



Potential climate-driven changes to seabird demography: implications for assessments of marine renewable energy development

Kate R. Searle^{1,*}, Adam Butler², James J. Waggitt³, Peter G. H. Evans^{3,4}, Lucy R. Quinn⁵, Maria I. Bogdanova¹, Tom J. Evans⁶, Janelle E. Braithwaite⁷, Francis Daunt¹

¹UK Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK

²Bioinformatics and Statistics Scotland, James Clerk Maxwell Building, Peter Guthrie Tait Road, The King's Buildings, Edinburgh EH9 3FD, UK

³School of Ocean Sciences, Bangor University, Menai Bridge, Isle of Anglesey LL57 2DG, UK

⁴Sea Watch Foundation, Ewyn y Don, Bull Bay, Amlwch, Isle of Anglesey LL68 9SD, UK

⁵NatureScot, Great Glen House, Leachkin Road, Inverness IV3 8NW, UK

⁶Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK

⁷Marine Scotland, Victoria Quay, Edinburgh EH6 6QQ, UK

ABSTRACT: Europe has set ambitious green energy targets, to which offshore renewable developments (ORDs) will make a significant contribution. Governments are legally required to deliver ORDs sustainably; however, they may have detrimental impacts on wildlife, especially those already experiencing declines due to climate change. Population viability analysis (PVA) is the standard method for forecasting population change in ORD assessments, but PVAs do not currently account for climate effects. We quantified climate effects on seabird breeding success for 8 UK species breeding in the North Sea. We assessed the potential for seabirds to mitigate climate-driven changes in breeding success by accessing wider resources through increased foraging ranges around colonies. We demonstrate strong links between breeding success and climate in 5 species. In 4 of these species, future climate projections indicated large declines in breeding success relative to current rates. Only one species was predicted to increase breeding success under future climate. In all 5 species, there was limited opportunity for species to increase breeding success by expanding foraging ranges to access more suitable future climatic conditions. Climate change will have significant ramifications for future breeding success of seabirds breeding in the North Sea, an area undergoing extensive and rapid offshore renewable energy development. We recommend 3 methods for including climate-driven changes to seabird breeding success within ORD assessments: development of predictive climate-driven habitat use models to estimate ORD-wildlife interactions; delivery of a new ORD assessment framework that includes dynamic predictions of climate-driven habitat use and demography of wildlife populations; and consideration of climate-driven changes in the implementation of compensatory measures.

KEY WORDS: Breeding success · Climate change · Demography · North Sea · Offshore renewable energy · Population viability analysis · Seabirds

1. INTRODUCTION

Governments across Europe have set ambitious targets for electricity generation from renewable sources, with offshore renewable developments (ORDs) set to

make a significant contribution (Schillings et al. 2012, European Commission 2020). Governments are legally required to deliver ORDs in a sustainable manner, conserving protected wildlife populations and, should developments go ahead where protected

*Corresponding author: katrle@ceh.ac.uk

wildlife populations are deemed to be adversely affected, securing appropriate compensatory measures. ORDs may have detrimental impacts on protected seabirds, notably through collisions with turbine blades, disturbance and barrier effects and displacement from important habitats (Drewitt & Langston 2006, Masden et al. 2010, Scottish Government 2011). Many of these affected species are already experiencing marked declines due to climate change and other anthropogenic factors (Carroll et al. 2015, MacDonald et al. 2015, Dias et al. 2019, Mitchell et al. 2020, Pearce-Higgins 2021). Consequently, the delivery of offshore renewable targets risks being constrained by uncertainties over the extent to which ORDs will compound the effects that protected populations are already experiencing from environmental change.

There is considerable uncertainty about the population-level consequences of ORDs on seabirds due to a lack of information on demography, distribution and behaviour, along with knowledge gaps on the impacts of ORDs. This uncertainty is hampering marine spatial planning, as it seeks to balance objectives for the economy, society and the environment for sustainable use of marine resources. The marine environment is experiencing rapid changes in climate, and many top predator species, including seabirds, have shown marked declines associated with bottom-up effects of warming on the abundance and quality of their prey (Frederiksen et al. 2006, Howells et al. 2017, Sydeman et al. 2021). Climate change can affect top predators indirectly (via changes in food supply) or directly (such as through mortality from extreme weather events) and has been identified as a primary pressure on the conservation status of UK seabirds (Daunt et al. 2017, Mitchell et al. 2018, 2020, Dias et al. 2019). The effects of ORDs on seabirds are likely to be intrinsically linked to variation in distribution and abundance associated with changes in climate. Yet current ORD assessment frameworks that forecast population projections over the lifespan of the wind-farms do not account for effects of environmental change. This key shortcoming in assessments presents challenges for decisions that need to be made now on how and where ORDs should be located. Lease agreements for ORDs in the UK can be up to 60 yr (Round 4; The Crown Estate 2019), spanning a timeframe that seabirds will likely experience significant effects from climate change. Accordingly, regulatory frameworks should take into account the consequences of ORDs on marine biodiversity within the context of a changing climate.

For seabirds, population viability analyses (PVAs) that forecast future population change under different scenarios currently assume that climate-induced effects on species are implicit within vital rates used in model parameterisations, but there is no explicit accommodation for potential future climatic influence on such rates. Previous work has demonstrated that climate projections for the period 2070–2099 will lead to potential declines in black-legged kittiwake *Rissa tridactyla* breeding success of around 21–43% (Carroll et al. 2015), suggesting a clear potential for rapid change in a key demographic rate for this protected species in UK waters. 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 to improving estimates of the effects of ORDs on future population change in protected seabird populations (Daunt et al. 2017, Mitchell et al. 2020).

We examined the potential impacts of climate change on 8 seabird species by quantifying relationships between climate and seabird breeding success for seabirds breeding at 119 species-by-colony combinations in the North Sea. We chose this region because it is home to a range of protected seabird species, many of which are showing strong responses to climate change (Burthe et al. 2014, Carroll et al. 2015, Pearce-Higgins 2021), and because this region of the North Sea is set to experience rapid and extensive development of offshore wind in the coming decades (Schillings et al. 2012, European Commission 2020). We estimated relationships using climate variables with known links to seabird breeding success to develop future estimates for breeding success using a scenario (SRES A1B) of future emissions (2070–2099) from the UKCP09 climate projections (<https://data.gov.uk/dataset/fd2b1c2d-3156-4eed-98c1-12155878cdc2/ukcp09-land-and-marine-past-climate-and-future-scenario-projections-data-for-the-uk>). We chose this future time period because it represents the end period of likely lease agreements (up to 60 yr) for ORDs currently being scoped for construction in the North Sea (Offshore Wind Leasing Round 4 and ScotWind). We were unable to use the more recent UKCP18 climate projections because not all of the required marine variables were available at the time of analysis. Under this scenario, we used statistical models to produce projections of future breeding success at seabird breeding colonies along the eastern seaboard of the UK. We also considered the benefits of seabird behavioural plasticity by estimating potential seabird breeding success achieved by simulating

access to more suitable climate through extended foraging ranges at focal seabird breeding colonies under climate projections. We compared these future projections against the current 'baseline' values (2014–2018) for breeding success to estimate the likely impacts of climate change. Finally, we provide a set of recommendations for adapting offshore wind assessments to include the dynamic effects of changing climate on wildlife vital rates, such as the development of predictive climate-driven habitat-use models to estimate interactions between wildlife and ORDs; creation of a new ORD assessment framework that includes dynamic predictions of climate-driven habitat-use and demography of wildlife populations; and consideration of climate-driven changes in the implementation of compensatory measures.

2. MATERIALS AND METHODS

We developed statistical models to link breeding success with key climate-related variables for 8 species of seabirds breeding at 119 species-by-colony combinations on the east coast of the UK: northern gannet *Morus bassanus*, black-legged kittiwake, common guillemot *Uria aalge*, razorbill *Alca torda*, Atlantic puffin *Fratercula arctica*, herring gull *Larus argentatus*, great black-backed gull *L. marinus* and European shag *Phalacrocorax aristotelis*. The climate variables we selected provide proxies for prey distribution, abundance and availability via bottom-up processes propagating up through lower trophic levels (Frederiksen et al. 2006, Shultz et al. 2009, van Deurs et al. 2009, Régnier et al. 2019). We conducted the statistical analyses of breeding success using colony-specific and year-specific values.

2.1. Data on demography and abundance

Annual colony-level seabird breeding success data were derived primarily from the UK Seabird Monitoring Programme (SMP) and augmented by breeding success data for black-legged kittiwakes, common guillemots, razorbills and European shags for the Isle of May National Nature Reserve (Newell et al. 2016; updated). We considered colonies within the region from Kent to Caithness, together with Orkney and Shetland. We restricted our analysis to the eastern seaboard of the UK to ensure that statistical modelling covered the range of climates that might be expected to occur within the region under future climate change (a 'climate envelope' modelling ap-

proach). Basing the modelling upon a wider spatial area, such as the whole of the UK, would likely include populations that are influenced by biological mechanisms different from those operating in the North Sea (Frederiksen et al. 2007, Lauria et al. 2012). Successful modelling is only possible with sufficient temporal coverage. Therefore, we imposed a minimum data requirement that colonies must have at least 9 yr of breeding success data since 1986 (i.e. >25% coverage). This resulted in a range of breeding colonies to use in the demographic modelling for each species, from 4 colonies for Atlantic puffin, up to 40 colonies for black-legged kittiwakes (see Text S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m690p185_supp.pdf).

2.2. Data on climate and other environmental characteristics

Previous studies have identified relationships between seabird breeding success and climate variables including terrestrial temperature and precipitation (Smith & Gaston 2012, Watanuki & Ito 2012, Christensen-Dalsgaard et al. 2018, Michielsen et al. 2019) as well as marine climate variables including spring North Atlantic Oscillation (NAO), winter NAO, sea surface temperature (SST) and sea surface salinity (SLM) (Jones et al. 2007, Watanuki & Ito 2012, Monticelli et al. 2014, Carroll et al. 2015). Terrestrial winter temperature and rainfall have been linked to survival in seabirds, thought to be driven by physiological stress arising from more extreme weather conditions, such as cooler and wetter phases increasing exposure risk (Smith & Gaston 2012) as well as high terrestrial temperatures during breeding causing heat stress (Smith & Gaston 2012, Michielsen et al. 2019). Breeding success has also been linked with impacts from terrestrial temperature and rainfall via an expected relationship between air temperature and precipitation, with chick survival decreasing due to exposure and cooling of chicks (Christensen-Dalsgaard et al. 2018, Michielsen et al. 2019). Previous research has demonstrated a relationship between the chilling effect of terrestrial temperature on chick growth rate in black-legged kittiwakes (Christensen-Dalsgaard et al. 2018). Terrestrial air temperature has also been hypothesized to affect incubation via increased energetic demands of incubating parents in low temperatures potentially causing reduced parental attentiveness and periodic cooling of the clutch below the developmental optimum (Michielsen et al. 2019). Accordingly, we

selected the following terrestrial variables taken from empirical measurements from the nearest UK Met Office weather station: mean of daily minimum air temperature and summed daily precipitation (Table 1). We downloaded UK Met Office data from the Centre for Environmental Data Analysis (CEDA) (Met Office 2019), selecting the nearest weather station with relevant data for each breeding colony (Fig. S1). We also selected 3 marine climate variables previously demonstrated to correlate with seabird demography: winter NAO (monthly values averaged over December, January and February), SST and SLM (Table 1). NAO values represent differences in the air pressure between Iceland and the Azores, which is a good predictor of general weather patterns in the northern Atlantic (Hurrell et al. 2001). Negative NAO indices are associated with cold, dry and calm weather; positive NAO indices represent mild, wet and windy weather. Winter NAO indices are commonly used, as this seasonal period is when the indices best explain annual weather conditions. Moreover, winter weather conditions may strongly affect populations of seabirds by impacting survival rates of individuals (e.g. Sandvik et al. 2005) or the abundance of sandeel, an important prey species for breeding seabirds in this region (e.g. Arnott & Ruxton 2002). Models were parameterised using simulated estimates (hindcast variables) from 1985–2018, with oceanography (SST [°C], SLM [ppt]) sourced from FOAM AMM7 models (O’Dea et al. 2012, available from the Marine Environmental Monitoring Service [MEMS] <https://marine.copernicus.eu/>) and climatic indices (NAO) sourced from HadCM3 models provided by the UK Met Office (Tinker et al. 2016).

The marine environmental data for SST and SLM relate to a spatial grid. Marine variables were resam-

pled from their original 7 km resolution to 2.5 km resolution using bilinear interpolation in the R package ‘raster’ (Hijmans & van Etten 2012) and covered all locations of marine habitat within the foraging range of each colony. The gridded data were translated into a weighted mean of the environmental variable for each breeding colony, following Carroll et al. (2015). We needed to calculate values for pre-breeding seasons as well as the breeding season rather than taking the approach of Carroll et al. (2015) of basing the weights upon estimated utilisation distributions derived from GPS tracking data that only relate to the chick-rearing period. Accordingly, we based the weights upon a simpler distance-decay rule that allocated more weight to locations close to the breeding colony:

$$w \propto \exp(-\lambda d) \quad (1)$$

where d represents the distance by sea from the grid cell midpoint to the breeding colony, and λ represents the decay rate. The value of λ for each species was defined as 95% of all weights that would, in an area of sea without land, be allocated to locations within the published mean-max foraging range (mean of maximum foraging ranges observed across colonies for a species; see Thaxter et al. 2012). We then set the weights equal to zero for locations beyond the mean-max foraging range and then rescaled so that the weights summed to 1 by dividing each weight by the sum of the weights across all grid cells. This rescaling step was included because the weights were used solely to provide information on the relative importance of each grid cell within the foraging range calculations, so the absolute values of the weights did not matter.

Table 1. Terrestrial and marine climate variables used in modelling spatial distribution of seabirds on the east coast of the UK

Climate variable	Details	Spatial scale	Temporal scale
Mean of daily minimum air temperature	Terrestrial weather station data in Celsius	Nearest Met Office weather station	Daily values averaged up to seasonal level
Summed daily precipitation	Terrestrial weather station in mm	Nearest Met Office weather station	Daily values averaged up to seasonal level
SST	Sea surface temperature in Celsius	Resampled to 2.5 × 2.5 km grid from ~7 km resolution using bilinear interpolation	Monthly values averaged up to seasonal level
SLM	Sea surface salinity in parts per thousand	Resampled to 2.5 × 2.5 km grid from ~7 km resolution using bilinear interpolation	Monthly values averaged up to seasonal level
NAO	North Atlantic Oscillation	Not applicable	Annual values based on normalized winter average (Dec, Jan, Feb)

2.3. Statistical models for effects of climate on breeding success

The basic structure of our statistical modelling was to assume that breeding success is related to a range of annual, colony-specific climate variables. We constructed separate models for each species. Breeding success relates to the number of chicks fledged relative to the number of nests. Random variation in breeding success (demographic stochasticity) can be modelled using a binomial distribution, which imposes an absolute upper limit. The denominator for the binomial model is the number of nests multiplied by maximum brood size, which is necessary to accommodate those species in which clutch size exceeds 1; the binomial model, therefore, models the ratio of expected breeding success to maximum brood size, which must lie between 0 and 1.

The binomial generalised linear mixed model (GLMM) that was implemented assumed that the logit of expected breeding success (as a ratio of maximum brood size: Atlantic puffin, common guillemot, northern gannet, razorbill: 1; black-legged kittiwake: 2; great black-backed gull, herring gull: 3; European shag: 4) was a linear function of a range of climate variables, with random effects for 'site', 'year' and the interaction of 'site' and 'year', to account for the spatial and temporal variation in breeding success unrelated to the climate variables.

2.4. Inference: parameter estimation and uncertainty

We fitted the models as GLMMs via maximum likelihood, using the 'glmer' function within the 'lme4' package (version 1.1-26; Bates et al. 2015) in R version 4.0.1. The model for breeding success was fitted to the nest monitoring data, allowing us to estimate the breeding success for each colony in each year. To estimate productivity rates from the model, it was necessary to multiply model estimates by maximum brood size. All climate variables were checked for cross-correlation, and for all species, variables were correlated (Pearson's correlation coefficient < 0.7).

2.5. Model selection

For each species, model selection was performed by applying full subset variable selection using Akaike's information criterion (AIC) to identify the model best supported by the data containing alternative combi-

nations of winter NAO, SST, SLM, terrestrial summed precipitation and terrestrial mean minimum temperature. We also assessed support in the data for alternative seasonal periods over which climate variables were derived: pre-breeding period, breeding season or combined pre-breeding and breeding season periods (see Texts S2 & S3 and Tables S2 & S3 in the Supplement). Because we were interested in assessing support in the data for the most influential seasonal period, we did not mix variables across seasonal periods within models. Rather, we identified the best-supported model using variables from a single seasonal period by performing full subset variable selection within each seasonal period and selecting the best overall model from the 3 seasonal periods with the lowest AIC. This resulted in a final best-supported model for breeding success 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.

2.6. Goodness of fit assessment

We assessed goodness of fit using the marginal and conditional R^2 value for GLMMs representing the proportion of variation in breeding success explained by the fixed effects (marginal) and by both fixed and random effects (conditional) (Nakagawa & Schielzeth 2013), calculated using the 'rsquaredGLMM' function in the 'MuMin' package (version 1.43.17; Barton 2017).

2.7. Predicting demography under future climate change

All predictions for future climate were made using forecasted variables from UKCP09 projections for the SRES Scenario A1B (medium). The UK Climate Projections (UKCP) provide forecasts and hindcasts of environmental conditions between 1950 and 2100 from the HadRM3 (Hadley Regional Climate Model) PPE (perturbed physics ensemble) simulation model, which is an 11 member-ensemble model (Lowe et al. 2009). The simulations in the UKCP09 project were the most up-to-date versions available at the time of analysis. The SRES Scenario A1B represents estimates under medium omission conditions characterised by rapid economic growth, increases in efficient technologies, declining population growth and reliance on diverse energy sources (Nakicenovic & Swart 2020). Spatiotemporal forecast variables rep-

represent an average over a 30 yr future period (2070–2099) and are therefore represented by a single average value. On average, the climate variables relating to temperature increased (SST, daily terrestrial temperature), whilst those relating to precipitation (daily terrestrial precipitation) and NAO decreased, with SLM remaining relatively constant with a slight decrease (Table S4). Projected values for each colony and year, expressed as a proportion of maximum brood size, were generated using the 'predict.merMod' function from the 'lme4' package, and uncertainty in these projected values was calculated via bootstrapping using the 'bootMer' function from 'lme4' package. The results were converted into projections of absolute productivity by multiplying by the maximum brood size for the species. Projected values and bootstrap samples were then averaged across colonies and (for the baseline reference period 2014–2018) across years to produce overall measures of change over time between the baseline period (2014–2018) and the future period (2070–2099), together with estimates of associated uncertainties.

2.8. Potential for adaptation to climate change

To assess the potential for species to reduce the magnitude of negative climate change impacts via adaptation, we also generated predictions of breeding success for the future period (2070–2099) under SRES Scenario A1B in which the foraging range was allowed to vary such that different values of the spatial decay parameter, λ , and hence different spatial weights, were used in calculating the local SST and SLM of each colony. We considered foraging ranges that varied from 40–400 km in steps of 40 km. We used this range of potential foraging ranges to modify the spatial area defining the set of values of the relevant marine environmental variables for each colony. These colony-specific values of the marine environmental variables were calculated to be weighted averages of the gridded values of these variables within each of the foraging range values, where the weights depended upon distance from colony. The rate of decay of the weights with distance was fixed such that 95% of the predicted distribution of birds lay within the foraging range. Altering the foraging range therefore adjusts the rate of decay with distance, which changes the weights and thereby the colony-specific values of the marine environmental variables used to predict future breeding success. We then used the estimated relationships between breeding success and the environ-

mental variables to predict the possible impact of changes in foraging range upon breeding success

Because increases in foraging range would impose penalties on individuals (e.g. by increasing the energy required for flight), it is not clear that this adaptation would always be realised. We did not introduce additional complexity to our test by attempting to model this increased energy requirement; instead, we provide a simplified assessment of potential benefits by looking at whether individuals could improve predicted breeding success by varying foraging range to access a wider range of climatic conditions.

3. RESULTS

Observed breeding success showed considerable variation across colonies and years in all species (Fig. S2).

We only considered predictions for future changes to breeding success for species in which the best-supported model explained more than 10% of the variation observed in the data and in which the best-supported model received support in the data more than 2 Δ AIC units different from the null model containing no effects of climate. Accordingly, we did not make projections for European shag, herring gull or razorbill (Table 2).

3.1. Atlantic puffin

The best-supported model for the Atlantic puffin included 2 marine climatic variables from the pre-breeding period, indicating a strong negative effect of SST on breeding success (mean effect: -0.680 , $p < 0.001$; Table 2) and a close to significant positive effect of SLM (mean effect: 0.679 , $p = 0.067$; Table 2).

Fourteen other models received some support in the data compared to the best-supported model for Atlantic puffin (Δ AIC < 5 ; Table S5). All of these alternative models included SST, with a model including only SST receiving similar support to the best model (Δ AIC = 1.51 ; Table S5). Seven of the 14 alternative models included SLM (Table S5). Several other models also included terrestrial temperature, terrestrial rain or NAO (Table S5). All of the 14 alternative models included covariates averaged over the pre-breeding season period (Table S5). Together, these results detailed support in the data for alternative environmental variables, suggesting that the environmental correlation with breeding success in Atlantic puffin is primarily driven by SST, with SLM

Table 2. Best-supported models for climatic influence (North Atlantic Oscillation, sea surface temperature [SST], sea surface salinity [SLM], mean temperature [Temp], and summed precipitation [Rain]) on breeding success of 8 species of seabird breeding on the east coast of the UK. Models for each species were fitted to 3 seasonal definitions: pre-breeding period, breeding season and 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 \times year. Significance ($**p \leq 0.05$) shown in **bold**. R^2 refers to the variance explained (as a proportion [0,1]) for fixed effects or for both fixed and random effects (including the individual-level random effect). Variables were not standardised

Species	Best model	Estimates					R^2
		Variable	Estimate	SE	z	p	
Atlantic puffin	Pre-breeding: SST** + SLM*	SST	-0.6800	0.170	-3.992	<0.001	Fixed only: 0.187
		SLM	0.679	0.370	1.833	0.067	Fixed + random: 0.958
	Random effects	Year	0.076	0.276			
		Colony	0.055	0.235			
		Colony \times year	0.366	0.605			
Black-legged kittiwake	Pre-breeding: SLM** + Temp** + Rain**	SLM	-2.163	0.365	-5.921	<0.001	Fixed only: 0.189
		Temp	-0.266	0.102	-2.613	0.0099	Fixed + random: 0.999
		Rain	0.6667	0.273	2.441	0.015	
	Random effects	Year	0.850	0.922			
Colony		0.766	0.875				
Colony \times year		1.898	1.378				
Common guillemot	Pre-breeding: SST** + Rain	SST	-0.866	0.160	-5.405	<0.001	Fixed only: 0.203
		Rain	0.374	0.252	1.483	0.138	Fixed + random: 0.994
	Random effects	Year	0.822	0.907			
		Colony	0.056	0.237			
		Colony \times year	0.806	0.898			
European shag	Pre-breeding: Temp**	Temp	-0.120	0.049	-2.456	0.014	Fixed only: 0.046
							Fixed + random: 0.984
	Random effects	Year	0.071	0.266			
		Colony	0.098	0.313			
		Colony \times year	0.332	0.576			
Great black-backed gull	Breeding: SLM** + Temp**	SLM	-0.338	0.147	-2.302	0.021	Fixed only: 0.169
		Temp	-0.619	0.176	-3.516	<0.001	Fixed + random: 0.981
	Random effects	Year	<0.001	<0.001			
		Colony	0.000	0.000			
		Colony \times year	1.137	1.066			
Herring gull	Null model						
Northern gannet	Breeding season: SLM**	SLM	-0.686	0.298	-2.306	0.021	Fixed only: 0.133
							Fixed + random: 0.958
	Random effects	Year	<0.001	0.009			
		Colony	0.066	0.256			
		Colony \times year	0.102	0.319			
Razorbill	Breeding season: SLM**	SLM	-0.848	0.398	-2.130	0.033	Fixed only: 0.148
							Fixed + random: 0.978
	Random effects	Year	0.152	0.390			
		Colony	0.227	0.476			
		Colony \times year	0.811	0.900			

having an important, but lesser, effect. There was essentially no support for models containing any effects of covariates averaged over the breeding season or the pre-breeding and breeding season combined (Table S5).

The null model with no environmental variables received very little support compared to the best-fitting model for Atlantic puffin ($\Delta AIC = 9.07$). Model validation showed that the best fitting model accounted for approximately 19% of the variation

observed in the data when not including the individual-level random effect (Table 2).

The best-supported model for Atlantic puffin estimated a current mean breeding success during 2014–2018 climate conditions of 0.727 (95% CI: 0.623, 0.793), and of 0.534 during 2070–2099 (95% CI: 0.371, 0.681). Predicted access to suitable marine climatic conditions showed some evidence for a slight increase from 50 km up to a foraging range of around 150 km under future projections in contrast to a very slight decline with increasing foraging range under current conditions (Fig. 1).

3.2. Black-legged kittiwake

The best-supported model for breeding success in the black-legged kittiwake included marine and terrestrial climate variables from the pre-breeding period only, indicating strong negative effects of SLM (mean: -2.163 , $p < 0.001$) and terrestrial temperature (mean: -0.266 , $p = 0.0099$) and a strong positive effect of terrestrial rain (mean: 0.667 , $p = 0.015$) (Table 2).

Six other models received some support in the data compared to the best-supported model for black-legged kittiwake ($\Delta\text{AIC} < 5$; Table S5). All of these alternative models included SLM, 5 included terrestrial rain and 4 of the 6 models included terrestrial temperature (Table S5). Three of the alternative models also included SST and 2 also included NAO (Table S5). A model including only SLM and terrestrial temperature received some support compared to the best model ($\Delta\text{AIC} = 3.93$; Table S5), whilst a model containing only SLM and terrestrial rain received minimal support compared to the best model ($\Delta\text{AIC} = 4.86$; Table S5). All 6 alternative models included covariates averaged over the pre-breeding season (Table S5). Together, these results suggest that the environmental correlation with breeding success in black-legged kittiwakes is primarily driven by SLM, with terrestrial rain and terrestrial temperature having important, but lesser, effects. There was essentially no support in the data for models containing any effects of covariates averaged over the breeding season or the pre-breeding and breeding season combined (Table S5). The null model with no environmental variables received very little support compared to the best-fitting model for the black-legged kittiwake ($\Delta\text{AIC} = 36.15$). Model validation showed that the best fitting model accounted for approximately 19% of the variation observed in the data when not including the individual-level random effect (Table 2).

The best-supported model for the black-legged kittiwake estimated a current mean breeding success during 2014–2018 climate conditions of 0.576 (95% CI: 0.322, 0.790), and of 0.411 for 2070–2099 (95% CI: 0.269, 0.563). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for this species, either under current or future projections, but rather showed a general decrease in suitability with increasing foraging distance, and little change beyond a foraging range of around 200 km (Fig. 1).

3.3. Common guillemot

The best-supported model for the common guillemot included marine and terrestrial climate variables defined over the pre-breeding period, suggesting strong evidence for a negative effect of SST (estimate = -0.866 , $\text{SE} = 0.106$, $z = -5.405$, $p < 0.001$) and a non-significant effect of terrestrial rainfall (estimate = 0.374 , $\text{SE} = 0.252$, $z = 1.483$, $p = 0.138$; Table 2).

There were 23 other models that received some support in the data compared to the best-supported model for common guillemot ($\Delta\text{AIC} < 5$; Table S5). Fifteen of these alternative models included SST, with a model including only SST receiving similar support to the best model ($\Delta\text{AIC} = 0.80$; Table S5). Sixteen of the 23 alternative models included terrestrial rain (Table S5). Several other models also included various other covariates not included in the best-supported model, including SLM, terrestrial temperature and NAO (Table S5). In terms of the more parsimonious models, a model including only effects of SST and terrestrial temperature received some support in relation to the best model ($\Delta\text{AIC} = 2.42$; Table S5), as did models including only SST and NAO ($\Delta\text{AIC} = 2.49$; Table S5), and SST and SLM ($\Delta\text{AIC} = 2.67$; Table S5). A model including only effects of terrestrial rain and terrestrial temperature received marginal support in the data compared to the best model ($\Delta\text{AIC} = 3.64$; Table S5). The top 12 best-supported models (all with $\Delta\text{AIC} < 3.0$) for common guillemot included only covariates averaged across the pre-breeding period; 5 of the top 23 other models included covariates averaged across the pre-breeding and breeding periods, but all 5 of these models received only minimal support in the data in comparison to the best model (all with $\Delta\text{AIC} > 3.0$). Together, these results suggest that the environmental correlation with breeding success in common guillemots is primarily driven by SST, with terrestrial rainfall having an important, but lesser, effect. There

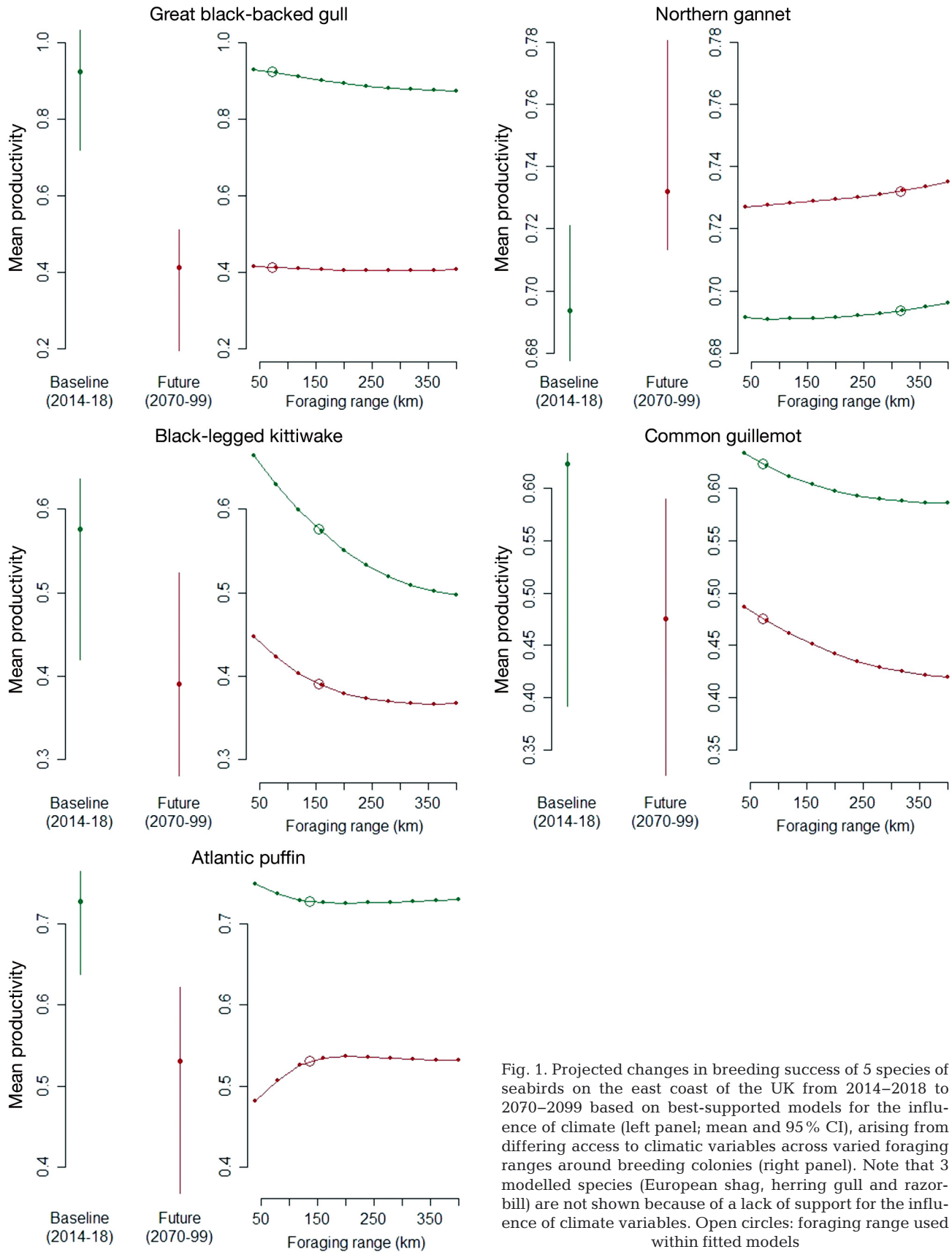


Fig. 1. Projected changes in breeding success of 5 species of seabirds on the east coast of the UK from 2014–2018 to 2070–2099 based on best-supported models for the influence of climate (left panel; mean and 95% CI), arising from differing access to climatic variables across varied foraging ranges around breeding colonies (right panel). Note that 3 modelled species (European shag, herring gull and razorbill) are not shown because of a lack of support for the influence of climate variables. Open circles: foraging range used within fitted models

was very little support in the data for models containing any effects of covariates averaged over the pre-breeding and breeding season combined and essentially no support in the data for models containing covariates averaged over only the breeding season (Table S5). The null model received essentially no support in comparison to the best-supported model ($\Delta\text{AIC} = 12.75$).

The best-supported model for common guillemot explained approximately 20% of the variation in the data, not including the individual-level random effect (Table 2), and estimated a current mean breeding success during 2014–2018 climate conditions of 0.609 (95% CI: 0.412, 0.700), and of 0.408 for 2070–2099 (95% CI: 0.309, 0.514). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for common guillemot, either under current or future projections (Fig. 1).

3.4. European shag

The best-supported model for breeding success in European shag included only the terrestrial climate variable for temperature defined over the pre-breeding period, suggesting strong evidence for a negative effect of this variable on breeding success (estimate = -0.120 , SE = 0.049, $z = -2.456$, $p = 0.014$; Table 2).

There were, however, 51 other models that received some support in the data in comparison to the best-supported model for European shag ($\Delta\text{AIC} < 5$; Table S5). Of these alternative models, 5 received similar support relative to the best model ($\Delta\text{AIC} < 2$), and all 5 included terrestrial temperature plus one of the other climate variables averaged over the pre-breeding period (+terrestrial rain: $\Delta\text{AIC} = 0.75$; +SLM: $\Delta\text{AIC} = 1.55$; +NAO: $\Delta\text{AIC} = 1.83$; +SST: $\Delta\text{AIC} = 1.86$; Table S5) or included one other variable averaged over the pre-breeding plus breeding period (terrestrial temperature and SLM: $\Delta\text{AIC} = 1.93$; Table S5). Together, these results suggest that the environmental correlation with breeding success in European shag is primarily driven by terrestrial temperature in the pre-breeding period, with very minimal influence of other covariates or seasonal periods. The null model received only slight support in comparison to the best-supported model ($\Delta\text{AIC} = 4.10$).

The best-supported model for European shag explained only around 5% of the variation in the data, not including the individual-level random effect (Table 2), and estimated a current mean breeding success during 2014–2018 climate conditions of 1.309 (95% CI: 0.968, 1.396).

3.5. Great black-backed gull

Defining climate variables over the breeding period only, including one marine and one terrestrial variable, resulted in the best-supported model for breeding success in the great black-backed gull. This model included strong evidence for negative relationships between breeding success and SLM (mean = -0.338 , SE = 0.147, $z = -2.302$, $p = 0.021$) and terrestrial temperature (mean = -0.619 , SE = 0.176, $z = -3.516$, $p < 0.001$; Table 2). Twelve other models received some support in the data compared to the best-supported model ($\Delta\text{AIC} < 5$; Table S5). All of these 12 alternative models included terrestrial temperature and 7 also included SLM (Table S5). A model including only terrestrial temperature received moderately similar support compared to the best-supported model, also including SLM ($\Delta\text{AIC} = 2.70$; Table S5). Other than this model, the 5 alternative models with the most support ($\Delta\text{AIC} < 3.0$) all included both SLM and terrestrial temperature and one or more of the other climate variables (+NAO: $\Delta\text{AIC} = 1.02$; +terrestrial rain: $\Delta\text{AIC} = 1.79$; +SST: $\Delta\text{AIC} = 1.91$; +NAO and terrestrial rain: $\Delta\text{AIC} = 2.88$; +NAO and SST: $\Delta\text{AIC} = 2.93$; Table S5). All 12 alternative models included variables averaged over the breeding season (Table S5). Together, these results suggest that the environmental correlation with breeding success in great black-backed gulls is primarily driven by terrestrial temperature in the breeding period with important, but lesser, effects of SLM. The null model received essentially no support in comparison to the best-supported model ($\Delta\text{AIC} = 8.04$) and explained approximately 17% of the variation in the data, not including the individual-level random effect (Table 2).

The best-supported model for breeding success in the great black-backed gull estimated a current mean breeding success during 2014–2018 climate conditions of 0.962 (95% CI: 0.811, 1.14), and of 0.415 for 2070–2099 (95% CI: 0.227, 0.731). Predicted access to suitable marine climatic conditions did not improve with increasing foraging range for this species, either under current or future projections (Fig. 1).

3.6. Herring gull

The null model containing no climate effects was best supported by the data for breeding success in the herring gull (Table 2, Table S5).

3.7. Northern gannet

The best-supported model for breeding success in the northern gannet included only SLM defined over the breeding season, indicating a strong negative correlation between this variable and breeding success (mean = -0.686 , SE = 0.298 , $z = -2.306$, $p = 0.021$; Table 2). There were, however, 72 other models that received some support compared to the best-supported model for this species ($\Delta\text{AIC} < 5$; Table S5), including the null model ($\Delta\text{AIC} = 2.72$; Table S5). Of the alternative models receiving greater support than the null model ($\Delta\text{AIC} < 2.7$; Table S5), the 4 most parsimonious included only one climate variable (SLM defined over the pre-breeding and breeding periods: $\Delta\text{AIC} = 0.35$; NAO defined over the pre-breeding period, the breeding season or both the pre-breeding and breeding seasons: all 3 $\Delta\text{AIC} = 2.62$; Table S5). All other alternative models included SLM and one or more other variables (Table S5). Together, these results suggest that the environmental correlation with breeding success in the northern gannet is primarily driven by SLM, with some ambiguity over which seasonal period is most influential. The null model received only slight support in comparison to the best-supported model ($\Delta\text{AIC} = 4.10$), explaining approximately 15% of the variation in the data, not including the individual-level random effect (Table 2).

The best-supported model for northern gannet estimated a mean breeding success in 2014–2018 of 0.693 (95% CI: 0.633 , 0.732), with a predicted slight increase to 0.713 in 2070–2099 (95% CI: 0.662 , 0.760). Predicted access to suitable marine climatic conditions did not tend to vary with foraging range for this species, either under current or future projections (Fig. 1).

3.8. Razorbill

The best-supported model for breeding success in razorbill included only SLM defined over the breeding season, indicating a strong negative correlation between this variable and breeding success (mean = -0.848 , SE = 0.398 , $z = -2.130$, $p = 0.033$; Table 2). However, an alternative 80 models received some support ($\Delta\text{AIC} < 5.0$; Table S5), only 7 of which received greater support than the null model ($\Delta\text{AIC} = 1.13$; Table S5). Of these 7 models, 4 included only a single climate variable (SST defined over the pre-breeding period: $\Delta\text{AIC} = 0.25$; SLM over the pre-breeding and breeding periods: $\Delta\text{AIC} = 0.33$; SST

defined over the pre-breeding and breeding periods: $\Delta\text{AIC} = 0.85$; and SLM over the pre-breeding period: $\Delta\text{AIC} = 1.10$; Table S5). In summary, there was ambiguity over the strongest climatic variable and seasonal period influencing breeding success in razorbill, with similar support in the data for the null model containing no effects of climate. The best-supported model for this species explained approximately 15% of the variation in the data, not including the individual-level random effect (Table 2), and estimated a mean breeding success in 2014–2018 of 0.564 (95% CI: 0.424 , 0.637).

4. DISCUSSION

Climate change poses a significant threat to marine wildlife, ecosystems and the societies that rely on these natural resources. Reducing emissions and achieving net-zero targets to address climate change will require the development of extensive renewable energy sources. In northern Europe, much of this shift to greener energy will be derived from offshore wind developments in the North Sea. Whilst offshore ORDs will bring long-term benefits to seabird species by combating climate-driven changes to ecosystems, they may also bring medium-term adverse impacts to protected seabird populations through effects such as habitat displacement, barrier effects and collisions (Drewitt & Langston 2006, Masden et al. 2010, Scottish Government 2011). We found strong impacts of marine and terrestrial climate on seabird breeding success rates, with climate over the pre-breeding period having a strong influence over subsequent breeding success in 4 species and climate during the breeding season affecting breeding success in 3 species. In 4 of the 5 species for which strong effects of climate were detected (Atlantic puffin, common guillemot, black-legged kittiwake and great black-backed gull), future climate projections resulted in a predicted decline in breeding success, which was often fairly severe over the future time period 2070–2099. In only one species (northern gannet) was breeding success predicted to increase under the future climate scenario. Our results build upon previous findings that have demonstrated the importance of climate on breeding success and other vital rates in seabirds globally, but which have tended to focus on single breeding colonies or species (Jones et al. 2007, Barbraud et al. 2011, Jenouvrier et al. 2014, Monticelli et al. 2014, Carroll et al. 2015, Christensen-Dalsgaard et al. 2018; but see Sydeman et al. 2021) or on abundance,

not vital rates (Johnson et al. 2013). Very few studies have estimated future vital rates for seabirds under projected future climates (but see Carroll et al. 2015) or across broad regions such as the North Sea (but see recent review by Pearce-Higgins 2021). Critically, with the exception of the positive outlook for the northern gannet, which likely reflects its broader diet (Hamer et al. 2000), our results corroborate recent reviews suggesting that potential declines in the future are likely to occur in a wider suite of seabird species than has been demonstrated before (Pearce-Higgins 2021). These predicted changes will likely result in significant shifts in UK seabird population demography, trends and distribution over the coming decades, with consequences for the interaction of these species with ORDs in the North Sea.

The most likely mechanism underpinning the observed temperature effects on breeding success in seabirds is via changes in the quality, abundance and trophic matching of lower trophic levels, with negative consequences on the availability of key prey species (notably lesser sandeels *Ammodytes marinus*) during the period of high energy demand in the breeding season (van Deurs et al. 2009, Eerkes-Medrano et al. 2017, Régnier et al. 2019, von Biela et al. 2019). Our results for the black-legged kittiwake failed to indicate a strong relationship between SST and breeding success, supporting findings from studies at some individual colonies (Carroll et al. 2015, Eerkes-Medrano et al. 2017). However, the results did include strong negative effects of terrestrial temperature on breeding success in this species (Table 3), which may be linked to heat stress in chicks as hypothesized in previous studies (Smith & Gaston 2012, Michielsen et al. 2019). SLM also played a role in breeding success

declines in 5 species (Table 3), a variable that has previously been linked to seabird distribution and abundance in other regions, most likely via bottom-up influences on prey (Serratosa et al. 2020). We detected a negative link between breeding success and SLM in 4 species (black-legged kittiwake, great black-backed gull, northern gannet and razorbill) and a positive link in just one species (Atlantic puffin) (Table 3). This evidence points to SLM being a potentially strong indicator of breeding success in the region and warrants further investigation into the mechanisms linking SLM to seabird demography. The mechanisms underpinning the positive effect of terrestrial rain on breeding success in one species (black-legged kittiwake) are not clear, and indeed other studies have previously documented negative effects of high terrestrial rainfall on burrow nesting species (Rodway et al. 1998). However, another study suggested more nuanced impacts of rainfall in black-headed gulls, with rainfall during egg-laying positively affecting clutch size and decreasing clutch predation, rainfall during the early post-natal period negatively affecting chick growth, and rain during the later post-natal phase positively affecting fledging success and reducing brood predation (Thyen & Becker 2006). Overall, the negative effects of increasing temperature resulted in a predicted overall decline in breeding success in the future across most species. An alternative mechanism underpinning the strong effect of pre-breeding climatic conditions is a carry-over effect, whereby conditions experienced by seabirds in one season (in this case, late winter) have downstream consequences on subsequent seasons via changes in the abundance and extent of trophic mismatch of their prey (Daunt et al. 2014).

Table 3. Significant climate effects on breeding success for seabird colonies on the eastern seaboard of the UK. Grey shading indicates the null model, containing no climatic effects, received the greatest support in the data (assessed using Akaike's information criterion [AIC]). Significance denoted by ** $p \leq 0.05$; NS: non-significant; direction of effect: negative (-) or positive (+). Empty cells denote that the variable was not included in the best-supported model (based on AIC)

Species	Marine	Terrestrial	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 -**	Rainfall NS	Pre-breeding
European shag		Temperature -**	Pre-breeding
Great black-backed gull	Sea surface salinity -**	Temperature -**	Breeding
Herring gull			
Northern gannet	Sea surface salinity -**		Breeding
Razorbill	Sea surface salinity -**		Breeding

Behavioural plasticity is an important process contributing to the resilience of seabird populations (Paiva et al. 2010, Pettex et al. 2012, Gilmour et al. 2018). However, our results indicate that the ability of breeding seabirds to adapt to a changing climate by extending their foraging range around breeding colonies may have little impact on buffering breeding success by extending access to more climatically suitable resources. There is a growing evidence base from UK seabird-tracking studies estimating foraging ranges during the breeding season (Woodward et al. 2019), which we considered when setting the upper limit to our foraging range distances in this analysis (400 km). Of the 5 species for which projections were made in our analysis, all had reported mean maximum foraging ranges below this range (Atlantic puffin: 137.1 km; black-legged kittiwake: 156.1 km; common guillemot: 73.2 km; great black-backed gull: 73.0 km; northern gannet: 315.2 km; Woodward et al. 2019). Only 2 of the species showed evidence for maximum recorded foraging ranges above 400 km (black-legged kittiwake: 770 km and northern gannet: 709 km; Woodward et al. 2019). This suggests the upper bound of 400 km used in our projections is likely an overestimate of the potential range over which these species may increase foraging around breeding colonies based on current data. Therefore, based on current evidence, it appears unlikely that populations of these species would increase foraging ranges beyond those used within our analysis, suggesting that their ability to access wider, more beneficial resources is limited. This limitation would be further constrained by heterogeneity in other habitat features, such as those affecting prey habitat suitability, as well as anthropogenic pressures such as fisheries activity. Moreover, there is emerging evidence that larger foraging distances may impose constraints on chick condition and subsequent breeding success, highlighting potentially important trade-offs between wider access to resources and subsequent fitness (Horswill et al. 2017, Campbell et al. 2019, Gulka et al. 2020).

Broadly across the study species, our models explained a limited amount of the observed variation in breeding success (~13–20% for the 5 species for which future predictions were made), despite identifying significant relationships between climate variables and demographic rates. This is not uncommon with ecological data, particularly where there is likely to be significant sampling variation, such as with the breeding success data within the SMP. 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. These limitations engender caution when interpreting our results quantitatively for projected changes in future breeding success. However, taking our results holistically within the background of growing evidence for negative effects of climate change on UK seabird populations (Carroll et al. 2015, Daunt et al. 2017, Pearce-Higgins 2021), the qualitative reliability of the predicted decreases appears to be supported, warranting further investigation and concern. A key priority for future research will be to identify stronger associations between demographic rates and more refined, lagged climate variables, ideally collected with greater spatio-temporal coherence to the habitat usage of individual populations across different seasons. It is also likely that responses of demographic rates to changing climate may vary regionally, as suggested by documentation of considerable variation in trends in breeding success for some seabird species (e.g. Horswill et al. 2022). Therefore, future work should seek to understand regional variation in demographic rates across vulnerable seabird populations as well as potential regional variation in inter-relationships between demographic rates and changing climate.

Our projections for future climatically driven changes in breeding success are limited by the use of a single emissions scenario (SRES A1B, medium) and through the use of climate projections for a single future period, representing an average over 2070–2099. This limits the extent to which strong ecological inference can be drawn from these projections. However, the intent behind the analysis—to demonstrate correlations between climate variables and seabird demography in a rapidly changing North Sea ecosystem and to consider the implications of these for offshore renewable energy assessments—is corroborated by our findings. The demonstration of potentially significant climate-driven changes to seabird demography under future climate reinforces the need for offshore wind assessment methods to integrate climate change within its approaches.

4.1. Implications for ORD and the use of PVA

PVA methods use population models to quantify the projected impacts of ORDs upon seabird abundance using estimates of annual effects on demography. The PVAs used in assessing the impacts of ORDs do not currently account for climate change, nor do they

currently account for existing drivers of directional change in demography (Horswill et al. 2022). However, our results demonstrate the importance of integrating climate variables because of the strong potential for significant changes in seabird demographic rates as a result of these processes over multiple decades, which the lease agreements for offshore wind farms will span. Climate change impacts on breeding success were estimated to be negative for 4 species, implying that the baseline condition or conservation status of populations that would be subject to ORD impacts (e.g. quasi-extinction probabilities) may be substantially underestimated if the impacts of climate change are ignored within PVAs. Underestimation of relative comparisons of ORD impacts and baseline conditions may occur if there are interactions between climate and ORD effects, such as non-linear or threshold effects where climate stress pushes populations into conditions where an additional impact from an ORD could result in disproportionately large changes to breeding success or other vital rates. Additional work is needed, for instance using mechanistic individual-based modelling approaches, to understand the form and strength that this non-linear interaction of multiple pressures may take.

We recommend that methods for conducting assessments of ORD impacts should be developed to allow for a dynamic, year-by-year prediction of the spatial habitat use, demography and abundance of protected seabird populations, exploiting the newly available yearly future estimates of key climate variables (UKCP18). This approach would allow estimated impacts to evolve dynamically through time as climate-driven changes to species' ecology occur. Developing such a framework is currently hindered by a lack of empirical understanding of how seabird space-use and demography will change as future climate change occurs. This understanding requires the projection of both seabird distribution and demography for each future year in which an assessment is required. These year-by-year dynamic predictions would allow for the estimation of ORD impacts in a predictive way that robustly accounts for climate-induced changes to demographic rates within PVAs. Inputs to ORD assessment tools would then be derived dynamically for each year of impact in accordance with predicted changes in distribution, demography and abundance, allowing for full integration of ORD impacts on demographic rates against prevailing climate-driven changes to species' ecology. This represents a considerable source of uncertainty in offshore wind assessments in the UK and is a priority area for future research (Ruffino et al. 2020).

4.2. Summary of recommendations

For assessment frameworks to account for climate-driven changes to demographic rates requires an understanding of the impacts of climate upon demographic rates such as breeding success and survival and on the distribution and space-use of marine wildlife. Therefore, we provide the following set of recommendations for future research and adaptation of assessment methods used in predicting impacts such as those arising from ORDs on protected seabirds and wildlife populations in general:

(1) Development of predictive models for seabird at-sea habitat use in relation to climate variables to estimate interactions with ORDs in each future year using yearly climate projections;

(2) Refinement of colony-specific relationships between climate and seabird demographic rates, including breeding success and survival, allowing climate-driven changes to demographic rates to be included in population forecasts used to underpin PVA in ORD assessments;

(3) Adaptation of the ORD assessment process to include a year-by-year prediction of the space-use and demographic rates of protected seabird populations under future annual projections of marine and terrestrial climate; and

(4) Consideration of potential climate change impacts on population demography and trends in the implementation of compensatory measures for ORD impacts and subsequent adaptive management.

Data availability. All data used in the analysis are freely available from the Joint Nature Conservation Committee (JNCC Seabird Monitoring Programme, <http://jncc.defra.gov.uk/page-4460>) and the Environmental Information Data Centre (EIDC).

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