



Predicting seabird distributions in response to climate change using habitat modelling

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Executive Summary

Seabirds are one of the world's most endangered avian groups and face a variety of threats including responding to a rapidly changing environment. As a result, an understanding of how seabird population dynamics and distributions may respond to climate change is required to facilitate effective seabird conservation. The MarPAMM project focusses on seabirds within the INTERREG VA region; an area covering western Scotland and Northern Ireland that supports important populations of many breeding seabirds. Previously, work conducted as part of the MarPAMM project used a range of climatic variables to model spatio-temporal variation in the abundance of seabird colonies within the MarPAMM region in response to future projections of climate change (Davies et al. 2021). The following report combines the predicted changes in seabird abundance provided by Davies et al. (2021), with pre-existing species distribution models for seven seabird species (Black-legged Kittiwake, *Rissa tridactyla*; Common Guillemot, *Uria aalge*; Razorbill, *Alca torda*; European Shag, *Phalacrocorax aristoteli*; Arctic Tern, *Sterna paradisaea*; Common Tern, *Sterna hirundo*; Sandwich Tern, *Sterna sandvicensis*) to estimate changes in at sea distributions for each species under changing climatic conditions within the MarPAMM region. Parameter estimates for species distribution models for each Tern species were obtained from Wilson et al. (2014) a Joint Nature Conservation Committee (JNCC) report that focussed upon quantifying usage of the marine environment around UK breeding colony Special Protection Areas (SPA). Parameter estimates for Kittiwake, Guillemot, Razorbill and European Shag were obtained from Wakefield et al. (2017) an RSPB-led research project that modelled colony-level habitat usage for these species across the UK and Ireland. While the species distribution models identified were designed to predict current seabird distributions, they contained various dynamic environmental covariates that will be affected by climate change and, in turn, influence future seabird distributions. In addition, the at sea distribution of central-place foragers such as seabirds will be influenced by changes in the abundance of birds at different colonies in response to climate change and subsequent changes in density dependent competition. Here, predictions from existing species distribution models were updated by conditioning on projected values of relevant oceanographic variables that were included in such models and for which climate projections were available (Sea Surface Temperature, SST; Potential Energy Anomaly, PEA; Thermal Front Gradient Density, TFGD). Projections for these oceanographic variables were calculated from climate models under a RCP8.5 (business-as-usual) climate change scenario equivalent to approximately 2°C global warming by 2050 compared to 1986-2005 levels using an existing hydrodynamic oceanographic model (Scottish Shelf Model, SSM). Estimates of changes in colony abundance as well as the resulting changes in both sympatric conspecific competition and parapatric conspecific competition under the same climate change scenario were obtained from Davies et al. (2021). Updated maps of seabird at-sea distributions under future climate change predictions were then compared to similar maps

constructed under current / historical conditions to determine the nature and extent of shifts in seabird distribution patterns as a result of projected climate change within the MarPAMM region (similar comparisons done at the UK and Ireland scale are also presented in an Appendix).

Within the MarPAMM region, three of the four species included in Wakefield et al. (2017) - Kittiwake, Guillemot and Razorbill - were predicted to decline in abundance across most of their at-sea distribution under projections of future climate change. In Razorbills there appeared to be a pattern of increased density in the immediate vicinity of colonies before abundance declined further from colonies. In addition, both 50% and 95% UD in this species were predicted to encompass a smaller area under future climate projections. Therefore, the results for Razorbill suggest a decline in population abundance combined with a contraction of foraging range in the MarPAMM region. While Kittiwake and Guillemot abundance was predicted to decline, both 50% UD and 95% UD contours expanded slightly, possibly due to reductions in parapatric competition between birds from neighbouring colonies as species abundance declined across the MarPAMM region. Unlike the other species included in Wakefield et al. (2017) the abundance of European Shag was expected to increase under future climate projections and the density of birds in the vicinity of breeding colonies was predicted to increase. However, declines in the size of 50% and 95% UDs under future climate conditions were also predicted. One potential explanation is that European Shag distributions were strongly influenced by values for the PEA covariate for which climate projections were available. Under the climate change projections assessed here PEA is expected to increase across most of the MarPAMM region and therefore the size and location of areas with optimal PEA values may become more localised and occur mostly in coastal regions, altering Shag distributions.

Species distribution models for the three Tern species considered here included relatively few static covariates all of which remained the same between predictions based on current or future climate projections. As such, we observed little difference in the at sea distribution of birds across all Tern species at the colony level and, even when aggregating across colonies within the MarPAMM region, there was little change in the predicted distribution of Terns. Arctic and Sandwich Tern populations were predicted to decline based on the outputs from Davies et al. (2021) and we predicted corresponding declines in Tern at-sea density across the MarPAMM region. Unlike Arctic and Sandwich Terns, Common Tern abundance was predicted to increase under future climate change but increases in density were not uniform across the

MarPAMM region with some colonies increasing in size and others decreasing. As such, predicted shifts in the spatial distribution of Common Tern arises from changes in the relative size of different colonies under climate change.

Developing accurate predictions of seabird responses to climate change will require consideration of the feedbacks between habitat quality, population size and density dependant competition within a rapidly changing environment. As such, combining demographic models of population abundance with species distribution models is likely to be an area that sees further development in the future. The modelling work presented here, in conjunction with Davies et al. (2021), represents one of the first attempts to model changes in seabird population abundance as a function of both terrestrial climate and oceanographic variables and to link such changes in population demography with habitat usage in order to predict seabird distributions. Under future projections of climate change the highest density of birds occurred within the vicinity of the largest breeding colonies reflecting a key mechanistic constraint of central-place foraging. Consequently, sea areas around large breeding colonies are likely to reliably contain high densities of breeding seabirds even under future climate projections. Therefore, assessing how the size and distribution of seabird colonies will change in response to climate change is crucial to conservation efforts. Seabird at sea distributions are also predicted to shift in response to climate change, contracting in some species (Razorbill) while expanding in others (Guillemot, Kittiwake). Thus, conservation efforts will also need to consider how seabird home ranges shift over time, particularly in response to changes in density dependent competition or dynamic oceanographic features that will be impacted by climate change.

Introduction

Seabirds are one of the world's most endangered avian groups (Croxall et al. 2012) and face a variety of interacting threats including invasive species, fisheries bycatch and pollution (Dias et al. 2019). Alongside these threats, climate change has also been identified as a potential driver of seabird declines (Grémillet & Boulinier 2009). Britain and Ireland are home to internationally important populations of breeding seabirds (Mitchell et al. 2004). However, given long-term warming of our climate and seas, they are also widely regarded as potentially highly vulnerable to climate change (Mitchell et al. 2020). The MarPAMM project focusses on seabirds across western Scotland and Northern Ireland, an area which supports breeding populations of many seabird species, to understand the potential vulnerability of these species to climate change. Specifically, the project aims to understand how seabird abundance and at sea distributions is predicted to change under future climate projections.

The following report describes an update to pre-existing predictions of at-sea distributions for seven seabird species derived from two published sources, Wilson et al. (2014) and Wakefield et al. (2017) in response to future climate change predictions. Wilson et al. (2014) is a Joint Nature Conservation Committee (JNCC) report that focussed upon quantifying usage of the marine environment by four tern *Sterna* species around their breeding colony Special Protection Areas (SPA) in the UK. Similarly, the main aim of Wakefield et al. (2017) was to generate colony-level maps of habitat usage for four species of seabirds (Black-legged Kittiwake, *Rissa tridactyla*; Common Guillemot, *Uria aalge*; Razorbill, *Alca torda*; European Shag, *Phalacrocorax aristotelis*) breeding in Britain and Ireland in order to aggregate colony-level distribution maps up to the national scale maps. However, missing substrate data (a covariate included as part of the distribution modelling process) meant that Wakefield et al. (2017) did not estimate usage by Shag, Guillemot, and Razorbill outside the UK Exclusive Economic Zone (EEZ) or for parts of the Northern and Western Isles. While the modelling process differed somewhat between Wilson et al. (2014) and Wakefield et al. (2017) both studies used the same class of habitat usage model commonly referred to as habitat (or resource) selection functions (Aarts et al. 2008, Aarts et al. 2012). Broadly speaking, habitat associations were assessed by tracking the movement of individual birds using either a visual tracking method (Wilson et al. (2014) or GPS loggers (Wakefield et al. 2017) and linking the density of observed tracking locations to a suite of underlying environmental covariates recorded at these locations. In addition, a covariate for distance from the breeding colony was included in both Wilson et al. (2014) and Wakefield et al. (2017) to reflect assumptions that breeding seabirds should seek prey close to the breeding site (Orlans & Pearson 1979).

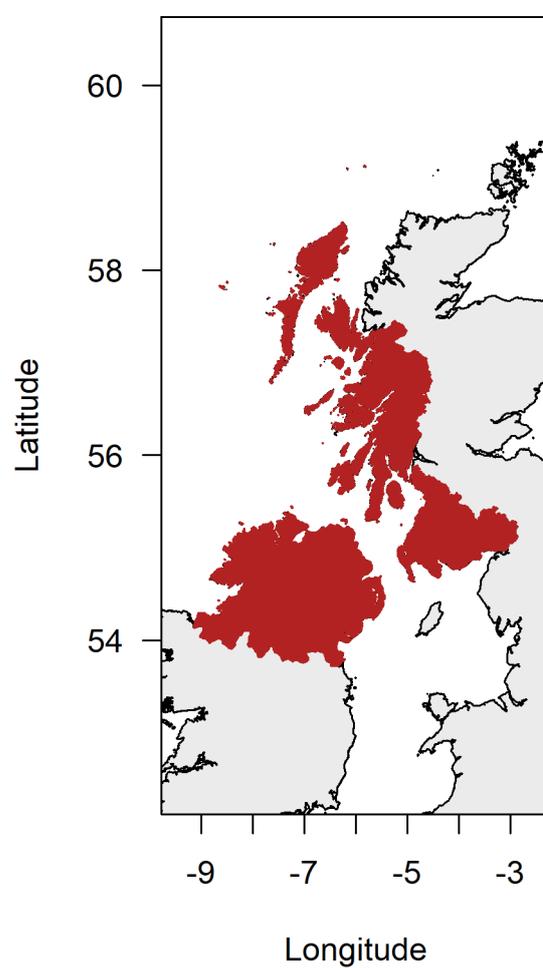
Wakefield et al. (2017) also included covariates linked to population abundance to reflect how competition both within and between colonies can influence seabird distributions (e.g. Grémillet et al. 2004, Wakefield et al. 2013).

The habitat models presented in both Wilson et al. (2014) and Wakefield et al. (2017) represent estimated patterns in observed habitat usage over the years in which birds were tracked (2009 – 2011 in Wilson et al. (2014); 2010 – 2014 in Wakefield et al. (2017)). However, many of the environmental covariates examined in these models are expected to change in the future under various climate change scenarios. For example, warming of UK shelf seas is projected to continue over the coming century with most models suggesting an increase of between 0.25°C and 0.4°C per decade (MCCIP Report Card, 2020) and could affect the food-webs upon which seabirds rely (Scott et al. 2006, Bedford et al. 2020, Mitchell et al. 2020). More specifically, the distribution of key dynamic environmental variables such as sea surface temperature (SST) and potential energy anomaly (PEA) that feature in the habitat models of Wakefield et al. (2017) are expected to alter significantly in the coming decades (see: Fig. 3c,d in MarPAMM Lot 2.1 Report, Davies et al. 2021) which, in turn, could result in changes in seabird distributions.

Alongside changes in environmental variables, long-term trends in population abundance in response to climate change are also likely to have important impacts on predicted seabird distributions. In part this will occur due to the relative changes in the size of different colonies throughout the UK and Ireland. The at-sea distribution of central-place foragers such as seabirds will be also constrained by colony location and as distance from the colony increases habitat usage is expected to decline. The exact nature of the relationship between distance from the colony and habitat usage is likely to be shaped in part by levels of competition from other individuals from the same colony (sympatric competition) as well as individuals from neighbouring colonies (parapatric competition) which will themselves be influenced by estimates of population abundance. For example, as a colony grows, local prey depletion or interference competition may require birds at larger colonies to travel further to find food (Ashmole 1963). Likewise, individuals may tend to avoid areas where the level of parapatric competition from birds from another colony is high (Grémillet et al. 2004, Wakefield et al. 2011, Wakefield et al. 2013). Consequently, changes in colony size under different climate change scenarios could have an important influence on seabird distributions by changing patterns of intra-specific competition.

The current report focusses specifically on the predicted at-sea distributions of seabirds originating from within the INTERREG VA area that is the focus of the MarPAMM project (see Fig. 1). Predictions from existing habitat models were updated by conditioning on projected values of relevant oceanographic variables calculated from climate models under a RCP8.5 (business-as-usual) climate change scenario equivalent to approximately 2°C global warming by 2050 compared to 1986-2005 levels via the Scottish Shelf Model (IPCC 2014 , De Dominicis et al. 2018a, 2019, Davies et al. 2021). In addition, estimates of colony abundance as a result of projected changes in climate and oceanography were obtained from Davies et al. (2021) to account for changes in seabird abundance throughout the UK and Ireland, as well as changes in sympatric conspecific competition (birds from same colony) and parapatric conspecific competition (birds from other colonies). Updated maps of seabird at-sea distributions were then compared to similar maps constructed under current / historical conditions to determine the nature and extent of shifts in seabird distribution patterns as a result of projected climate change within the MarPAMM region. Moreover, while this report concentrates on reporting mapped distribution changes for the MarPAMM region, distributional maps were also made for the whole of the UK and Ireland and are presented as supplementary material.

Fig. 1. Map showing the location of the terrestrial MarPAMM region within the UK and Ireland. MarPAMM region highlighted in red. All seabird colonies within a 2 km buffer of this region were selected when creating density maps of birds from this region.



2. Methods

2.1. Modelling Approach of Wakefield et al. 2017

The approach used in Wakefield et al. (2017) involved modelling the intensity of tracking locations at a given point in space as a function of various explanatory variables (Table 1) using numerical quadrature methods to fit an Inhomogeneous Poisson Process (IPP) model. The response variable for the IPP was created by scoring all point locations in which tracking was observed as 1 and then creating a set of dummy points on a regular grid across the study area and scoring them as 0. Point locations from tracking (1) and dummy points (0) were then combined into a single vector of quadrature points that can be used to estimate the pseudo-likelihood of an IPP model. Grids were constructed at 1 km² resolution for Kittiwakes, Guillemots and Razorbills and at a 0.5 km² scale for Shags. Separate models were run for each species, but within a species data was provided by multiple colonies. For each colony the spatial grid over which habitat usage was assessed was designed to encompass the sea area accessible from that colony and was defined as 1.1x the maximum foraging range observed across colonies tracked during the study (Shags 35 km, Kittiwakes 300 km, Guillemots 340 km, Razorbills 305 km). Weights were then assigned to quadrature points in relation to how many quadrature points occurred within the same grid cell as a given point. Thus, the response variable is proportional to the expected density of tracking locations and the IPP model is equivalent to a weighted Poisson model. Model selection proceeded using a *k*-folds cross-validation approach to compare the out-of-sample predictive performance of models based on the similarity between the observed and predicted utilization distributions while holding out data for the *k*th colony.

For each species, the intensity of usage and thereby the Utilisation Distribution (UD) for birds from each Seabird 2000 site were predicted using the fixed-effects part of the best fitting models selected during the cross-validation process (Table 2). Model predictions from each colony were normalized to sum to 1.0 to ensure they met the definition of a UD as a spatial probability distribution describing the expected density of a population at a particular place. When weighted by population size estimates, UD's of neighbouring colonies can also be aggregated to depict relative or absolute expected density of breeding birds in a specified area. In this case, relative measures of density represent a probability density associated with a set of spatial coordinates (i.e. a UD that sums to 1.0) whereas absolute usage is defined as

an absolute amount that integrates to the total population size over the space considered (Matthiopoulos et al. 2020). Wakefield et al. (2017) displays a national-level UD for each species. However, because the original outputs from Wakefield et al. (2017) are predictions for individual colonies they can be combined in a variety of different ways depending on the scale of interest. Therefore, the absolute density (AD) of birds originating from a selected set of colonies can be calculated as:

$$AD_{P,i} = \sum_{All\ x} UD_{s,x} N_s$$

Where $AD_{P,i}$ represents the absolute density surface for a defined population P for the i^{th} species (see also: equation 10 in Wakefield et al. 2017) and will sum to total population size of colonies considered. The population in question is defined by a list of colonies, *set x*, over which to perform the operation. For example, at the UK-level, *set x* contains all Seabird 2000 sites that are located within the UK. N_s represents the size of colony s and is calculated as two times the number of Apparently Occupied Nests (AON) recorded during the Seabird 2000 census for Kittiwakes and Shags or the number of individuals recorded for Guillemots and Razorbills. While $AD_{P,i}$ represents an absolute measure of seabird density it can be converted to a relative measure of density, or population-level UD, by normalizing predictions to sum to unity.

Table 1. A list of covariates used in Wakefield et al. (2017) habitat modelling. Wakefield et al. (2017) tested a variety of potential environmental covariates when modelling seabird habitat usage based upon tenets of central place foraging theory as well as previously reported habitat associations within the seabird literature. Table details covariates that were retained in final models for at least one of the four species examined. Note that regional mean for each environmental covariate was included as an additional covariate during model selection to capture potential nonlinearities in habitat usage (Matthiopoulos et al. 2011). For more details see Wakefield et al. (2017).

Variable	Description	Justification
Distance from colony, d	The minimum distance by sea between a focal colony and each grid cell	Describes constraint associated with central place foraging
Log-transformed cumulative area of sea available to birds, A	Area of sea available to birds from each breeding site, which varies with coastal geometry. Density-dependent competition may be higher among birds foraging from colonies with restricted access to the open sea	Measure of sympatric competition
Number of sympatric breeders at the colony, N	Colony size as reported in Seabird 2000 census (Mitchell et al. 2004)	Measure of sympatric competition
Inverse-distance weighted number of breeding conspecifics from neighbouring colonies, θ	Combines estimate of colony size with influence of size of neighbouring colonies.	Measure of sympatric competition
Ratio of the expected intensity of locations at a grid cell for a given focal breeding site to the sum of those from all other sites in the region, ρ	Birds may avoid locations at which the density of conspecifics from other colonies is high (see Wakefield et al. 2013)	Measure of parapatric competition
Seabed Depth	Source: ETOPO2 Global Relief 2v2, provided by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center, 2006)	Previously reported habitat association
Seabed Slope	Calculated from the Seabed Depth in ArcGIS 10 (ArcGIS10 manufactured by ESRI based in Redlands, California, USA)	Previously reported habitat association
Distance from Coast	Minimum distance to the coast from centre of grid cell, calculated in ArcGIS 10	Previously reported habitat association

Proportion of gravel in seabed sediment	Derived from British Geological Survey 1:250,000 maps	Previously reported habitat association
Sand:Mud ratio in seabed sediment	Derived from British Geological Survey 1:250,000 maps	Previously reported habitat association
Potential Energy Anomaly (PEA)	Quantifies the intensity of thermohaline stratification. Data from the UK Met Office Forecasting Ocean Assimilation Model Atlantic Margin model.	Previously reported habitat association
Sea Surface Temperature (SST)	AVHRR sea surface temperature (SST), supplied by the Natural Environment Research Council Earth Observation Data Acquisition and Analysis Service (NEODAAS)	Previously reported habitat association
Thermal Front Gradient Density (TFGD)	Thermal front gradient density (TFGD), estimated following (Scales et al. 2014) using AVHRR SST to provide an index of the mean intensity and persistence of thermal fronts.	Previously reported habitat association

Table 2. Summary of fixed effects in inhomogeneous Poisson point process models of the density of seabird tracking locations as functions of colony distance, coastal geometry, intra-specific competition, and habitat. More details in Wakefield et al. (2017).

Species	Covariate	Estimate	S. E
Black-legged Kittiwake	Intercept	-6.785	0.189
	d	-1.432	0.009
	$\log(A)$	-0.477	0.005
	θ	-0.323	0.182
	$\log(\rho)$	1.84	0.013
	$\log(\text{seabed slope})$	-0.011	0.004
	$\text{mean log}(\text{seabed slope})$	-1.467	0.246
	SST	-0.961	0.006
	$\log(A) \times \theta$	0.153	0.003
	$\log(\text{seabed slope}) \times \text{mean log}(\text{seabed slope})$	0.621	0.005
Common Guillemot	Intercept	-7.753	0.172
	d	-1.589	0.027
	$\log(A)$	-1.033	0.007
	square-root (θ)	0.387	0.162
	$\log(\rho)$	1.247	0.029
	TFGD	0.294	0.004
	$\text{mean}(\text{TFGD})$	-1.763	0.322
	Distance from Coast	-1.230	0.023

	$\log(A) \times \text{square-root}(\theta)$	0.374	0.005
	TGFD \times mean (TGFD)	0.272	0.008
Razorbill	Intercept	-5.314	0.093
	d	-0.998	0.009
	$\log(A)$	-1.251	0.004
	$\text{square-root}(N)$	0.572	0.095
	SST	-0.163	0.008
	mean (SST)	0.354	0.113
	Sand:Mud ratio	-0.310	0.006
	Sand:Mud ratio ²	-0.278	0.005
	$\log(\text{seabed slope})$	0.020	0.005
	mean $\log(\text{seabed slope})$	-0.365	0.164
	$\log(A) \times \text{square-root}(N)$	0.353	0.003
	SST \times mean (SST)	-0.816	0.009
	$\log(\text{seabed slope}) \times \text{mean} \log(\text{seabed slope})$	-0.573	0.015
European Shag	Intercept	-6.080	0.210
	d	-1.578	0.017
	$\log(A)$	-1.445	0.008
	θ'	0.583	0.219
	% Gravel	0.530	0.011
	mean (% Gravel)	-0.303	0.337
	$\text{square-root}(\text{PEA})$	-2.007	0.020
	$\log(A) \times \theta'$	0.149	0.005
	% Gravel \times mean (% Gravel)	-0.742	0.017

2.2. Updating Wakefield et al. (2017) models under new climate change scenarios

In order to update habitat usage predictions under the future climate change projections investigated by Davies et al. (2021) we identified which of the covariates listed in Table 2 it was possible to update with future climate projections. Ultimately, we were able to update the following environmental covariates: Sea Surface Temperature (SST), Potential Energy Anomaly (PEA) and Thermal Front Gradient Density (TFGD). Updated values for SST and PEA were obtained as bespoke outputs from the Scottish Shelf Model averaged (weekly mean) over the period 2038-62 (see also: Davies et al. 2021). The original data was provided on an unstructured grid and was subsequently aggregated to the same grid cell resolution as used in Wakefield et al. (2017). SST and PEA outputs from the SSM were then averaged over the months of May and June which is the period when most of the GPS tracking data was collected

during Wakefield et al. (2017). TFGD was calculated using SST outputs averaged over May – June following (Scales et al. 2014) via the R package ‘grec’ (Lau-Medrano 2020). Other environmental covariates in the Wakefield et al. (2017) were not updated with climate predictions either because they were deemed as static variables, or it was not possible to source a relevant climate change prediction. However, additional seabed sediment data for Ireland was downloaded from the Geological Survey of Ireland at the same resolution (1:250k) as used in Wakefield et al. (2017) and using the same Folk schema of substrate classification (<https://www.gsi.ie/en-ie/data-and-maps/Pages/Marine.aspx#Habitats>) to allow prediction of seabird distributions along the west coast of Ireland, an area which included colonies located within the MarPAMM region. In the original work of Wakefield et al. (2017) sediment data for such areas was not available and therefore predictions for three species in which sediment was retained in habitat usage models (Guillemot, Razorbill and Shag) did not extend into these regions.

Variables relating to both sympatric and parapatric competition were updated using the median estimates of population size produced as part of Davies et al. (2021). Results from the population abundance modelling by Davies et al. (2021) defined seabird sites at a coarser level than in Wakefield et al. (2017) in which Seabird 2000 sites were split into smaller nodes in some instances by splitting the coastline into the minimum possible number of segments ≤ 1 km long and dividing population size equally between each. To match up the colony labels used by Davies et al. (2021) to the finer sub-divisions used in Wakefield et al. (2017) we split the population size estimates from Davies et al. (2021) amongst these finer sub-divisions in proportion to their size in Wakefield et al. (2017). A table detailing which variables were updated for each species are displayed in Table 3.

Table 3. Details of the covariates included in habitat models for each species and whether they were updated with future climate change projection (Y) or included as static covariates (-).

Variables	Kittiwake	Guillemot	Razorbill	Shag	Source for climate-projected versions
Intraspecific competition	Y	Y	Y	Y	Davies et al. (2021)
Sea Surface Temp (SST)	Y		Y		Scottish Shelf Model
Potential Energy Anomaly (PEA)				Y	Scottish Shelf Model
Thermal Front Gradient Density (TFGD)		Y			Scottish Shelf Model (Derived from SST)
Distance to Colony	NA – static
Distance to Coast		.			NA – static
Seabed Slope	.		.		NA – static
% Gravel		.		.	NA – static
Sand:Mud ratio			.		NA – static

2.3. Mapping predicted seabird distributions from Wakefield et al. (2017) in the MarPAMM region

We used the fixed-effects coefficients reported in Wakefield et al. (2017) to predict habitat usage for individual colonies within the MarPAMM region. Where appropriate we substituted in updated values for covariates for which we had climate change predictions. For example, rather than use the observed SST during the period 2010 – 2014 during which Wakefield et al. (2017) was conducted, we used updated maps of projected SST from the SSM and so on. We defined *set x* in equation (1) as all seabird colonies located within the MarPAMM region displayed in Figure 1 or within a 2 km buffer of this region. We used a 2 km buffer to ensure that spatial errors in coordinates when matching spatial data from different datasets (coordinates of seabird colonies from Seabird 2000 and MarPAMM shapefiles) did not lead to us removing colonies from *set x* on the fringes of the MarPAMM region. Once colony-level distributions for each colony within the MarPAMM were constructed they were then combined to create a single density map. In addition to producing relative density maps at the MarPAMM region levels we also produced similar maps in which *set x* was defined as all seabird colonies within the UK and Ireland to generate broader seabird distribution predictions.

2. 4. Modelling Approach of Wilson et al. 2014

Wilson et al. (2014) used a similar habitat modelling approach to that used in Wakefield et al. (2017) when estimating the distribution of tern species (Arctic Tern, *Sterna paradisaea*; Common Tern, *Sterna hirundo*; Roseate tern, *Sterna dougallii*; Sandwich Tern, *Sterna sandvicensis*). However, because there is only one regularly breeding colony of Roseate terns in the UK, we did not include this species in our population distribution modelling, instead focussing upon the remaining three tern species. Whereas Wakefield et al. (2017) modelled the intensity of usage as an IPP Wilson et al. (2014) used a logistic regression. Using this approach, the response variable takes the value 1 for tracking observations and 0 for the control (available environment) points (Aarts et al. 2008). However, note that the slope parameters of a logistic regression model will converge to those of an IPP model as the number of available points increases (i.e. modelling approaches are connected, Warton & Sheperd (2010)). Wilson et al. (2014) used visual tracking to follow individuals as opposed to GPS loggers which were used in Wakefield et al. (2017). One benefit of visual tracking compared to GPS tracking is that the spatial location of foraging events was directly recorded by human observers. Therefore, Wilson et al. (2014) modelled the intensity of habitat usage on a sub-set of tracking observations where birds were classified as foraging. In contrast, Wakefield et al. (2017) used all tracking locations for an individual over a 24-hour period regardless of the behaviour of the bird. By focussing on spatial locations classed as foraging signals of habitat selection in the data may be stronger as during periods of other behaviours such as commuting or resting on the water individuals may not be engaged in active habitat selection (Beyer et al. 2010, Wilson et al. 2012). However, in practice it is not clear how much difference focussing on only foraging behaviour or including all behaviours would be expected to alter predicted distributions. For example, recent work conducted by the RSPB (Cleasby et al. 2021, in prep.) suggests that mapped outputs from species distributions models for three diving species (Guillemot, Razorbill, Shag) built using foraging locations identified by dive loggers showed a high degree of similarity to the distribution maps presented in Wakefield et al. (2017). Wilson et al. (2014) also conducted their tracking during the chick-rearing period but were unable to confirm the breeding stage of birds followed. Thus, while their data was probably dominated by breeding individuals this could not be stated with certainty. Habitat usage models in Wilson et al. (2014) were used to generate predicted foraging distributions on a data grid extending out to the maximum foraging range around the colonies of interest and predictions were made to the centre points of grid cells of 500 m² resolution. The maximum foraging range

was taken from Thaxter et al (2012) and was either 30 km (Arctic and Common Terns) or 54 km (Sandwich Terns).

Wilson et al. (2014) provides a generic model for each tern species based upon a combined dataset including information from all colonies tracked. Because we wish to predict usage over large numbers of untracked tern colonies both within the MarPAMM region and beyond we chose to use these generic models of habitat usage when creating tern density maps. While Wilson et al. (2014) tested a suite of environmental covariates not all were subsequently retained in the best fitting habitat models identified (Table 4). Most variables in the generic tern models could be calculated directly but it was not possible to obtain access to the seabed depth data used in Wilson et al. (2014) due to licencing issues. Therefore, we used a freely available source of bathymetry data for information on seabed depth downloaded from EMODnet (<https://www.emodnet-bathymetry.eu/data-products>). EMODnet provides a Digital Terrain Model (DTM) of seabird depth with a resolution of ~ 115 m². For context, the resolution of bathymetry data in Wilson et al. (2014) had a resolution that varied from 30 m² to 180 m². Details on the fixed estimates from generic habitat models for Arctic, Common and Sandwich Terns displayed in Table 5.

Table 4. Details of the covariates included in the generic tern models presented in Wilson et al. (2014).

Covariate	Description	Species for which covariate was included in habitat model
Distance from Colony	Euclidean (straight-line) distance was used rather than distance by sea	Arctic Tern, Common Tern, Sandwich Tern
Seabed Depth	Calculated using Defra's Digital Elevation Model. However, we could not access this data so depth data in the current work was sourced from EMODnet	Arctic Tern, Common Tern, Sandwich Tern
Distance from Shore	Shortest distance between centre of a grid cell and land	Common Tern, Sandwich Tern

2.5. Mapping tern distributions under current conditions and new climate change scenarios

Wilson et al. (2014) provides maps of tern distributions at specific SPAs around the UK but does not provide tern distributions at larger scales. Therefore, for each tern species the intensity of usage and thereby the UD for birds from each Seabird 2000 site were predicted using the fixed-effects part of the best fitting models described in Wilson et al. 2014 (Table 5). We chose colony definitions that aligned with those used in outputs from Davies et al. (2021) allowing for easy one-to-one matching between different datasets. Predicted distributions from each site were normalized to sum to 1.0 to ensure they met the definition of a UD. Colony-level UDs were then transformed to relative density surfaces by weighting them by population size estimates from the Seabird 2000 census and aggregating colony-level distributions across all colonies within the MarPAMM region and 2 km buffer (similar maps including all colonies within the UK and Ireland can be found within the Appendix). Multiplying relative density surfaces by the absolute number of terns within the MarPAMM regions also provided maps of absolute tern density. In addition, relative density surfaces were calculated using predictions for every coastal tern colony counted as part of the Seabird 2000 census to provide UK-wide distribution maps. However, we did not include distributions for tern colonies recorded as inland colonies during the Seabird 2000 census due to the implausibility of calculating variables such as distance from coast and at sea distributions across large parts of their foraging range.

When generating updated maps of tern distributions in response to climate change we were unable to access any climate predictions for the covariates described in Table 4. Therefore, we used the same values for these covariates in both current and future predictions of tern distributions. However, colony size projections were available as part of the population modelling presented in Davies et al. (2021) and we chose the median colony size estimate for each tern colony as our updated measure of colony size under climate change. Because we used the same set of covariates when estimating both current and projected tern distributions, colony-level distributions will not differ but differences in the relative sizes of tern colonies under climate change may drive differences in broader scale tern distributions when aggregating distributions across multiple colonies.

Table 5. Summary of fixed effects from generic habitat models in Wilson et al. (2014). Note that no standard errors around coefficient estimates were provided in JNCC report.

2.6. Estimation of Uncertainty

Modelled predictions of seabird density under climate change are subject to multiple sources of uncertainty. In the current work two important sources of such uncertainty are: 1) uncertainty in population sizes estimates obtained from Davies et al. 2021, and 2) uncertainty in parameter estimates from the habitat models used. Of these two sources of uncertainty,

Species	Covariate	Estimate
Arctic Tern	Intercept	-0.96
	Distance from Colony	-0.22
	Seabed Depth	-0.01
Common Tern	Intercept	-0.74
	Distance from Colony	-0.19
	Seabed Depth	-0.001
	Distance from Coast	-0.10
Sandwich Tern	Intercept	0.28
	Distance from Colony	-0.09
	Seabed Depth	0.03
	Distance from Coast	-0.20

it was judged that uncertainty in predictions of colony size will have a larger impact on mapped outputs than uncertainty associated with habitat modelling, particularly given uncertainty in colony size projections was high some species (see: Davies et al. 2021). This judgement was made on the basis that variation in estimates of population size at each colony will have a direct influence on the density / abundance of birds at sea when aggregating the relative density of birds across colonies to a single map. Therefore, we quantified spatial variation in the relative uncertainty of predicted seabird distributions by plotting the coefficient of variation (CV) in density across the study area. To achieve this, we used a re-sampling approach in which we estimated the relative density of birds at each colony using equation 1 and drawing estimates of colony size from the posterior distribution of colony sizes available in Davies et al. (2021). For each seabird colony we performed 100 simulations in which relative density was calculated using randomly sampled estimates of colony size. We then aggregated colony-level simulations to generate 100 maps of seabird density throughout the MarPAMM region and used these simulations to calculate CV at each grid cell (similar results for UK and Ireland available in Appendix).

In addition to estimating the relative uncertainty arising from variation around estimates of population size we ran simulations that incorporated uncertainty from both population

modelling and habitat modelling. However, because no standard errors are reported for the tern habitat models this approach was restricted to the four species included in Wakefield et al. (2017). In addition, because of the prohibitive computing time required to perform the re-sampling approach outlined below across large number of colonies and multiple species (current estimates of time to perform 100 simulations are ~25 hours per 100 colonies for a given species), we restricted our focus to investigating the spatial uncertainty arising from both population and habitat modelling to colonies found within the Rathlin Island SPA. The Rathlin Island SPA was chosen as it represents an important site for each of the four species in Wakefield et al. (2017) that also lies within the MarPAMM region. We used a re-sampling approach in which the sampling distribution of fixed effects within each habitat model in Wakefield et al. (2017) was estimated using the standard errors around each coefficient to generate 100 sets of fixed-effects parameters. We combined these 100 sets of fixed effect parameters with simulated values for those covariates in habitat models that related to intraspecific competition by drawing 100 estimates of population size for each colony from posterior distributions of colony size from Davies et al. (2021). These simulated values were then used to create 100 colony-level UD's for each colony. Each of these colony-level UD's was then converted to a relative density map by multiplying the UD by the same estimate of population size used to update covariates relating to intraspecific competition. Relative density maps were then aggregated across individual colonies within the Rathlin Island SPA resulting in 100 maps of seabird density that were used to calculate CV at each grid cell. A summary of results relating to uncertainty modelling is included within the Appendix.

3. Results

3. 1. Black-legged Kittiwake

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 2. In general, there was a decrease in the density of Kittiwake throughout the MarPAMM region under future climate scenarios reflecting the expected decreases reported in Davies et al. (2021). Areas of relatively high density were found around Rathlin Island under both current and future conditions. However, reductions in predicted density under climate change were apparent throughout

the Inner Seas off the West coast of Scotland. Such patterns are also apparent in plots of the predicted absolute change in density of Kittiwakes throughout the region (Fig. 3). There was also evidence of an increase in the predicted density of birds in the area immediately surrounding Rathlin Island under the future climate projections. Other areas in which the density of Kittiwakes was expected to increase under future climate projection typically occurred at the fringes of Kittiwake distributions and involved relatively small increases in density. For example, much of the area in which Kittiwake distributions were predicted to increase fell out-with the boundaries of estimated 95% UD contours (Fig. 4). Overall, both the 95% and 50% UD contours of Kittiwakes within the MarPAMM region showed large areas of overlap between current and projected future conditions. However, the 95% UD contour under climate change extended slightly further west. More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 2. The predicted density of breeding Black-legged Kittiwakes (No. birds per km²) based on habitat models in Wakefield et al. (2017). Density represents the density of birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wakefield et al. (2017) based on current conditions. b) Predictions based upon future climate modelling of key oceanographic variables and updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S2 in Appendix.

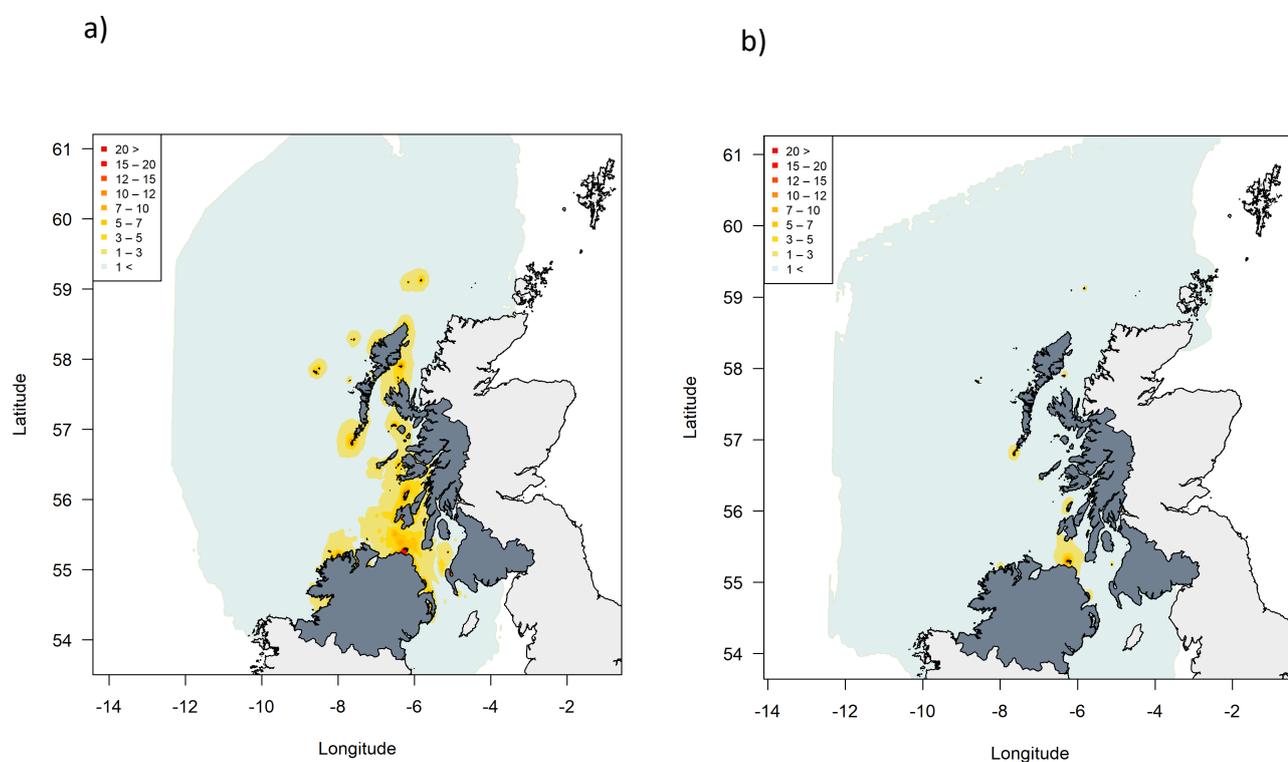


Fig. 3. Absolute change in the density of breeding Kittiwakes (change in No. birds per km²) between current conditions (Wakefield et al. 2017) and under future climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S3 in Appendix.

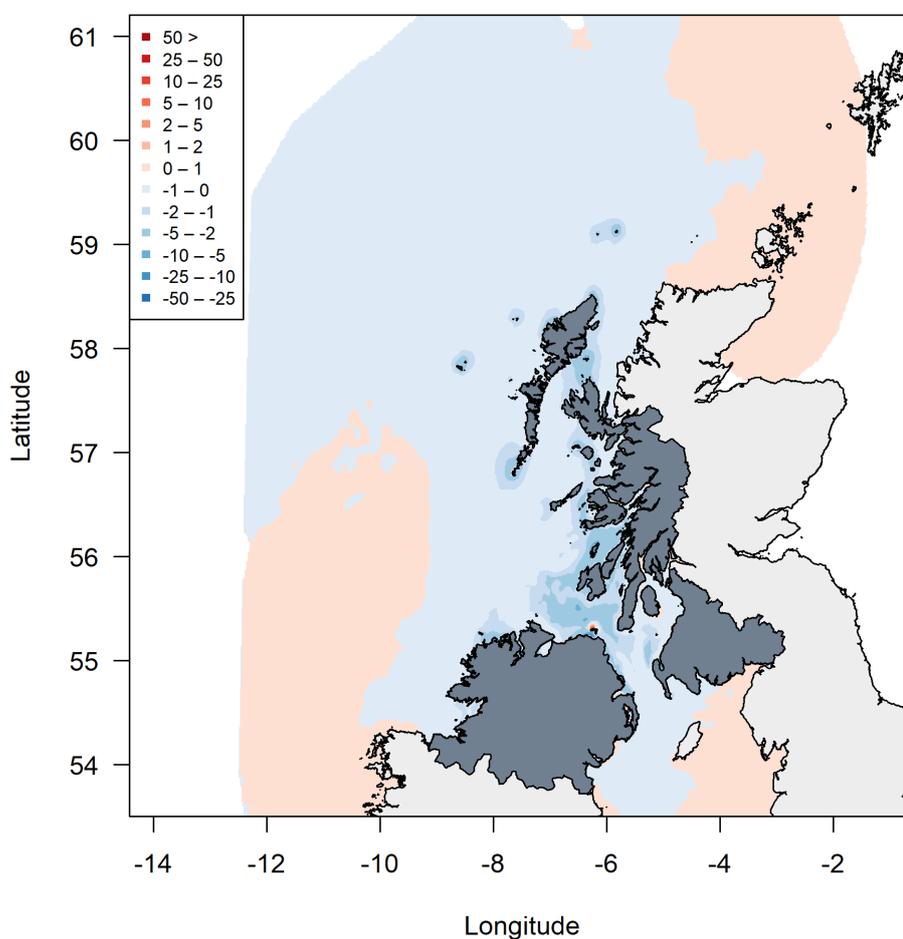
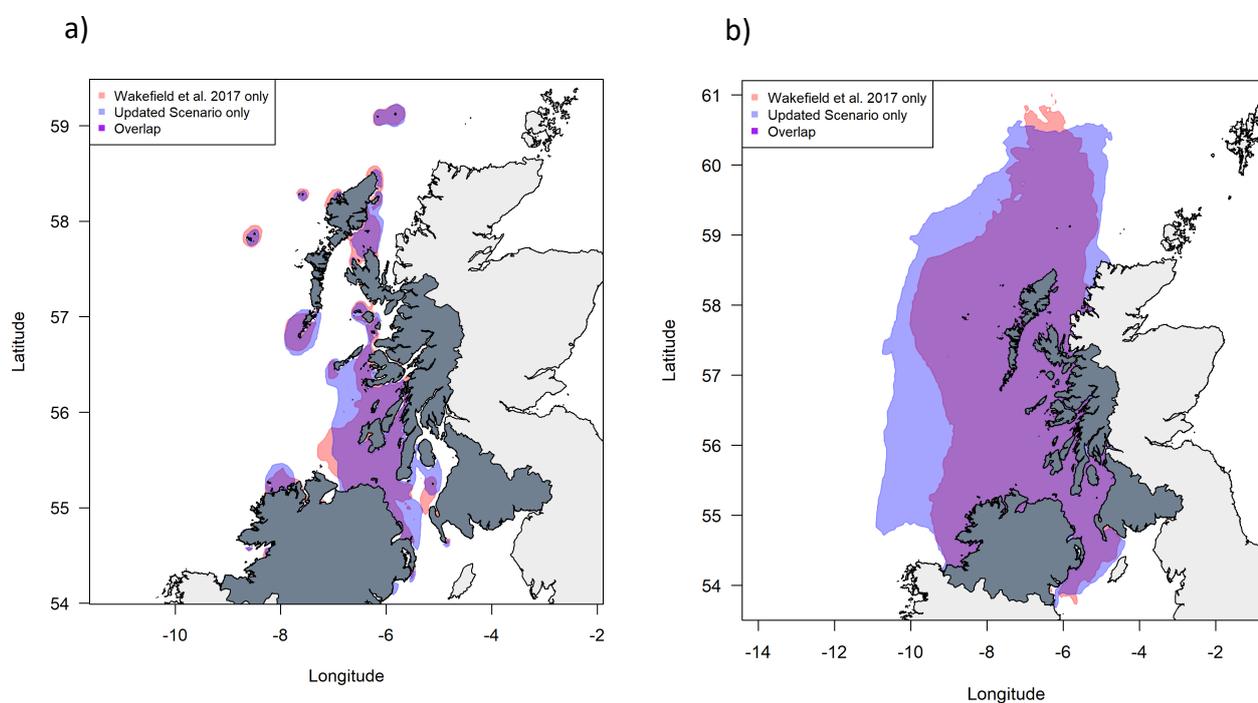


Fig. 4. Overlap of 50% (core range) and 95% (home range) UD contours for breeding Kittiwakes originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wakefield et al. 2017) or projected future conditions. a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S5 in Appendix.



3. 2. Common Guillemot

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 5. In general, maps of the change in density showed declines in Guillemot density throughout most of the MarPAMM region. Such declines were particularly apparent in the vicinity of larger Guillemot colonies throughout the MarPAMM region (Fig. 6.). Increases in Guillemot density were predicted in certain localized areas within the Inner Seas off the West coast of Scotland, but the magnitude of density increases in such areas were relatively small compared to the predicted decreases in other areas. However, within a national-scale context such increases

in Guillemot density are higher than observed increases in other areas of the UK and Ireland outside of Northern Scotland (Fig. S8). Other areas in which the density of Guillemot was expected to increase in the MarPAMM region under future climate projection typically occurred at the fringes of Guillemot distributions and involved relatively small increases in density outside of predicted 95% UD contours (Fig. 6 and Fig. 7). A general decrease in the density of Guillemot throughout the MarPAMM region under future climate scenarios reflects the expected decreases in Guillemot abundance reported in Davies et al. (2021). Both the 95% and 50% of Guillemot within the MarPAMM region showed large areas of overlap between current and projected future conditions. However, 50% and 95% UD contours covered a slightly larger area under future climate change projections. More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 5. The predicted breeding density of Common Guillemot (No. birds per km²) based on habitat models in Wakefield et al. (2017). Density represents the density of breeding birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wakefield et al. (2017) based on current conditions. b) Predictions based upon future climate modelling of key oceanographic variables and updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S7 in Appendix.

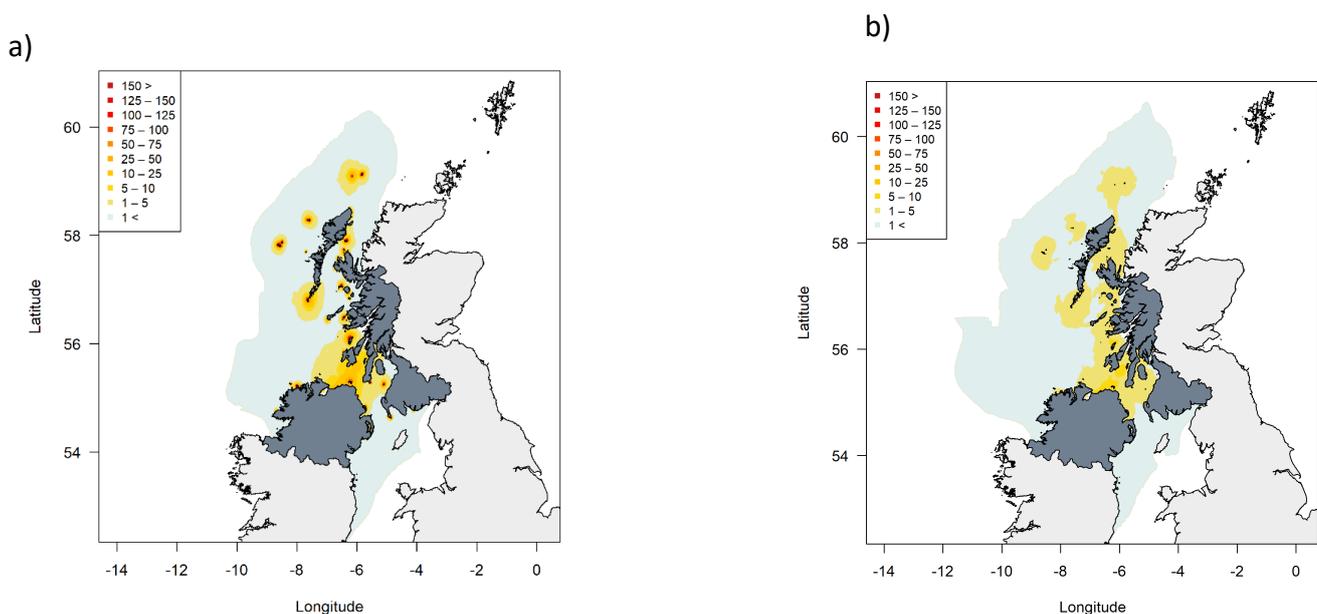


Fig. 6. Absolute change in the density of breeding Common Guillemot (change in No. birds per km²) between current conditions (Wakefield et al. 2017) and under future climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S8 in Appendix.

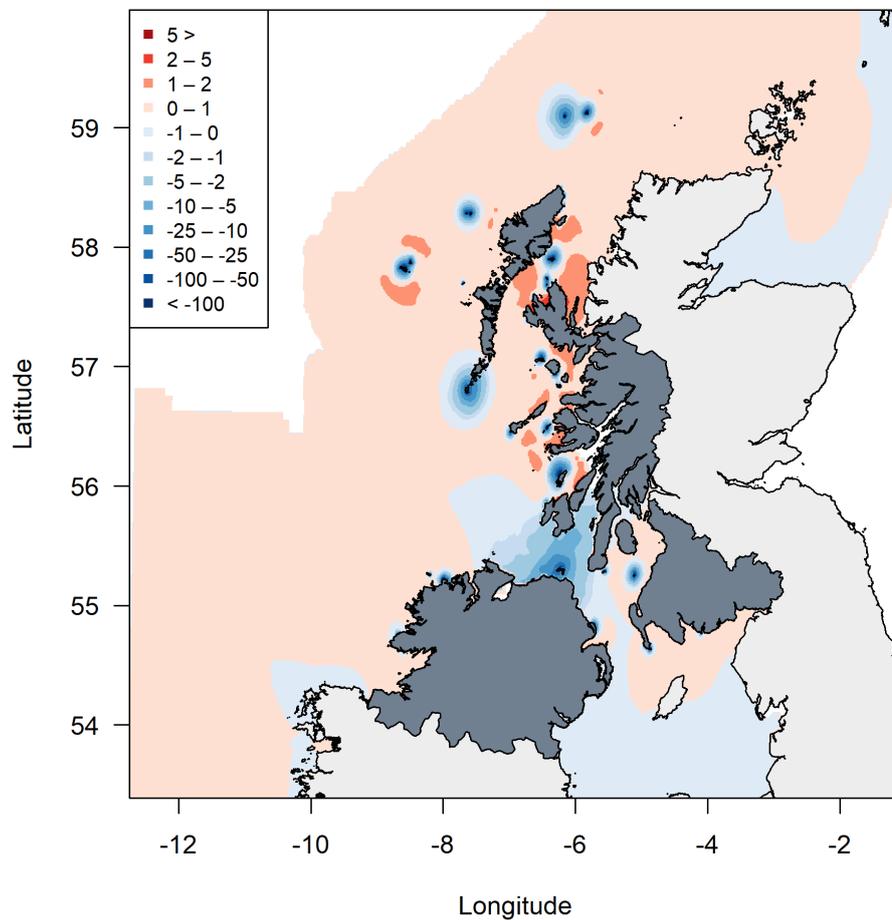
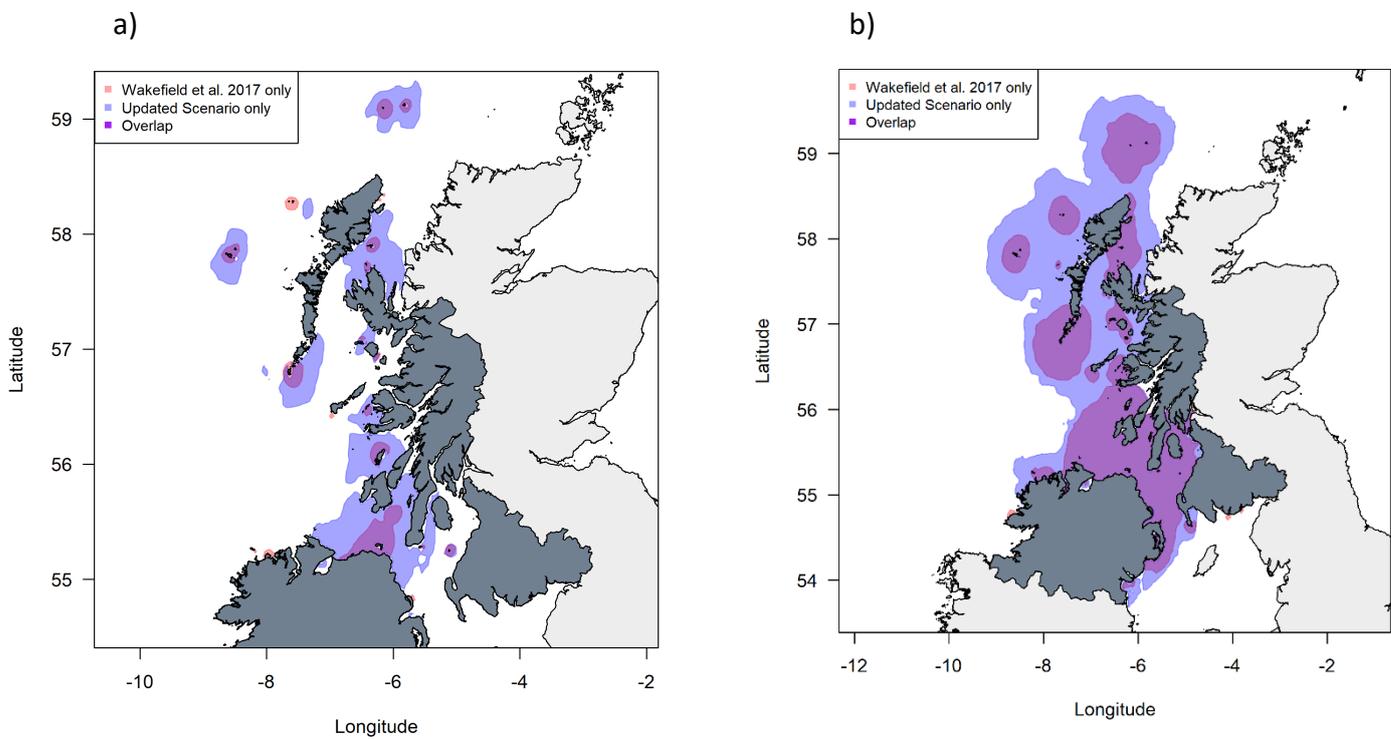


Fig. 7. Overlap of 50% (core range) and 95% (home range) UD contours for breeding Common Guillemot originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wakefield et al. 2017) or future projected conditions. a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S10 in Appendix.



3. 3. Razorbill

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 8. In general, Razorbill density declined throughout the MarPAMM region under climate change projections mirroring similar findings related to Razorbill population abundance in Davies et al. 2021. However, some areas of higher Razorbill density concentrated around larger Razorbill colonies were still predicted. Indeed, maps of change in absolute density show that the density of Razorbills was predicted to increase in areas directly surrounding large colonies under climate change projections while declining in areas further from such colonies (Fig. 9). Other areas in which the density of Razorbill was expected to increase under future climate projection typically occurred at the fringes of Razorbill distributions and involved relatively small increases in density outside of predicted 95% UD contours (Fig. 9 and Fig. 10). While the 95% and 50% of Razorbill within the MarPAMM region showed large areas of overlap between current and projected future conditions there were some noticeable differences. Firstly, both 50% and 95% UDs covered a greater area under current conditions than under climate change projections. For example, based on 50% UD calculated under future climate change projections. Razorbill core areas were concentrated around colony locations. In contrast, such 50% UDs were predicted to cover most of the Inner Seas off the West coast of Scotland under current conditions. More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 8. The predicted density of breeding Razorbill (No. birds per km²) based on habitat models in Wakefield et al. (2017). Density represents the density of birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wakefield et al. (2017) based on current conditions. b) Predictions based upon climate modelling of key oceanographic variables and updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S12 in Appendix.

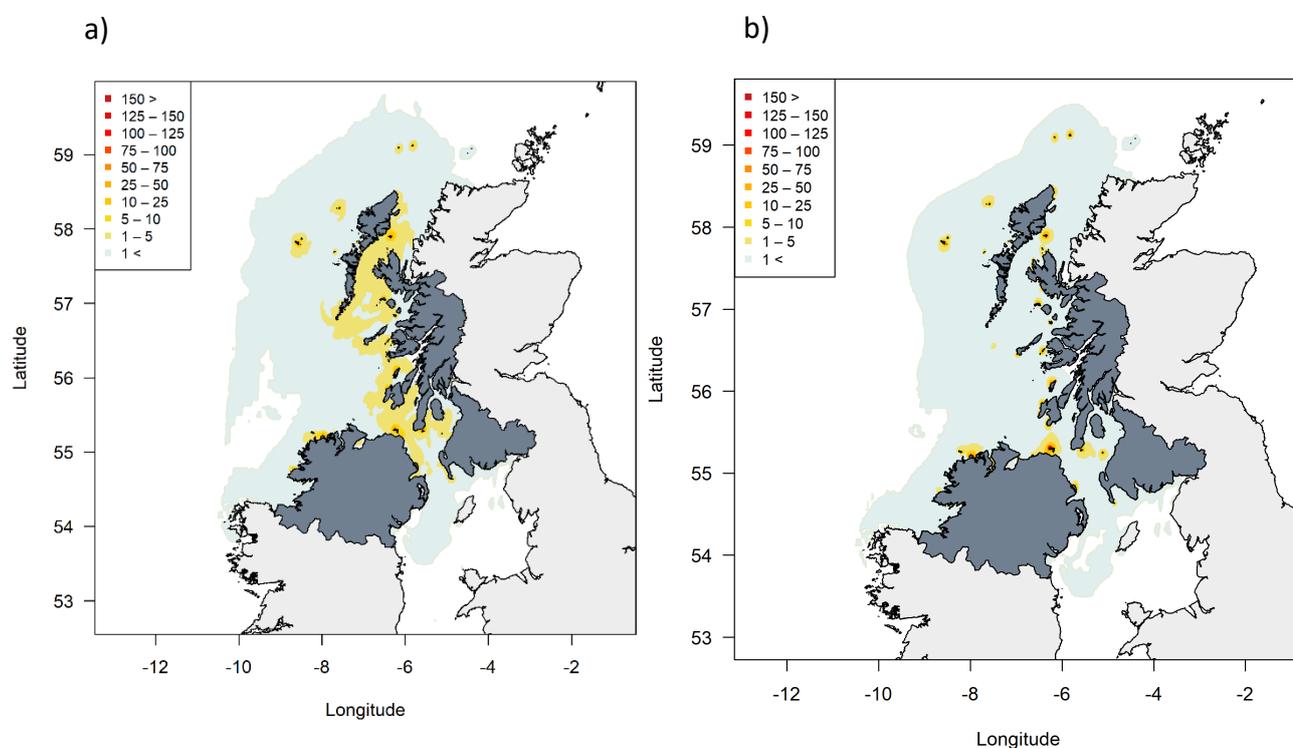


Fig. 9. Absolute change in the density of breeding Razorbill (change in No. birds per km²) between current conditions (Wakefield et al. 2017) and under future climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S13 in Appendix.

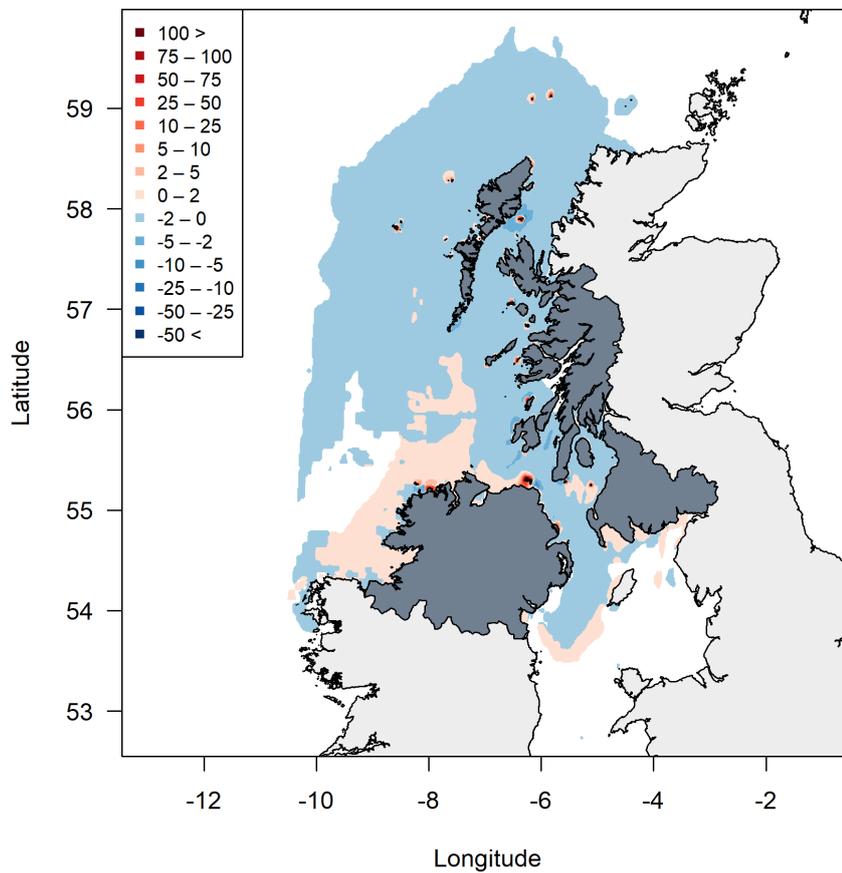
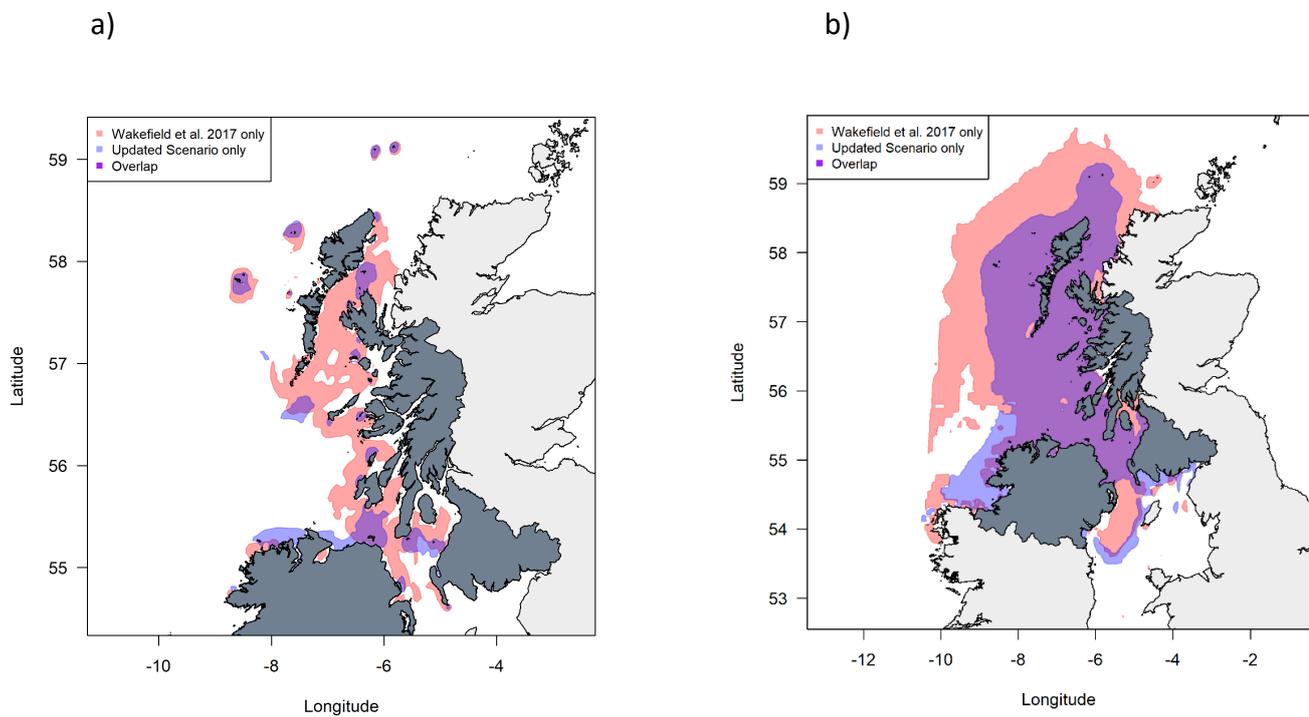


Fig. 10. Overlap of 50% (core range) and 95% (home range) UD contours for breeding Razorbill originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wakefield et al. 2017) or future projected conditions. a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S15 in Appendix.



3. 4. European Shag

Maps displaying the predicted density of breeding birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 11. In general, European Shag density increased throughout the MarPAMM region under climate change projections as expected based on results reported in Davies et al. 2021. More noticeable increases in Shag density occurred to the south of Rathlin Island at various points around the coast of the Inner Hebrides and along the west coast of the Mull of Kintyre (Fig. 12). Such density increases were concentrated in the vicinity of large colonies. Both 50% and 95% UD covered a greater area under current conditions than under climate change projections (Fig. 13). For example, based on 95% UD calculated under climate change predictions the home range of Shags in the areas were more concentrated around colony locations under climate change projections than under current conditions. Similar patterns were also seen in 50% UD contours but are more difficult to visualize given the small area covered by such contours. More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 11. The predicted density of breeding European Shag (No. birds per 0.5 km²) based on habitat models in Wakefield et al. (2017). Density represents the density of breeding birds originating from colonies located within the terrestrial MarPAMM region which is hatched with horizontal lines for ease of visualisation. a) Original predictions from Wakefield et al. (2017) based on current conditions. b) Predictions based upon future climate modelling of key oceanographic variables and updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S17 in Appendix.

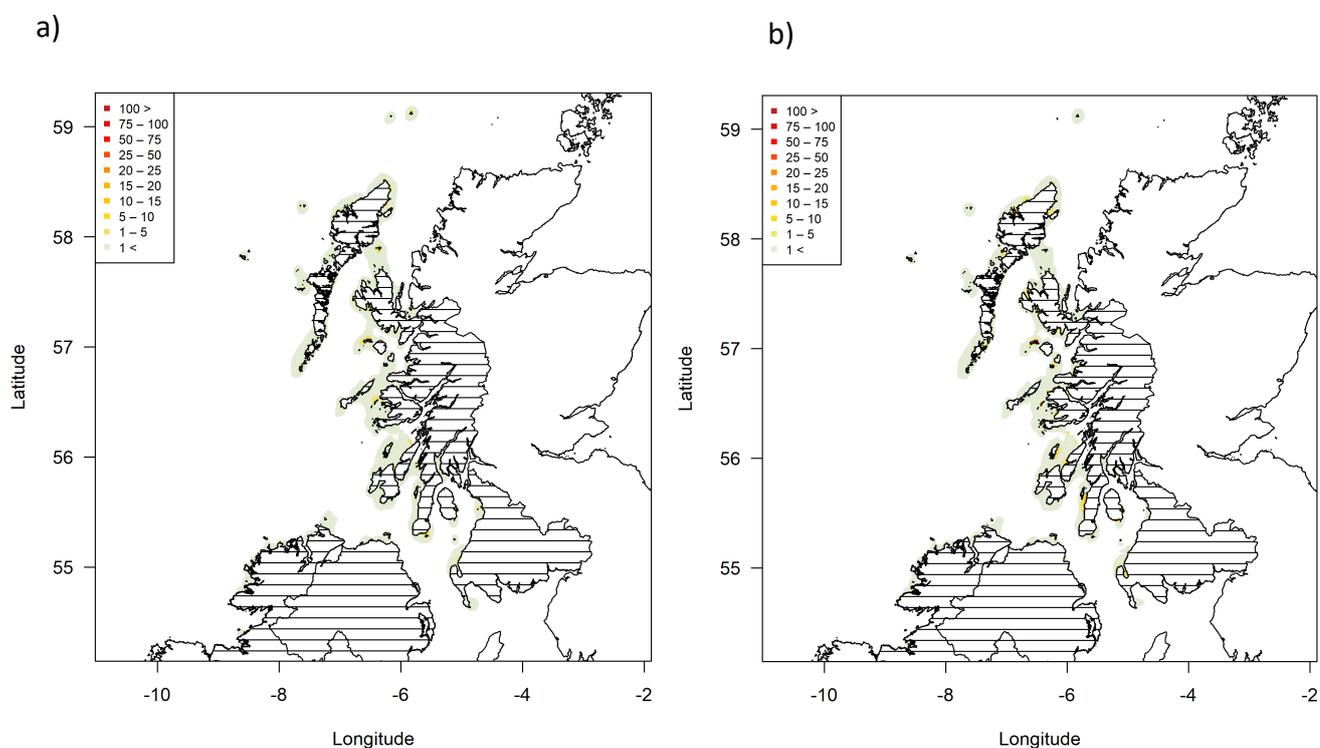
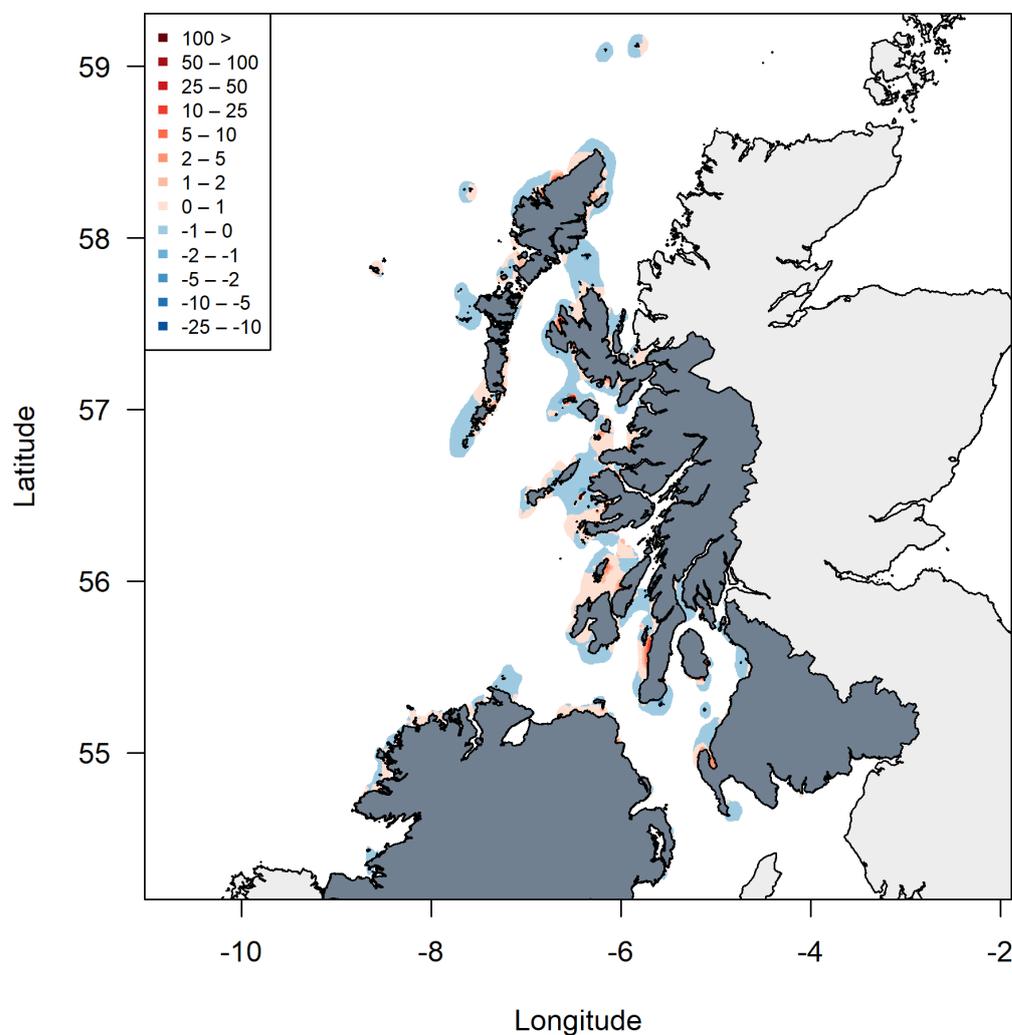
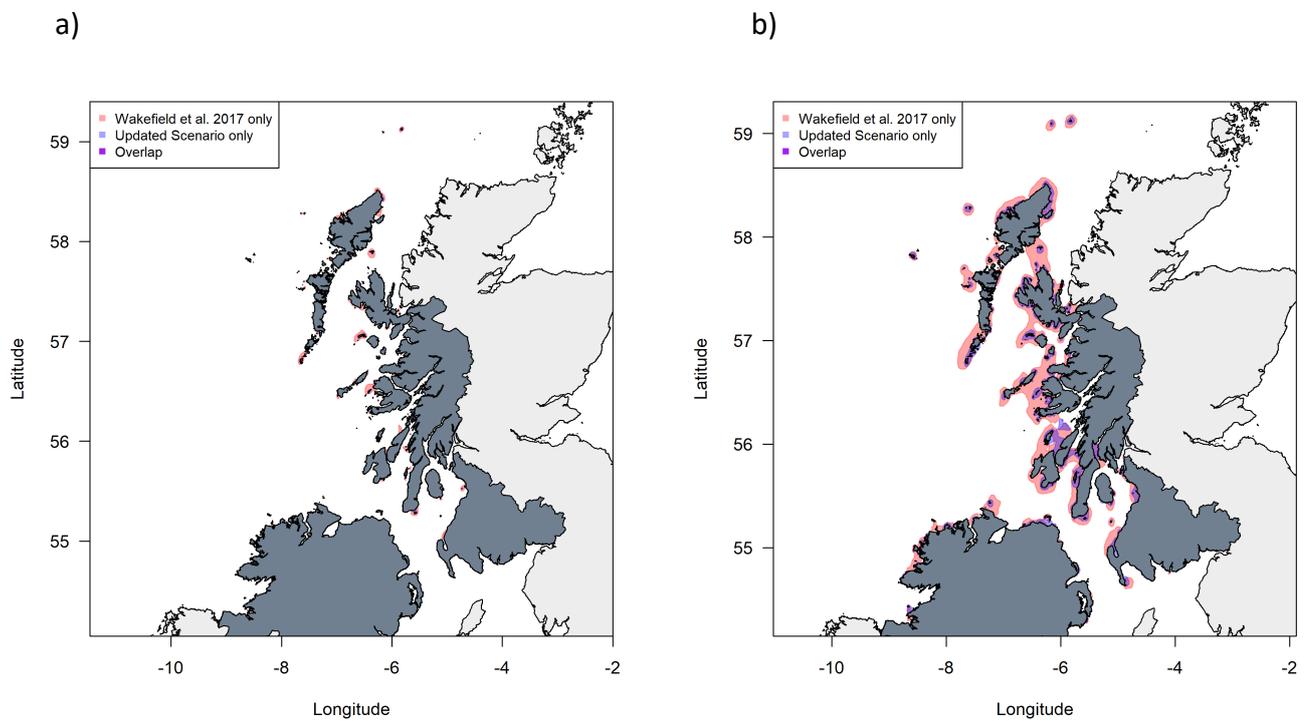


Fig. 12. Absolute change in the density of breeding European Shag (change in No. birds per 0.5 km²) between current conditions (Wakefield et al. 2017) and under climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours



indicating greater increases. For UK and Ireland equivalent map see Fig. S18 in Appendix.

Fig. 13. Overlap of 50% (core range) and 95% (home range) UD contours for breeding European Shag originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wakefield et al. 2017) or projected conditions. a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S20 in Appendix.



3. 5. Arctic Tern

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 14. The predicted density of Arctic Terns declined throughout the entire MarPAMM region in line with the steep declines in abundance (greater than 50%) predicted for Arctic Tern in Davies et al. (2021). As such, we did not identify any part of the range of Arctic Tern within the MarPAMM region where density was predicted to increase (Fig. 15). The 50% and 95% UD of Arctic Terns in the MarPAMM showed a high degree of overlap between current and projected future conditions suggesting little change in the distribution of Arctic Terns even as their abundance was predicted to decline (Fig. 16). More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 14. The predicted density of Arctic Tern (No. birds per 0.5 km²) based on habitat models in Wilson et al. (2014). Note breeding status of birds was unknown. Density represents the density of birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wilson et al. (2014) based on current conditions. b) Predictions based upon updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S22 in Appendix.

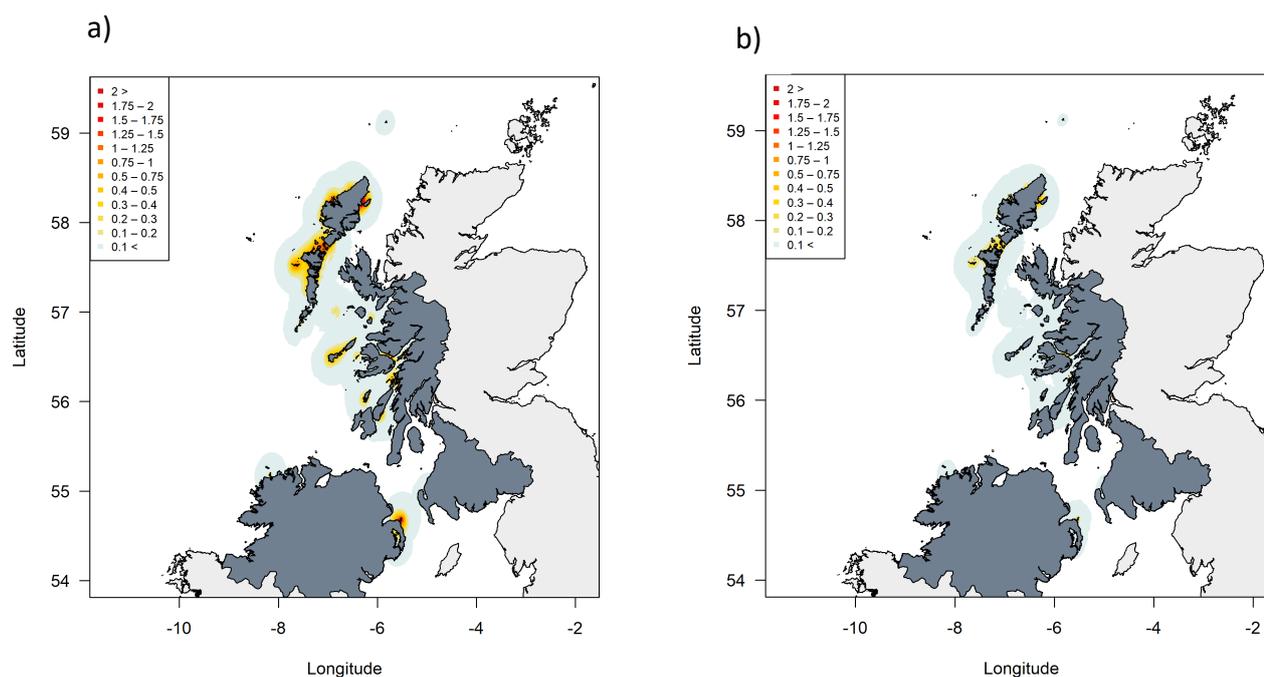


Fig. 15. Absolute change in the density of Arctic Tern (change in No. birds per 0.5 km²) between current conditions (Wilson et al. 2014) and under climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S23 in Appendix.

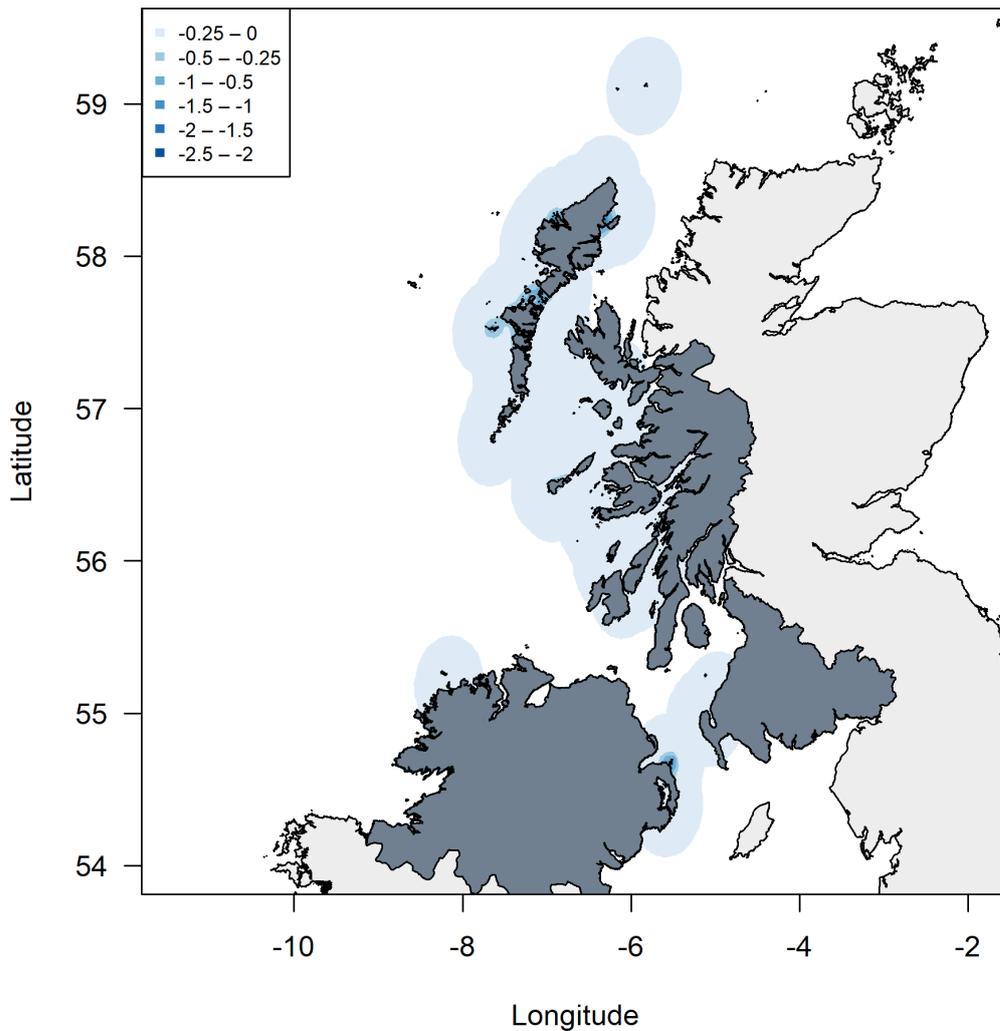
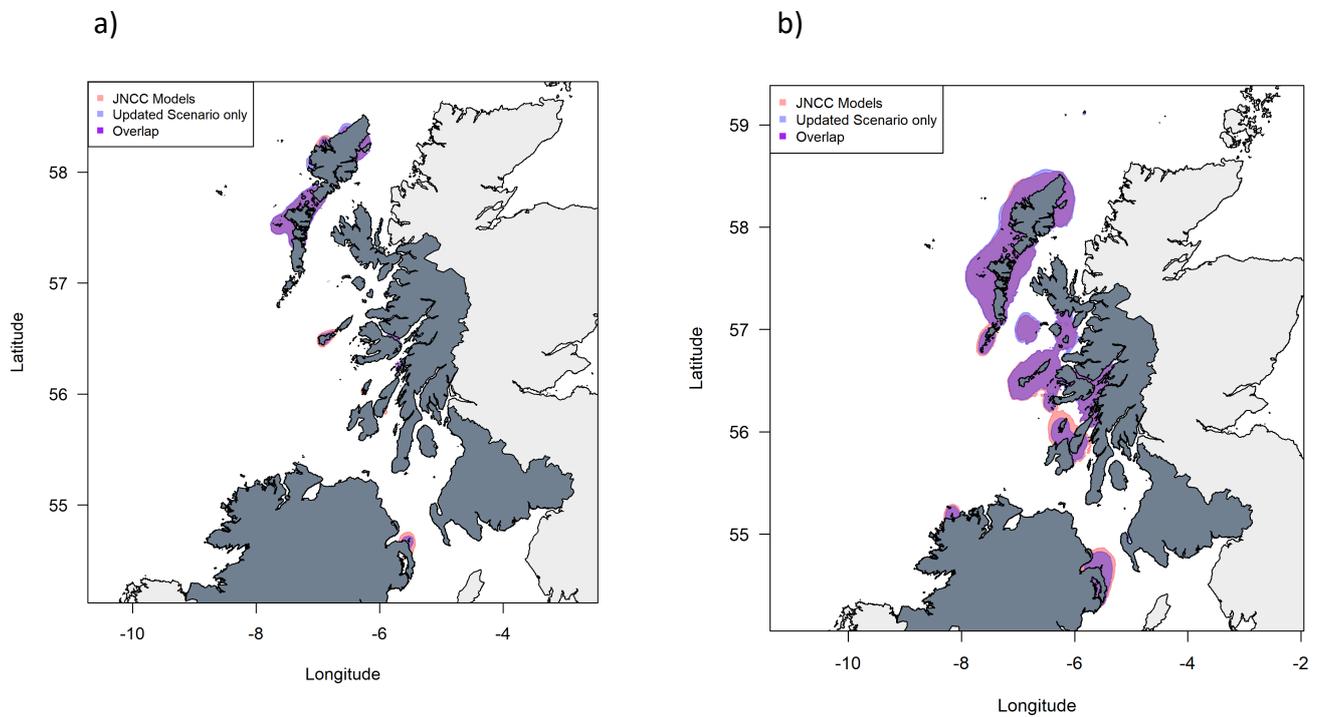


Fig. 16. Overlap of 50% (core range) and 95% (home range) UD contours for Arctic Tern originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (JNCC Models - Wilson et al. 2014) or projected conditions (Updated Scenario). a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S2 in Appendix. For UK and Ireland equivalent map see Fig. S25 in Appendix.



3.6. Common Tern

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 17. Davies et al. (2021) predicted slight increases in Common Tern population abundance throughout the UK and Ireland. Across the MarPAMM region increases in Common Tern density were predicted to occur around the coast of south-west Scotland, in coastal areas around the Inner and Outer Hebrides and along certain sections of the north coast of Ireland (Fig. 18). Increases in absolute density within the MarPAMM region were relatively small but contrast with expected declines in predicted Common Tern densities in southern areas of the UK and Ireland (see Appendix). The 50% and 95% UD of Common Terns in the MarPAMM region showed a high degree of overlap between current and projected future climate conditions (Fig. 19). More detailed maps containing extra information on more UD contours as well as similar results at the UK and Ireland scale are presented in the Appendix.

Fig. 17. The predicted density of Common Tern (No. birds per 0.5 km²) based on habitat models in Wilson et al. (2014). Note breeding status of birds was unknown. Density represents the density of birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wilson et al. (2014) based on current conditions. b) Predictions based upon updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S27 in Appendix.

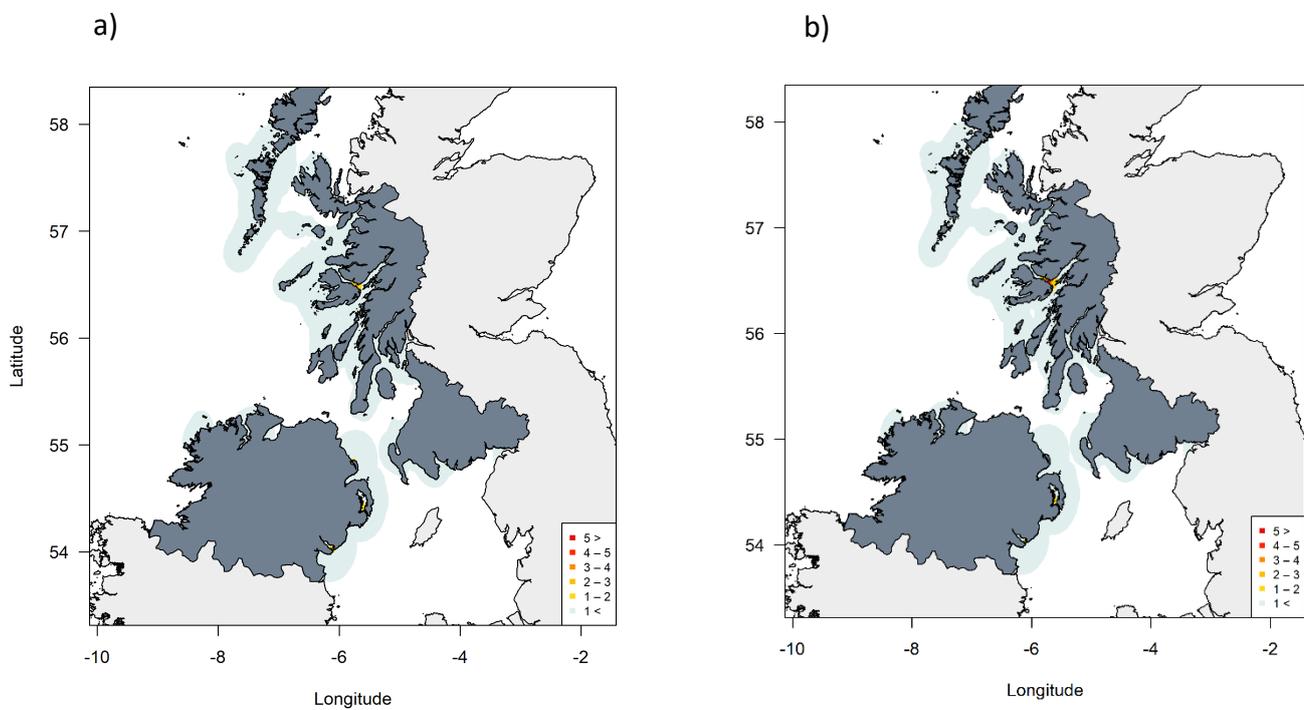


Fig. 18. Absolute change in the density of Common Tern (change in No. birds per 0.5 km²) between current conditions (Wilson et al. 2014) and under climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S28 in Appendix.

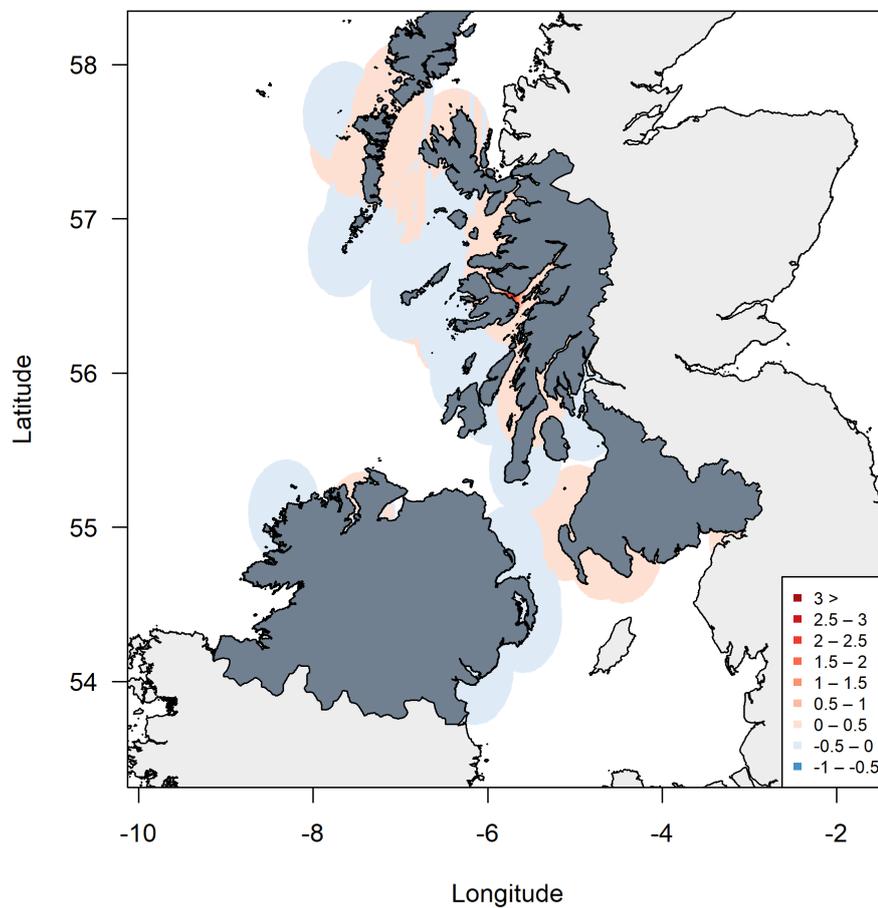
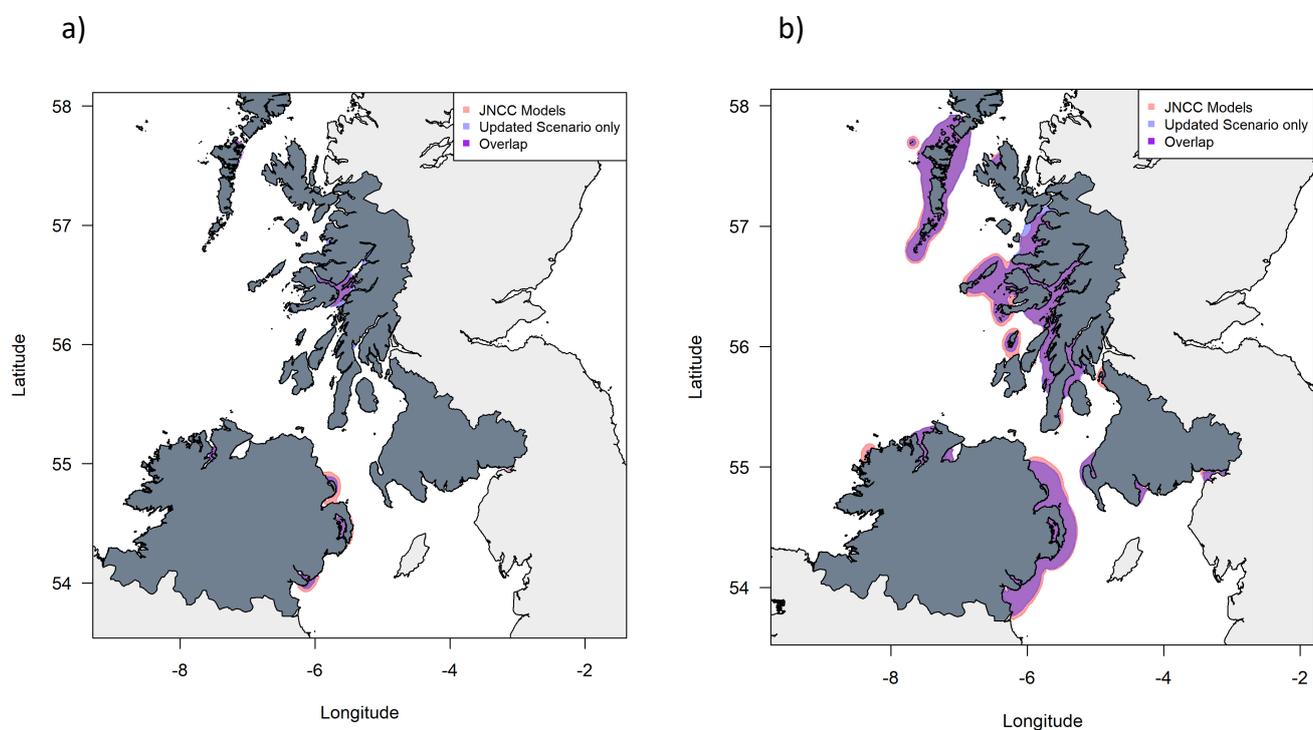


Fig. 19. Overlap of 50% (core range) and 95% (home range) UD contours for Common Tern originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wilson et al. 2014 – JNCC models) or projected conditions (Updated Scenario). a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S30 in Appendix.



3.7. Sandwich Tern

Maps displaying the predicted density of birds from colonies within the MarPAMM region under both current and future climatic conditions are displayed in Fig. 20. However, it should be borne in mind that relatively few Sandwich Tern colonies were identified within the MarPAMM region centered in two main regions, County Down and County Donegal. Plots of the change in absolute Sandwich Tern density show that declines in population abundance were predicted around Sandwich Tern colonies in County Down, but increases were predicted around colonies in County Donegal (Fig. 21). However, the magnitude of these changes was very small. The 50% and 95% UD of Sandwich Terns in the MarPAMM region showed a high degree of overlap between current and projected future climate conditions (Fig. 22). However, both the 50% and 95% UD contours were slightly smaller in marine areas off the coast of County Down and extended further off the coast of County Donegal reflecting shifts in the relative size of Sandwich Tern populations in these areas.

Fig. 20. The predicted density of Sandwich Tern (No. birds per 0.5 km²) based on habitat models in Wilson et al. (2014). Note breeding status of birds was unknown. Density represents the density of birds originating from colonies located within the terrestrial MarPAMM region which is highlighted in dark grey. a) Original predictions from Wilson et al. (2014) based on current conditions. b) Predictions based upon updated estimates of population size from Davies et al. (2021). For UK and Ireland equivalent map see Fig. S32 in Appendix.

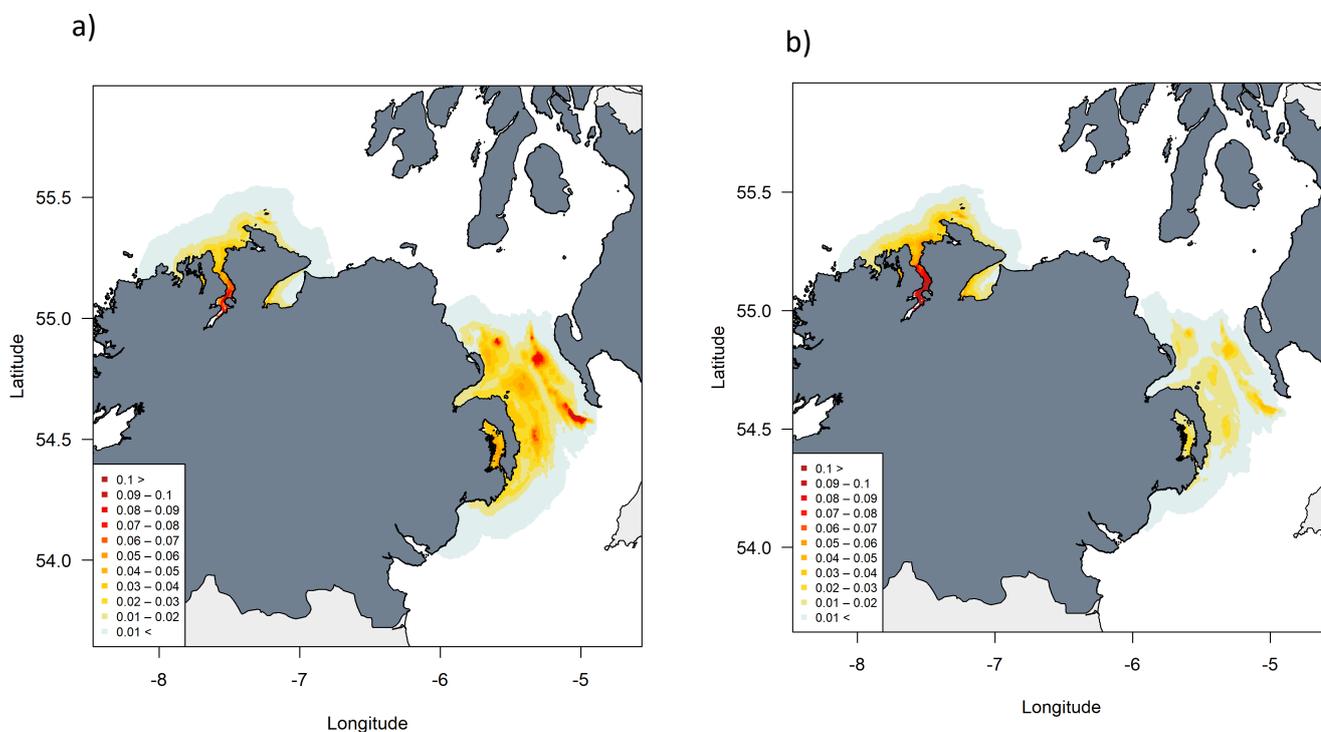


Fig. 21. Absolute change in the density of Sandwich Tern (change in No. birds per 0.5 km²) between current conditions (Wilson et al. 2014) and under climate change projections for birds originating from colonies within the terrestrial MarPAMM region. Blue colours indicate reductions in absolute density with darker blue colours indicating greater reductions. Red colours indicate an increase in absolute density with darker red colours indicating greater increases. For UK and Ireland equivalent map see Fig. S33 in Appendix.

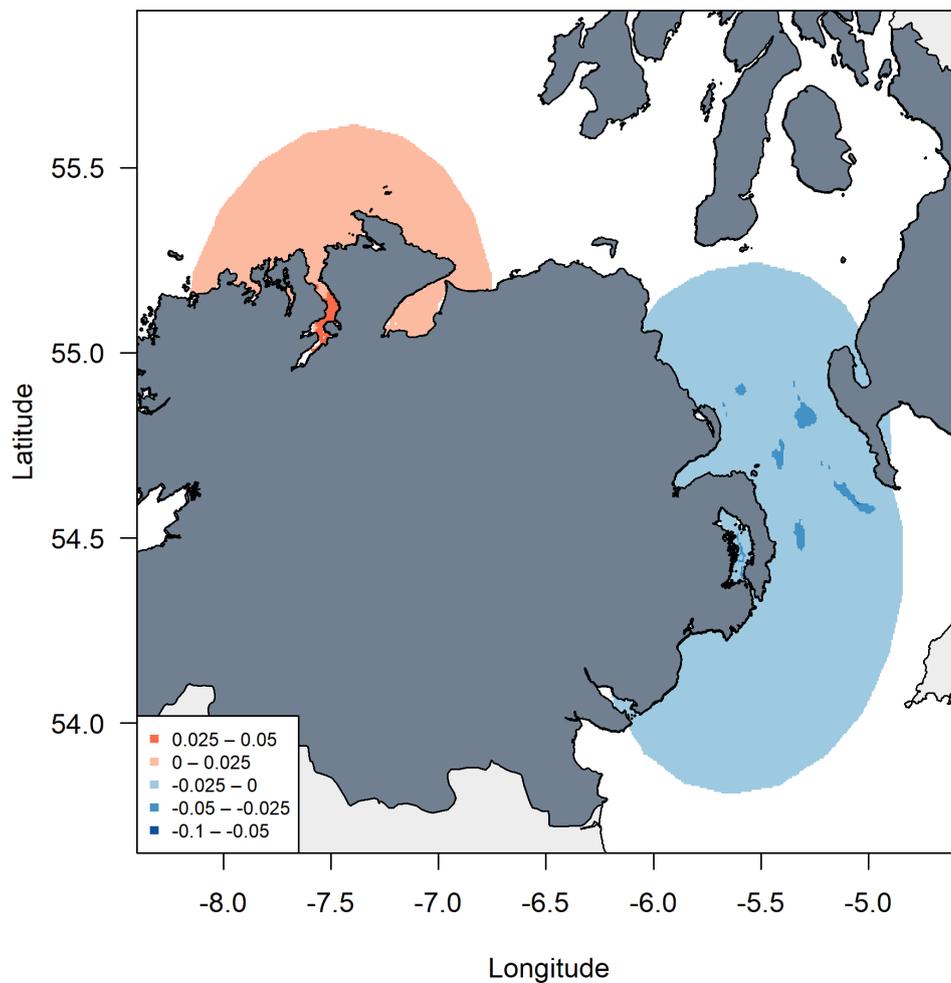
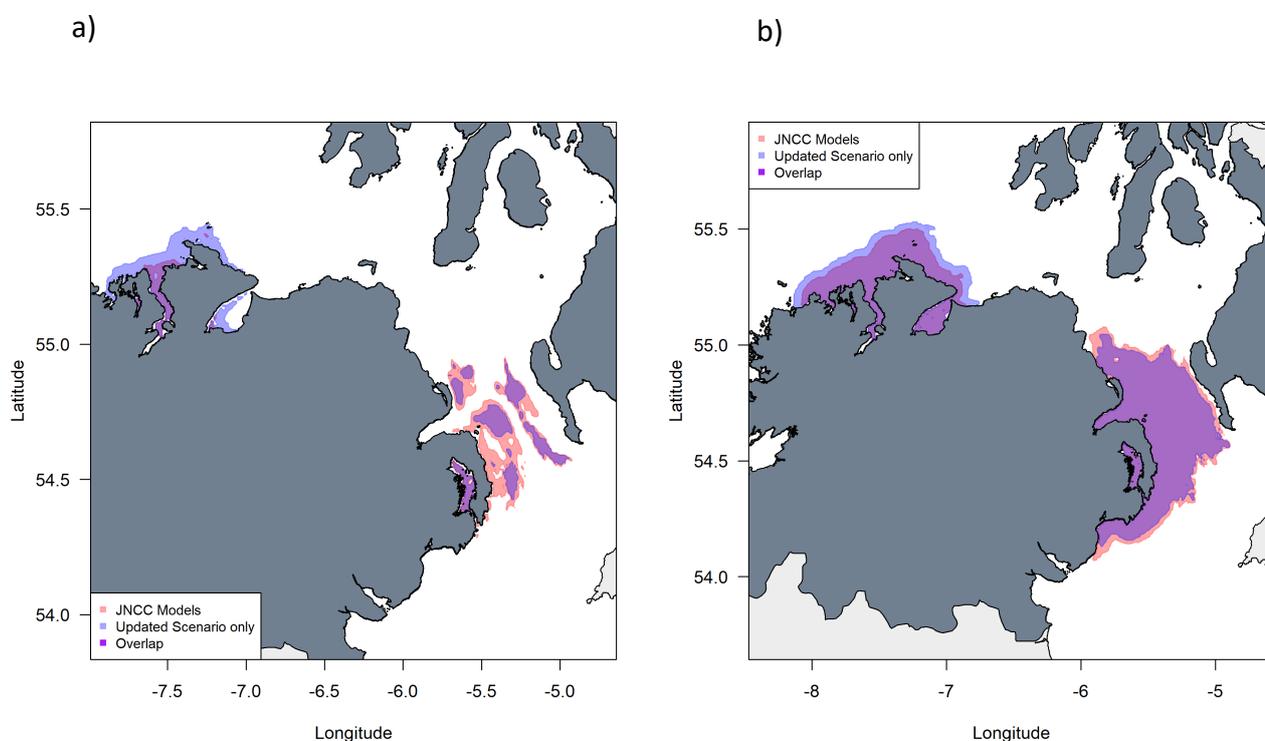


Fig. 22. Overlap of 50% (core range) and 95% (home range) UD contours for Sandwich Tern originating from colonies within the terrestrial MarPAMM region highlighting areas where UD contours overlap or diverge under current (Wilson et al. 2014 – JNCC Models) or projected conditions (Updated Scenario). a) 50% UD contour; b) 95% UD contour. For UK and Ireland equivalent map see Fig. S35 in Appendix.



3.8. Seabird distributions at the UK scale

While the current report focuses on the distribution and abundance of species within the MarPAMM region, species distribution maps covering the entire UK and Ireland are available in the Appendix. Broader scale maps suggest that declines in Razorbill distributions are most marked in the southern part of the species range. For example, Razorbill 50% and 95% UD contours shifted northwards and covered a smaller area of English and Welsh waters under climate change projections (Fig. S15). Similarly, Guillemot density tended to decline across most of the species range and any predicted increases in density appeared to be concentrated in northern Scotland (Fig. S8). In Kittiwakes predicted increases in density under climate change projections were observed in North Sea coastal areas in the vicinity of breeding colonies and along a stretch of the eastern coast of Ireland centred around Dublin bay (Fig. S3). Predicted distributions of European Shag are difficult to visualise at the national scale due to their restricted foraging ranges. However, the results reported for Shag within the MarPAMM region appear to be repeated at the larger scale throughout the UK and Ireland. Namely, increases in Shag density close to breeding colonies but also a contraction of UD contours (Fig. S20).

At the UK and Ireland scale the abundance of Arctic Terns was predicted to decline throughout the species range under future climate projections. However, declines in species 95% UD occurred largely in the southern part of the species range at colonies located around the Welsh and Irish coasts. In contrast, no such range contractions were predicted in colonies from the Northern Isles or the Outer Hebrides (Fig. S24 and S25). For Common Terns increases in predicted density tended to occur in more Northern and Eastern areas of the UK (Fig. S28). As a result, the distribution of Common Tern was predicted to shift in this direction and areas along the Southern and South-Eastern coasts of England declined in importance slightly (Fig. S30). Sandwich Tern distributions shifted northwards alongside general declines in species abundance under projected climate change (Fig. S35).

4. Discussion

Distribution Predictions for Black-legged Kittiwake, Common Guillemot, Razorbill and European Shag

Based on population abundance modelling provided as outputs from Davies et al. (2021) three of the four species included in Wakefield et al. (2017) were predicted to decline in abundance under projections of future climate change (Kittiwake, Guillemot and Razorbill). Therefore, the pattern of general declines in the abundance of these species across most of their at-sea distribution observed when comparing current to future conditions was not unexpected. In Razorbills there appeared to be a pattern of increased density in the immediate vicinity of colonies, and especially larger colonies, before abundance declined further from breeding colonies under future climate change projections. This pattern is reinforced by the observation that both 50% and 95% UD in this species were predicted to encompass a smaller area under future climate projections. Therefore, the results for Razorbill suggest a decline in population abundance combined with a contraction of foraging range in the MarPAMM region. In Wakefield et al. (2017) the relationship between sympatric competition and foraging range is captured by the interaction between the cumulative area at distance available to birds (A) and measures of population size in habitat usage models (see also: Table 2). Therefore, one explanation for observed results in Razorbill is that reductions in colony size as population abundance decreases lead to reduced sympatric competition between individuals within a breeding colony and thereby a reduction in foraging range. This result echoes the observation that foraging range is positively dependent on colony size in many seabirds (Lewis et al. 2001, Gaston et al. 2007, Wakefield et al. 2013, Jovani et al. 2016). Consequently, even though Razorbill density declined overall, remaining birds may tend to concentrate in areas closer to their colony.

Kittiwake and Guillemot abundance were also predicted to decrease in the same manner as Razorbill abundance, but in these species 50% UD and 95% UD expanded slightly rather than contracting as they did in Razorbill. However, the same pattern of localized increase in density around large breeding colonies was observed in Kittiwakes around Rathlin Island within the MarPAMM region. Moreover, at the national (UK and Ireland) scale increases in Kittiwake density were also predicted around larger colonies within the North Sea as well. In contrast, Guillemot 50% and 95% UDs were predicted to expand markedly under future climate

projections. Shifts in environmental covariates may also play a role and unlike Razorbill and Kittiwake, habitat models included a covariate for TFGD (for variable definition see Table 1) which was not included within similar models for Razorbill and Kittiwake. However, TFGD was derived from SST which was included on both Razorbill and Kittiwake models so responses across the different covariates should be linked. Alternatively, habitat models for Guillemot and Kittiwake included a covariate (ρ) that was designed to capture the influence of parapatric competition that was not included with Razorbill habitat models. As a result, both Kittiwakes and Guillemots were predicted to avoid areas at which the ratio of the density of birds from the home colony to those from other colonies was lower in contrast to Razorbill where this covariate was not included in habitat models. Among-colony segregation is also evident in other non-UK and Ireland Kittiwake populations (Ainley et al. 2003, Paredes et al. 2012) though has only previously been noted in UK Guillemot populations by Wakefield et al. (2017). Therefore, one reason why UD contours expanded in Guillemot was that reductions in parapatric competition as a result of declines in population abundance throughout the UK led to birds within the MarPAMM region utilising a broader range of areas. Such an explanation rests upon the assumption that parapatric competition was currently limiting the use of these areas by birds within the MarPAMM region but is reduced under future climate projections as UK Guillemot population size declines. Such results highlight that an understanding of how different sources of both sympatric and parapatric competition interact to shape foraging ranges (e.g. Wakefield et al. 2011) and patterns of spatial segregation between different colonies may be required to understand population responses to climate change.

Unlike the other species included in Wakefield et al. (2017) the abundance of European Shag was expected to increase under the climate projections presented in Davies et al. (2021). As such, the predicted increases in the density of birds in the vicinity of breeding colonies was expected. However, the decline in the size of 50% and 95% UDs under future climate conditions was less expected given that population abundance increased. Under the assumption that foraging range is positively dependent on colony size in many seabirds increases in Shag abundance should have led to birds travelling further while foraging and therefore to increases, not decreases, in the size of UD contours. One potential explanation is that European Shag distributions are strongly influenced by values for the PEA covariate for which climate projections were available. For example, estimated coefficients from Shag habitat models were of a larger magnitude for PEA than any other covariates included in the model. Based on model coefficients in Table 2 Shags are expected to avoid areas with high

PEA values. Previously, PEA was reported to be negatively associated with habitat usage in a variety of marine species including Guillemot and Kittiwake by Sadykova et al. (2020), which may represent animals avoiding strongly stratified waters when foraging (Scott et al. 2010). Under the climate change projections assessed here PEA is expected to increase across most of the MarPAMM region and therefore the size and location of areas with preferred PEA values may become smaller and more localised. In general, PEA increases with distance from the shore (Holt & Proctor 2008) and areas with lower PEA appear to occur mostly in coastal regions under future climate projections, which may explain why European Shag UD's decreased in size even as Shag abundance was predicted to rise (see Appendix). If so, the importance and spatial distribution of a particularly important environmental predictor, PEA, and how it reflects changes in water column stratification may be more important in driving changes in spatial distributions than intraspecific competition for this species.

Distribution predictions for Tern species

The generic habitat models for the three Tern species considered here included relatively few covariates all of which remained the same between predictions based on current or future climate projections. Moreover, while a term for distance from the colony was included as a covariate in these models and could perhaps capture some nuances of sympatric competition in determining foraging ranges, no interaction term between colony size and distance travelled was examined. Therefore, the models would not be expected to predict changes in species foraging ranges due to changes in Tern population abundance predicted in Davies et al. (2021). As such, we observed little difference in the colony-level distribution of birds across all Tern species and, even when aggregating across colonies within the MarPAMM region, there was little change in the predicted distribution of Terns as seen in the high overlap between 50% and 95% UD contours. Arctic and Sandwich Tern populations were predicted to decline throughout the UK and Ireland based on the outputs from Davies et al. (2021) and we predicted corresponding declines in Arctic Tern density across the entire MarPAMM region. In the case of Sandwich Tern, reductions in density were observed in some areas but slight increases in others. Such increases were small and did not compensate completely for reductions in bird numbers from other colonies in the MarPAMM region but did result in predicted UD's for this species shifting slightly towards these colonies. Unlike Arctic and Sandwich Terns, Common Tern abundance was predicted to increase under future climate change projections (Davies et al. 2021). Increases in Common Tern abundance were also observed in distribution maps of the MarPAMM region but increases in density were not

uniform across different areas with some colonies increasing and others decreasing. As such, predicted shifts in the spatial distribution of Common Tern arises from changes in the relative size of different colonies predicted by Davies et al. (2021).

Conservation and Management Implications

Marine ecosystems are vulnerable to climate change (Lotze et al. 2019, Pinsky et al. 2019) and there is a growing awareness that the planning and design of Marine Protected Areas (MPA) should account for the influence of climate change (Tittensor et al. 2019). A variety of approaches to how to incorporate climatic resilience have been developed (MacLeod et al. 2009, Wilson et al. 2020) and often promote the idea of monitoring key conservation features (both species and habitat features) and responding adaptively. Ultimately, this could lead to a combined network of static and dynamic MPAs (Game et al. 2009, D'Aloia et al. 2019). While static MPAs are easier to implement the development of dynamic MPAs with boundaries that can be altered if required has been discussed in some UK contexts (e.g. MMO 2016). However, the limited availability of climatic data and forecasts at suitable spatial scales as well as modelling subsequent impacts on animal populations and distributions represents a challenge.

Together with Davies et al. (2021), the work presented demonstrates the importance of reliably being able to predict changes in the size of breeding colonies and linking such changes to seabird distributions. Under future projections of climate change the highest density of birds occurred within the vicinity of the largest breeding colonies reflecting a key mechanistic constraint of central-place foraging. Consequently, static MPAs centred around large breeding colonies are likely to contain high density of seabirds even under future climate projections. Identifying where we expect large breeding colonies to be located is crucial. For example, Northwards shifts in the distribution of Kittiwake, Guillemot and Razorbill may mean such colonies represent an increasingly important proportion of species breeding population. In contrast, population declines at more Southerly colonies may be difficult for MPAs alone to combat if they represent more general latitudinal shifts in marine ecosystems as a result of climate change. The ability to design more dynamic MPAs may rely upon identifying key environmental covariates linked to habitat suitability and habitat profitability. Our work shows that predicted seabird distributions may shift in response to climate change, contracting in some species (Razorbill) while expanding in others (Guillemot, Kittiwake). Thus, offshore MPAs designed to cover important seabird foraging hotspots may need to consider

how seabird home ranges shift over time, particularly if such MPAs are based on features that are more susceptible to climate change (e.g. tidal mixing fronts, De Dominicis et al. 2018b).

Interpretation of habitat models and future research

For each of the species distributions modelled and presented an important consideration when interpreting results is how the population of interest is defined. A terrestrial, colony-based approach (as used here) reflects the importance of colony location in determining seabird distributions as well as how such populations are often described and censused by researchers. In the current report the distribution maps presented represent the distribution of birds originating from colonies within the terrestrial MarPAMM area defined in Figure 1. However, the at sea distributions of birds originating from within and without the MarPAMM area will overlap to some extent particularly towards the edges of the MarPAMM area. Consequently, the overall density of birds in some areas may be higher than predicted when focusing solely on birds from within the MarPAMM region. This can most clearly be seen by comparing maps of the predicted density of Guillemots when set x in equation 1 was defined as colonies with the MarPAMM region or as all colonies within the UK. For example, the predicted density of Guillemot in marine areas of the coast of County Down and County Lough is greater when using data from all UK and Ireland colonies than just from the MarPAMM regions (Fig. 5 and Fig. S8). In this case Guillemot from Irish colonies outside of the terrestrial MarPAMM region may be the main birds foraging in these areas. Likewise, the predicted density of Guillemot in sea areas in the North-west of the terrestrial MarPAMM regions increases when considering the distributions of birds from all UK and Irish colonies.

An approach based on defining marine areas of interest represents an alternative approach and could incorporate contributions from all colonies where birds are predicted to visit such an area to estimate seabird density. The main difficulty with such an approach is defining a suitable marine area that reflects the ecology of the different species studied here. For example, the scale of marine areas that are relevant to European Shag that have relatively localized home ranges may be quite different to that relevant to, say, Kittiwakes that range further. Nevertheless, because we provide seabird distribution at the UK-scale, incorporating predictions from all colonies located within the UK and Ireland, one could overlay the locations of important marine areas onto these outputs to get a picture of the overall density of birds in an area

Maps of changes in the distribution of birds from the habitat models based on the results of Wilson et al. (2014) and Wakefield et al. (2017) rest upon the predictive performance of said models. Therefore, variation in the predictive performance of habitat models between species should be considered when comparing predicted seabird distribution. In both Wilson et al. (2014) and Wakefield et al. (2017) habitat models were selected for predictive performance using cross-validation scores, but performance varied across the species examined. For example, habitat models in Wakefield et al. (2017) performed equally well for Shags, Kittiwakes and Guillemots but did not perform as well for Razorbill. Wakefield et al. (2017) suggested poorer model performance in Razorbills may occur because a relatively large proportion (48%) of Razorbills tracked during the study were from the Northern Isles, where populations have been in decline (JNCC 2014) due to reductions in forage fish availability (Cook et al. 2014). Razorbills from these colonies typically travelled further during foraging trips than birds at other tracked colonies during Wakefield et al. (2017). Consequently, their behaviour may reflect the behaviour of birds at other colonies less accurately thereby reducing overall model performance. The predictive performance of habitat models for Terns in Wilson et al. (2014) also varied by species, with models performing best for Sandwich Terns, followed by Common Tern and then Arctic Tern. However, all scores fell within typical benchmark values of 'fair' to 'good' for the Area Under Curve scoring metric used (Swets et al. 2000). Moreover, because underlying covariates in habitat models for Terns were static across current and future scenarios any changes in Tern distribution will arise from changes in predicted Tern abundance by Davies et al. (2021). It should also be borne in mind that the number of Tern colonies within the MarPAMM region is relatively small and that population abundance predictions for Sandwich Terns were highlighted as less reliable in Davies et al. (2021).

Basing predictions on modelled outputs also assumes that seabird responses to environmental covariates remain static over time. The generalized functional response (GFR) approach used by Wakefield et al. (2017) may allow some interpolation of species responses to as-yet unobserved changes in certain environmental covariates (Matthiopoulos et al. 2019). However, it is likely that part of the updated seabird distributions rest upon out-of-sample predictions as environmental conditions are predicted to change, potentially generating unique covariation combinations at certain sites that were not experienced by any birds in the original study. Such considerations are more relevant when considering outputs based on Wakefield et al. (2017) as habitat models for Terns were restricted to static variables that did not change between current and future conditions. Even considering the results of

Wakefield et al. (2017) many of the covariates identified were deemed to be relatively static including seabed slope, distance from the coast and sediment type. Such features may describe how seabed geomorphology drives physical mechanisms that indirectly affect prey availability (Scott et al. 2010, Cox et al. 2013). Thus, the fixed locations of such features may constrain seabirds' ability to track changes in more dynamic oceanographic variables. A further caveat is that some important covariates describing usage may have been absent from habitat models or the temporal or spatial grain of those covariates included may not correspond precisely to the scale at which seabird habitat selection operates.

While the fine-scale distribution of individual animals will be shaped by habitat selection processes, the distribution of all organisms in a population will be shaped by demographic parameters that depend on the spatial distribution of environmental variables (i.e. Demographic Sorting *sensu* Matthiopoulos et al. 2020). Consequently, habitat selection patterns may vary in response to the densities of both consumers and resources, requiring an understanding of potential feedbacks between species abundance, habitat covariates and levels of competition in determining species distributions. As the models of Wakefield et al. (2017) include estimates of sympatric and parapatric competition they may capture some aspects of this relationship. For example, interactions between estimates of local population size and cumulative sea area were interpreted as showing foraging range was positively dependent on colony size and the availability of suitable habitat (open sea). Moreover, because Davies et al. (2021) provided estimates of population abundance under climate change this interaction was updated when generating predicted seabird distributions from Wakefield et al. (2017). As a result, the population modelling results provided by Davies et al. (2021) are likely to have a large effect on resulting distribution maps, and predicted changes in density between current and future conditions because they influence our predictions in multiple ways. Firstly, estimates of colony size, and hence intra-specific competition, are included as covariates in species distribution models. Secondly, because outputs from Davies et al. (2021) indicate the size and location of seabird colonies that are used when creating weighted density distributions across multiple colonies (see equation 1). Finally, the uncertainty around estimates of population size are larger than those reported around individual parameters from species distribution models (see Appendix). In contrast, potential relationships between population size and foraging range were not incorporated within Tern habitat models however the updated population size estimates from Davies et al. (2021) will still play an important role when creating weighted density distributions across multiple colonies.

Currently, it remains unclear how seabird responses to environmental covariates may change in concert with changes in population size and whether changes in the strength of competition from conspecifics (density dependence) alter the availability or utility of resources. Distributional shifts are likely to be driven by the combined and interacting influences of competition and resource density. The influence of habitat on individual fitness is important because high density areas do not necessarily reflect underlying habitat quality (Loiselle et al. 2003, Railsback et al. 2003). Therefore, linking species distribution predictions to measures of animal performance can begin to help us understand biological consequences of habitat use and assist conservation and management efforts (Aldridge & Boyce, 2008; Gaillard et al., 2010). To achieve this greater integration of habitat usage and population modelling may prove a useful avenue of future research and such techniques are currently being developed and employed (Matthiopoulos et al. 2019, Avgar et al. 2020). For example, Matthiopoulos et al. (2015) developed a modelling framework, subsequently termed the Habitats-to-Populations approach, to link patterns of habitat selection to predicted changes in population abundance. One advantage to such an approach is the ability to link habitat composition and its influence on individual fitness to feed back into population size projections. A key part of such an approach would involve sampling multiple seabird colonies to ensure a range of different habitats were sampled together with sufficient demographic information to calculate population growth rate across different time-points. Once acquired such data may allow us to model in greater detail the context-dependent nature of habitat selection often observed in natural animal populations (van Beest et al. 2016, Avgar et al. 2020, O'Neil et al. 2020).

Conclusions

Composite maps of seabird distributions based on the habitat models of Wakefield et al. (2017) and Wilson et al. (2014) arise from a combination of two different processes. Firstly, the influence of usage covariates that describe colony-level distributions. Secondly, variation in relative population size among neighbouring colonies when aggregating colony-level density maps on a broader scale. Of these, we believe that the size and location of breeding colonies had more effect on predicted species distributions than shifts in response to changes in oceanographic variables in most cases. This is because breeding sea birds are central place foragers, and this places significant constraints on foraging movements during this period of the annual cycle. For example, distance from the colony was an important predictor in all habitat models used in the current study. The habitat models provided by Wakefield et al.

(2017) also include covariates derived from estimates of population abundance to estimate the impact of competition. In these models changes in population size influence colony-level distributions and influence spatial patterns when results from neighbouring colonies are aggregated through variation in relative population size. Therefore, we believe the population modelling results provided by Davies et al. (2021) are likely to have a larger effect on resulting distribution maps, and predicted changes in density between current and future conditions, than the updated projections of environmental covariates. Indeed, because no environmental covariates were updated when modelling Tern habitat usage any resulting shifts in distribution must arise from the population modelling performed by Davies et al. (2021). The one exception were the results in Shag where one covariate (PEA) that was updated as part of climate modelling was an important predictor of habitat usage and appeared to have an impact on predicted distributions. Changes in population abundance may play a key role in determining seabird distributions through their role in driving density dependent competition for resources. Moreover, the quality and distribution of resources will also be influenced by climate change. Changes in population size are not independent of changes in the distribution of environmental covariates and hence resource availability. Linking of demographic population models to species distribution models is likely to be an area that sees further development in the future (Matthiopolous et al. 2019). However, the modelling work presented by Davies et al. (2021) represents one of the first attempts to model changes in seabird population abundance as a function of both terrestrial climate and oceanographic variables and link population demography to habitat characteristics. Likewise, by combining results from Davies et al. (2021) and SSM climate projections within the framework of existing habitat models the current report provides a link between updated population size estimates and oceanographic climate projections to predict seabird distributions within the MarPAMM region and across the UK.

5. References

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Supplementary material

Appendix A: Additional distribution maps and uncertainty modelling outputs

Appendix B: Rasters of predicted seabird distributions under future climate change projections at MarPAMM scale and at UK and Ireland scale.

All appendices are available to download online:

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

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