account for these changes in ORD assessments may lead to misidentification of the key affected populations, as well as misjudgement of the

extent to which seabirds are likely to interact with ORDs over time, and inclusion in assessments could be considered at the scoping stage of the Environmental Impact Assessment (EIA) process. Any directional shift in habitat use, from South to North, will mean that the number and source populations of individual birds interacting with specific OW footprints will alter over time. This could mean that a static assessment identifying the protected populations of concern using apportioning methods applied to current day distributions could fail to identify populations that would come to interact with those footprints as their population sizes evolve over time, and their spatial habitat use changes in coming decades.

- Similarly, the evidence supporting potential seasonal shifts in habitat use of the North Sea for two species (common guillemot and razorbill) suggests that the seasonal period of greatest importance for ORD impacts on protected populations may change as climate alters. If species begin to use the North Sea proportionately more in the overwinter period than the breeding season, ORD impact assessments in the non-breeding season will become more critical to performing robust and accurate assessments. This is particularly challenging because at present, available methods for assessing impacts of ORD in the non-breeding season, and apportioning impacts back to protected colonies, are much cruder than those available for the breeding season. Moreover, it will become increasingly important that cross-border efforts to assess impacts for seabirds originating from different countries are better developed, because the ratio of seabirds from UK and non-UK populations in the North Sea during winter is likely to alter under future climate change.

Introduction

Offshore Renewable Developments (ORDs) can make a significant contribution to the Scottish Government's target to generate 50% of overall energy consumption from renewable sources by 2030 and have decarbonised the energy system almost completely by 2045 (Scottish Government, 2022). However, the Scottish Government has a duty to ensure that ORDs are delivered in a sustainable manner, in accordance with the requirements of the Marine Strategy Framework Directive (EC/2008/56), the Habitats Directive (EC/92/43) and the Birds Directive (EC/79/409). Offshore renewable developments have the potential to affect seabirds that are protected by the EU Birds Directive, and transposed domestic legislation, notably from collisions with turbine blades and through displacement from important habitat (Drewitt & Langston 2006; Masden *et al*. 2010; Scottish Government 2011).

A key current concern is that assessments of ORDs on seabird populations, in particular Population Viability Analyses that forecast future population change, do not account for any potential changes to seabird populations arising from environmental change. However, there is widespread evidence that seabirds are being affected by changes in marine ecosystems as a result of climate change. Over one third of UK seabird species have experienced declines in breeding abundance of 20-30% or more since the early 1990s (Mitchell *et al*. 2018) and 6 of the 25 UK breeding seabird species are Red-listed (Eaton *et al*. 2015). Climate change is considered to be one of the primary causes of these declines (Daunt & Mitchell 2013; McDonald *et al*. 2015; Carroll *et al*. 2015; Daunt *et al*. 2017, Dias 2019, Daunt & Mitchell 2020). Climate change can affect seabird populations via two main processes: indirect effects via changes in food supply, and direct effects such as mortality from extreme weather. These effects could interact with the effects of ORDs additively, synergistically or antagonistically (Crain *et al*. 2008; Burthe *et al*. 2014). Factoring in these processes to assessments is therefore critically important in improving estimates of the effects of ORDs on future population change in protected seabird populations (Daunt *et al*. 2017, Daunt & Mitchell 2020)*.*

In this project, we examined the potential impacts of climate change on Scottish seabirds breeding on the eastern seaboard by exploring relationships between climate and seabird behaviour, demographics, abundance and distribution. We developed future estimates for seabird distribution and demography using a scenario (SRES A1B) of future emissions from the UKCP09 climate projections (2018), and hence climate. Under this scenario, we used statistical models to produce projections of:

  i.   The spatial distribution of seabird foraging areas;
 ii.   Overall species seasonal abundance based on density maps of seabirds at sea;
iii.   Demographic rates at seabird breeding colonies (productivity and adult survival);
iv.   Demographic rates achieved under varying foraging ranges at seabird breeding colonies;

We compared these future projections against the current "baseline" values for key population and distribution characteristics to estimate the likely impacts of climate change, analysed in a way that accounts for uncertainty. Finally, we discuss the implications of our findings for offshore wind assessments.

Methods

We constructed statistical models to link existing data sources (at-sea survey data on the spatial distribution of birds, nest monitoring data on productivity and colony abundance data) to key climate-related variables. The analyses of at-sea survey data built upon previous models developed for the NERC/DEFRA funded MERP (Waggitt et al. 2020) and ORJIP Sensitivity Mapping (Searle et al. 2019) projects. We conducted the statistical analyses of productivity and abundance using colony-specific and year-specific values, for breeding colonies throughout the region of interest. We used these models to generate projections of future spatial distributions and demography under one future scenario of climate change. We also estimated the change in foraging range that would be required in order for each seabird species to maintain their current prey intake at each breeding colony. This was estimated using proxies for prey distribution, abundance and availability, which are determined by bottom-up processes propagating through lower trophic levels (Frederiksen et al. 2006; van Deurs et al. 2009).

Data on demography and abundance

This project considered eight species of seabirds, all breeding on the east coast of Scotland:

- northern gannet *Morus bassanus*
- black-legged kittiwake *Rissa tridactyla*
- common guillemot *Uria aalge*
- razorbill *Alca torda*
- Atlantic puffin *Fratercula arctica*
- herring gull *Larus argentatus*
- great black-backed gull *Larus marinus*
- European shag (spatial distribution not modelled) *Phalacrocorax aristotelis*

We obtained annual colony-level seabird abundance and productivity data, derived primarily from the Seabird Monitoring Programme (SMP), but augmented by additional count data for northern gannet from Prof. Sarah Wanless (UKCEH fellow); breeding success for black-legged kittiwakes, common guillemots, razorbills and European shags for the Isle of May NNR (UKCEH); and additional plot count data for these four species, also from the Isle of May NNR (UKCEH). For the additional plot count data, we used a regression model to link the colony level counts to plot counts within each colony (Poisson GLM: colony pairs ~ plot pairs). Finally, adjustment factors ('k' values) were used to convert raw counts of individuals to breeding pairs for common guillemots and razorbills, obtained from the Isle of May long-term study (Harris et al. 2015a; 2015b; updated).

The primary aim of the modelling was to predict the impact of future climate change within the Forth-Tay region. However, generating such predictions require colonies beyond this region to be included in the statistical modelling to ensure that the statistical modelling covers the range of climates that might be expected to occur within the Forth-Tay region under future climate change (a "climate envelope" modelling approach). Basing the model upon a very wide spatial area would, however, risk including populations that are influenced by different biological mechanisms to those operating in the Forth-Tay region. It was decided, in discussion

with the project steering group (PSG), that the best compromise was to consider colonies along the east coast of Britain – i.e., within the region that stretches from Kent to Caithness, together with Orkney and Shetland.

Successful modelling of the empirical relationship with climate is only possible for colonies that have sufficient data. Therefore, we imposed a minimum data requirement that colonies must have at least nine years of data since 1986 (e.g. >25% coverage) for either breeding success or abundance. The threshold (25% coverage) is somewhat arbitrary, as there is no obvious rule for determining the appropriate level of coverage to consider, but ensures that the analysis focuses on colonies with a reasonable level of temporal coverage, which is important given that focus here is upon change over time.

The SMP is structured as "Sites" that are contained within "Master Sites". The latter, higher level, of site definitions are generally of most practical interest (as, for example, they often correspond to SPAs), but as data are provided at the lower "Site" level it is not always possible to extract data at the "Master Site" level (e.g., if only some of the "Sites" within a "Master-site" have been counted within a particular year). Where possible, we aggregated 'Sites' up to 'Master Sites' in the SMP to better represent biological populations: aggregation was done for sites where the number of years with complete counts for all 'sites' within the 'master-site' was within four years of the number of years of counts for the best observed site within that master-site (i.e., if the best observed 'site' had ten years with counts, sites were only aggregated up to 'master site' if there were complete counts for all 'sites' within the 'master site' in at least six years). We chose a threshold of four years to ensure that the aggregation approach could be used reasonably often (if we were to apply a threshold of zero years, for example, then aggregation would be possible in far fewer cases), whilst ensuring that the number of years dropped from the analysis as a result of aggregating is not too large (because the aggregation means that only years with data for all sites within the master-site can be included in the analysis).

Applying this methodology resulted in a range of breeding colonies to use in the demographic modelling for each species. For analyses of productivity this ranged from four colonies for northern gannet, up to 40 colonies for black-legged kittiwakes (Table 1), with lower numbers for analyses of survival. Full details of the selected colonies are in the appendix.

Table 1. Summary of number of colonies that mean the minimum data requirements (9 or more years of data of the relevant type) for the analyses of abundance, productivity and survival.

Species	Abundance	Productivity	Survival
Atlantic puffin	11	4	2
Common guillemot	15	10	5
European shag	39	19	12
Northern gannet	7	6	4
Razorbill	17	9	6
Herring gull	42	19	12
Great black-backed gull	46	12	8
Black-legged kittiwake	76	40	23

Survival data

Adult survival rates for the eight species in this study have been published in the peer-review literature and reviewed in contract reports (Horswill & Robinson 2015; Searle et al. 2020). We used the published rates for adult survival from these reports for each species in the demographic modelling (Table 2).

Table 2. Summary of adult and juvenile survival rates (mean and standard deviation) used in the demographic modelling in relation to climate variables. All values taken from Horswill & Robinson (2010) or MS PVA report (Searle et al. 2019) except for juvenile survival for greater black-backed gull where no data was available, this value was set to match that for herring gull juvenile survival to 2 decimal places.

Species	Adult		Juvenile
	Mean survival	SD	Mean survival
Atlantic Puffin	0.906	0.083	0.737
Common Guillemot	0.939	0.015	0.786
Herring Gull	0.834	0.034	0.794
Great Black-Backed Gull	0.930	0.034	0.790
Kittiwake	0.854	0.051	0.790
Northern Gannet	0.919	0.042	0.728
Razorbill	0.895	0.067	0.794
Shag	0.858	0.194	0.615

Data on climate and other environmental characteristics

Terrestrial climate variables

To identify climate variables of relevance to seabird demographics, we conducted a literature review using Web of Science (WoS) and the terms 'seabirds', 'climate', 'productivity', 'breeding success', 'survival' and 'demography'. This identified 20 published studies (Appendix A), which we summarised into two sets of climate variables relating to either breeding success or adult survival (Table 3). Of these, we selected the following monthly terrestrial variables to use within the demographic modelling, all of which were taken from data for the nearest UK Met Office weather station:

Breeding success:

- Mean of daily minimum air temperature
- Summed daily precipitation
- Mean wind speed

Adult survival:

- Mean of daily minimum air temperature
- Max precipitation
- Mean wind speed

For breeding success, each terrestrial variable was aggregated into a value across the set of months most relevant to each species in terms of pre-breeding attendance

at colonies, incubation and chick-rearing. For adult survival, variables were aggregated into the non-breeding season, or over the whole year. The biological periods are based on those used within the NERC MERP at-sea seabird distribution modelling, and were selected to reflect when a substantial portion of the local population of a the particular species remains close to the colony (Waggitt et al. 2020; Table 4, Table 5).

Table 3. Summary of terrestrial and marine climate/weather variables used to correlate with breeding success (or parameters related to breeding success) and adult survival in seabirds based on literature review.

Demographic rate	Climate parameters	References
Breeding success	Air temperature/effective temperature/min temp Mean wind speed Wind direction Prevailing wind Precipitation (max or summed) Spring NAO, winter NAO Chlorophyll SST	*(Jones et al. 2007, Lewis et al. 2009, Smith and Gaston 2012, Watanuki and Ito 2012, Monticelli et al. 2014, Lewis et al. 2015, Zuberogoitia et al. 2016, Howells et al. 2017, Christensen-Dalsgaard et al. 2018, Pakanen 2018, Gardarsson and Jonsson 2019, Michielsen et al. 2019)*
Adult survival	Wind magnitude/wind speed/onshore wind Mean winter SST, SST anomalies Winter NAO AO (non-breeding season) Min temp (winter) Winter precipitation	*(Jones et al. 2007, Frederiksen et al. 2008, Hario et al. 2009, Tomita et al. 2009, Tranquilla et al. 2010, Smith and Gaston 2012, Genovart et al. 2013, Zuberogoitia et al. 2016, Guery et al. 2017, McKnight et al. 2019)*

Table 4. Definition of breeding season months for each of the eight species; note that 'breeding season' includes both the main breeding season and outlying periods (pre-laying and post-fledging) for all species.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Atlantic puffin												
Black Legged-kittiwake												
Common guillemot												
European shag												
Herring gull												
Great Black-backed Gull												
Northern gannet												
Razorbill												

This results in a set of 'pre-breeding' months, 'breeding season' months, 'preceding year' definitions, and 'non-breeding' months for each of the eight species (Table 5), which were used within the demographic models.

Table 5. Set of months used to define the biological periods to be used to create synthesised climate variables within the demographic models.

Species	Pre-breeding months	Breeding season months	Preceding year based on post breeding season census	Winter months
Atlantic puffin	February - March	April – August	May - April	September – March
Black-legged kittiwake	February – March	April – August	May – April	September – March
Common guillemot	February – March	April – July	May – April	August – March
European Shag	February – March	March – August	April – March	September – February
Herring gull	February – March	April – July	May – April	August – March
Great black-backed gull	February – March	April – July	May – April	August – March
Northern gannet	February – March	April – October	May – April	November - March
Razorbill	February - March	April – July	May – April	August – March

All UK Met Office data were downloaded from CEDA (Met Office, 2019). The nearest UK weather stations for each selected breeding colony are shown below:
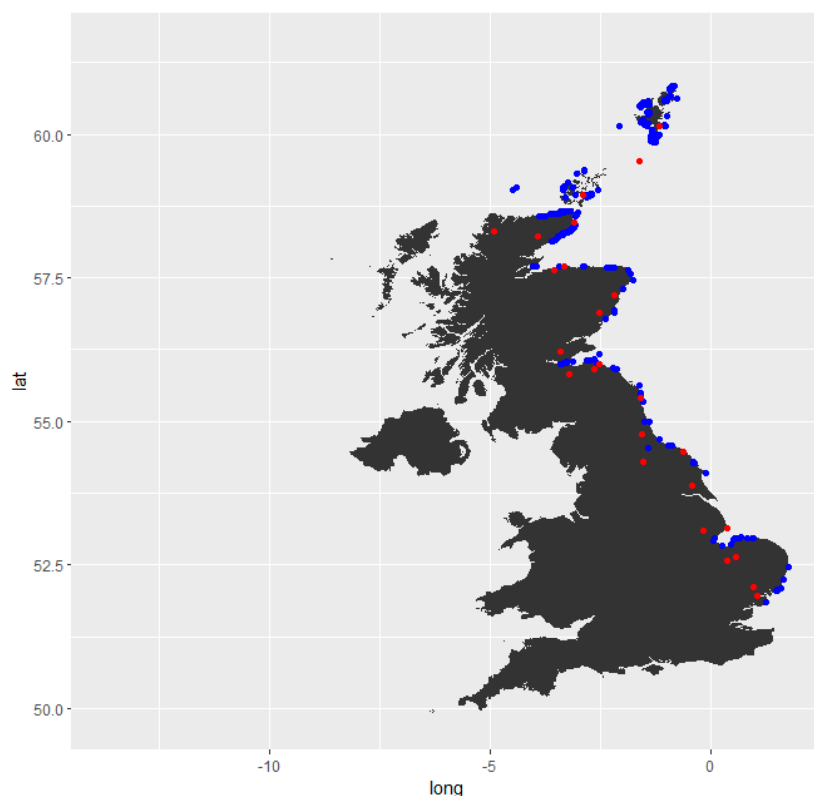
Figure 1. Locations of nearest UK weather stations (red) for the selected seabird breeding colonies (blue) on the East coast of the UK.

Marine climate variables

We selected marine climate variables previously demonstrated to correlate with seabird distribution and demography, all of which were used in the spatial distribution modelling, with only three marine variables (NAO, sea surface temperature and sea surface salinity) used in the demographic modelling (Table 6). Models were parameterised using hindcast variables from 1985 to 2018, with oceanography (temperature, salinity) sourced from FOAM AMM7 models (O'Dea *et al* 2014, available from the Marine Environmental Monitoring Service: MEMS (2022)) and climatic indices (AMO, NAO) sourced from the MET Office (Tinker et al 2016). Distribution models were also parameterised using static/non-dynamic variables including topographic values (depth) from EMODNet (2022) and oceanography (mean current speed) from FOAM AMM15 models (Tonani *et a*l 2019, available from MEMS). All predictions for future climate were made using forecasted variables from UKCP09 projections for the SRES Scenario A1B (medium). Spatiotemporal forecast variables represent an average over a 30 year future (2070-2099). Note that at the time of project commencement all required marine variables were not available from the updated UKCP18 climate projections, hence we were forced to use the older UKCP09 projections in the modelling.

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Table 6. Summary of marine climate variables to be used in modelling of spatial distribution of seabirds on the East coast of the UK.

Column	Details	Spatial Scale	Temporal Scale	Notes
Date	MMM - YY	-		1975 = average conditions in 1961-1990 from Hindcast. 2085 = average conditions in 2070-2099 from Forecast.
Year	Year	-		1975 = average conditions in 1961-1990 from Hindcast. 2085 = average conditions in 2070-2099 from Forecast.
Month	Month	-		
Lon	Eastings in UTM30N	-		
Lat	Northings in UTM30N	-		
SST	Sea Surface Temperature in Celsius	2.5km	Monthly	Resampled to 2.5km from ~7km resolution using bilinear interpolation.
SLM	Sea Surface Salinity in ppt	2.5km	Monthly	Resampled to 2.5km from ~7km resolution using bilinear interpolation.
BAT	Depth in m	2.5km	Monthly	Resampled to 2.5km from <1km resolution using block-averaging.
FEA	Seabed Roughness in m	2.5km	-Static	Derived from BAT using a terrain ruggedness index (TRI) to identify topographic features including banks, trenches and ridges.
SPM	Mean Depth-Averaged Current Speed in ms-1	2.5km	-Static	Resampled to 2.5km resolution from ~2km resolution using bilinear interpolation.
HU3	Simpson-Hunter Stratification Index	2.5km	-Static	Derived from BAT and SPM to identify mixed, frontal and stratified water columns.
NAO	North Atlantic Oscillation	-	Annual	Normalised Winter Average (Dec, Jan, Feb). In 1975 represents average in 1961-1990. In 2085 represents average in 2070-2099.
AMO	Atlantic Multidecadal Oscillation	-	Annual	Normalised Annual Average. In 1975 represents average in 1961-1990. In 2085 represents average in 2070-2099.

The annual marine environmental data relate to a spatial grid. The gridded data were used directly within the models of distribution, but for the models of demography they were translated into a single annual summary metric of each environmental variable for each breeding colony. The approach used was similar to that used by Carroll et

al. (2015): we calculated a weighted mean of the environmental variable. Because we needed to calculate values for non-breeding and pre-breeding seasons as well as the breeding season, rather than basing the weights upon estimated utilisation distributions derived from GPS tracking data (which only relate to the chick rearing period) we based the weights upon a simpler distance-decay rule that allocates more weight to locations close to the breeding colony than to locations that are far away. Specifically, we assumed that the weight of each grid cell is the form

$$w \propto \exp(-\lambda d)$$

where d represents the distance by sea from the grid cell midpoint to the breeding colony, and where λ represents the decay rate for the species. The weights are rescaled so that they sum to one across all grid cells. We estimated the decay rate λ for each species to be the value such that 95% of all weights would, in an area of sea without land, be allocated to locations within the published mean-max foraging range (Thaxter et al., 2012) of the colony. Note that foraging ranges were derived from Thaxter et al. (2012) rather than the more recent Woodward et al. (2019) data because during the initial stages of the project inception Woodward et al. (2019) had not yet been published.

Statistical models for spatial distribution of birds

Climate change may be expected to alter the spatial distribution of prey, and hence to alter the areas that are most suitable for foraging. We are using a statistical model to quantify the likely impact of climate change in altering the spatial distribution of foraging locations.

As part of the NERC/DEFRA funded Marine Ecosystems Research Programme (MERP), a species distribution model (SDM) was developed to predict the at-sea distribution and densities (animals per km^2) of 12 prevalent species; Atlantic puffin, black-legged kittiwake, common guillemot, razorbill, European shag, European storm-petrel *Hydrobates pelagicus*, herring gull, lesser black-backed gull, Manx shearwater *Puffinus puffinus*, northern fulmar *Fulmarus glacialis*, and northern gannet (Waggitt et al, 2020). SDMs quantify relationships between densities and ecologically-relevant environmental descriptors, and then use the relationships to predict distributions in particular regions and/or times. Using a series of environmental variables (temperature, temperature variance, fronts, depth and bathymetric roughness) averaged across the study period (1985-2018), this SDM predicted monthly distributions for a typical year in the North-East Atlantic (Waggitt et al, 2020) and Scottish waters (Searle et al. 2019), respectively.

In this project, we have extended this SDM framework to predict seabird distributions for a specific month and year, in both current and future scenarios (e.g. Evans and Waggitt 2019). To do so, we replaced the averaged environmental variables with corresponding concurrent environmental variables. Influential climatic indices including the North Atlantic Oscillation (NAO) and Atlantic Multi-decadal Oscillation (AMO) were also included. These climatic indices describe regional-scale meteorological and oceanographic conditions (e.g. wind events, storm events, precipitation). Because species responses to physical changes can be complex, the SDMs we have developed include interactive terms between environmental variables. For example, previous work on marine mammals has demonstrated that

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harbour porpoise *Phocoena phocoena* concentrations have moved from the northern North Sea (NNS) to the southern North Sea (SNS) in recent decades (Hammond et al. 2013). However, using concurrent temperature alone will not detect these profound changes, because animals have moved from the cool-water NNS to the warm-water SNS. Importantly, using an interaction between annual temperature and AMO will detect these changes; increasing AMO has likely caused declines in cool-water prey in the NNS, encouraging animals to exploit warm-water prey in the SNS.

Overview

Predictions of distributions under previous (1969-1990), current (2017) and future scenarios (2070-2099) were based on GEE-GLM approaches developed in Waggitt *et al*. (2020). GEE-GLMs use a hurdle-model approach divided into a presence-absence and density component. The presence-absence component uses relationships between a species presence and environmental conditions to predict spatio-temporal variations in the probability of encountering a species. The density component then uses relationships between numbers of individuals and environmental conditions to predict the density of a species if encountered. The final predicted density of a species is the product of these two components. These components are parameterised using sightings of seabirds from at-sea aerial and vessel surveys. Further details on GEE-GLM setup and associated data are provided in Waggitt *et al*. (2020). However, several changes were implemented to adapt the GEE-GLM for predictions across scenarios. These changes are discussed in detail in the following sections.

At-Sea Aerial and Vessel Surveys

Because of data-sharing constraints associated with some of the survey data used in Waggitt *et al* (2020), GEE-GLM parameterisation only used freely-available subsets of this collation. This subset included the data used in Bradbury *et al*. (2014) (ESAS and WWT), and additional data provided by Marine Scotland Science (MSS) and Natural England (NE).

Environmental Variables

Original GEE-GLM were developed to predict monthly (January – December) variations in densities in a typical year across several decades (1980-2018). Because of these aims, original GEE-GLM were parameterised using average environmental variables across this time period. Environmental variables were divided into spatial and temporal components. The spatial components were quantified per grid cell and consisted of colony indices, breeding season, depth, average temperature and temperature variance across the study period (1980-2018), seabed roughness and front intensity; the temporal components were quantified per month (January – December) and consisted of mean temperature across the study region (NE Atlantic). Variables anticipated to influence the overall range of a species were included in the presence-absence model, namely, colony indices, breeding season, depth, average temperature and regional temperature. An interactive term between regional temperature and depth/average temperature/temperature variance was included, capturing seasonal movements across environmental gradients i.e. between deep and shallow water, higher and lower latitudes. Variables anticipated to cause

aggregation within the overall range of a species were included in the density model, specifically, seabed roughness and front intensity.

To predict spatial variations in densities across scenarios (past, present, future), average temperatures and temperature variance across the overall survey period (1980-2015) were replaced with average temperatures in the five years preceding the survey in question. Regional temperatures were retained as previously, because their role was to represent seasonal cycles (relative increases and decreases across months) rather than absolute temperatures *per-se*. In addition, the collinearity between average and regional temperatures could exaggerate trends in species presence linked to increasing or decreasing temperatures. The replacement of annual temperatures across the overall survey period with those of the five years preceding the survey period should better identify thermal associations of species, improving the ability of GEE-GLM to predict across scenarios. In all instances, sea surface temperatures rather than average temperatures in the upper 150m of the water column were used because HadRM3 scenarios only provided the former (Hadley Centre for Climate Prediction and Research, 2008).

Because of their known influence on seabird ecology, climatic indices (North Atlantic Oscillation and Atlantic Multidecadal Oscillation) were tested (Mitchell *et al*., 2020). Specifically, interactive terms between climatic indices and annual temperature/depth were included to capture any movement of populations between the northern and southern North Sea in response to associated conditions. In a previous analysis using GEE-GLM approaches (Waggitt *et al*, unpublished), these interactions successfully detected well-documented shifts in harbour porpoise from the northern to the southern North Sea in the late 1990s (see, for example, Hammond *et al*., 2013). Whilst initially successful in the current analyses, additional scrutiny of analysis and outputs revealed that model parameters were particularly sensitive to model-setup and data input. Moreover, predicted densities were unrealistically high for some species, suggesting that model parameters exaggerated interactions between climatic indices and annual temperature/depth. Therefore, climatic indices were omitted from GEE-GLM. Consequently, predictions only consider the thermal associations of each species and do not consider potential movements between the northern and southern North Sea in response to conditions associated with these climatic indices.

Platform-type (vessel versus plane) was included alongside environmental variables. The GEE component of GEE-GLM accounts for correlations in encounter rate and densities amongst surveys from the same supplier in the same month, whereas detection functions account for differences in the area covered (km^2) from different platforms and sea states. However, some important differences in animal behaviour and associated consequences on survey data were not accounted for in the original GEE-GLM. Specifically, detections of scavenging species (northern gannet and *Laridae*) will be intrinsically higher from vessels due to animal attraction; detections of pursuit-diving species (*Alcidae*) could also be higher because slower moving vessels have a lower minute per km^2 coverage. As vessel surveys have largely been replaced by aerial surveys in recent times, not accounting for these differences may produce misleading model parameters. Including platform-type as a categorical variable helped account for differences between vessels and planes.

In addition to the changes required for GEE-GLM to predict across scenarios, front intensity was replaced with the Simpson-Hunter stratification index (HU3: Simpson

and Sharples, 2012). This index combines measurements of mean current speeds (ms^{-1}) and depth (m) into a single measurement which identifies mixed (<1.9), frontal (~1.9), and stratified (>1.9) water columns. This index not only has a strong influence on seabird distributions at regional scales (<100km^2) in shelf-seas (Scott *et al*., 2010, Cox *et al*., 2013, Waggitt *et al*., 2018) but identifies a greater range of associations than front intensity when modelled as a quadratic term, i.e. associated with mixed, frontal or stratified water. The Simpson-Hunter stratification index was modelled as a quadratic and continuous variable. All processing was performed in the 'raster' package in R.

Table 7. Summary of the environmental variables used in GEE-GLM. [+] see Waggitt et al (2020).

Name	Type	Scale	Description
Platform	Temporal	Survey	Whether a survey was performed from a vessel or plane.
Colony Index	Spatiotemporal	Grid Cell	Location of colonies, weighted by their population and breeding season+.
Breeding Season	Temporal	Regional	Non-breeding (0), pre/post (0.5) or breeding season (1) +.
Depth	Spatial	Grid Cell	Seabed Depth (m)
Annual Temperature Variance	Spatiotemporal	Grid Cell	Variation on sea surface temperature over the preceding five years.
Annual Temperature	Spatiotemporal	Grid Cell	Mean sea surface temperature over the preceding 5 years.
Regional Temperature	Temporal	Regional	Mean sea surface temperature for that month (1961-2099).
Seabed Roughness	Spatial	Grid Cell	Terrain Ruggedness Index (TRI) identifying topographic features.
Simpson-Hunter Stratification Index	Spatial	Grid Cell	Discriminates between water columns likely to mix or stratify.

[*]For species specific breeding seasons see Table 5

Model Selection

As in Waggitt *et al*. (2020), forwards-model selection based on the Quasilikelihood Information Criteria (QIC) was performed for the presence model. Following the inclusion of platform as an environmental variable, forwards-model selection was also performed for the density model. Environmental variables were introduced in a scale-dependent manner, starting with those deemed to have the greatest and ending on those deemed to have the lowest influence at the North-East Atlantic scale. Table 8 summarises the forwards-model selection.

Table 8. Summary of the forwards-model selection used for the presence and density model. 2 = Quadratic Term; * = Interactive Term.

Presence Model
Stage 1
Platform
Stage 2
Colony Index
Breeding Season
Colony Index + Breeding Season
Stage 3
$Depth^2$
$Depth^2$ + Annual Temperature Variance
Stage 4
Annual $Temperature^2$
Annual $Temperature^2$ + Regional Temperature * Annual Temperature
Annual $Temperature^2$ + Regional Temperature * Depth
Annual $Temperature^2$ + Regional Temperature * Annual Temperature Variance
Density Model
Stage 1
Platform
Stage 2
Seabed Roughness
Simpson-Hunter Stratification $Index^2$
Seabed Roughness + Simpson Hunter Stratification $Index^2$

Nested Models

Whilst this study focused on the North Sea region, the presence-absence component used data from across the North-East Atlantic (see Waggitt *et al*., 2020). The inclusion of data outside the North Sea improved the likelihood of GEE-GLM parameters identifying a species' overall thermal association. For instance, if a species was prevalent throughout the North Sea then GEE-GLM focused on this area would identify weak or absent thermal associations, underestimating responses to changing temperatures. Conversely, if a widespread species was concentrated in certain parts of the North Sea then such GEE-GLM would identify strong thermal associations, overestimating responses to changing temperatures. However, the density model only used data from inside the North Sea. The focus on data in the

North Sea should increase the accuracy of GEE-GLM parameters identifying important habitats within this region, which could contrast those in neighbouring regions (Celtic Sea, English Channel, Hebrides) due to differences in prey communities and associated foraging strategies.

The presence-absence component was performed at 10 km resolution whilst the density component was performed at 2.5 km resolution. These differences in resolution were due to computing power, as processing and analysing data at 2.5 km resolution across the NE Atlantic was not possible. However, the broad-scale environmental variables included in the presence-absence model do not differ greatly in a 10 x 10 km cell. Therefore, thermal associations identified at 10 km resolution are suitable for prediction at 2.5 km resolution.

Predictions

GEE-GLM predictions of species densities (animals per km^2, modelled separately for each species) were made at 2.5 km and monthly resolution for each scenario (1961-1990, 2017, 2070-2099). A population estimate was then produced by estimating numbers of animals in each cell and summing estimations across all cells. The influence of breeding colonies was omitted from predictions because the relative size and absolute locations of nesting aggregations could change substantially across a 140 year period (1961-2099). Retaining their influence could cause misleading and irregular patterns in predictions; for instance, high densities around breeding colonies in habitats suitable now but perhaps not suitable in the future. Despite their omission, GEE-GLM predictions from present scenarios (2017) appeared accurate, with the highest densities centred on regions currently supporting large breeding colonies. These predictions suggest that accurate and appropriate environmental associations had been identified. Finally, predictions were based on measured densities from vessels rather than planes because population estimates from the latter were unrealistically low in comparison to published estimates from breeding colonies obtained from national seabird censuses (Mitchell *et al*., 2004). If we assume that estimates from breeding colonies are broadly correct, this adjustment suggests that measurements from vessel-based surveys provide more representative measurements of densities. However, measurements from aerial-based surveys were not adjusted for availability bias in diving seabirds (Alcidae, northern gannets), which could be underwater in the short-period that a plane is overhead. Accounting for these biases would provide more accurate densities, although this requires further information on dive-times of birds and time-in-area of surveys.

Statistical models for effects of climate on demographics

The basic structure of our statistical modelling was to assume that productivity, annual growth rate and adult survival are each related to a range of annual, colony-specific climate variables. We constructed separate models for each species.

Models for productivity and population growth rate

We assumed that productivity and population growth rate were each related to climate via generalized linear mixed models (GLMMs). GLMMs are very widely used in statistical ecology (Bolker *et al*., 2009), and provide a natural framework for modelling the relationship between multi-site and multi-year count data and explanatory variables (such as climate variables).

Productivity relates to the number of chicks fledged, relative to the number of nests. Random variation in the number of chicks fledged (demographic stochasticity) can either be modelled using a Poisson distribution, with log(number of nests * maximum brood size) as an offset term, or modelled as a binomial distribution with the number of nests multiplied by maximum brood size as the binomial denominator. These two modelling approaches are conceptually similar: both model the ratio (expected productivity = expected number of chicks / (number of nests * maximum brood size)), but they differ in whether they constrain this ratio to be less than or equal to one (the binomial) or impose no upper limit (the Poisson). Equivalently, the difference between the two approaches is that they either impose an absolute upper limit upon brood size (the binomial) or they do not (the Poisson). Because maximum brood size for the species used in this analysis is biologically unambiguous, we only considered the binomial model.

The binomial GLMM implemented assumed that the logit of expected productivity was a linear function of a range of climate variables, but also depended upon "random effects" – sources of unexplained, but structured, variation not accounted for in fixed effects ("environmental stochasticity"). We considered random effects for "site", "year" and the interaction of "site" and "year" within all of our models, to account for the spatial and temporal variation in productivity unrelated to the climate variables used within our models.

We estimated the impacts of climate variables upon population annual growth rate (which incorporates productivity, adult survival and juvenile survival) using abundance data. Specifically, we used a Poisson GLMM to model abundance (count), with the log of (count) in the previous year being an offset, and included the same explanatory variables and random effects as in the models for productivity. The inclusion of the offset means that this model is equivalent to modelling the log of the growth rate between this year and the previous year.

Inference: parameter estimation and uncertainty

We fitted the models as generalised linear mixed models (GLMMs) via maximum likelihood, using the glmer function within lme4 package for R (Bates et al, 2015). The model for productivity can be fitted directly to the nest monitoring data, and this model allowed us to estimate the productivity rate for each colony in each year. The model for growth rate can, similarly, be fitted directly to data on abundance (colony

counts), and this model allowed us to estimate the growth rate for each colony in each year.

Alternative approach via Bayesian inference

We also considered the use of Bayesian inference for fitting each of the models, as an alternative to the more standard non-Bayesian approach. There is a long-standing and complex philosophical argument about the validity and interpretation of Bayesian and non-Bayesian approaches to statistical inference. The key advantage in this context, however, is that the Bayesian approach is able to more comprehensively account for uncertainty – in particular, it enables the uncertainty involved in estimating random effect variances in the GLMMs to be accounted for, whilst the non-Bayesian approach does not.

Given the computational demands of the Bayesian approach we used the non-Bayesian approach for exploratory analyses (which involve fitting a large number of models, and so were infeasible in this project using the Bayesian approach), and only refit the "final" sets of models for each species using the Bayesian approach. We fitted the models using JAGS (Plummer 2003), a widely-used and flexible environment for statistical modelling via Bayesian inference. We called JAGS from within R using the jagsUI package (Kellner 2017). The full JAGS code for our models can be found in Appendix E.

Model selection

For each species, we decided upon the set of climate variables to consider, in relation to productivity, adult survival and trend, based upon biological judgement and the existing literature. This approach reduced the dangers of "data dredging", avoiding the practical and conceptual difficulties associated with automated model selection, and was the only feasible approach for a project of this timescale. Model selection was performed in the non-Bayesian context (using GLMMs), and was run in a forward selection manner, using categories of climate variables. All models considered four marine climate variables identified as being of relevance to seabird productivity and survival (NAO, AMO, sea surface temperature and sea surface salinity); note that we were able to include the additional marine climate variable, AMO, because non-identifiability is less problematic within the Bayesian framework. We then tested whether support in the data for each model was improved by adding terrestrial climate variables for summed precipitation and mean minimum temperature. If the addition of terrestrial climate variables improved support in the data (assessed using AIC), then both variables were retained in the model, otherwise both were dropped. Finally, we tested whether adding terrestrial mean wind speed improved model fit, and if so, this variable was retained within the final model for each demographic rate and species. The order of this categorical selection was in response to the strength and importance of previously demonstrated links between seabird demography and marine, terrestrial and terrestrial wind variables. This selection process resulted in final models either including:

- Marine climate variables only
- Marine and terrestrial climate variables
- Marine climate variables plus terrestrial wind
- Marine and terrestrial climate variables plus terrestrial wind

At all stages of model selection we also assessed support in the data for alternative seasonal periods over which climate variables were derived. These were:

- Productivity:
  - Pre-breeding period only
  - Breeding season only
  - Pre-breeding plus breeding season periods
- Adult survival
  - Non-breeding period
  - Whole year
- Population growth rate models
  - All seasonal periods defined above

This resulted in a final best supported model for population growth rate and productivity in each species, defined by a set of climate variables, over a selected seasonal period. We also always assessed support in the data for a null model containing no climate variables.

Goodness of fit assessment

We assess goodness of fit using the marginal R-squared value for GLMMs proposed by Nakagawa & Schielzeth (2012). This value can be calculated from the fitted models using a simple formula (Equation 29 in the reference), which defines the marginal R-squared for a GLMM to be:

> Marginal GLMM R-square =
> (Variance of predictions from fixed effect part of the model) /
> (Variance of predictions from fixed effect part of the model + Sum of random effect variances + Variance from overdispersion + Distribution-specific variance)

We calculate this using the r.squaredGLMM function in the MuMin package (Barton 2017). Nakagawa & Schielzeth (2012) also define another quantity, the conditional R-squared, which also includes the sum of random effect variances in the numerator. The conditional R-squared will always be higher than, or equal to, the marginal R-squared, but in situations where, as here, the random effects are essentially nuisance variables and it is the fixed effects (the climate variables in this context) that are of primary interest, the marginal R-square value will be of much more practical relevance than the conditional R-square value. In this context, the marginal R-square value effectively provides information on the proportion of variation in the raw data that can be explained by the climate variables.

Predicting demography and abundance under climate change

The models that we have developed allowed productivity and annual population growth rate to be readily predicted under a future scenario of climate change, so long as annual projections of all environmental variables (whether terrestrial or marine) used in fitting the models are available for the scenario(s) and future year(s) of interest.

Within the Bayesian context the uncertainty within these predictions can also be fully quantified in a straightforward way, simply by generating predictions separately for

each MCMC sample, and then using the results sample of predicted values to represent uncertainty in the predictions.

Some elements of uncertainty quantification are also straightforward in the non-Bayesian context: the uncertainties resulting from inter-annual variability and uncertainty in estimating the direction/magnitude of the environmental effects can both be readily accounted for via a simple simulation-based approach, but other elements of uncertainty quantification (e.g. uncertainty in the level of inter-annual or inter-colony variation) are more problematic, and were not considered here.

Accounting for adaptation

Our methodology assumed that birds do not adapt to change in their environment; in reality, adaptation is likely to occur, in situations where successful adaptation mitigates against the demographic consequences of environmental change. One obvious adaptation strategy for breeding seabirds is to increase their foraging range, providing a potential mechanism for birds to track climate-driven shifts in foraging areas.

Using the outputs of our models we estimated the direct demographic consequences of birds increasing their foraging range, to assess whether increasing their foraging ranges could lead them to avoid any negative consequences of climate change on demographic rates. We did this by generating predictions under a range of possible future foraging ranges, and estimating how predicted productivity and population growth rate varied as the foraging range increased, changing the foraging range changes the distance decay parameter used in estimating the weighted mean of the marine climate variables.

Ultimately, decisions regarding adaptation depend upon whether the benefits outweigh the cost; this is a difficult question to answer, as the costs and benefits refer to different quantities, which cannot be readily translated into each other, and a quantification of the optimal decisions that birds make in trading off between costs and benefits is beyond the scope of this project.

Note that the foraging ranges used here from Thaxter et al. (2012) are generally lower than the updated values in Woodward et al. (2019), which were not available for this analysis. As such, our analysis may overestimate the capacity to expand foraging range.

Models for survival

The population growth rate depends upon productivity and survival, both of adults and of juveniles. If it is possible to examine the effects of climate variables upon productivity and growth rate it should, therefore, also be possible to quantify their effects upon survival. We attempted this, using the two sources of data used in the main analyses (colony counts and nest monitoring data), because insufficient direct data on survival (e.g., mark-recapture) are available to be able to run a multi-colony analysis of climate effects. Data issues mean that the results should be interpreted with caution, however, so we relegate the methodology and results to Appendix C.

Results

Spatial distribution modelling

For each of the seven seabird species examined, GEE-GLM predictions of their thermal niches were derived using data on sea surface temperatures across the North-East Atlantic (Figure 2). Several species showed greatest abundance in waters at mean annual temperatures of between 4°C and 10°C. Atlantic puffin and black-legged kittiwake favoured coldest waters and therefore were most likely to respond negatively to climate warming in the region. Great black-backed gull and herring gull also showed a general association with cooler temperatures. There was a general trend towards warmer thermal associations from common guillemot to razorbill, and then to northern gannet, suggesting that these species would be less likely to be negatively affected by climate warming. Trends are assessed qualitatively in terms of large, moderate or small changes in abundance, noting also whether changes are widespread or local.

Summer (June) and winter (January) North Sea distributions for past (1961-1990), present (using 2017 data), and future (2070-2099) scenarios were derived showing spatial variation in estimated densities (animals per km²) and differences between past and future scenarios for each species from GEE-GLM predictions. These are shown in Figures 3-9, along with graphs indicating monthly variation in estimated abundances for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM, they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions.

Atlantic puffin occurs at greatest densities in summer in coastal waters of north-east Scotland and the Northern Isles (Figure 3). Those areas currently show reduced densities, and the prediction for the latter part of this century is for densities to decline further leading to a large decline in abundance. Winter distributions are at lower densities and more dispersed since many puffins winter outside the region, the remainder being concentrated in the north-western sector of the North Sea (Harris *et al.*, 2010); they show a similar long-term trend.

Black-legged kittiwake densities are more evenly distributed in summer and although they are slightly higher in coastal waters of north-east Britain, they are widely distributed across the North Sea (Figure 4). There has been a moderate decline in abundance compared with the period 1961-1990, and that change is predicted to continue under the future climate scenario. The species occurs at higher densities during winter months, potentially due to the presence of migrant birds from breeding areas outside the North Sea. Densities are greatest all along the eastern seaboard of Britain, but have also shown moderate decline compared with 1961-1990 and are predicted to do so further under the future climate scenario, particularly in the southern North Sea.

Common guillemot occurs at greatest densities in summer in coastal waters of north-east Britain (Figure 5). Densities have declined since 1961-1990, and are predicted to continue to do so under the future climate scenario, particularly along the eastern seaboard of Britain. The species occurs at higher densities in winter and is more widespread, reflecting seasonal immigration of birds from outside the North Sea

(Harris & Swann, 2002). There has been little change since 1961-1990. Predictions under the future climate scenario suggest a decline in occupation of the southern and central North Sea with greater concentrations in a band across the northern North Sea from southern Scandinavia to eastern Scotland.

During summer, great black-backed gull occurs at highest densities in the southern North Sea, with a relatively coastal distribution (Figure 6). There has been little change in distribution patterns since 1961-1990 and the prediction is for little further change under the future climate scenario. However, overall abundance has declined and is predicted to continue to do so. Densities are higher in winter, presumably reflecting birds spending more time offshore. Although more widespread in winter, densities remain greatest in the southern North Sea. Moderate and widespread declines in abundance are predicted, particularly in coastal waters of East Anglia and in the south-eastern North Sea under the future climate scenario.

The predicted distribution of great-black backed gulls in summer contrasts with the distribution of breeding colonies in the North Sea region, which is centred on Orkney and Shetland (Mitchell et al 2004). This discrepancy is primarily linked to the omission of the breeding colony index (see Methods) and an environmental association with shallow and unstable (high temperature variance) water-columns, which are prominent in the southern North Sea. The inability to detect aggregations around Orkney and Shetland without including the colony index may indicate that influential environmental drivers are absent from the GEE-GLM. Alternatively, this inability may suggest that breeding birds remain on landmasses or intertidal habitats. For example, breeders may be reliant on terrestrial and intertidal prey (e.g. nesting seabirds, rabbits, domestic refuse: Westerberg et al 2019), meaning that at-sea surveys do not detect aggregations around breeding colonies. If correct, then the predicted distribution of great black-backed gulls could be representative of the non-breeding population in summer.

Herring gull densities in the North Sea in summer are generally higher than in great black-backed gull. As with that species, densities are greatest in the southern North Sea, with a relatively coastal distribution (Figure 7). Distribution patterns have changed little since 1961-1990 and the prediction is for little further change under the future climate scenario. However, overall abundance has declined and is predicted to continue to do so. As with the other gull species, densities are higher in winter, reflecting a more offshore distribution though greatest in the southern North Sea particularly in coastal waters of East Anglia and the south-eastern sector of the North Sea. Moderate and widespread declines in abundance are predicted, particularly in coastal waters of East Anglia and in the south-eastern North Sea under the future climate scenario.

Densities of northern gannet in summer are greatest in the north-western North Sea, around eastern Scotland and the Northern Isles (Figure 8). These show a general increase in densities and overall abundance compared with 1961-1990. Under the future climate scenario, the prediction is for further increases particularly in the northern North Sea. Densities are lower and distribution more dispersed during winter, with increases, albeit less pronounced, since 1961-1990. These increases are also predicted to continue under the future climate scenario, remaining greatest in the northern half of the North Sea, particularly around eastern Scotland and southern Scandinavia.

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Razorbill densities in summer in the North Sea are greatest along the eastern seaboard of Britain (Figure 9). These have shown moderate declines since 1961-1990. Under the future climate scenario, those are predicted to continue, mainly in the southern sector of the North Sea. During winter, on the other hand, densities have slightly increased since 1961-1990, and are predicted to result in moderate increases in abundance in the northern North Sea under the future climate scenario but a decline in the southernmost North Sea.

In terms of seasonal use of the North Sea (Table 9), Atlantic puffin and northern gannet are primarily summer species and those patterns are predicted to remain under the future climate scenario. Black-legged kittiwake occurs throughout the year and will likely remain so in the future. Common guillemot, razorbill, great black-backed gull and herring gull show higher numbers across the North Sea in winter, and under the future climate scenario, the two auks (common guillemot and razorbill) could become primarily species present in winter.

Predicted changes in summer abundance between the 1960s and the 2090s under the future climate scenario (Table 10) indicate large declines for Atlantic puffin, moderate declines for black-legged kittiwake, razorbill, common guillemot and herring gull, little change for great black-backed gull, and large increases for northern gannet. During winter, similar trends are predicted though less pronounced for northern gannet, little change for common guillemot and herring gull, whereas razorbills are predicted to show moderate increases.

Two species are predicted to show general changes in distribution under the future climate scenario (Figure 5, Figure 9). These are common guillemot and razorbill both of which are expected to show increases in the north and decreases in the south. Only northern gannet is predicted to show a widespread increase, the rest showing moderate or widespread declines.
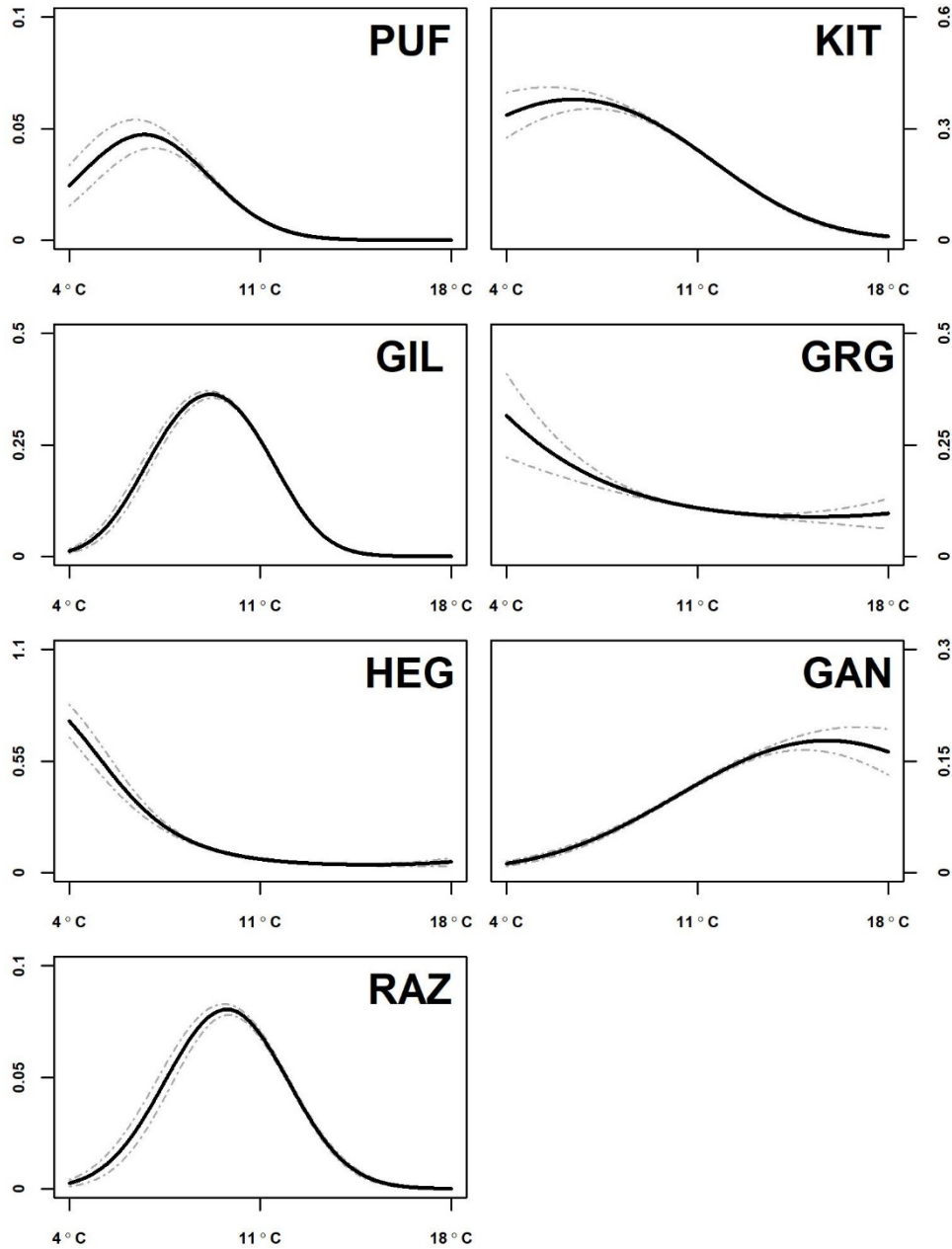
Figure 2. GEE-GLM predictions of thermal associations for Atlantic puffin (PUF), black-legged kittiwake (KIT), common guillemot (GIL), great black-backed gull (GRG), herring gull (HEG), northern gannet (GAN) and razorbill (RAZ) in the North-East Atlantic. Specifically, figures illustrate GEE-GLM predicted variations in species occurrence (probability ± standard error of encounters per km2) across gradients in mean annual temperature (°C).
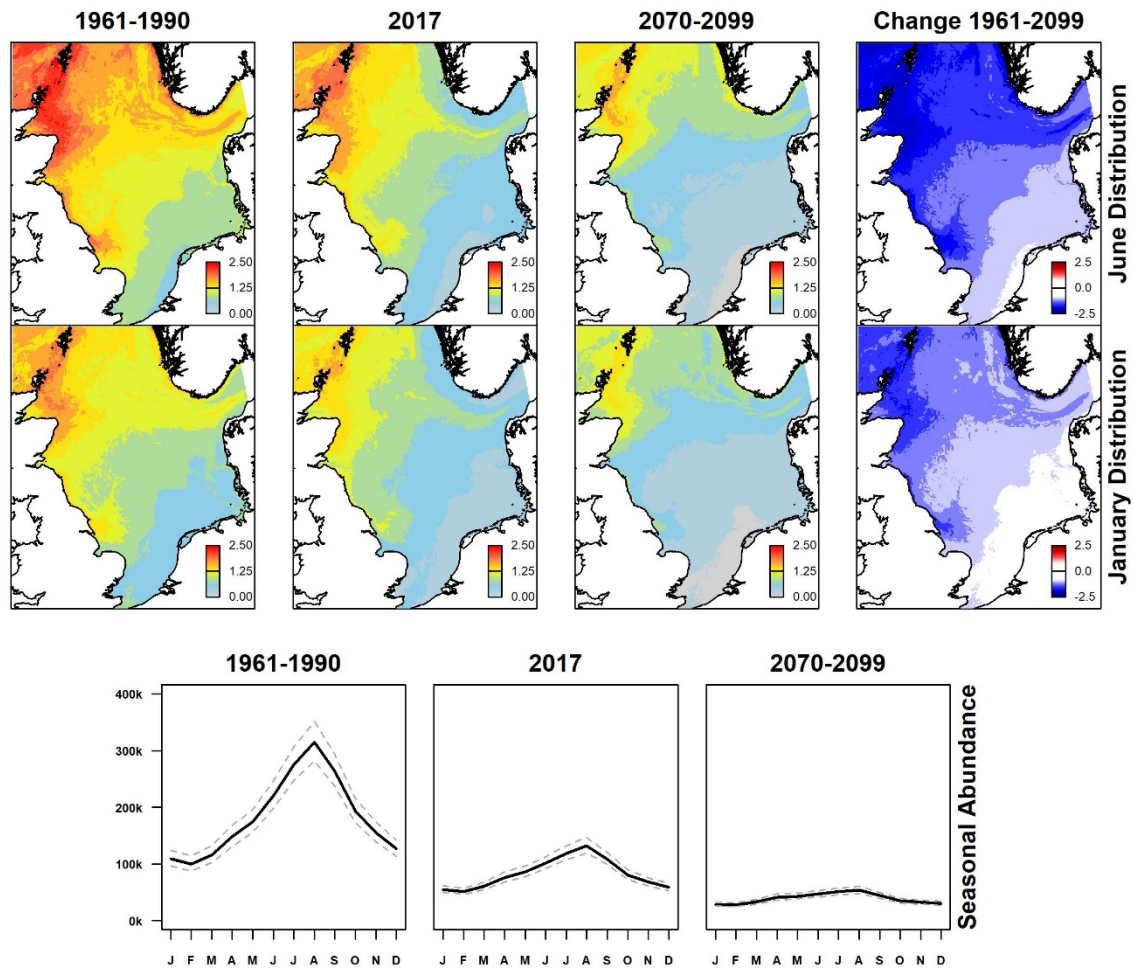
Figure 3. GEE-GLM predictions for Atlantic puffin in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.
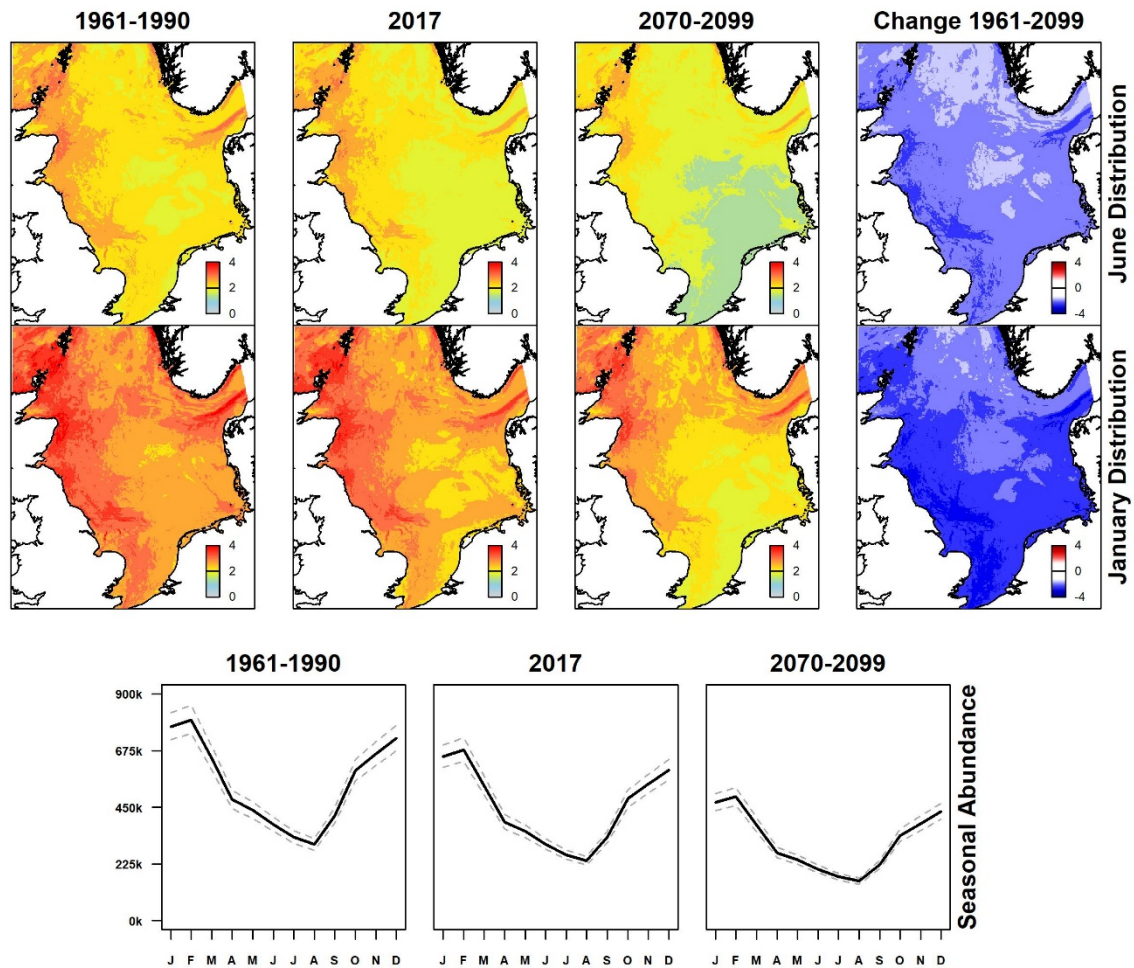
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Figure 4. GEE-GLM predictions for black-legged kittiwake in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue = decrease in estimated densities.
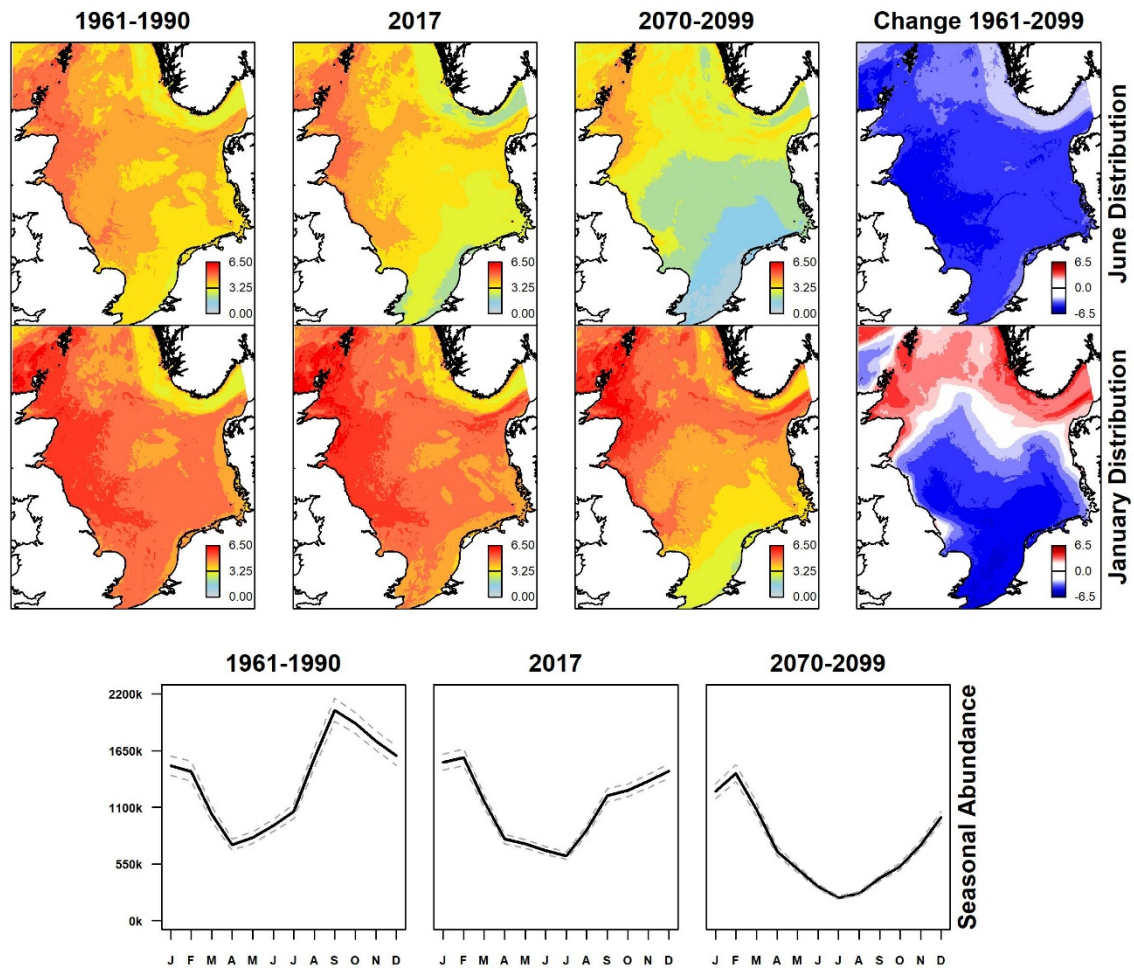
Figure 5. GEE-GLM predictions for common guillemot in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.

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Figure 6. GEE-GLM predictions for great black-backed gull in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.
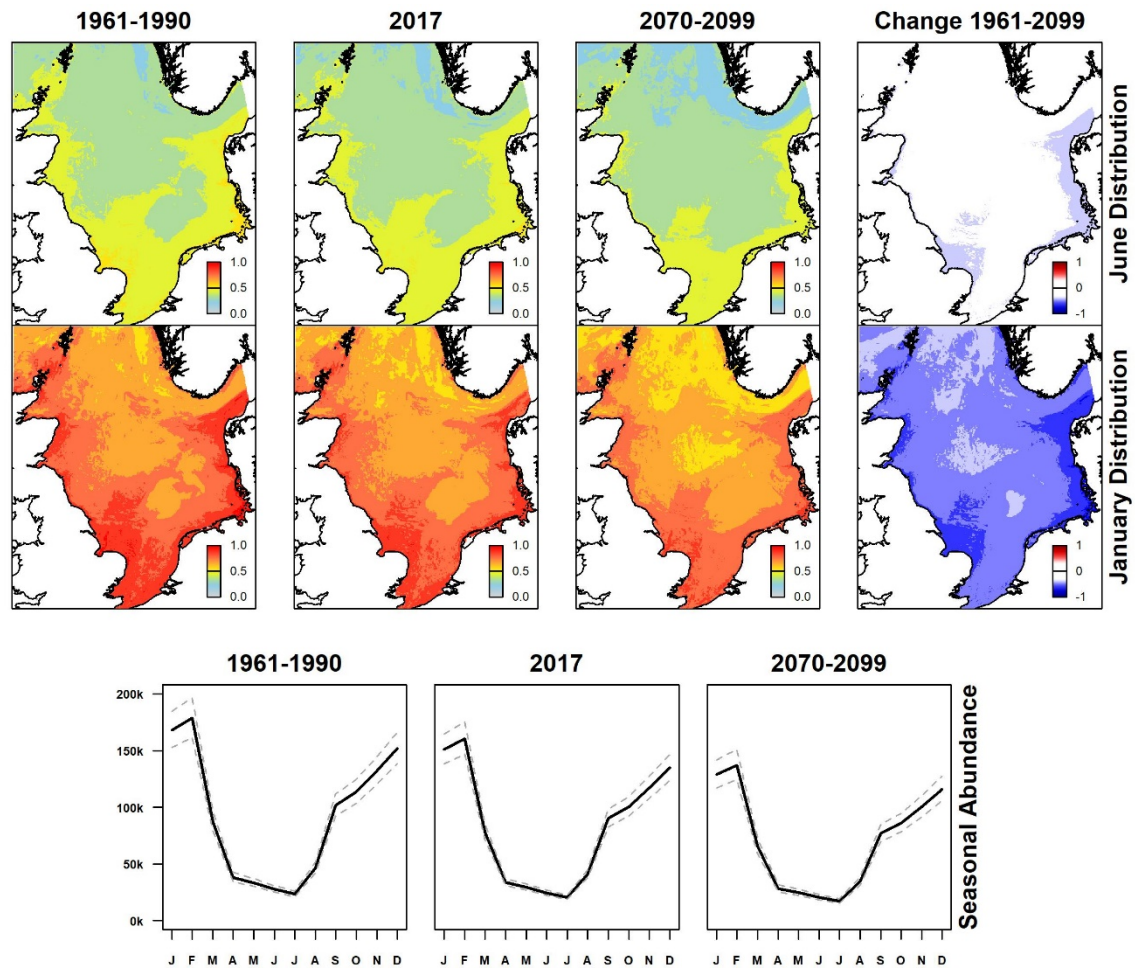
Figure 7. GEE-GLM predictions for herring gull in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.
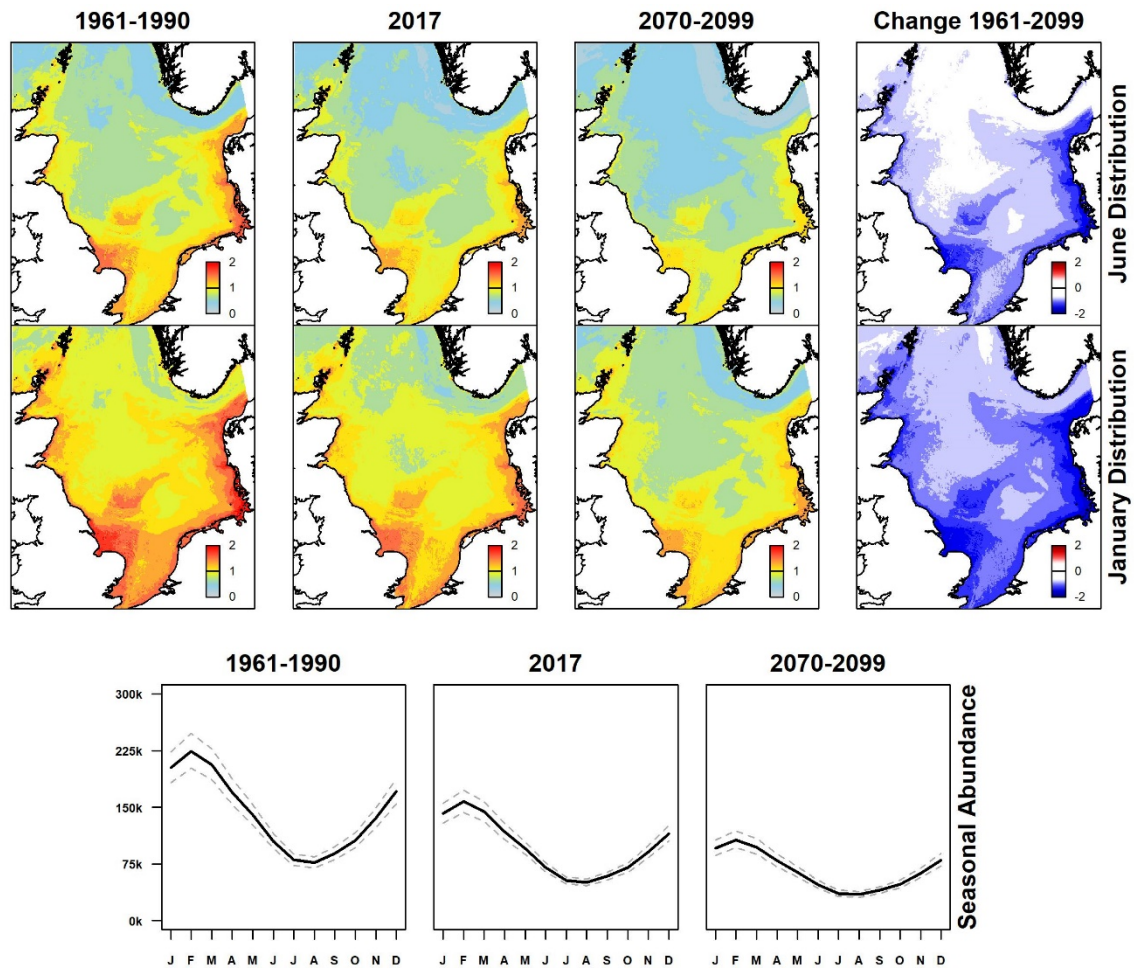
Figure 8. GEE-GLM predictions for northern gannet in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.

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Figure 9. GEE-GLM predictions for razorbill in previous (1961-1990), present (2017) and future (2070-2099) scenarios. Maps indicate spatial variation in estimated densities (animals per km2) in January and June for all scenarios and associated differences in densities between previous and future scenarios. Graphs indicate monthly variation in estimated abundances in the North Sea for all scenarios. Whilst the location and sizes of breeding colonies were included in GEE-GLM they were omitted from predictions as both can change considerably across time. The omission of breeding colonies prevented bias towards present locations of large colonies in predictions. Six left-hand panels: red = higher densities, blue = lower densities. Two right-hand panels: red = increase in estimated densities; blue =decrease in estimated densities.
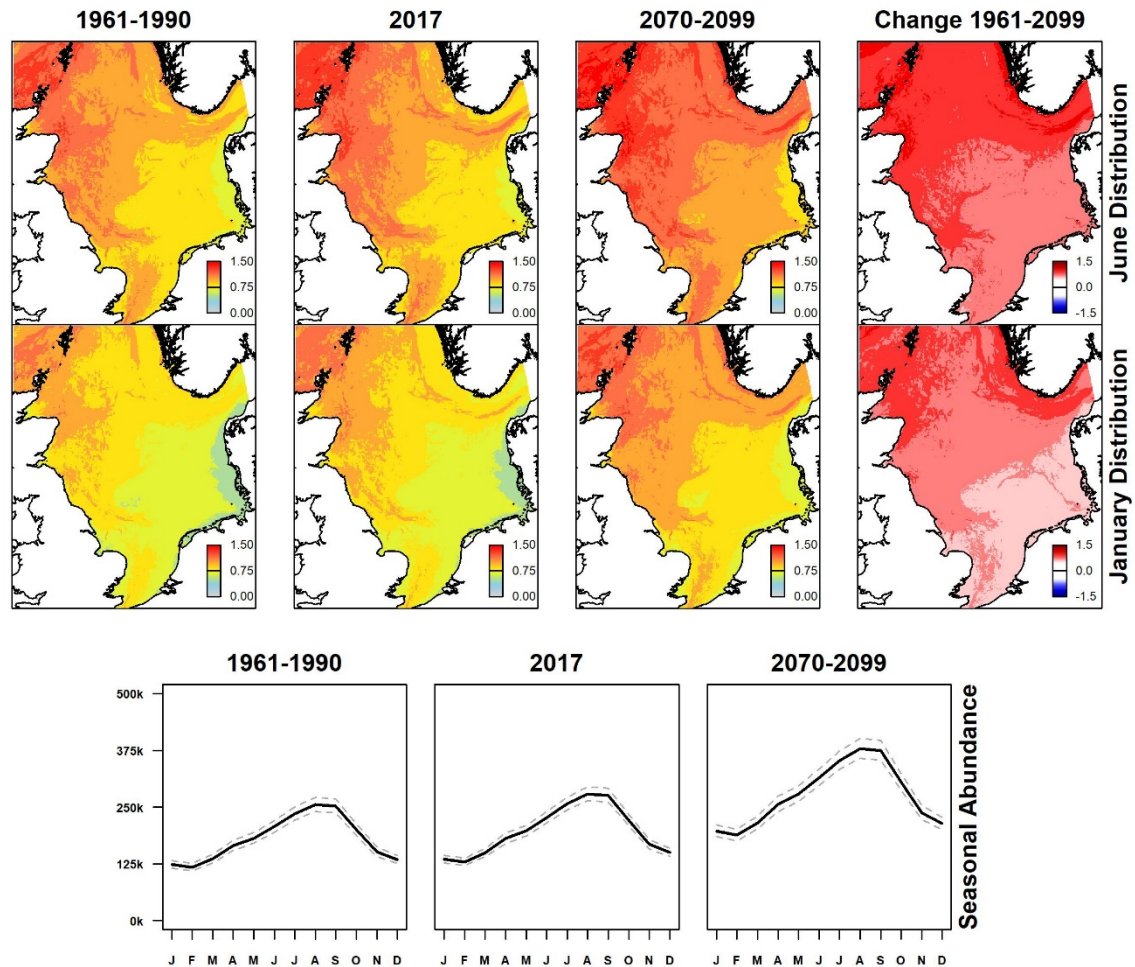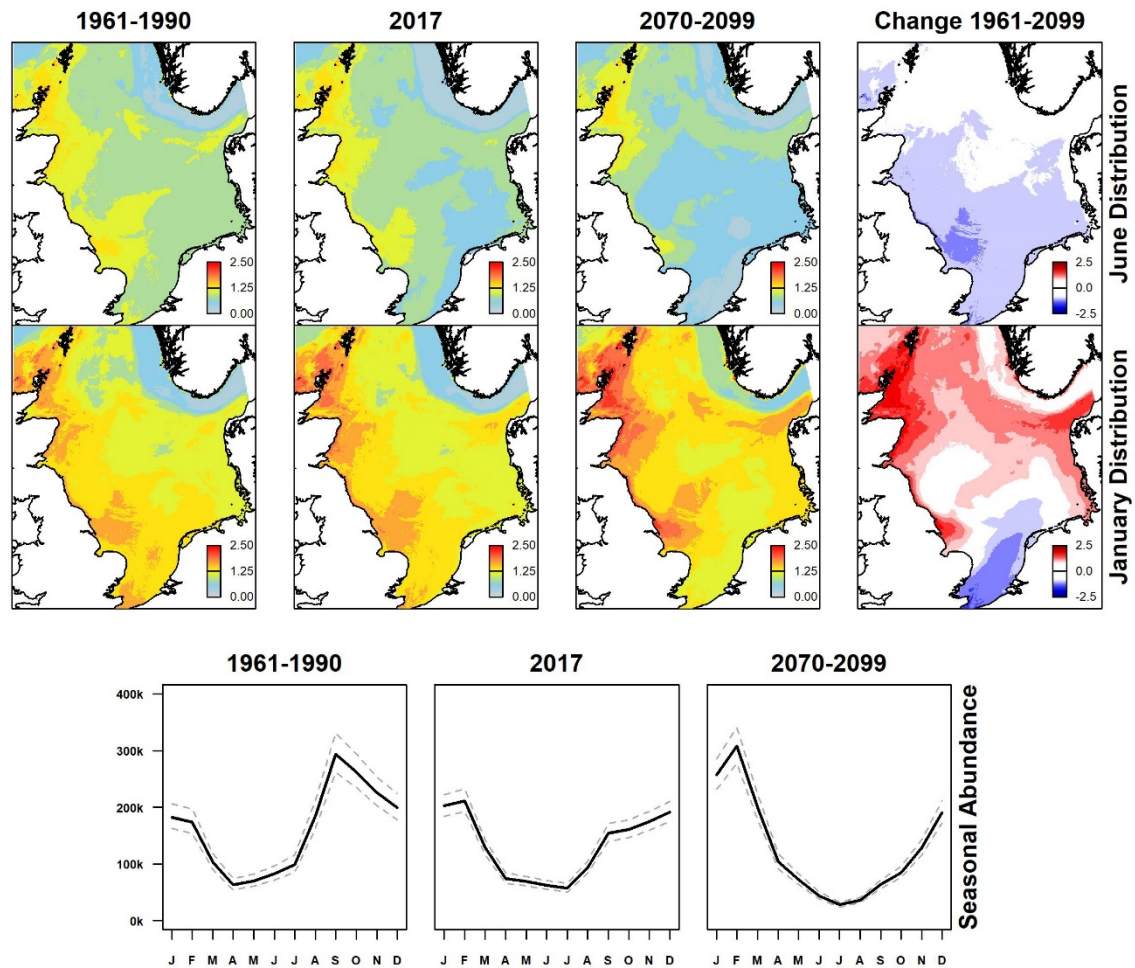
Table 9. Qualitative summary of GEE-GLM predicted changes in in at-sea abundance for Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, herring gull, northern gannet and razorbill across seasons in the North Sea. The division of animals between marine foraging areas and terrestrial nest sites during breeding seasons was considered in the summary text, i.e. a species occupying the North Sea in similar numbers across the annual cycle would decrease during breeding seasons. More detailed predictions on a species-level are shown in Figures 2-9.

Species	1961-1990	2017	2070-2099	Change 1961-2099
Atlantic puffin	Primarily Summer	Primarily Summer	Primarily Summer	No Change
Black-legged kittiwake	All Year	All Year	All Year	No Change
Common guillemot	All Year	All Year	Primarily Winter	Becoming a Winter species
Great black-backed gull	Primarily Winter	Primarily Winter	Primarily Winter	No Change
Herring gull	Primarily Winter	Primarily Winter	Primarily Winter	No Change
Northern gannet	Primarily Summer	Primarily Summer	Primarily Summer	No Change
Razorbill	All Year	All Year	Primarily Winter	Becoming a Winter Species

Table 10. Qualitative summary of GEE-GLM predicted changes (1961–2099) in at-sea abundance for Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, herring gull, northern gannet and razorbill in the North Sea. More detailed predictions on a species-level are shown in Figures 2-9.

Species	January	June
Atlantic puffin	Large Declines	Large Declines
Black-legged kittiwake.	Moderate Declines	Moderate Declines
Common guillemot	Similar	Moderate Declines
Great black-backed gull	Moderate Declines	Similar
Herring gull	Similar	Moderate Declines
Northern gannet	Moderate Increases	Large Increases
Razorbill	Moderate Increases	Moderate Declines

Table 11. GEE-GLM predicted changes (1961-2099) in at-sea distribution for Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, herring gull, northern gannet and razorbill in the North Sea.

Species	January	June
Atlantic puffin	Widespread decline	Widespread decline
Black-legged kittiwake	Widespread decline	Widespread decline
Common guillemot	Increase in North – Decrease in South	Widespread decline
Great black-backed gull	Widespread decline	Widespread decline
Herring gull	Widespread decline	Widespread decline
Northern gannet	Widespread increase	Widespread increase
Razorbill	Increase in North – Decrease in South	Moderate Declines

Demographic modelling

Productivity

In the main report, we present inference from the non-Bayesian analysis of the effects of climate on seabird productivity. For additional inference from Bayesian analyses of productivity see Appendix B.

Atlantic puffin

The best supported model for Atlantic puffin breeding success included only marine climatic variables from the pre-breeding period. This model included a strong negative relationship between sea surface temperature (SST) and productivity (mean effect: -0.683, P<0.001; Table 12), and a close to significant positive relationship between sea surface salinity and productivity (mean effect: 0.679, P: 0.066; Table 12). A model that also included terrestrial wind received some support in the data (delta AIC hereafter 'ΔAIC' 2.0), as did the model including marine and terrestrial variables (ΔAIC 3.2), with the model containing all climate variables receiving less support (ΔAIC 4.9) (Table 12). The null model with no environmental variables received very little support in the data compared to the best-fitting model (ΔAIC 7.41; Table 12). Finally, there was essentially no support in the data for models containing climate variables defined over the pre-breeding and breeding seasons combined (ΔAIC 9.93) or when defined over only the breeding season (ΔAIC 11.9) (Table 12). Model validation showed that the best-fitting model accounted for very little variation in the data (approx. 6%) when not including the individual level random effect (year by colony), with the climate variables explaining only around 3% of the total variation in the data (Table 12).

The best supported model estimated a current mean productivity during 2014-2018 climate conditions of 0.728 (95%CI: 0.628, 0.812), and for future conditions during 2085 of 0.531 (95%CI: 0.444, 0.690). Predicted access to suitable marine climatic conditions did not tend to vary much with increasing foraging range for this species, either under current or future projections (Figure 10).

Black-legged kittiwake

For this species, the best supported model for productivity included marine and terrestrial climate variables from the pre-breeding period only. These included strong negative effects for sea surface salinity (SLM; mean: -2.120, P <0.001) and terrestrial temperature (Temp; mean: -0.251, P 0.033), and a strong positive effect of terrestrial rain (Rain; mean: 0.669, P 0.014) (Table 12). A model that also included terrestrial wind received similar support in the data to the best supported model (ΔAIC 2.0; Table 12), with models including only marine (ΔAIC 7.5) or marine and terrestrial wind (ΔAIC 9.4) received very little support in the data compared to the best supported model (Table 12). The null model with no climate variables received essentially no support in the data in comparison to the best supported model (ΔAIC 32.8, Table 12). Models in which climatic variables were derived over the pre-breeding and breeding periods combined (ΔAIC 16.4) or over the breeding season only (ΔAIC 25.8) also received essentially no support in the data when compared to the best supported model using climate metrics in the pre-breeding period only (Table 12). Model validation showed that the best supported model for this species explained approximately 32% of the variation in the data, not including the individual level random effect (year by colony), with the fixed climatic parts of the model explaining around 11% of the variation in the data (Table 12).

The best supported model estimated a current mean productivity during 2014-2018 climate conditions of 0.576 (95%CI: 0.395, 0.753), and for future conditions during 2085 of 0.390 (95%CI: 0.242, 0.640). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for this species, either under current or future projections (Figure 10).

Common guillemot

The best supported model for productivity in this species included all climate variables (marine, terrestrial and wind) defined over the pre-breeding period only. None of the climate variables were strongly significant (P>0.05), but there was some evidence for negative effects of sea surface temperature (P 0.102) and sea surface salinity (P 0.101), along with a positive effect of terrestrial rainfall (P 0.058) (Table 12). There was very little separation between this best supported model and alternative models with different combinations of climate variables; a model including marine and terrestrial variables (ΔAIC 0.1), or including marine variables and terrestrial wind (ΔAIC 0.2), or including marine variables only (ΔAIC 0.8) all received essentially equal support in the data when compared to the best supported model (Table 12). However, the null model containing no climate effects received essentially no support in the data in comparison to the best supported model (ΔAIC 9.23), nor did models in which climate effects were derived over the breeding period only (ΔAIC 9.21). However, there was some support when climate variables were derived over the pre-breeding and breeding periods combined (ΔAIC 3.19) (Table 12). Model validation showed that the best supported model for this species explained approximately 24% of the variation in the data, not including the individual level random effect (year by colony), with the fixed climatic parts of the model explaining around 9% of the variation in the data (Table 12).

We were unable to generate predictions for the best supported model because it contained terrestrial wind, for which predictions were not available at the time of the project. We therefore used the second best supported model, containing marine and terrestrial variables, to generate current and future predictions for productivity for this

species. This model estimated a current mean productivity during 2014-2018 climate conditions of 0.624 (95%CI: 0.495, 0.691), and for future conditions during 2085 of 0.476 (95%CI: 0.359, 0.639). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for this species, either under current or future projections (Figure 10).

European shag

In this species, the null model containing no climate effects was best supported by the data (Table 12).

Great black-backed gull

Defining climate variables over the breeding period only, including marine and terrestrial variables, resulted in the best supported model for productivity in this species. The model included strong negative relationships with both sea surface salinity (mean: -0.328, P 0.034) and terrestrial temperature (mean: -0.656, P 0.0011) (Table 12). A model that also included terrestrial wind received similar support in the data when compared to the best supported model (ΔAIC 1.9), as did models including marine only (ΔAIC 3.2) or marine and wind (3.2) (Table 12). The null model also received some support in the data for this species (ΔAIC 3.25; Table 12). Finally, defining climate variables over pre-breeding and breeding periods combined (ΔAIC 6.80) or over just the pre-breeding season (ΔAIC 8.91) did not result in strong support in the data in comparison to the best supported model where variables were defined over the breeding period only (Table 12). Model validation showed that the best supported model explained very little of the variation in the data (approx. 5% including colony and year random effects, but without the individual level random effect of colony by year), with the fixed climate effects contributing most of this explanatory power (Table 12).

The best supported model estimated a current mean productivity during 2014-2018 climate conditions of 0.923 (95%CI: 0.829, 1.06), and for future conditions during 2085 of 0.414 (95%CI: 0.338, 0.688). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for this species, either under current or future projections (Figure 10).

Herring gull

In this species, the null model containing no climate effects was best supported by the data (Table 12).

Northern gannet

In this species, the best supported model for productivity included only marine variables defined over the breeding season. This model included a strong negative correlation between sea surface salinity and productivity (mean: -0.630, P 0.032; Table 12). A range of other models received similar support in the data as the best supported model, including those including marine variables and terrestrial wind (ΔAIC 0.5), marine and terrestrial variables and wind (ΔAIC 0.5), marine and terrestrial variables (not including wind; ΔAIC 1.3). The null model also received similar support in the data (ΔAIC 1.86; Table 12). There was also very similar support for the model including only marine variables that were derived over the pre-breeding and breeding seasons combined (ΔAIC 0.22), and some support for the same model in which climate effects were derived over the pre-breeding period only (ΔAIC 3.50; Table 12). Model validation showed that the best supported model for this species

explained very little of the variation in the data (approx. 3%), not including the individual level random effect (year by colony), with the fixed climatic parts of the model explaining just 1% of the variation in the data (Table 12).

The best supported model estimated a current mean productivity of 0.694 (95%CI 0.647, 0.726) for this species, with a future predicted increase to 0.732 (95%CI 0.664, 0.790). Predicted access to suitable marine climatic conditions did not tend to vary with foraging range for this species, either under current or future projections (Figure 10).

Razorbill

In this species, the null model containing no climate effects was best supported by the data (Table 12).

Table 12. Summary of best supported models for climatic influence on productivity of eight species of seabird breeding on the east coast of the UK. All models include NAO, AMO, SST (sea surface temperature), and SLM (salinity). Model selection using AIC was used to assess if adding terrestrial variables improved model fit (Temp and Rain). Finally, model selection was conducted using AIC to assess if adding WS (terrestrial wind speed) improved model fit. Models for each species were fitted to three seasonal definitions: PB: pre-breeding period; BS: breeding season period; and PBBS: pre-breeding plus breeding season periods. A null model was also fitted to all species and seasonal periods containing random effects for colony, year, and colony*year. Significance shown in bold and denoted by ** P<=0.05, * P<=0.10. ΔAIC refers to the difference in AIC units between the final best supported model and alternative model formulations including: marine only (M), marine and terrestrial variables (M+T), marine and wind (M+W), and marine, terrestrial and wind (M+T+W). R^2 refers to the variance explained (as a proportion [0,1]) for only fixed effects, or for both fixed and random effects (excluding the individual-level random effect). Variables were not standardised.

Species	Best Model	Estimates					ΔAIC	R^2
Atlantic puffin	Pre-breeding: NAO + SST** + SLM*		**Estimate**	**SE**	**z**	**P**	Null: 7.41 PBBS: 9.93 BS: 11.90 M+T: 3.2 M+W: 2.0 M+T+W: 4.9	Fixed only: 0.032 Fixed + random: 0.064
		NAO	0.090	0.155	0.585	0.559		
		SST	**-0.683**	**0.169**	**-4.036**	**<0.001**		
		SLM	**0.679**	**0.369**	**1.841**	**0.066**		
Black-legged kittiwake	Pre-breeding: NAO + SST + SLM** + Temp** + Rain**		**Estimate**	**SE**	**z**	**P**	PBBS: 16.37 BS: 25.80 Null: 32.79 M+T+W: 2.0 M: 7.5 M+W: 9.4	Fixed only: 0.111 Fixed + random: 0.318
		NAO	0.249	0.317	0.787	0.431		
		SST	-0.046	0.230	-0.199	0.843		
		SLM	**-2.120**	**0.441**	**-4.802**	**<0.001**		
		Temp	**-0.251**	**0.118**	**-2.128**	**0.033**		
		Rain	**0.66933**	**0.273**	**2.448**	**0.014**		
Common guillemot	Pre-breeding: NAO + SST* + SLM* + Temp + Rain* + WS		**Estimate**	**SE**	**Z**	**P**	PBBS: 3.19 Null: 9.23 BS: 9.21 M+T: 0.1 M+W: 0.2 M: 0.8	Fixed only: 0.087 Fixed + random: 0.244
		NAO	0.240	0.310	0.772	0.440		
		SST	**-0.536**	**0.328**	**-1.637**	**0.102**		
		SLM	**-0.762**	**0.464**	**-1.641**	**0.101**		
		Temp	-0.136	0.156	-0.874	0.382		

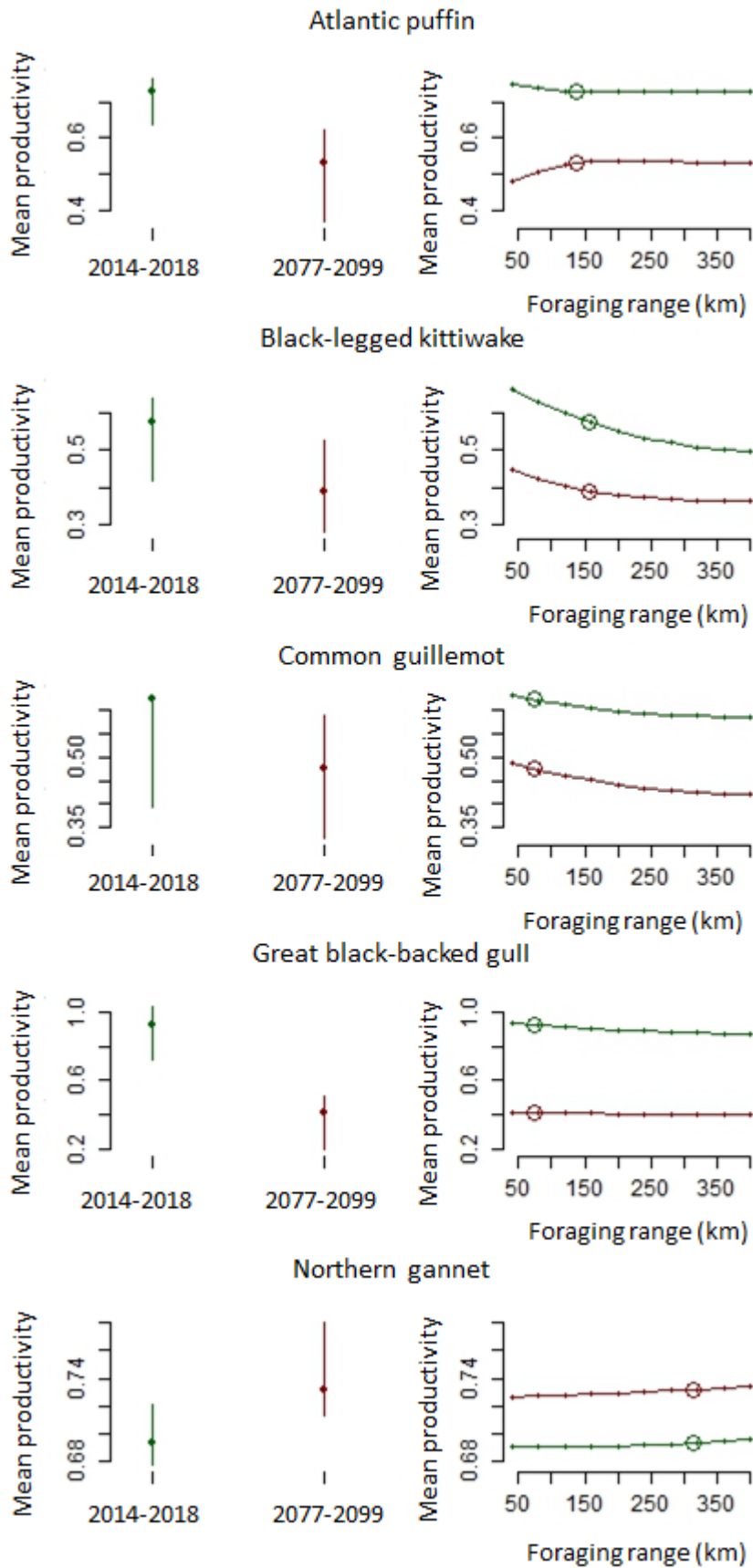|							
		Rain	**0.470**	**0.248**	**1.898**	**0.058**	
		WS	0.086	0.059	1.452	0.147	
European shag	Null model	**ΔAIC**	PB: 2.72; PBBS: 0.26; BS: 0.50				
Great black-backed gull	Breeding season: NAO + SST + SLM** + Temp** + Rain		**Estimate**	**SE**	**z**	**P**	PBBS: 6.80 PB: 8.91 Null: 3.25 M+T+W: 1.9 M: 3.2 M+W: 3.2	Fixed only: 0.054 Fixed + random: 0.054
		NAO	0.110	0.115	0.957	0.339	
		SST	0.058	0.197	0.292	0.770	
		SLM	**-0.328**	**0.155**	**-2.116**	**0.034**	
		Temp	**-0.656**	**0.202**	**-3.251**	**0.0011**	
		Rain	-1.521	4.189	-0.363	0.717	
Herring gull	Null model	**ΔAIC**	BS: 3.45; PBBS: 3.74; PB: 4.83				
Northern gannet	Breeding season: NAO + SST + SLM**		**Estimate**	**SE**	**z**	**P**	Null: 1.86 PBBS: 0.22 PB: 3.50 M+T: 1.3 M+W: 0.5 M+T+W: 0.5	Fixed only: 0.010 Fixed + random: 0.029
		NAO	-0.023	0.015	-1.517	0.129	
		SST	0.070	0.062	1.131	0.258	
		SLM	**-0.630**	**0.293**	**-2.150**	**0.032**	
Razorbill	Null model	**ΔAIC**	PB: 2.25; PBBS: 1.53; BS: 1.40				

Figure 10. Predicted changes in breeding success from best-supported models
(marine only: M; marine and terrestrial variables: M+T) for influence of climate on

breeding success for four species of seabirds on the east coast of the UK between 2014-2018 (Green; top line in the first four graphs and bottom line on the fifth graph) and 2077-2099 (Red; left panel bottom line in the first four graphs and top line on the fifth graph). Predicted change in breeding success arising from differing access to climatic variables across varied foraging ranges around breeding colonies (right panel). For common guillemot the second best supported model had to be used for predictions due to a lack of available climate projections for wind speed at the time of the analysis. Note that for three species there is no graph displayed because of a lack of support for influence of climate variables in the models.

Population growth rate

In general, models for population growth rates derived from abundance data performed very poorly in explaining variation in the data, ranging from just 2-7% (Table 13). Therefore, we did not use these models to generate future predictions for population growth rate using climate projections. However, we did detect some significant effects of climate on population growth rates for some species.

Atlantic puffin

In this species, the null model containing no climate effects was best supported by the data (Table 13).

Black-legged kittiwake

The best supported model for population growth rate in this species included marine variables and terrestrial wind, derived over the pre-breeding period (Table 13). This model included a significant positive correlation between terrestrial wind speed and growth rate (effect: 0.042, P 0.004; Table 13), a close to significant negative effect of sea surface salinity (effect: -0.162, P0.055; Table 13), and some support for an additional positive effect of NAO on growth rate (effect: 0.190, P 0.09; Table 13).

Common guillemot

In this species, the null model containing no climate effects was best supported by the data (Table 13).

European shag

The best supported model included only marine variables during the non-breeding period, with a significant positive effect of NAO on population growth rate (effect: 0.423, P 0.003; Table 13).

Great black-backed gull

In this species, the best supported model included effects of marine, terrestrial and wind speed climate variables, derived over the breeding season (Table 13). A significant positive effect was detected for terrestrial wind speed (effect: 0.089, P 0.013), and a marginally significant positive effect of terrestrial rain (effect: 1.664, P 0.066; Table 13).

Herring gull

The best supported model included effects for marine climate variables and terrestrial wind speed throughout the whole year, with a significant positive effect of sea surface salinity (effect: 0.195, P <0.001), and significant negative effects for sea surface

temperature (effect: -0.114, P <0.001) and terrestrial wind speed (effect: -0.043, P 0.005; Table 13).

Northern gannet

In this species, the best supported model for population growth rate included effects of marine and terrestrial climate variables, derived over the non-breeding season (Table 13). This model showed a significant positive effect on population growth rate for terrestrial temperature (effect: 0.268, P <0.001) and marginal support for a positive effect of NAO (effect: 0325, P 0.095; Table 13). The model also included a significant negative effect of sea surface temperature on population growth rate (effect: -0.384, P <0.001; Table 13).

Razorbill

The best supported model for population growth rate included marine climate variables and terrestrial wind speed, derived over the non-breeding season (Table 13). There was a significant negative effect of sea surface salinity (effect: -0.207, P 0.01) and a significant positive effect of terrestrial wind (effect: 0.038, P 0.023; Table 13).

Bayesian models for population growth rate using abundance data

Bayesian models for trends in abundance using the SMP data proved intractable. There were major issues of non-convergence when fitting the trends models in a Bayesian framework, which is the most appropriate framework for modelling data such as these with high levels of missing-ness and potential observation error. We therefore do not report the results from these models here, but see Appendix B for a summary of results. These issues are likely to arise because the abundance data contain insufficient information to be able to meaningfully constrain the parameters of model, which may in turn be because of the high proportion of missing counts within the SMP meaning that the proportion of colony-by-year combinations for which count data were available was relatively low.

Table 13. Summary of best supported models for climatic influence on population trends of eight species of seabird breeding on the east coast of the UK. All models include NAO, AMO, SST (sea surface temperature), and SLM (salinity). Model selection using AIC was used to assess if adding terrestrial variables improved model fit (Temp and Rain). Finally, model selection was conducted using AIC to assess if adding WS (terrestrial wind speed) improved model fit. Models for each species were fitted to five seasonal definitions: NB: non-breeding period; AY: all year; PB: pre-breeding period; BS: breeding season; and PBBS: pre-breeding and breeding season periods. A null model was also fitted to all species and seasonal periods containing random effects for colony, year, and colony*year. Significance shown in bold and denoted by ** P<=0.05, * P<=0.10. ΔAIC refers to the different in AIC units between the final best supported model and alternative model formulations including: marine only (M), marine and terrestrial variables (M+T), marine and wind (M+W), and marine, terrestrial and wind (M+T+W). R^2 refers to the variance explained (as a proportion [0,1]) for only fixed effects, or for both fixed and random effects (excluding the individual-level random effect). Variables were not standardised.

Species	Best Model	Estimates					ΔAIC	R²
Atlantic Puffin	Null	**ΔAIC** AY: 7.98; NB: 8.40; PB: 8.66; PBBS: 8.08; BS: 8.35						
Black-legged kittiwake	All year: NAO* + SST + SLM* + WS**		**Estimate**	**SE**	**z**	**P**	NB: 0.25 AY: 0.36 PBBS: 4.66 BS: 4.96 Null: 8.02 M+T+W: M: M+T:	Fixed only 0.0045 Fixed + random 0.025
		NAO	**0.190**	**0.113**	**1.678**	**0.093**		
		SST	0.0055	0.035	0.157	0.875		
		SLM	**-0.162**	**0.084**	**-1.916**	**0.055**		
		WS	**0.042**	**0.015**	**2.884**	**0.0039**		
Common guillemot	Null	**ΔAIC** BS: 4.27; PBBS: 3.67; PB: 2.86; AY: 8.54; NB: 8.08						
European shag	Non-breeding: NAO** + SST + SLM		**Estimate**	**SE**	**Z**	**P**	AY: 0.27 Null: 2.21 PBBS: 7.63 PB: 7.57 BS: 7.72 M+W: M+T: M+T+W:	Fixed only 0.0078 Fixed + random 0.028
		NAO	**0.423**	**0.141**	**2.992**	**0.0027**		
		SST	0.027	0.044	0.624	0.533		
		SLM	-0.0095	0.019	-0.502	0.616		
Great black-backed gull	Breeding season: NAO + SST + SLM + Temp + Rain** + WS**		**Estimate**	**SE**	**Z**	**P**	Null: 5.04 AY: 5.30 PBBS: 4.19 NB: 5.62 PB: 9.24 M+W: M: M+T:	Fixed only 0.025 Fixed + random 0.071
		NAO	0.030	0.022	1.379	0.168		
		SST	-0.020	0.061	-0.329	0.742		
		SLM	0.0018	0.092	0.019	0.985		
		Temp	0.0574	0.045	1.267	0.205		
		Rain	**1.664**	**0.903**	**1.842**	**0.066**		
		WS	**0.089**	**0.036**	**2.491**	**0.013**		
Herring gull	All year: NAO + SST** + SLM** + WS**		**Estimate**	**SE**	**z**	**P**	NB: 1.84 BS: 0.06 PBBS: 0.97 PB: 7.63 Null: 17.09 M+T+W: M: M+T:	Fixed only 0.020 Fixed + random 0.023
		NAO	-0.011	0.133	-0.083	0.934		
		SST	**-0.114**	**0.033**	**-3.401**	**0.00067**		
		SLM	**0.195**	**0.040**	**4.895**	**<0.001**		
		WS	**-0.043**	**0.015**	**-2.805**	**0.0050**		

Species	Model	Variable	Estimate	SE	z	P	Model selection	
Northern gannet	Non-breeding: NAO* + SST** + SLM + Temp** + Rain	**NAO**	**0.325**	**0.195**	**1.672**	**0.095**	Null: PB: AY: PBBS: BS: M+T+W: M: M+W:	Fixed only 0.042 Fixed + random 0.046
		SST	**-0.384**	**0.103**	**-3.746**	**0.00018**		
		SLM	-0.033	0.194	-0.171	0.865		
		Temp	**0.268**	**0.054**	**4.916**	**<0.001**		
		Rain	**0.0167**	**0.056**	**0.297**	**0.766**		
Razorbill	Non-breeding: NAO + SST + SLM** + Wind**		Estimate	SE	z	P	Null: 1.00 PB: 3.63 AY: 2.43 PBBS: 5.35 BS: 6.03	Fixed only 0.0084 Fixed + random 0.030
		NAO	-0.18922	0.17491	-1.082	0.2793		
		SST	0.07953	0.06860	1.159	0.2463		
		SLM	**-0.20696**	**0.08101**	**-2.555**	**0.0106**		
		Wind	**0.03834**	**0.01691**	**2.267**	**0.0234**		

Survival

Our analyses of the relationships between survival and climate were inconclusive, with the models having very low explanatory power, and frequently yielding implausible predictions of survival (e.g., survival rates higher than one). We have, therefore, not presented the results of these analyses in the main report, although the methodology and results are given in Appendix C.

Discussion

Changes to seabird distribution

A GEE-GLM modelling approach was used to predict the at-sea distribution and abundance of seven of the study species (Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, herring gull, northern gannet and razorbill; European shag could not be reliably modelled due to insufficient at-sea survey data and issues related to their very coastal distribution) in the past (1961-1990), present (2017) and future (2070-99) in both summer (June) and winter (January). The analyses built on models previously developed for the NERC/DEFRA funded MERP project (Waggitt et al. 2020) and ORJIP Sensitivity Mapping Tool (Searle et al. 2019).

Underpinning the results were thermal niches of each species. Atlantic puffin and black-legged kittiwake were most likely to respond negatively to climate warming because they favoured the coldest waters. Great black-backed gull and herring gull were also associated with cooler temperatures, and are therefore also likely to respond negatively to predicted future warming. In contrast, common guillemot, razorbill and in particular northern gannet showed an association with warmer temperatures, and were therefore likely to be least negatively affected by warming.

The results predicted widespread declines among the majority of species. For Atlantic puffin and black-legged kittiwake, this was apparent in both summer and winter, whereas it was only the case for summer in common guillemot, herring gull and razorbill, and in winter in great black-backed gull. In contrast, razorbill were in fact predicted to increase in winter, and the northern gannet was predicted to increase in both summer and winter.

The predicted declines were apparent across the North Sea in most cases, with relative distributional changes apparent only in common guillemot and razorbill, which were predicted to see increases in the northern North Sea and decreases in the southern North Sea. Changes in seasonal use were generally not forecasted. Atlantic puffin and northern gannet use the region more extensively in summer than winter and this pattern was predicted to remain under future climate scenarios. Black-legged kittiwake were predicted to continue to use the North Sea throughout the year. Common guillemot, razorbill, great black-backed gull and herring gull currently show higher numbers across the North Sea in winter, and under future climate scenarios, the difference between summer and winter densities were predicted to become more marked in common guillemot and razorbill.

These results are in keeping with past work which has investigated the effect of temperature on distribution and environmental suitability in the North Sea. Frederiksen et al. (2013) predicted that seabird habitat suitability will shift northward over the next century, and concluded that northern distributional shifts and reduced densities in the North Sea are likely in future. Russell et al. (2015) used climate envelope models to predict that 65% of seabird species that breed in the UK would show a decline in their European range, with some declining by as much as 80%. This work was focussed on colony location, which has a strong influence on at-sea distribution in particular in summer. The study estimated that, under a best case scenario of unlimited dispersal, the ranges of black-legged kittiwake and auks would

still decline significantly. The marked variation among species in their responses is challenging to interpret. The decline in kittiwake abundance supports past work on the negative effects of future predicted warming (Carroll et al. 2015), and the increase in gannets suggest the current situation of population increases under climate warming is set to continue. However, the reasons underpinning the variation in responses of the three auk species is unclear. A recent analysis of summer diet from the Isle of May suggests that common guillemots and razorbills are becoming less reliant on lesser sandeels *Ammodytes marinus*, whereas there is no such trend in puffins (Wanless et al. 2018). Puffins may thus be less able to switch prey under climate warming, and single prey loading may constrain guillemots if future warming results in further declines in prey size, which may have less impact on razorbills. However, it is not clear why puffin abundance was also predicted to decline in winter, and razorbills to increase. There are differences in winter distribution and trophic position between these species (Glew et al. 2018), but these do not provide a clear explanation for the decrease in puffins and increase in razorbills predicted in winter. Clearly, further mechanistic studies of diet and foraging ecology are needed to understand among-species variation in summer and winter distribution and abundance.

It is important to recognise that underlying at-sea survey data were an open-access subset of that used in Waggitt et al. (2020) – namely that used by Bradbury et al. (2014) plus additions from Marine Scotland and Natural England. As a consequence, coverage in the most recent decade (2010-2020) and in southern regions (Bay of Biscay, English Channel) is limited. The inclusion of data in the latest decade could have stabilised interaction terms based on climatic indices, identifying differences between the northern and southern North Sea. Whilst outside the study area, the inclusion of data in the southern region would have improved quantification of thermal associations. Further developments to the GEE-GLM would be enhanced if these data could be included.

Seabird Productivity

The effect of climate on productivity (the number of chicks fledged per breeding attempt) was investigated in eight species - the same seven species considered in the analyses of seabird distribution (Atlantic puffin, black-legged kittiwake, common guillemot, great black-backed gull, herring gull, northern gannet and razorbill) plus European shag. The statistical analyses were conducted using colony-specific and year-specific values for breeding colonies throughout the region of interest to estimate associations between productivity and climate variables, and to subsequently generate predictions of future productivity under a projected future climate scenario.

There was a strong negative effect of pre-breeding sea surface temperature and a strong positive effect of pre-breeding sea surface salinity on productivity of Atlantic puffins (Table 14). This resulted in a future projected decline in productivity from the present day to 2070-99, with limited opportunity to increase foraging range to compensate for these productivity declines. For the black-legged kittiwake, the best supported model for productivity included marine and terrestrial climate variables from the pre-breeding period, with a strong negative effect of sea surface salinity and terrestrial temperature and a strong positive effect of terrestrial precipitation (Table 14). As with Atlantic puffin, this resulted in a future projected decline in productivity in

2070-99, with no apparent opportunity to compensate for these declines by increasing foraging range. For common guillemots, the best supported model for productivity included marine and terrestrial climate variables, as well as terrestrial wind, during the pre-breeding period, with some evidence for negative relationships between productivity and sea surface temperature and sea surface salinity, and for a positive relationship with terrestrial rain (Table 14). Because we could not generate future predictions from this model due to the lack of reliable wind projections at the time of modelling, we used the second best supported model, which included both marine and terrestrial climate variables to generate future projections, which indicated a future projected decline in common guillemot productivity in 2070-2099. Again, there was no evidence that increasing foraging range would allow common guillemots to access better marine conditions. For productivity in great black-backed gull, there was a strong negative relationship with sea surface salinity, and a strong negative relationship with terrestrial temperature (Table 14). Interestingly, in great black-backed gull, there was more support for effects of climate over the breeding season, rather than over the pre-breeding period as for the previous three species (Table 14). Future productivity in great black-backed gull was projected to decline in common with the previous three species, and there was little evidence that this species would have the ability to compensate for predicted declines in productivity by increasing its foraging range around breeding colonies to access more climatically suitable conditions. The results for northern gannet were markedly different, with the model receiving the most support including a strong negative relationship between sea surface salinity and productivity (Table 14). As with great black-backed gull, there was more support for an effect of climate during the breeding season on subsequent productivity, rather than the pre-breeding period (Table 14). Notably, northern gannet was the only species for which productivity was predicted to increase in the future. The null model, including no climatic variables, was best supported in the three remaining species (European shag, herring gull and razorbill), suggesting that in these species there was insufficient information in the data to be able to detect relationships between productivity and climate variables.

Table 14. Summary of significant climate effects on seabird productivity for breeding colonies on eastern seaboard of the UK. Grey shading indicates the null model, containing no climatic effects, received the greatest support in the data (assessed using AIC). Significance denoted by ** P<=0.05, * P<=0.10, and direction of effect as negative (-) or positive (+).Empty cells imply the variables was either not included in the best supported model, or was included but the effect was not significant. For more detailed results see Table 12.

Species	Marine	Terrestrial	Wind speed	Season
Atlantic puffin	Sea surface temperature -** Sea surface salinity +*			Pre-breeding
Black-legged kittiwake	Sea surface salinity -*	Temperature -** Rainfall +**		Pre-breeding
Common guillemot	Sea surface temperature -* Sea surface salinity -*	Rainfall +*		Pre-breeding
European Shag				
Great black-backed gull	Sea surface salinity -**	Temperature -**		Breeding
Herring gull				
Northern gannet	Sea surface salinity -**			Breeding
Razorbill				

Our results support previous findings that have demonstrated the importance of temperature on productivity in seabirds in the northern hemisphere (Frederiksen et al. 2004; Jones et al. 2007, Lewis et al. 2009, Smith and Gaston 2012, Watanuki and Ito 2012, Cook et al. 2014; Burthe et al. 2014; Monticelli et al. 2014, Lewis et al. 2015, Zuberogoitia et al. 2016, Howells et al. 2017, Christensen-Dalsgaard et al. 2018, Pakanen 2018, Gardarsson and Jonsson 2019, Michielsen et al. 2019). The most likely mechanism underpinning temperature effects is via changes in the abundance and trophic matching of lower trophic levels with negative consequences on the availability of key prey to seabirds, notably lesser sandeels *Ammodytes marinus* (van Deurs et al. 2009, 2014; Engelhard et al, 2014; McDonald et al, 2015; Eerkes-Medrano et al. 2017; Regnier et al. 2019). Note that evidence for negative effects between temperature and productivity have not always been found - indeed, recent studies at two North Sea colonies did not find significant relationships between sea surface temperature and black-legged kittiwake breeding success (Carroll et al., 2017; Eerkes-Medrano et al. 2017). However, our results predicting a future decline in black-legged kittiwake productivity of approx. 19% (percentage points), linked to warming, matched closely the findings of Carroll et al. (2015) who showed that kittiwake breeding success is predicted to decline by 21-43% between 1961−90 and 2070−99. Sea surface salinity also played a role in resulting predictions for productivity declines in five species (Table 14). We detected a negative link between productivity and sea surface salinity in four species (black-legged kittiwake, common guillemot, great black-backed gull and northern gannet), and a positive link in just

one species, Atlantic puffin (Table 14). Fewer studies have examined the relationship between seabird distribution or density and sea surface salinity than for sea surface temperature, and in general those studies that have considered salinity tend to suggest a positive association between seabird distribution or density with increasing salinity, linked to the degree of ocean mixing and its effects on prey availability (e.g., Balance 2007, Serratosa et al. 2020). However, this relationship has been shown to vary by species; Garthe (1997) found positive associations between sea surface salinity and the density of two species in the southern North Sea (Northern fulmar and common guillemot), but a negative association for five other species in that region, including black headed gull, common gull, herring gull, common tern and arctic tern. In our study, only one species (Atlantic puffin) showed a positive relationship between salinity and productivity, with four other species showing evidence for a negative relationship. This evidence points to sea surface salinity being a potentially strong indicator of seabird breeding success, and as such warrants further investigation as to the underlying mechanisms linking sea surface salinity to seabird demography. The mechanisms underpinning the positive effects of terrestrial rain on productivity apparent in some species is not clear, but overall these were not sufficiently strong to counteract the negative effects of temperature and, across most species, a predicted overall decline in breeding success in future.

An important finding was that pre-breeding conditions were generally more important than conditions during the breeding season, which may result from the effect of such conditions on the quality or abundance of prey during the period of peak energy demand during breeding, or may represent a carry-over effect whereby conditions experienced by seabirds in one season (in this case late winter) have downstream consequences on subsequent seasons (Daunt et al. 2014).

These declines in productivity, together with declines in at-sea density and shifts in range in certain species support past work on effects of climate warming on distribution and demography that threaten the future well-being of many breeding seabirds in the UK. However, a more positive outlook is apparent for northern gannet, whose productivity is predicted to increase and likely reflects its more catholic diet, with less dependence on prey species that are negatively affected by warming.

Seabird Survival

We used count and productivity data to estimate survival because it was the only approach that would allow us to study climate effects across multiple populations and species. Mark-recapture data are only available for a few species and sites, and therefore do not allow for a UK-wide multi-species assessment of relationships between adult survival and environmental variables. However, survival estimates derived from mark-recapture data are a significantly more powerful and reliable approach for estimating drivers of change in survival. For example, using that approach, Frederiksen et al. (2008) demonstrated the effect of wind on survival of European shags, whereas we could not detect any climatic effects in this species. Of more concern are cases where we found opposing results than published survival studies using mark recapture, such as the effects of warming on survival of black-legged kittiwakes. This, together with predictions of survival in our models that exceeded one, and the very low levels of explanatory power, leads us to conclude

that estimating survival from counts and productivity using this method was not reliable within the timeframes of this project.

A further challenge is that for several species in this study – notably black-legged kittiwake and northern gannet – a considerable proportion of the adult population spends the winter outside UK waters. As such, the environmental variables used here may not be particularly relevant to survival prospects, because most adult mortality occurs at this time. Thus, incorporating environmental drivers at wintering grounds would potentially have provided important insights (Reiertsen et al. 2014).

Seabird Population Growth Rates

Using SMP count data to estimate population trends for seabirds has proved very difficult in previous projects (Searle et al. 2020). This is because of missing counts and extremely high uncertainty associated with model estimates. It is likely that the abundance data contain insufficient information to meaningfully constrain the parameters of trend models. Fitting models using non-Bayesian methods resulted in the detection of some significant effects of climate on population growth rates, however these models will have underestimated uncertainty, and could only be fitted to complete time-series of counts as they are unable to estimate counts in missing years. This means results from the non-Bayesian models are very limited in their application, and should be treated with considerable caution. Similarly, all population growth rate models had extremely low explanatory power, and therefore we were unable to generate predictions for future population growth rates using climate projections.

Given the strong influence of adult survival on population trends in seabirds, and the tendency for most adult mortality to occur overwinter, we might expect climate during the non-breeding period to exert the most influence on population growth rates, as was detected for three species (European shag, northern gannet, razorbill; Table 15). One species showed evidence for effects of climate on population growth rate over the whole year (herring gull), with two species having more evidence for climate impacts occurring over the summer (black-legged kittiwake, pre-breeding; great black-backed gull, breeding season; Table 15). These results suggest that both immediate effects of prevailing conditions and carry-over effects of previous seasons are important in determining demographic rates and, in turn, population growth rate, in line with findings from other studies (Oro & Furness 2002; Frederiksen et al. 2008; Erikstad et al. 2009; Bogdanova et al. 2011; Reiertsen et al. 2014; Daunt et al. 2014). Our results are in line with previous studies that have found links between population trends and sea surface temperature, with higher sea surface temperatures associated with lower population growth rates in both herring gull and northern gannet (Table 15). Similarly, we found a positive association between the strength of NAO and population growth rates in black-legged kittiwake, European shag and northern gannet. Finally, for marine variables, as with seabird productivity, we also detected significant effects of sea surface salinity on population growth rates in three species, with higher salinity associated with lower growth rates in black-legged kittiwake and razorbill, but with higher growth rates in herring gull (Table 15).

Table 15. Summary of significant climate effects on seabird population growth rates for breeding colonies on eastern seaboard of the UK. Grey shading indicates the null model, containing no climatic effects, received the greatest support in the data

(assessed using AIC). Significance denoted by ** P<=0.05, * P<=0.10, and direction of effect as negative (-) or positive (+).Empty cells imply the variables was either not included in the best supported model, or was included but the effect was not significant. For more detailed results see Table 13.

Species	Marine	Terrestrial	Wind speed	Season
Atlantic puffin				
Black-legged kittiwake	NAO +* Sea surface salinity -*		Wind speed +**	Pre-breeding
Common guillemot				
European shag	NAO +**			Non-breeding
Great black-backed gull		Rain +*	Wind speed +**	Breeding
Herring gull	Sea surface temp -** Sea surface salinity +**		Wind speed -**	All year
Northern gannet	NAO +* Sea surface temp -**	Temp +**		Non-breeding
Razorbill	Sea surface salinity -**		Wind speed +**	Non-breeding

Conclusions

The future predictions of seabirds under projected warming of the climate investigated in this project suggest that there will be marked changes in at-sea density and productivity and moderate changes in distribution, which accords with previous work in this field largely undertaken in single populations and/or species. Importantly, our results suggest that potential declines in the future are expected to occur in a wider suite of species than has been demonstrated before. We have demonstrated important links between climate variables and seabird productivity. Strong declines in future productivity associated with climate change were predicted for four of the five species in which climate effects were detected. These changes will likely result in significant shifts in seabird population demography, trends and distribution over the coming decades, with consequences for the interaction of these species with offshore wind developments in the North Sea.

We also found evidence suggesting widespread declines in spatial habitat use among the majority of species, particularly for Atlantic puffin, but also for black-legged kittiwake, great black-backed gull, common guillemot, herring gull and razorbill. Puffin and kittiwake were predicted to decline in both summer and winter, whereas it was only the case for summer in common guillemot, herring gull and razorbill, and in winter in great black-backed gull. One species, razorbill, was predicted to increase its spatial habitat use of the North Sea in winter, and only one species, northern gannet, was predicted to increase its spatial habitat use of the North Sea in both summer and winter. This suggests that interactions between

razorbill and northern gannet and ORDs may increase in the North Sea in coming decades. Relative distributional changes were apparent only in common guillemot and razorbill, which were predicted to see increases in the northern North Sea and decreases in the southern North Sea. This suggests that for these two species, impacts from offshore wind may be more strongly felt in Scottish populations than in English populations over future decades. Importantly, although changes in seasonal use were generally not forecasted, we did detect some evidence for a greater proportional use of the North Sea in winter for guillemots and razorbills, which implies a greater importance of assessing offshore wind impacts during the non-breeding season in coming decades for some species.

In general, our models for seabird productivity and population growth rates performed poorly in explaining the observed variation in the SMP dataset, despite identifying significant relationships between climate variables and demographic rates. This is not uncommon with ecological data, particularly, as is the case with the SMP, where there is likely to be significant sampling or observer error in counts and productivity data. Moreover, seabird demography will respond to environmental fluctuations from year to year, including lag effects, which are difficult to capture precisely with environmental variables that have relatively coarse spatial and temporal resolution. This is particularly true during the non-breeding season when a lack of knowledge inhibits strong spatio-temporal coherence between the habitats seabird populations are utilising and their associated climatic and environmental characteristics used within models. It is therefore, unsurprising that the models for productivity performed better, when individuals are constrained to forage within the vicinity of their breeding colony. The lack of explanatory power very much hinders our ability to make reliable future predictions for changes to seabird demography in response to changing climate. A key priority for future research will be to identify stronger associations between demographic rates and population trends and more refined, lagged climate variables, ideally collected with a greater spatio-temporal coherence to the habitat usage of individual populations across different seasons. In addition, there are other drivers of seabird population growth rate whose investigation was beyond the scope of this study. For example, the patterns observed in large gull species may have been affected by historic culls and current licensing regimes. Future modelling would ideally consider these additional factors in order to more accurately assess the effect of future climate change on these populations.

The results on survival rates derived from models using count and productivity data with assumed species-level estimates for juvenile survival, do not appear to have produced robust or defensible results. This arises from the inability to accurately estimate survival from population count data and productivity in datasets such as the SMP with a high incidence of missing data, considerable potential for observer variation and the potential influence of other factors (notably variation in immature survival rates and net movements) that may affect the link between productivity, adult survival and population size. Accordingly, a future priority is to increase the number of survival estimates obtained from mark-recapture data, which in some cases will require the development of new empirical studies of individually marked birds. A second priority is to address the drastic shortage of estimates of juvenile survival and net movements, which are only available for very few populations of a subset of species. A third priority is to undertake analyses using environmental variables that are more directly related to seabird distribution and demography, such as direct measures for prey availability and the inclusion of extreme weather events. However,

although these will improve our explanatory power in retrospective analyses, there remains the limitation of working only with variables that are available in climate projections.

Implications for offshore wind assessments

The results of these analyses suggest that climate change will potentially have substantial impacts on demography and abundance of seabirds in the North Sea over the 21st century, and the impacts are likely to vary, in magnitude and form, between species.

Estimation of impacts

A failure to account for these changes in ORD assessments may lead to misidentification of the key affected populations, as well as misjudgement of the extent to which seabirds are likely to interact with ORDs over time, and inclusion in assessments could be considered at the scoping stage of the EIA process. Climate-induced changes to the spatial distribution of seabirds within the North Sea reveal that habitat use in UK seabirds will not be static over the coming decades. Any directional shift in habitat use, from South to North, will mean that the number and source populations of individual birds interacting with specific ORD footprints will alter over time. This could mean that a static assessment identifying the protected populations of concern using apportioning methods applied to current day distributions could fail to identify populations that would come to interact with those footprints as their population sizes evolve over time, and their spatial habitat use changes in coming decades. For example, smaller populations to the North may increase in abundance as climate shifts prey suitability northwards, expanding their foraging ranges as a result of density-dependent interactions with conspecifics, and thereby starting to interact with an ORD footprint with which they previously had no contact. Similarly, the evidence supporting potential seasonal shifts in habitat use of the North Sea for two species suggests that the seasonal period of greatest importance for ORD impacts on protected populations may change as climate alters. If species begin to use the North Sea proportionately more in the overwinter period than the breeding season, ORD impact assessments in the non-breeding season will become more critical to performing robust and accurate assessments. This is particularly problematic because at present, available methods for assessing impacts of ORD in the non-breeding season, and apportioning impacts back to protected colonies, are much cruder than those available for the breeding season. Moreover, it will become increasingly important that cross-border efforts to assess impacts for seabirds originating from different countries are better developed (e.g., MarPAMM project, 2022), because the ratio of seabirds from UK and non-UK populations in the North Sea during winter is likely to alter under future climate change.

Population Viability Analysis

Population Viability Analysis (PVA) methods use population models to quantify the projected impacts of offshore renewable energy developments (ORD) upon seabird and abundance, using estimates of annual effects on demography as a result of collision, displacement and barrier effects.

The PVAs used in assessing impacts of ORD developments do not currently account for climate change, but the results of this project imply that it could be potentially important to account for climate change when running PVAs. Climate change impacts on productivity were estimated to be negative for four species in this study, which implies that the absolute condition or conservation status of populations under ORD impacts (e.g., quasi-extinction probabilities) may be substantially under-estimated when the impacts of climate change are ignored within PVAs. It is not clear, however, that relative comparisons relating to ORD (e.g. comparisons of growth rates under ORD impacts and baseline conditions) would necessarily be systematically under-estimated as a result of failing to account for climate change effects. Under-estimation of relative impacts may occur if there are interactions between climate and ORD effects, but additional work would be needed (e.g. via individual-based modelling) to understand whether such interactions actually exist, and what form they take. The implications of the current project are also complicated by the fact that our assessments, of necessity, focused upon change over a longer period (baseline period until 2070-2099) than the periods, of up to 30 years, typically considered in assessments of ORD impacts, so it is not clear if the consequences of climate change for estimates of ORD impacts will be as great, over these shorter periods, as the results of this project may initially suggest.

It is technically feasible to modify PVAs so that they can incorporate the sort of climate impacts that we have estimated within this project, because the models used in PVAs have the same basic structure (stochastic Leslie matrix models) as the models considered here. One key practical challenge in incorporating climate change into PVA models, however, would be the need to consider much shorter periods of time than those considered here (e.g. changes over the next 10 years or 30 years, rather than over the entire course of the 21st century), and the need to consider multiple emissions scenarios (to reflect uncertainty about actual future emissions). The models that we have developed in this project could easily be used to produce projections of seabird demography and abundance for other periods, or under other scenarios, once relevant marine and terrestrial climate projections become available (e.g. through UKCP18). Similarly, climate projections would need to be available for each future year within the PVA so as to be able to generate climate-driven changes to demographic rates at each time step.

The other key challenge in incorporating climate change into PVA models is the low explanatory power of the models considered in this project, which implies that the models are not capturing the full range of climate and non-climate variables that influence changes in population demography and abundance. This low explanatory power means that the predictions produced by models should be treated with substantial caution. We would suggest that the predictions produce by the models we have fitted here should not be over-interpreted, but that there is likely to be value in applying PVA models with and without climate change impacts, to see the extent to which these differ, and to examine whether PVAs that ignore climate change are likely to systematically under-estimate key metrics of ORD impacts.

Compensatory measures

It is increasingly recognised that the scale of ORD development in the North Sea will necessitate the use of compensatory measures to counteract the negative impacts arising from collision, displacement and barrier effects on seabirds. Compensatory

measures are best applied strategically across the Natura 2000 Network in order to maintain the coherence of the Natura 2000 network. Strategic implementation of compensatory measures for ORDs requires an understanding of the population status and trends across colonies comprising the network, and the mechanisms for any strong declines. This is because the application of compensatory measures in strongly declining populations are unlikely to result in a net gain of individuals, potentially applying efforts that ultimately fail to contribute to the overall coherence and integrity of the Natura 2000 network. Similarly, a lack of understanding for the reasons of climate-induced changes to population trends could undermine the success of specific compensatory measures. For example, if a population is declining primarily due to declines in prey availability within the foraging range of the breeding colony then compensatory measures such as artificial nest creation may not result in an increase in productivity due unless nest site availability is also limiting breeding population size.

Recommendations and future work

Ideally, methods for conducting assessments of ORD impacts should be developed so as to allow for a year by year prediction of the spatial habitat use, demography and abundance of protected seabird populations. This would allow estimated impacts to evolve dynamically through time as climate-driven changes to species' ecology occur. This is true for both the estimation of impacts (changes to demographic rates and abundance arising from collision, displacement and barrier effects), and their use within PVA models incorporating climate-induced changes to demographic rates. Developing such a framework is, in principle, straightforward, but is currently hindered by a lack of empirical understanding for how seabird space use and demography will change through time as future climate change occurs. This understanding requires the projection of seabird distribution and demography for each future year in which an assessment is required. Without this empirical quantification it is not currently possible to estimate ORD impacts on a year by year basis in a predictive way, or to robustly account for climate induced changes to demographic rates within PVAs.

Our results have also demonstrated the difficulty in estimating survival rates of seabird populations from abundance and productivity data. More sophisticated statistical methods may yield more defensible estimates of survival, but this is only likely to be successful if these approaches can accurately capture the observation processes associated with collection of count and nest monitoring data within the SMP. This is not straightforward, and requires considerable understanding of the form and magnitude of the errors and biases associated with the data collection process. For example, whole colony counts are typically undertaken once in a given year, precluding an estimate of error in the estimate. Further, levels of observation error are likely to be higher in colonies where these have been derived from plot counts that in colonies where whole colony counts have been taken, but this difference can only be quantified through detailed modelling of the relationship between plot-level and colony-level counts – and this relies, in turn, upon modelling the process by which plots are selected. Collection of empirical data on adult survival at more colonies and for more species, through mark-recapture studies, is a critical data gap which would facilitate more defensible use of survival rates within PVA models. Another key priority is to obtain more empirical data on immature survival rates and net movements between colonies, in order to improve accuracies of

population forecasts. However, these would not immediately help with identifying climate effects on survival because this requires long time-series of survival data to robustly link with climate variables.

A key finding is that the overwintering period may become more dominant in determining ORD impacts on two UK seabird species, and this highlights the need for future work to develop both impact estimation and apportioning methods in this critical seasonal period. Overall, our results are important because these effects of climate change are of direct relevance to assessments of ORDs, creating complex interactions that could have a significant bearing on the effect of the ORD on protected populations over the lifespan of the project. Our results are also relevant to other key policy initiatives, such as marine protection. We strongly encourage that climate change effects are incorporated into ORD assessments and conservation designation in future.

Acknowledgements

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Appendix A: Data used in modelling

Table 16. Selected breeding colonies on the East coast of Scotland to include in the demographic modelling with climate variables. Atlantic puffin (ATPU), common guillemot (COGU), European shag (EUSH), northern gannet (NOGU), razorbill (RAZO), herring gull (HEGU), great black-backed gull (GBBG), black-legged kittiwake (BLKI).

Species	Colony name (SMP Site or Mastersite name)	SMP Site or Mastersite?	Years of data available for analyses of:		
			Abundance	Productivity	Survival
ATPU	Bass Rock	Site	3	0	0
ATPU	Coquet Island	Site	14	4	4
ATPU	Craigleith	Site	2	0	0
ATPU	Fair Isle	Site	1	32	0
ATPU	Farne Islands	Site	0	22	0
ATPU	Fidra	Site	9	0	0
ATPU	Inchcolm	Site	14	0	0
ATPU	Inchkeith	Site	16	0	0
ATPU	Inchmickery	Site	16	0	0
ATPU	Isle of May	Site	1	33	1
ATPU	St Abb's Head NNR	Site	27	0	0
ATPU	The Lamb	Site	7	0	0
BLKI	Auskerry	Site	12	0	0
BLKI	Bass Rock	Site	21	0	0
BLKI	Boulby Cliffs	Site	29	0	0
BLKI	Brei Wick to Virdick	Site	2	0	0
BLKI	Buchan Ness to Collieston	Site	0	23	0
BLKI	Burga Stacks to Caves	Site	4	0	0
BLKI	Calders Geo	Site	3	0	0
BLKI	Castle Headland	Site	18	0	0
BLKI	Clett Head	Site	3	3	0
BLKI	Compass Head	Site	6	8	1
BLKI	Coquet Island	Site	30	26	26
BLKI	Costa Head	Site	0	24	0
BLKI	Craigleith	Site	24	0	0
BLKI	Cross-voe-sand to Caves	Site	0	14	0
BLKI	Cullernose Point	Site	6	0	0
BLKI	Dunnet Head RSPB	Site	0	10	0
BLKI	Dunstanburgh Castle	Site	6	0	0

BLKI	East Caithness Cliffs SPA	Mastersite	0	9	0
BLKI	East Yell	Site	1	0	0
BLKI	Fair Isle	Site	5	33	1
BLKI	Farne Islands	Site	32	29	26
BLKI	Fidra	Site	31	0	0
BLKI	Firth of Forth SPA	Mastersite	21	30	17
BLKI	Fitful Head	Site	1	0	0
BLKI	Flamborough Head and Bempton Cliffs	Site	1	32	0
BLKI	Foula	Site	15	29	10
BLKI	Fowlsheugh RSPB	Site	1	31	0
BLKI	Grand Hotel	Site	14	0	0
BLKI	Harbourside Houses	Site	11	0	0
BLKI	Hartlepool Fish Quay 1	Site	9	0	0
BLKI	Hermaness	Site	1	29	1
BLKI	Hich Holm	Site	2	3	0
BLKI	Holm	Mastersite	0	30	0
BLKI	Hopeman Bay	Mastersite	29	3	1
BLKI	Horse Island; Colsay; Little and Ladies Holm to Fitful Head	Mastersite	4	0	0
BLKI	Huntress Row	Site	5	0	0
BLKI	Inchcolm	Site	28	0	0
BLKI	Inchkeith	Site	33	0	0
BLKI	Isle of May	Site	33	33	30
BLKI	Kettlaness	Site	3	10	0
BLKI	Lowestoft	Site	28	32	24
BLKI	Marsden Cliffs	Site	20	2	2
BLKI	Marwick Head SPA	Mastersite	1	32	0
BLKI	Maywick to Scalloway	Mastersite	4	0	0
BLKI	Mousa RSPB	Site	7	0	0
BLKI	Muckle Flugga	Site	1	0	0
BLKI	Mull Head - cliff-nesters	Site	2	25	1
BLKI	Nelson Pub and Foreshore	Site	9	0	0
BLKI	Ness of Ireland	Site	2	0	0
BLKI	No Ness to Levenwick and Boddam to Virkie	Mastersite	11	23	5
BLKI	North Caithness Cliffs SPA	Mastersite	0	9	0

BLKI	North Sutor to Shandwick	Mastersite	23	29	20
BLKI	Noss SPA	Mastersite	3	32	1
BLKI	Old Britannia Inn/Eastborough	Site	10	0	0
BLKI	Outer Brough	Site	4	0	0
BLKI	Outer Thames Estuary SPA	Mastersite	13	0	0
BLKI	Papa Westray (North Hill and Holm) SPA	Mastersite	8	26	2
BLKI	Portknockie	Site	27	0	0
BLKI	Reawick	Mastersite	6	0	0
BLKI	River Tyne to Seaton Sluice	Mastersite	11	27	8
BLKI	Row Head	Site	1	28	1
BLKI	Royal Hotel	Site	5	0	0
BLKI	Saltburn Cliffs (Huntcliff)	Site	28	23	18
BLKI	Sands of Forvie	Site	29	20	14
BLKI	Sandside	Site	5	0	0
BLKI	Saxavord	Site	1	0	0
BLKI	Scarvister to Culswick	Mastersite	0	17	0
BLKI	SE Yell (inc. Burravoe)	Site	3	12	0
BLKI	Sea Cadets	Site	10	0	0
BLKI	Siggar Ness	Site	1	0	0
BLKI	Skeld; Westerwick and Culswick	Site	3	0	0
BLKI	Spa Bridge	Site	7	0	0
BLKI	St Abb's Head NNR	Site	33	32	30
BLKI	St. Ninian's Isle	Site	7	0	0
BLKI	Stenness	Site	1	0	0
BLKI	Sulman's	Site	2	0	0
BLKI	Sumburgh Head	Site	5	33	4
BLKI	Swallow Cove - Crawton	Site	1	0	0
BLKI	The Lamb	Site	29	0	0
BLKI	The Poil	Site	3	0	0
BLKI	Town Hall	Site	10	0	0
BLKI	Troswick Ness	Site	13	10	2
BLKI	Troup; Pennan and Lion's Heads	Site	0	9	0
BLKI	Vaila	Site	4	0	0
BLKI	West Burra	Site	4	0	0

BLKI	West Burra - Shetland	Mastersite	0	23	0
COGU	Bass Rock	Site	21	0	0
COGU	Craigleith	Site	26	0	0
COGU	Deerness	Mastersite	0	25	0
COGU	Fair Isle	Site	1	32	0
COGU	Farne Islands	Site	32	9	5
COGU	Fidra	Site	31	0	0
COGU	Flamborough Head and Bempton Cliffs	Site	0	18	0
COGU	Fowlsheugh RSPB	Site	22	0	0
COGU	Hermaness	Site	3	0	0
COGU	Inchcolm	Site	17	0	0
COGU	Inchkeith	Site	33	0	0
COGU	Isle of May	Site	33	33	28
COGU	Marwick Head SPA	Mastersite	0	30	0
COGU	North Sutor to Shandwick	Mastersite	0	17	0
COGU	Papa Westray (North Hill and Holm) SPA	Mastersite	2	27	1
COGU	Sands of Forvie	Site	21	0	0
COGU	St Abb's Head NNR	Site	27	4	2
COGU	Sumburgh Head	Site	12	30	6
COGU	The Lamb	Site	31	0	0
EUSH	Auskerry	Site	9	0	0
EUSH	Bass Rock	Site	26	0	0
EUSH	Carr Craig	Site	32	0	0
EUSH	Craigleith	Site	31	0	0
EUSH	Cumlewick Ness	Site	4	0	0
EUSH	Fair Isle	Site	0	33	0
EUSH	Farne Islands	Site	32	29	28
EUSH	Fidra	Site	33	2	2
EUSH	Foula	Site	0	19	0
EUSH	Haystack	Site	22	0	0
EUSH	Hermaness	Site	4	5	0
EUSH	Holm Of Papa Westray	Site	3	1	0
EUSH	Hopeman Bay	Mastersite	17	0	0
EUSH	Howick - Cullornose Point - Dunstanburgh Castle Point	Mastersite	6	0	0
EUSH	Inchcolm	Site	27	0	0
EUSH	Inchkeith	Site	33	0	0

EUSH	Inchmickery	Site	28	1	1
EUSH	Isle of May	Site	33	33	32
EUSH	Kettlaness	Site	3	2	0
EUSH	Mousa RSPB	Site	10	4	2
EUSH	Muckle Roe	Site	2	0	0
EUSH	Noness	Site	27	4	4
EUSH	North Hill RSPB; Papa Westray	Site	7	12	6
EUSH	North Sutor Of Cromarty/Castlecraig	Site	24	27	23
EUSH	Noss	Site	31	3	3
EUSH	Portknockie	Site	27	0	0
EUSH	Reawick	Mastersite	3	0	0
EUSH	Sands of Forvie	Site	19	0	0
EUSH	Sandwick to Virkie: Boddam to Virkie within SPA	Site	9	0	0
EUSH	SE Yell (inc. Burravoe)	Site	2	4	0
EUSH	Silwick - Westerwick	Site	2	0	0
EUSH	Skeld; Westerwick and Culswick	Site	3	0	0
EUSH	Skelda Ness-Burga Stacks (Sh.) (all inc. traces)	Site	1	0	0
EUSH	St Abb's Head NNR	Site	33	29	30
EUSH	Strathlene to Portknockie	Mastersite	11	0	0
EUSH	Sumburgh Head	Site	31	31	30
EUSH	The Lamb	Site	31	0	0
EUSH	Troswick Beach to Boddam	Site	10	0	0
EUSH	Troswick Ness	Site	10	5	2
EUSH	Vaila	Site	3	0	0
EUSH	West Of The Nev - Stead Of Culswick	Site	1	0	0
EUSH	Whaness	Site	0	10	0
GBBG	Auskerry	Site	10	0	0
GBBG	Bass Rock	Site	5	0	0
GBBG	Birsay Moors RSPB	Site	6	2	0
GBBG	Car Craig; Eyebroughy and Haystack	Mastersite	18	0	0
GBBG	Ceann Leathad nam Bo 1	Site	11	0	0

GBBG	Ceann Leathad nam Bo 2	Site	11	0	0
GBBG	Cleit Bheag	Site	9	0	0
GBBG	Craigleith	Site	31	0	0
GBBG	Fair Isle	Site	8	0	0
GBBG	Farne Islands	Site	22	0	0
GBBG	Fidra	Site	31	0	0
GBBG	Fowlsheugh RSPB	Site	4	0	0
GBBG	Halberry Head	Site	8	0	0
GBBG	Havergate Island	Site	8	5	1
GBBG	Helman Head	Site	9	0	0
GBBG	Hich Holm	Site	4	0	0
GBBG	Hobbister RSPB	Site	7	2	0
GBBG	Holburn Head 2	Site	11	0	0
GBBG	Holm Of Papa Westray	Site	3	2	0
GBBG	Inchcolm	Site	23	0	0
GBBG	Inchgarvie	Site	23	0	0
GBBG	Inchkeith	Site	22	0	0
GBBG	Inchmickery	Site	25	1	1
GBBG	Isle of May	Site	27	4	2
GBBG	Latheronwheel	Site	9	0	0
GBBG	Little Clett	Site	10	0	0
GBBG	Llama Farm	Site	11	0	0
GBBG	Loch of Strathbeg RSPB	Site	10	6	3
GBBG	Melvich 1	Site	7	0	0
GBBG	Mousa RSPB	Site	5	3	1
GBBG	Nigg Ferry	Site	5	0	0
GBBG	Nigg Oil Terminal	Site	17	15	11
GBBG	North Hill RSPB; Papa Westray	Site	21	14	11
GBBG	Noss SPA	Mastersite	32	17	17
GBBG	Occumster	Site	11	0	0
GBBG	Ord of Caithness 1	Site	9	0	0
GBBG	Ord of Caithness 2	Site	4	0	0
GBBG	Orford Ness 1	Site	8	0	0
GBBG	Poll Gallon	Site	9	0	0
GBBG	Sands of Forvie	Site	28	0	0
GBBG	Sarclet Head	Site	10	0	0
GBBG	St Johns Point	Site	9	0	0
GBBG	St. Ninian's Isle	Site	1	0	0

GBBG	Stack of Ulbster	Site	6	0	0
GBBG	The Brough	Site	11	0	0
GBBG	The Lamb	Site	23	0	0
GBBG	Whaness	Site	0	10	0
HEGU	Bass Rock	Site	5	0	0
HEGU	Birsay Moors RSPB	Site	4	0	0
HEGU	Blakeney Point	Site	24	5	1
HEGU	Boulby Cliffs	Site	29	0	0
HEGU	Car Craig; Eyebroughy and Haystack	Mastersite	26	0	0
HEGU	Coquet Island	Site	30	9	8
HEGU	Craigleith	Site	3	0	0
HEGU	Eyebroughy	Site	13	0	0
HEGU	Fair Isle	Site	6	0	0
HEGU	Farne Islands	Site	9	0	0
HEGU	Fidra	Site	18	0	0
HEGU	Flamborough Head and Bempton Cliffs	Site	0	10	0
HEGU	Fowlsheugh RSPB	Site	1	3	0
HEGU	Freiston Shore RSPB	Site	8	1	1
HEGU	Havergate Island	Site	19	5	5
HEGU	Hobbister RSPB	Site	8	1	0
HEGU	Holkham NNR	Site	9	2	1
HEGU	Hollesley Marsh	Site	2	1	0
HEGU	Holm Of Papa Westray	Site	2	3	0
HEGU	Hunstanton Town	Site	11	11	7
HEGU	Inchgarvie	Site	25	0	0
HEGU	Inchmickery	Site	22	1	1
HEGU	Isle of May	Site	22	19	17
HEGU	Long Craig	Site	17	0	0
HEGU	Longnewton Res.	Site	15	0	0
HEGU	Minsmere Scrape & Beach	Site	14	0	0
HEGU	Mousa RSPB	Site	5	1	0
HEGU	Nigg Ferry	Site	5	0	0
HEGU	Nigg Oil Terminal	Site	17	0	0
HEGU	North Hill RSPB; Papa Westray	Site	13	9	4
HEGU	Noss	Site	32	19	18
HEGU	Orford Ness 1	Site	19	0	0

HEGU	Outer Trial Bank	Site	19	0	0
HEGU	Saltburn Cliffs (Huntcliff)	Site	28	0	0
HEGU	Sands of Forvie	Site	22	0	0
HEGU	Scolt Head Island NNR	Site	9	4	2
HEGU	Snettisham RSPB	Site	9	1	0
HEGU	St Abb's Head NNR	Site	33	0	0
HEGU	St Cyrus NNR	Site	23	0	0
HEGU	St Fergus Gas Terminal	Site	6	0	0
HEGU	Stiffkey	Site	1	0	0
HEGU	The Lamb	Site	12	0	0
HEGU	Titchwell Marsh RSPB	Site	8	2	1
NOGA	Fair Isle	Site	31	32	26
NOGA	Flamborough Head and Bempton Cliffs	Site	13	21	8
NOGA	Foula	Site	4	0	0
NOGA	Hermaness; Saxa Vord and Valla Field SPA	Mastersite	0	29	0
NOGA	Noss SPA	Mastersite	1	32	0
NOGA	Sule Skerry	Site	2	0	0
NOGA	Troup; Pennan and Lion's Heads SPA	Mastersite	13	21	7
NOGA	West Westray SPA	Mastersite	12	14	8
RAZO	Bass Rock	Site	18	0	0
RAZO	Boulby Cliffs	Site	18	0	0
RAZO	Craigleith	Site	25	0	0
RAZO	Fair Isle	Site	0	28	0
RAZO	Farne Islands	Site	21	19	13
RAZO	Fidra	Site	27	2	1
RAZO	Flamborough Head and Bempton Cliffs	Site	0	10	0
RAZO	Hermaness	Site	3	0	0
RAZO	Inchcolm	Site	21	0	0
RAZO	Inchkeith	Site	31	0	0
RAZO	Isle of May	Site	33	33	29
RAZO	Marsden Cliffs	Site	4	0	0
RAZO	North Sutor to Shandwick	Mastersite	0	21	0
RAZO	Papa Westray (North Hill and Holm) SPA	Mastersite	2	13	1
RAZO	Portknockie	Site	5	0	0
RAZO	Saltburn Cliffs (Huntcliff)	Site	6	0	0

RAZO	Sands of Forvie	Site	26	0	0
RAZO	St Abb's Head NNR	Site	19	3	1
RAZO	Sumburgh Head	Site	9	8	6
RAZO	The Lamb	Site	25	0	0

Table 17. Detailed summary of climate/weather variables used to correlate against seabird demographic parameters identified in Web of Science literature search ("seabirds and productivity and survival and breeding success and climate"). BLKW = black-legged kittiwake. IOM = Isle of May.

Demographic rate and Species	Metrics	Ref
Survival (fledglings, post-recruitment) BLKW (Alaska)	- Winter **PDO** (Nov-Feb prior to BS, averaged monthly data) - Winter **ENSO** 3.4 index values (Nov-Feb prior to BS, averaged monthly data) - Mean monthly autumn (sept-oct), winter (nov-feb) and spring (mar-apr) **wind magnitudes** - Mean monthly **SST** (nov-feb)	(McKnight et al. 2019)
Chick growth and survival BLKW (Norway)	- Weather station data hourly for wind speed and temp, daily ppt: - **Effective temp** (chill factor using eqn for temp and wind speed) - Mean **wind speed** - **Wind direction** (NE, S, NW) - **Prevailing wind** direction in 5d periods (direction with >50% prevalence) - Day with **highest ppt** in 5d periods	(Christensen-Dalsgaard et al. 2018)
Adult survival (in relation to migration) Eiders (Canada, Svalbard, Norway)	- Winter **NAO** (from monthly values, Dec-Mar) - Time lags of 1, 2, 3 years	(Guery et al. 2017)
Survival and breeding success European storm petrel (Spain)	- Mean monthly **NAO for winter** (Dec-Mar) - Mean monthly **NAO for spring** (apr-Jun)	(Zuberogoitia et al. 2016)
Breeding: hatching date, egg size, hatching success, fledging success Lesser noddies (Seychelles)	- **Chlorophyll** (weekly averaged then found 'peak productivity' over Apr-Jun and Jun-Aug) - **SST** (weekly averaged over Apr-Jun and Jun-Aug) - **Wind speed** (weekly averaged over Apr-Jun and Jun-Aug; and 'extreme wind' either very low or very high)	(Monticelli et al. 2014)
Breeding success (hatching success,	All at nest sites: - **Air temperature** - **Wind speed**	(Michielsen et al. 2019)

Demographic rate and Species	Metrics	Ref
chick growth, chick survival) **Wilson's storm petrel (Antarctic)**	- **Wind direction** - **Precipitation** - Snow cover	
Adult survival, breeding success (Cory's shearwater, Mediterranean)	- SOI (annual mean – Jan-Dec) - **NAO** (annual winter NAO – Dec-Mar, 1 yr lag) - Number of hurricanes during study period	(Genovart et al. 2013)
Breeding success, chick diets, timing of breeding Rhinoceros auklet, Japanese cormorant, black-tailed gulls (Japan)	- Average monthly **air temp** (Feb-Jul) - Monthly **rainfall** - Total snowfall in March - Mean monthly **SST** - Current - **Chlorophyll** in spring (mar-may) - PDO (Pacific Decadal Observation) - NPI (North Pacific Index) - AO (Arctic Oscillation)	(Watanuki and Ito 2012)
Adult survival, breeding success, chick diet, chick mass Thick-billed murres (Canada)	- **NAO** annual and winter (Dec-Mar) - **AO** monthly mean – non-breeding (sep-apr) - Lag effects of up to 3 years for above - Monthly mean **SST** (jan-Mar & apr) - Mean **min temp** (monthly) – winter (jan-mar) - Mean monthly **ppt** - winter (jan-mar) - **Wind speeds** (monthly means BS – May-aug)	(Smith and Gaston 2012)
Adult survival Common eiders (Baltic)	- **NAO** (annual index, with lags up to 4 years)	(Hario et al. 2009)
Breeding (first egg dates, clutch sizes, egg volume) Black-tailed gulls (Japan)	- **SST anomalies** (difference to long-term mean, March, April)	(Tomita et al. 2009)
Timing of arrival to breeding grounds Little terns (Finland)	- **NAO** (Apr-May, May, June) - **Air temperature** (Spring, based on earliest sighting and earliest egg laying dates, split into 10, 20 or 30 day periods)	(Pakanen 2018)

Demographic rate and Species	Metrics	Ref
Breeding success Northern fulmar (Orkney)	- **NAO** (winter, current and lag 1 year)	(Lewis et al. 2009)
Breeding – chick diet Shags (IOM)	- **SST** (mean of Feb + Mar) - **Wind speeds** (mean daily wind speed) - **Precipitation** (total daily rainfall)	(Howells et al. 2017)
Breeding (nest numbers, habitat use of nests, brood size, breeding density, fecundity – proportion of juveniles) Great cormorant (Iceland)	- **Subpolar gyre index** - **SST** - **AMO** - **NAO** - **Average monthly temp** (jan-feb)	(Gardarsson and Jonsson 2019)
Juvenile survival Emperor penguins (Antarctica)	- **Southern Annular Mode (SOM,** Jul-Dec**)** - **Sea ice concentration**	(Abadi et al. 2017)
Foraging effort Shags (IOM)	- **Wind speed** (mean daily wind speed, mean daily wind direction – E or W of N)	(Lewis et al. 2015)
Adult mortality (wreck event) Brünnich's guillemots (Newfoundland)	- **Sea ice** (timing of blocking of coastal leads) - **Onshore winds (NE)**	(Tranquilla et al. 2010)
Adult survival and productivity Whiskered auklets (Alaska)	- **Aleutian Low Pressure climate index** (Dec-Mar) - **SST** (Summer – Apr-Aug; Winter – Aug-Apr) - **PDO** (Aug-Apr) - **North Pacific Index NPI** (Aug-Apr)	(Jones et al. 2007)
Adult, 1st year, 2nd year survival Shags (IOM)	- Daily weather from WS for **February** - **Mean daily minimum air temperature** - **Total precipitation**	(Frederiksen et al. 2008)

Demographic rate and Species	Metrics	Ref
	- **Summed onshore wind component** (easterly component – mean daily wind speed(knots) x sin(mean daily wind direction; set to 0 if wind direction between 180-360 [westerly] – then summed over all days in February)	

Appendix B: Bayesian results of modelling

Productivity

Table 18. Summary of best supported models (JAGS) for the influence of climatic effects on breeding success of seabirds breeding on the east coast of the UK. Estimates, standard errors (SE) and limits of lower and upper 95% credible intervals (L95% and U95%) are shown, along with the proportion of the posterior density that is greater than, or less than, zero,(Proportion <0>), which is a measure of the strength of the effect. Note that the null model, including no climatic variables, was best supported in three species (Razorbill, European shag and Herring gull). Terms highlighted in bold indicate strong effects.

Species	Estimates					
Atlantic puffin		**Estimate**	**SE**	**L95%**	**U95%**	**Proportion <0>**
	NAO	0.0503	0.172	-0.290	0.378	0.624
	AMO	-0.735	0.994	-2.625	1.136	0.788
	SST	**-0.621**	**0.181**	**-0.962**	**-0.264**	**1.00**
	SLM	**0.886**	**0.587**	**-0.073**	**2.236**	**0.96**
Black-legged kittiwake						
	NAO	0.155	0.336	-0.572	0.804	0.674
	AMO	-1.770	1.936	-5.488	2.156	0.824
	SST	0.0086	0.231	-0.446	0.446	0.525
	SLM	**-2.190**	**0.436**	**-3.041**	**-1.287**	**1.00**
	Temp	**-0.263**	**0.125**	**-0.515**	**-0.026**	**0.985**
	Rain	**0.700**	**0.277**	**0.173**	**1.257**	**0.995**
Common guillemot						
	NAO	0.258	0.364	-0.483	0.962	0.785
	AMO	0.138	2.001	-3.990	3.982	0.526
	SST	**-0.480**	**0.339**	**-1.130**	**0.227**	**0.918**
	SLM	**-0.699**	**0.503**	**-1.704**	**0.289**	**0.921**
	Temp	-0.166	0.164	-0.473	0.157	0.845
	Rain	**0.472**	**0.259**	**-0.015**	**0.961**	**0.966**
	WS	**0.090**	**0.065**	**-0.033**	**0.219**	**0.929**
Great black-backed gull						
	NAO	-0.083	0.263	-0.606	0.417	0.619
	AMO	**-5.132**	**1.710**	**-8.503**	**-1.549**	**1.00**
	SST	-0.190	0.249	-0.694	0.291	0.799
	SLM	-0.096	0.248	-0.594	0.374	0.646
	Wind	**0.127**	**0.066**	**0.000047**	**0.259**	**0.975**
Northern gannet						
	NAO	-0.019	0.019	-0.055	0.018	0.853
	AMO	0.054	0.114	-0.171	0.285	0.696
	SST	0.046	0.073	-0.109	0.186	0.746
	SLM	**-0.632**	**0.327**	**-1.257**	**0.036**	**0.969**

Population growth rates

Table 19. Summary of best supported models (JAGS) for the influence of climatic effects on population trends of seabirds breeding on the east coast of the UK. Note that the null model, including no climatic variables, was best supported in three species (Atlantic puffin, Common guillemot and Razorbill). Estimates, standard errors (SE) and limits of lower and upper 95% credible intervals (L95% and U95%) are shown, along with the proportion of the posterior density that is greater than, or less than, zero,(Proportion <0>), which is a measure of the strength of the effect. Note that the null model, including no climatic variables, was best supported in three species (Razorbill, European shag and Herring gull).Terms highlighted in bold indicate strong effects.

Species	Best Model	Estimates					
			Estimate	SE	L95CI	U95CI	Proportion <0>
Black-legged kittiwake	All year: NAO + SST + SLM** + WS**	NAO	-6.714	31.057	-71.094	64.243	0.605
		AMO	13.245	31.216	-45.749	71.815	0.670
		SST	18.927	16.755	-9.285	42.584	0.816
		SLM	**-51.135**	**30.161**	**-121.95**	**1.839**	**0.966**
		WS	**75.030**	**1.870**	**72.232**	**78.376**	**1.00**
European shag	All year: NAO + AMO + SST** + SLM**	NAO	-4.605	20.955	-37.933	40.578	0.586
		AMO	-5.989	32.098	-70.451	49.957	0.488
		SST	**35.094**	**14.216**	**5.873**	**57.828**	**0.991**
		SLM	**36.522**	**10.264**	**21.130**	**59.625**	**1.00**
Great black-backed gull	Breeding season: NAO + AMO + SST + SLM** + Temp** + Rain** + WS**	NAO	0.483	0.556	-0.535	1.595	0.805
		AMO	2.636	3.483	-4.575	7.890	0.778
		SST	-0.150	0.895	-2.019	1.620	0.609
		SLM	**-5.766**	**2.200**	**-9.896**	**-0.742**	**0.994**
		Temp	**-0.470**	**0.153**	**-0.693**	**-0.154**	**1.00**
		Rain	**32.971**	**20.632**	**3.672**	**74.816**	**0.998**
		WS	**2.177**	**0.280**	**1.665**	**2.627**	**1.00**
Herring gull	All year: NAO + AMO** + SST** + SLM** + WS**	NAO	-31.512	23.669	-70.312	23.387	0.891
		AMO	**-45.071**	**18.660**	**-90.516**	**-13.842**	**1.00**
		SST	**78.735**	**1.982**	**74.728**	**82.538**	**1.00**
		SLM	**27.233**	**12.840**	**4.922**	**44.524**	**0.998**
		WS	**11.601**	**0.460**	**10.813**	**12.504**	**1.00**
Northern gannet	Non-breeding: NAO + AMO + SST** + SLM* + Temp** + Rain	NAO	-7.323	29.837	-66.327	47.681	0.594
		AMO	1.734	29.791	-53.953	65.698	0.518
		SST	**-51.852**	**38.880**	**-115.396**	**0.704**	**0.971**

Species	Best Model	Estimates					
		SLM	44.437	25.370	-5.503	88.764	0.938
		Temp	**120.041**	**15.024**	**99.654**	**155.175**	**1.00**
		Rain	-20.405	27.657	-75.478	31.934	0.773

Appendix C. Survival modelling

Models

The structure of the model for adult survival was similar to that of the binomial model for productivity; in this case the binomial numerator is equal to the number of breeding adults in year t that were already breeding adults in year $t - 1$, and the denominator is equal to the number of breeding adults in year t. The transformed annual adult survival probability is assumed to be a linear function of environmental variables (relating to climate, but, depending on the biology of the species, not necessarily the same variables that are assumed to impact productivity), and to also depend on random effects for "site", "year" and the interaction of "site" and "year". We initially considered a logit transformation (as the survival probability must lie between zero and one), but the resulting model encountered irresolvable estimation problems due to incompatibility between the model and data, and we therefore used a log transformation instead. The use of a log transformation means the survival probabilities are assumed to be positive, but not necessarily below one – although it is logically impossible to have survival probabilities above one, using a model that allows this (e.g. a log rather than logit transformation) was possible whereas a model that prevents this was not. This is probably because of inconsistencies between the productivity data and count data, which can only be resolved by allowing the survival probability to be greater than one in some instances.

The number of breeding adults in year t that were already breeding adults in year $t - 1$ is not something that can usually be observed directly, but it will be equal to:

Breeding adults in year t - Number of new recruits in year t

The former quantity is observable; under a standard Leslie matrix model (with three age classes) the latter quantity can be assumed to follow a Binomial distribution where the denominator is the number of chicks born in year $t - a$, where a denotes the age at first breeding, and the probability of survival is equal to $(\text{juvenile survival})^a$.

We considered two possible models for juvenile survival:

Model A: juvenile survival is a single unknown value, constant across time and space, whose value $\tilde{\psi}$ is derived from the species-level estimate in Horswill & Robinson (2015), so that juvenile survival is independent of climate and other environmental factors;

Model B: juvenile survival varies over time and space (i.e. depends on climate, and other environmental factors) in the same way as adult survival, but has a potentially different mean value, so that:

$$\log(\text{juvenile survival}) = \log(\text{adult survival}) + \log(\tilde{\psi}) - \log(\tilde{\phi})$$

where $\tilde{\phi}$ denotes the mean adult survival rate from Horswill & Robinson (2015).

Neither model is likely to be entirely plausible, but they offer two scenarios for how variations in juvenile survival are linked to adult survival (completely in Model B, not at all in Model A); applying both models and comparing the results will often be the most useful strategy, as without direct data on juvenile survival (which are rarely available) it is impossible to empirically select between the different models.

A full count of the number of chicks born at the colony in year $t - a$ was estimated from a sample, rather than observed directly from a census. We assumed that the productivity rate for sampled and unsampled birds was identical, and that the actual number of fledged chicks from unsampled nests followed the same distribution as chicks from sampled nests (i.e. binomial).

Non-Bayesian inference

Model A can be fitted using an approximate form of non-Bayesian inference. Specifically, if the number of newly recruited breeding adults at each colony in each year were known then the number of surviving breeding adults from year $t - 1$ can be calculated, and the model can be fitted directly to abundance data as a Binomial GLMM. For each year t at each colony we therefore estimated the number of new recruits deterministically, using the nest productivity data and juvenile survival rate, via the following steps:

Step 1. Estimated number of chicks born in year $t - a$

= (Number of breeding pairs in year $t - a$)

* (Number of fledged chicks in sampled nests in year $t - a$)

/ (Number of sampled nests in year $t - a$)

Step 2. Estimated number of new recruits in year t

= Estimated number of chicks born in year $(t - a)$ * (Juvenile survival rate)^a

Bayesian inference

Within the context of the survival models there are two key advantages in using a Bayesian approach, even though the non-Bayesian approach is computationally much faster to use, and can be applied in a more automated way (requiring less manual intervention and checking) than the Bayesian approach:

1. The Bayesian approach is more flexible, and so can be used in situations where the non-Bayesian approach is infeasible. Specifically, the Bayesian approach can be used to fit models in which juvenile survival is either assumed to either be linked to adult survival (Model B) or independent of adult survival (Model A), whereas the non-Bayesian approach can only be used to fit the latter. Model B is biologically more plausible than Model A, so it is a substantial restriction of the non-Bayesian approach that it can only be applied to Model A.
2. The Bayesian approach also accounts more fully for uncertainty. This is a general advantage of Bayesian methods, but is particularly important here, because the non-Bayesian analysis requires the strong assumption that the number of new recruits can be calculated deterministically - the number of new recruits can be treated as a stochastic random variable within the Bayesian analysis, avoiding this assumption.

The Bayesian approach that we used here is similar to that used by Freeman *et al*. (2014) and Jitlal *et al*. (2017). The key difference is that they used the model to

estimate juvenile survival, in a situation where no environmental/climate effects were considered and where a good independent estimate of adult survival was available. We focused instead upon estimating adult survival, and the relationship between adult survival and climate/environment, and assumed juvenile survival was known. Note that it is impossible to estimate both juvenile <u>and</u> adult survival empirically simultaneously, using abundance data, because the model is unidentifiable – i.e. the same observed series of abundance values can be obtained through a range of different possible combinations for juvenile and adult survival rates.

Model selection

Model selection within the context of Model A was performed using the non-Bayesian approach, as in the analyses for productivity and growth rate. The best supported model for adult survival under Model A was re-fitted in the Bayesian framework - we fitted both possible models for juvenile survival (Model A and Model B), and compared these using deviance information criterion (DIC).

Results

Having identified the best supported set of climatic variables and seasonal definitions for adult survival for each species using glmer models, we then assessed how support in the data differed when juvenile survival was assumed to be constant over time and space (Model A, Methods), derived from species-level estimates (Horswill & Robinson, 2015), versus models in which juvenile survival was allowed to vary over time and space in the same way as estimates for adult survival, derived from the model fitting (Model B, Methods). By necessity, these models could only be fitted using the Bayesian framework. We found that in all species, support for a constant value for juvenile survival vastly outweighed support in the data for varying juvenile survival rates, in line with variation in adult survival (Table 20).

We detected some differences in the strength, and occasional differences in the direction of effects when juvenile survival was allowed to vary in comparison to models where it was kept constant (Table 21). Relationships between climate variables and adult survival tended to be less strong in models in which juvenile survival was allowed to vary (Table 21).

Table 20. Summary of the support in the data for alternative model formulations for survival in eight species of seabirds breeding on the east coast of the UK. The set of best-fitting climate variables and seasonal definitions were identified using glmer models (see methods), and then Bayesian models were fitted including these best supported climate variables with juvenile survival either assumed to be constant, or varying over space and time in relation to variation in adult survival rates estimated by the model. DIC = Deviance Information Criterion.

Species	Best supported model	DIC constant juvenile survival	DIC varying juvenile survival
Atlantic puffin	Not fitted due to lack of data	-	-
Black-legged kittiwake	Marine + wind (AY)	11016.37	12627.53
Common guillemot	Marine + wind (NB)	1268.02	1299.621
European shag	Null	-	-
Great black-backed gull	Marine + terrestrial (AY)	216.23	272
Herring gull	Marine + wind (AY)	192.05	224.155
Northern gannet	Null	-	-
Razorbill	Marine + wind (NB)	1253.79	1568.579

Table 21. Comparison of strength and direction of climatic influence on adult survival in models in which juvenile survival was assumed to be constant, versus models in which juvenile survival was allowed to vary over space and time in accordance with variation in adult survival.

Species	Model	NAO	AMO	SST	SLM	Temp	Rain	Wind
Atlantic puffin	Not fitted	-	-	-	-	-	-	-
Black-legged kittiwake	Constant juvenile survival	-ve	+ve	+ve	-ve	-	-	+ve
Black-legged kittiwake	Varying juvenile survival	ns	ns	+ve	-ve	-	-	ns
Common guillemot	Constant juvenile survival	-ve	+ve	+ve	-ve	-	-	+ve
Common guillemot	Varying juvenile survival	-ve	ns	ns	ns	-	-	-ve
European shag	Null	-	-	-	-	-	-	-
Great black-backed gull	Constant juvenile survival	-ve	+ve	ns	ns	-ve	ns	-
Great black-backed gull	Varying juvenile survival	-ve	+ve	ns	+ve	ns	-ve	-
Herring gull	Constant juvenile survival	-ve	+ve	-ve	ns	-	-	ns
Herring gull	Varying juvenile survival	-ve	+ve	ns	ns	-	-	ns
Northern gannet	Null	-	-	-	-	-	-	-
Razorbill	Constant juvenile survival	-ve	ns	ns	-ve	-	-	+ve
Razorbill	Varying juvenile survival	-ve	-ve	ns	-ve	-	-	+ve

Models with juvenile survival as a constant

Here, we focus our report on the main results from models of adult survival in which juvenile survival was assumed to be constant over space and time, and was based on species level estimates from Horswill and Robinson (2015).

Models of survival would generally model the logit of the survival probability as a linear function of covariates, but in our analyses of adult survival we use a log, rather than logit, transformation. This was because initial attempts to fit the models using a logit transformation suggested that such models could not be fit to the SMP data - attempting to do so resulted in major issues of non-convergence that we could not resolve. This issue is likely to arise because of an irresolvable inconsistency between the assumptions of the model and the empirical characteristics of the data - e.g. the data suggest that the survival probability is sometimes above one, which is logically impossible. There are a number of possible reasons that such an inconsistency may occur:

a) the SMP counts and/or productivity data contain a higher level of observation error than our models can account for;
b) the productivity data do not always represent a representative sample from the colony, and so the productivity rates estimated from these data may provide biased estimates of the year-specific productivity rates for the entire colony;
c) the model makes biologically unrealistic modelling assumptions – in particular, both models (Model A and Model B) necessarily make strong assumptions about the relationship between juvenile survival and climate, which may not be realistic. More specifically, they either assume that juvenile survival is unrelated to climate [Model A], or assuming that the relationship between juvenile survival and climate is the same as that between adult survival and climate [Model B].

Using a log transformation provides a technical way of avoiding this issue, but introduces a degree of biological implausibility in to the model, since it implies that it is possible for adult survival to be greater than one. The results obtained with these models should therefore be treated with some caution, particularly when extrapolating (e.g., extending estimates of adult survival into the future).

Black-legged kittiwake

The best-supported model for survival in this species included effects of marine variables and terrestrial wind over the whole year (Table 22). This model included strong negative correlations with the North Atlantic Oscillation (NAO; posterior mean: -1.336, 95%CI: -3.647, 0.034) and sea surface salinity (SLM: posterior mean: -0.282, 95%CI: -0.321, -0.238), as well as strong positive correlations with the Atlantic Multidecadal Oscillation (AMO; posterior mean: 1.271, 95%CI: -0.108, 3.591, >92% posterior density positive), sea surface temperature (SST; posterior mean: 0.142, 95%CI: 0.133, 0.152) and terrestrial wind speed (WS; posterior mean: 0.052, 95%CI: 0.044, 0.059) (Table 22). There was some support in the data for models containing alternative combinations of climate variables (only marine variables ΔAIC 2.4; marine plus terrestrial plus wind ΔAIC 2.7; and marine plus terrestrial ΔAIC 3.1; Table 22).

The model containing marine and terrestrial wind variables defined over the non-breeding period also received similar support to the best supported model (ΔAIC 1.19), with the null model containing no climate variables also receiving some support (ΔAIC 3.64) (Table 22).

Common guillemot

In this species, the best supported model included effects of marine climate variables and terrestrial wind defined over the non-breeding period (Table 22). This model included strong negative correlations with the North Atlantic Oscillation (NAO; posterior mean: -0.749, 95%CI: -1.227, -0.013) and sea surface salinity (SLM: posterior mean: -0.114, 95%CI: -0.157, -0.070), as well as strong positive correlations with the Atlantic Multidecadal Oscillation (AMO; posterior mean: 0.748, 95%CI: 0.018, 1.213), sea surface temperature (SST; posterior mean: 0.018, 95%CI: -0.003, 0.038) and terrestrial wind speed (WS; posterior mean: 0.023, 95%CI: 0.014, 0.032) (Table 22). Models containing alternative combinations of climate variables received little support in the data compared to the best supported model (ΔAIC: 3.8 for all other combinations, Table 22), as did the null model containing no climate effects (ΔAIC: 3.78). Similarly, when marine climate variables and wind were defined over the whole year, the model received little support in the data comparted to the model where climate influence was defined over the non-breeding period (ΔAIC 3.66; Table 22).

Great black-backed gull

Results for this species indicated poor model fit (Table 22), suggesting the information in the data was insufficient to estimate model parameters and effects robustly. We therefore do not report further on the model for this species.

Herring gull

The best supported model for this species included effects of marine climate variables and terrestrial wind speed defined over the entire year (Table 22). The model included strong negative relationships between adult survival and NAO (posterior mean: -6.195, 95%CI: -13.545, -0.818) and sea surface temperature (posterior mean -0.375, 95%CI: -0.787, -0.070), and a strong positive relationships with AMO (posterior mean: 6.705, 95%CI: 1.359, 13.782) (Table 22). A model containing the same climate variables, but defined over the non-breeding season only, received essentially identical support in the data (ΔAIC 0.007; Table 22). Models containing other combinations of climate variables received little support in the data (ΔAIC 3.1 for all combinations; Table 22), as did the null model with no climate effects (ΔAIC 3.16; Table 22).

Razorbill

Adult survival in this species was best explained by a model including marine climate variables and terrestrial wind defined over the non-breeding period (Table 22). This model included strong negative relationships with NAO (posterior mean: -0.440, 95%CI: -0.609, -0.271) and sea surface salinity (posterior mean: -0.443, 95%CI: -0.567, -0.319), and a strong positive association with terrestrial wind speed (posterior mean: 0.095, 95%CI: 0.078, 0.116) (Table 22). Other models received considerably

less support in the data, with the next best model including marine, terrestrial and wind climate variables (ΔAIC 3.5), and other models receiving even less support in the data (marine variables only ΔAIC 6.8; marine and terrestrial variables ΔAIC 7.0), as did the null model with no climatic effects (ΔAIC 6.96). A model containing the same climate variables as the best supported model, but defined over the entire year also received little support in the data (ΔAIC 6.01).

Table 22. Summary of best supported non-Bayesian GLMM models for climatic influence on adult survival of eight species of seabird breeding on the east coast of the UK. All models include NAO, AMO, SST (sea surface temperature), and SLM (salinity). Model selection using AIC was used to assess if adding terrestrial variables improved model fit (Temp and Rain). Finally, model selection was conducted using AIC to assess if adding WS (terrestrial wind speed) improved model fit. Models for each species were fitted to two seasonal definitions: NB: non-breeding period; and AY: all year. A null model was also fitted to all species and seasonal periods containing random effects for colony, year, and colony*year. Significance shown in bold and denoted by ** P<=0.05, * P<=0.10. ΔAIC refers to the different in AIC units between the final best supported model and alternative model formulations including: marine only (M), marine and terrestrial variables (M+T), marine and wind (M+W), and marine, terrestrial and wind (M+T+W).

Species	Best Model	Estimates					ΔAIC	R^2
Atlantic Puffin	Not fitted							
Black-legged kittiwake	Non-breeding: NAO + SST + SLM + WS*		**Estimate**	**SE**	**z**	**P**	AY: 0.48 Null: 4.12 M: 0.9 M+T+W: 3.0 M+T: 3.1	Fixed only: 0.104 Fixed + random: 0.451
		NAO	0.7579	2.3470	0.323	0.747		
		SST	1.0269	0.6869	1.495	0.135		
		SLM	0.4806	2.2091	0.218	0.828		
		WS	**0.4834**	**0.2833**	**1.706**	**0.088**		
Common guillemot	Non-breeding: NAO + SST + SLM** + WS**		**Estimate**	**SE**	**z**	**P**	AY: 0.67 Null: 0.79 M: 0.8 M+T: 0.8 M+T+W: 0.8	Fixed only: 0.157 Fixed + random: 0.157
		NAO	-1.0411	2.3350	-0.446	0.65571		
		SST	0.8919	0.9463	0.942	0.34593		
		SLM	**-4.8414**	**2.3737**	**-2.039**	**0.04140**		
		WS	**1.2936**	**0.4663**	**2.774**	**0.00553**		
European shag	Null model	**ΔAIC** AY: 2.96; Null: 3.68						
Great black-backed gull	All year: NAO + SST + SLM + Temp + Rain*		**Estimate**	**SE**	**Z**	**P**	NB: 0.36 Null: 0.85 M: 0.3 M+W: 0.9 M+T+W: 0.9	Fixed only: 0.225 Fixed + random: 0.225
		NAO	1.9580	1.8153	1.079	0.2807		
		SST	0.1149	1.0274	0.112	0.9109		
		SLM	0.3054	0.5443	0.561	0.5747		
		Temp	-0.6752	0.7709	-0.876	0.3811		
		Rain	**13.6327**	**7.2221**	**1.888**	**0.0591**		
Herring gull	All year: NAO + SST** + SLM** +WS**		**Estimate**	**SE**	**z**	**P**	NB: 1.19 Null: 3.16 M: 3.1 M+T: 3.1 M+T+W: 3.1	Fixed + random: 0.189 Fixed + random: 0.379
		NAO	-1.3664	2.5029	-0.546	0.585120		
		SST	**-1.9820**	**0.6387**	**-3.103**	**0.001915**		
		SLM	**3.6337**	**1.1154**	**3.258**	**0.001123**		
		WS	**-0.7983**	**0.3156**	**-2.529**	**0.011438**		

Northern gannet	Null model	**ΔAIC** AY: 6.06; NB: 6.41						
Razorbill	Non-breeding: NAO* + SST + SLM** + WS**		**Estimate**	**SE**	**z**	**P**	AY: 4.95 Null: 5.90 M+T+W: 2.3 M: 4.4 M+T: 5.7	Fixed + random: 0.218
		NAO	-4.3609	2.5005	-1.744	0.08116		
		SST	1.7016	1.0433	1.631	0.10289		
		SLM	-7.0367	2.4305	-2.895	0.00379		Fixed + random: 0.218
		WS	1.1580	0.4649	2.491	0.01275		

Table 23. Summary of best supported Bayesian models (fitted using JAGS) for the influence of climatic effects on adult survival of seabirds breeding on the east coast of the UK. Note that the null model, including no climatic variables, was best supported in two species (European shag and Northern gannet), and the model was unable to be fitted for Atlantic puffin due to insufficient data. Note that results for great black-backed gull indicated very poor model fit, so parameter estimates for this species should not be interpreted.

Species	Best Model	Estimates					
			Estimate	**SE**	**L95CI**	**U95CI**	**Proportion <0>**
Black-legged kittiwake	All year: NAO** + AMO* + SST** + SLM** + WS**	**NAO**	**-1.336**	**1.101**	**-3.647**	**0.0339**	**0.955**
		AMO	**1.271**	**1.104**	**-0.108**	**3.591**	**0.924**
		SST	**0.142**	**0.005**	**0.133**	**0.152**	**1.00**
		SLM	**-0.282**	**0.022**	**-0.321**	**-0.238**	**1.00**
		WS	**0.052**	**0.004**	**0.044**	**0.059**	**1.00**
Common guillemot	Non-breeding: NAO** + AMO** + SST** + SLM** + WS**	**NAO**	**-0.749**	**0.281**	**-1.227**	**-0.013**	**0.980**
		AMO	**0.748**	**0.279**	**0.018**	**1.213**	**0.988**
		SST	**0.018**	**0.010**	**-0.003**	**0.038**	**0.960**
		SLM	**-0.114**	**0.023**	**-0.157**	**-0.070**	**1.00**
		WS	**0.023**	**0.005**	**0.0136**	**0.032**	**1.00**
Great black-backed gull	All year: NAO** + AMO** + SST + SLM + Temp** + Rain	**NAO**	**-31.181**	**14.964**	**-53.079**	**-2.563**	**1.00**
		AMO	**33.318**	**14.932**	**4.665**	**55.109**	**1.00**
		SST	-0.137	0.646	-1.623	1.158	0.589
		SLM	0.459	0.414	-0.287	1.583	0.888
		Temp	**-0.765**	**0.309**	**-1.375**	**-0.243**	**0.998**
		Rain	-7.125	6.489	-20.873	4.277	0.880
Herring gull	All year: NAO** + AMO** + SST** + SLM +WS	**NAO**	**-6.195**	**3.379**	**-13.545**	**-0.818**	**0.989**
		AMO	**6.705**	**3.300**	**1.359**	**13.782**	**0.998**
		SST	**-0.375**	**0.186**	**-0.787**	**-0.070**	**0.995**
		SLM	-0.078	0.272	-0.641	0.406	0.569
		WS	-0.013	0.078	-0.141	0.132	0.623
Razorbill	Non-breeding: NAO** + AMO +	**NAO**	**-0.440**	**0.088**	**-0.609**	**-0.271**	**1.00**
		AMO	0.010	0.400	-0.775	0.799	0.525
		SST	0.027	0.040	-0.048	0.101	0.744

Species	Best Model	Estimates					
	SST + SLM** + WS**	SLM	-0.443	0.066	-0.567	-0.319	1.00
		WS	0.095	0.010	0.078	0.116	1.00

Discussion

We fitted two alternative broad model formulations to estimate relationships between adult survival and climate variables. In the first of these (Model A), juvenile survival was assumed to be constant over time and space, with the value of juvenile survival derived from species-level estimates (Horswill & Robinson, 2015). In the second formulation (Model B), we allowed juvenile survival to vary over time and space in the same way in which estimates for adult survival were estimated to vary over time and space. Overwhelmingly, support in the data for models with constant juvenile survival outweighed that for models with varying juvenile survival. This result was surprising, given that ecologically we would expect juvenile survival to vary over time and space, and the model parameterisation forcing juvenile survival to vary in a similar pattern to that estimated for adult survival also follows from current ecological understanding of a degree of correlation in variation in survival rates across different age classes. We therefore focused our more detailed assessments of the influence of climatic factors on adult survival to those models in which juvenile survival remained constant over time and space.

We were unable to fit survival models for Atlantic puffins due to insufficient data on both abundance and productivity. Similarly, for two additional species, European shags and northern gannet, the best supported survival model contained no climatic effects, suggesting available data for these species was insufficient to detect the influence of climate on adult survival. Finally, one more species, great black-backed gull, demonstrated support in the data for a model including marine and terrestrial climate variables, but model fit was exceedingly poor and model estimates were implausible, again suggesting that in this species there was insufficient data to properly detect and estimate relationships of climate with adult survival.

Black-legged kittiwake and common guillemot showed very similar responses of adult survival to climate. In both species, adult survival was related to marine and terrestrial wind variables, although they differed in the seasonal definition used to aggregate climate impacts – with black-legged kittiwakes responding most to climate defined over the whole year, and common guillemot responding most to climate defined over the non-breeding period only. Adult survival in both species was lower when NAO and sea surface salinity were higher, and was greater when AMO, sea surface temperature and wind speed were higher. Projected future climate predicted higher future adult survival rates for both black-legged kittiwake and common guillemot, although there will little evidence that either species could substantially alter its adult survival rate through extending foraging range around breeding colonies, either now or under future climate scenarios.

Razorbill showed similar responses of adult survival to climate as was detected for black-legged kittiwakes and common guillemots, with adult survival being most strongly correlated with marine climate variables and terrestrial wind, as defined over the non-breeding period. This species also showed lower adult survival rates when NAO and sea surface salinity were higher, and higher adult survival rates when terrestrial wind speed was greater. Projected future climate also resulted in higher predicted adult survival rates for this species, again with no opportunity for this species to augment adult survival rates by extending foraging range around breeding colonies, either under current or future climate conditions.

Finally, adult survival in herring gull was also most strongly related to marine climate variables and terrestrial wind, as defined over the entire year. This species also showed lower adult survival when NAO was greater, and lower adult survival with higher sea surface temperatures. However, in contrast to the other species, herring gull showed higher adult survival when AMO was greater. Adult survival in herring gull was predicted to decline under future climate conditions, although there was considerable uncertainty around these estimates. As with other species, there was little to no predicted opportunity for this species to increase adult survival by extending foraging range around breeding colonies.

The fitted models, when applied to future climate conditions, often predicted adult survival rates of greater than one, which is clearly biologically unfeasible. Typically statistical models of probabilities using logit functions to ensure estimated rates lie between zero and one, however when applied to the SMP count and productivity data, these models did not converge, likely due to irreconcilable inconsistencies between the assumptions of the model and the empirical characteristics of the count and productivity data. For instance, there are various combinations of counts of breeding pairs and fledged young in some years which imply the adult survival rate is sometimes greater than one. In all survival models, we therefore had to use a log transformation to achieve model convergence. This parameterisation avoids non-convergence issues by relaxing the constraint that adult survival estimates must always lie between zero and one, allowing inconsistencies between data and modelled processes to be avoided. It does, of course, however introduce a degree of biological implausibility into the model. As such, the results obtained from these models, particularly the extrapolation of survival rates under future climate, should be treated with caution.

The underlying mechanism explaining the positive effect of wind on survival is not clear, and therefore warrants further investigation. Many climate models predict future changes in wind speeds. A key question revolves around the importance of effects across the range of speeds experienced by the birds which we considered here, and the frequency and severity of extreme events, which are predicted to increase in future in many regions (Rahmstorf and Coumou, 2011; IPCC 2018), because the effect of wind speed may be non-linear such that there is a positive effect overall but a negative effect of high winds (Frederiksen et al. 2008). Our results also show that temperature is having a strong positive effect on survival of black-legged kittiwakes and common guillemots. This relationship is in stark contrast to Frederiksen et al. (2004) who demonstrated a negative effect of temperature on survival in kittiwakes. Given the widespread evidence that warming is having a negative impact on prey of seabirds, this appears counterintuitive, but one possibility is that these potential impacts are more than compensated for by the reduced energetic costs of key activities such as foraging and resting that seabirds, as endotherms, experience at higher temperatures (Amelineau et al. 2018). The predicted large declines in productivity under future climate projections may also in part explain why these models predicted counter-intuitive increases in survival in relation to climate variables such as temperature.

We used count and productivity data to estimate survival because it was the only approach that would allow us to study multiple populations and species. Mark-recapture data are only available for a few studies, and therefore do not allow for a

UK-wide multi-species assessment of relationships between adult survival and environmental variables. However, survival estimates derived from mark-recapture data are a significantly more powerful and reliable approach for estimating drivers of change in survival. For example, using that approach, Frederiksen et al (2008) demonstrated the effect of wind on survival of European shags, whereas we could not detect any climatic effects in this species. Of more concern are cases where we found opposing results than published survival studies using mark recapture, such as the effects of warming on survival of black-legged kittiwakes. This, together with predictions of survival in our models that exceeded one, leads us to conclude that estimating survival from counts and productivity is not reliable where there are significant gaps as is the case with the SMP.

A further challenge is that for several species in this study – notably black-legged kittiwake and northern gannet – a considerable proportion of the adult population spends the winter outside UK waters. As such, the environmental variables used here may not be particularly relevant to survival prospects, since most adult mortality occurs at this time. Thus, incorporating environmental drivers at wintering grounds would potentially have provided important insights (Reiertsen et al. 2014).

Appendix D: technical specification of the demographic model

Notation

Item	Description (for year t and colony c)
Observed or known quantities	
m	Maximum brood size
a	Age at first breeding
n_{ct}	Count of number of breeding adults
b_{ct}	Number of breeding pairs for which productivity data are available
y_{ct}	Number of chicks born, from pairs for which productivity data are available
$\widetilde{\phi}$	Mean estimated adult survival from Horswill & Robinson (2015)
$\widetilde{\psi}$	Mean estimated juvenile survival from Horswill & Robinson (2015)
x_{ct}	Environmental variables (vector)
Unknown quantities and parameters	
Y_{ct}	Actual number of chicks born
R_{ct}	Number of newly recruited breeding adults
λ_{ct}	Productivity rate
ϕ_{ct}	Adult survival rate
ψ_{ct}	Juvenile survival rate

Model structure

Note: "linear predictor" refers to the sum of random effects and fixed effects (explanatory variables) multiplied by their parameters – i.e. the linear mixed model part

Model	Structure
Productivity	$y_{ct} \sim \text{Binomial}(b_{ct}m, \lambda_{ct})$ $\log\left(\dfrac{\lambda_{ct}}{1 - \lambda_{ct}}\right) = \text{linear predictor}$
Growth rate	$n_{ct} \sim \text{Poisson}\big((n_{c,t-1} + 1)\lambda_{ct}\big)$ $\log\left(\dfrac{\lambda_{ct}}{1 - \lambda_{ct}}\right) = \text{linear predictor}$

Model	Structure
Survival Models	$n_{ct} \sim \text{Binomial}(n_{c,t-1} - R_{ct}, \phi_{ct})$ $R_{ct} \sim \text{Binomial}(Y_{c,t-a}, \psi_{ct}^a)$ $(Y_{ct} - y_{ct}) \sim \text{Binomial}((n_{ct}/2) - b_{ct}, \lambda_{ct})$ *Adult survival submodel* $\log\left(\frac{\phi_{ct}}{1-\phi_{ct}}\right) = \text{linear predictor}$ *Juvenile survival submodel* **[Model A]** $\psi_{ct} = \tilde{\psi}$ or **[Model B]** $\log\left(\frac{\psi_{ct}}{1-\psi_{ct}}\right) = \log\left(\frac{\phi_{ct}}{1-\phi_{ct}}\right) + \log\left(\frac{\tilde{\psi}}{1-\tilde{\psi}}\right) - \log\left(\frac{\tilde{\phi}}{1-\tilde{\phi}}\right)$

Appendix E: JAGS model code

Productivity model

```
model{

  for(j in 1:nobs.prod){
    BS.Fledged[j] ~ dbin(p.prod[j], mbs * BS.Pairs[j])
    log(p.prod[j]) <- fixed.prod[j] + re.prod.year[iyear[j]] +
re.prod.site[isite[j]] + re.prod.ilre[j]
    fixed.prod[j] <- alpha.prod + sum(beta.prod[1:nxp] * x.prod[j,1:nxp])
    re.prod.ilre[j] ~ dnorm(0, tau.prod.ilre)
  }

  for(s in 1:nsites){
    re.prod.site[s] ~ dnorm(0, tau.prod.site)
  }

  for(t in 1:nyears){
    re.prod.year[t] ~ dnorm(0, tau.prod.year)
  }

  alpha.prod ~ dnorm(0, hyper.prod.alpha)

  for(k in 1:nxp){
    beta.prod[k] ~ dnorm(0, hyper.prod.beta)
  }

  tau.prod.site ~ dgamma(hyper.prod.site[1], hyper.prod.site[2])
  tau.prod.year ~ dgamma(hyper.prod.year[1], hyper.prod.year[2])
  tau.prod.ilre ~ dgamma(hyper.prod.ilre[1], hyper.prod.ilre[2])
}
```

Survival model

```
model{

  for(j in 1:nobs.asurv){

    Pairs[j] ~ dpois(Pairs.true[j])
    Pairs.true[j] <- Pairs.surv[j] + nrecuits.pairs[j]
    Pairs.surv[j] ~ dpois(p.asurv[j] * Pairs.prev[j])
    nrecuits.pairs[j] <- step(round(nrecruits[j] / 2))
    nrecruits[j] ~ dbin(p.recruit[j], Fledged.mafb[j])
    Fledged.mafb[j] <- BS.Fledged.mafb[j] + US.Fledged.mafb[j]
    BS.Fledged.mafb[j] ~ dbin(mup.prod[j], mbs * BS.Pairs.mafb[j])
    US.Fledged.mafb[j] ~ dbin(mup.prod[j], mbs * (Pairs.mafb[j] -
BS.Pairs.mafb[j]))
    p.recruit[j] <- pow(p.jsurv[j], afb)
    mup.prod[j] ~ dbeta(hyper.mup.prod[1], hyper.mup.prod[2])
    log(p.jsurv[j]) <- log(pe.jsurv) + link.jsurv * (log(p.asurv[j]) -
log(pe.asurv))
    log(p.asurv[j]) <- fixed.asurv[j] + re.asurv.year[iyear[j]] +
re.asurv.site[isite[j]]
    fixed.asurv[j] <- alpha.asurv + sum(beta.asurv[1:nxa] *
x.asurv[j,1:nxa])
  }
  for(s in 1:nsites){
    re.asurv.site[s] ~ dnorm(0, tau.asurv.site)
  }
  for(t in 1:nyears){
    re.asurv.year[t] ~ dnorm(0, tau.asurv.year)
  }
  alpha.asurv ~ dnorm(0, hyper.asurv.alpha)
  for(k in 1:nxa){
    beta.asurv[k] ~ dnorm(0, hyper.asurv.beta)
  }
  tau.asurv.site ~ dgamma(hyper.asurv.site[1], hyper.asurv.site[2])
  tau.asurv.year ~ dgamma(hyper.asurv.year[1], hyper.asurv.year[2])
}
```

Trend model

```
model{

  for(j in 1:nobs.trend){
    Pairs[j] ~ dpois(mu[j])
    mu[j] <- log(Pairs.prev[j] + 1) + ratmu[j]
    ratmu[j] <- fixed.trend[j] + re.trend.year[iyear[j]] +
re.trend.site[isite[j]] + re.trend.ilre[j]
    fixed.trend[j] <- alpha.trend + sum(beta.trend[1:nxt] *
x.trend[j,1:nxt])
      re.trend.ilre[j] ~ dnorm(0, tau.trend.ilre)
  }

  for(s in 1:nsites){
      re.trend.site[s] ~ dnorm(0, tau.trend.site)
  }

  for(t in 1:nyears){
      re.trend.year[t] ~ dnorm(0, tau.trend.year)
  }
  alpha.trend ~ dnorm(0, hyper.trend.alpha)

  for(k in 1:nxt){
      beta.trend[k] ~ dnorm(0, hyper.trend.beta)
  }

  tau.trend.site ~ dgamma(hyper.trend.site[1], hyper.trend.site[2])
  tau.trend.year ~ dgamma(hyper.trend.year[1], hyper.trend.year[2])
  tau.trend.ilre ~ dgamma(hyper.trend.ilre[1], hyper.trend.ilre[2])
}
```