LUND UNIVERSITY

The utility of relative environmental suitability (RES) modelling for predicting distributions of seabirds in the North Atlantic

Watson, Hannah; Hiddink, Jan G.; Hobbs, Matthew J.; Brereton, Tom M.; Tetley, Michael J.

Published in:
Marine Ecology - Progress Series

DOI:
10.3354/meps10334

2013

Link to publication

Citation for published version (APA):
Watson, H., Hiddink, J. G., Hobbs, M. J., Brereton, T. M., & Tetley, M. J. (2013). The utility of relative environmental suitability (RES) modelling for predicting distributions of seabirds in the North Atlantic. *Marine Ecology - Progress Series*, *485*, 259-273. https://doi.org/10.3354/meps10334

Total number of authors:
5

General rights
Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.
• Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
• You may not further distribute the material or use it for any profit-making activity or commercial gain
• You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: https://creativecommons.org/licenses/

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

The utility of relative environmental suitability (RES) modelling for predicting distributions of seabirds in the North Atlantic

Hannah Watson[1,5,*], Jan G. Hiddink[1], Matthew J. Hobbs[2], Tom M. Brereton[3], Michael J. Tetley[4]

[1]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

[2]Baker Shepherd Gillespie, Wyastone Business Park, Wyastone Leys, Monmouth NP25 3SR, UK

[3]MARINElife, 12 St Andrews Road, Bridport, Dorset DT6 3BG, UK

[4]Ecology and Marine Sciences Consultant, Montague House, Durham DH1 2LF, UK

[5]*Present address*: Institute of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

*Email: h.watson.1@research.gla.ac.uk

Running head: Watson et al.: Modelling seabird distributions and habitat suitability

ABSTRACT: Understanding spatial and temporal variability in the distribution of seabirds is fundamental for the conservation and management of marine ecosystems. In the absence of large-scale systematic survey data, the application of standard habitat modelling techniques to predict the at-sea distributions of seabirds at large spatial scales has been limited. In this study, we examine the utility of relative environmental suitability (RES) modelling to predict large-scale distributions and habitat suitability for 6 seabirds in the North Atlantic. An index of habitat suitability was derived by relating niche characteristics to environmental attributes. Predictive performance of models was evaluated with receiver-operating characteristic plots, using independent survey data from the Bay of Biscay. RES models performed significantly better than null models at predicting relative likelihood of occurrence for 5 out of 6 species. Qualitative assessment showed that model outputs corresponded well with published range maps, though a common discrepancy was the inclusion of enclosed seas in which species are not known to regularly occur. This study demonstrates that RES modelling can be used to predict large-scale habitat suitability for wide-ranging marine animals for which occurrence data are limited and biased in geographical extent. RES predictions represent simple, testable hypotheses concerning a species' potential niche in respect of a few environmental

predictors. RES modelling can help to identify biodiversity hotspots, predict effects of climate change and develop criteria for designating marine protected areas.

KEY WORDS: Ecological niche modelling · Habitat suitability · Seabird · Relative environmental suitability · Geographic range · Distribution · AquaMaps · Species distribution model · SDM

INTRODUCTION

The ability to accurately describe and understand processes that determine the distribution of species is central to the development and implementation of effective measures for conservation and management. Increasing the availability of biogeographic data and knowledge of species' ecological requirements can facilitate the identification of biodiversity hotspots (Nur et al. 2011), assessment of the impacts of climate change (Olivier & Wotherspoon 2006), establishment of conservation priorities (Maxwell et al. 2009) and design of reserve networks at large spatial scales (Airamé et al. 2003).

Predictive habitat modelling offers a range of tools to quantitatively delineate range extents based on species–environment relationships (for reviews, see Guisan & Zimmermann 2000, Guisan et al. 2002, Redfern et al. 2006, Zimmermann et al. 2010). Standard techniques typically employ records of species occurrence and associated environmental factors, which may determine – directly or indirectly – a species' distribution within an area. Species distribution models (SDMs) have been widely applied in terrestrial systems, yet their application for predicting occurrences of marine organisms remained limited until the last 10 yr (Elith & Leathwick 2009, Robinson et al. 2011). Many SDMs in marine systems have been applied in conservation planning (e.g. Guinotte et al. 2006, Oppel et al. 2012) and are typically biased towards commercially harvested animals (e.g. Maxwell et al. 2009, Hardy et al. 2011) and mammals (e.g. Redfern et al. 2006, Gregr & Trites 2008, Ready et al. 2010). The most widely used models require large presence–absence data sets (Guisan et al. 2002) and are therefore unsuitable for generating accurate predictions about species for which occurrence data are limited in spatial and temporal extent, which characterises the situation for many marine animals (Ready et al. 2010, Robinson et al. 2011). While occurrence data of marine animals are becoming increasingly available through online databases, such as the Ocean Biogeographic Information System (OBIS; www.iobis.org) and the Global Biodiversity Information Facility (GBIF; www.gbif.org), there is little published quantitative

information concerning large-scale patterns of diversity and distribution in the marine environment.

In the absence of point data spanning large spatial and temporal scales, Kaschner et al. (2006) proposed that the synthesis of available knowledge concerning species–habitat relationships could approximate a large-scale representative sampling scheme. They developed a novel rule-based envelope model to map global distributions of marine mammals and generate large-scale predictions of relative environmental suitability (RES) without the need for a huge input of presence–absence data – the limiting factor of standard modelling techniques. RES underlies the AquaMaps modelling system, which, compared with traditional methods of presence-only distribution modelling, was found to perform very well for a suite of marine taxa (Ready et al. 2010). AquaMaps is now used extensively for generating distribution maps in FishBase (www.fishbase.org). Gregr & Trites (2008) also demonstrated that species–habitat relationships can be accurately defined for wide-ranging marine top predators when limited observation data prevent the use of more common correlative approaches.

The behaviour and ecology of marine birds at sea is poorly understood, largely due to the practical and logistical difficulties associated with studying seabirds (Tasker & Reid 1997). Most data come from opportunistic sampling and sparse non-systematic records of occurrence (e.g. Huettmann & Diamond 2001). Sampling typically covers only a fraction of a species' range (e.g. Hobbs et al. 2003), and transects at sea can underestimate seabird distribution and abundance due to low detection rates and vast geographic ranges (Ostrand et al. 1998). Traditional range maps are generated subjectively, on the basis of limited occurrence records and expert opinion (Cramp & Simmons 1980, del Hoyo et al. 1992), and they do not provide quantitative information on the relative suitability of different areas. Predictive modelling of seabird distributions has been largely restricted to studies of waters within 200 km of the coast (e.g. Yen et al. 2004, Louzao et al. 2006, Oppel et al. 2012) and nesting habitat (e.g. Olivier & Wotherspoon 2006). A few larger-scale studies, however, have encompassed extensive areas of pelagic waters, such as the Southern Indian Ocean (Raymond & Woehler 2003) and the Arctic Circle (Huettmann et al. 2011).

The aims of the present study are to (1) predict the RES and geographic range extent for 6 seabirds in the North Atlantic, and (2) evaluate these models using independent point data. Using published information on species' distributions, foraging behaviour and life histories, species were assigned to broad-scale niche categories, defined by environmental parameters known to be key predictors of distribution. We build upon the approach developed by

Kaschner et al. (2006, 2010), incorporating temporal variability in environmental variables and species–habitat relationships – pertinent to wide-ranging migratory marine animals – into models. Model performance was evaluated using observation data collected by MARINElife in the English Channel and Bay of Biscay. The approach is designed to inform our understanding of seabird distributions and the development and evaluation of predictive habitat models relevant to the at-sea distribution of seabirds.

MATERIALS AND METHODS

Study species

RES modelling was applied to 6 species of seabirds, belonging to the order Procellariiformes, that are all abundant and widely distributed in the North Atlantic during part, or all, of their annual life cycle: northern fulmar *Fulmarus glacialis* (hereafter fulmar), Cory's shearwater *Calonectris diomedea*, great shearwater *Puffinus gravis*, sooty shearwater *P. griseus*, Manx shearwater *P. puffinus* and European storm petrel *Hydrobates pelagicus* (hereafter storm petrel). The selection of species was determined by the availability of data concerning species–habitat relationships and the availability of test data for model evaluation. The fulmar is restricted to the Northern Hemisphere during its breeding and non-breeding seasons and has a circumpolar distribution (del Hoyo et al. 1992). Cory's shearwater, Manx shearwater and storm petrel breed in the North Atlantic during the boreal summer, dispersing into the southern Atlantic during migration and the non-breeding season (del Hoyo et al. 1992). Great shearwater and sooty shearwater breed in the Southern Hemisphere during the austral summer and disperse into the Northern Hemisphere during their non-breeding season – the boreal summer (del Hoyo et al. 1992).

Quantifying species' ecological niches

Qualitative and quantitative data concerning species' habitat preferences were gathered from an extensive range of primary and secondary literature sources. A total of 35 sources of literature informed the quantification of species' ecological niches (see Table S1 inSupplement 1 at www.int-res.com/articles/suppl/mXXXpXXX_supp.pdf). Of these, 26 represented primary sources and 9 were secondary sources of literature. Not all species were represented equally in the literature, with the number of relevant data sources ranging from 4 (Cory's shearwater) to 17 (fulmar). There was high reliance on 8 sources of literature (5 primary, 3 secondary) for informing parameterisation of models. These sources, however,

represent comprehensive pieces of literature based on substantial quantities of data collected over large temporal and spatial scales.

This information was used to assign each species to an ecological niche defined by 4 ecogeographical variables (EGVs): depth, sea-surface temperature (SST), chlorophyll *a* (chl *a*) concentration (indicating phytoplankton biomass, a proxy for ocean productivity) and distance to land. Most available data were qualitative and habitat categories were consequently developed to facilitate quantification of a species' niche (Table 1). EGVs were selected on the basis of wide evidence in the literature of their significance in determining the distribution and abundance of seabirds at sea (Schneider 1997, Huettmann & Diamond 2001, Oedekoven et al. 2001, Louzao et al. 2006, Wakefield et al. 2009) and the availability of environmental data at appropriate scales.

Ecological niches were described by resource selection functions (RSFs) describing the relative suitability of an environment (Fig. 1). While true RSFs express the probability of use of a resource or area by an organism (Boyce et al. 2002), the RSFs applied here express the relative likelihood of use of an area; predicting probability of presence requires the incorporation of reliable information on prevalence (Elith et al. 2006). After Kaschner et al. (2006), it was assumed that the relative suitability of the environment is uniformly highest throughout a preferred parameter range, bounded by a minimum (MinP) and maximum (MaxP) value. Outside of this preferred range, suitability was assumed to decrease linearly towards an absolute minimum (MinA) and maximum (MaxA), being equal to 0 outside of those thresholds.

The availability of information concerning species' associations with chl *a* concentration was limited (see Table S1) and largely restricted to qualitative statements such as 'aggregates in productive waters' or 'attracted to fronts'. Procellariiformes occur in waters of all productivity but prefer eutrophic and enriched waters (Warham 1990, Louzao et al. 2006, Hedd et al. 2012). Insufficient information was available at the species level to distinguish different relationships; consequently, all species were assigned to identical niches with respect to chl *a* concentration.

Distinct niches were defined for a species' breeding and/or non-breeding season, as opposed to characterising an annual average niche. This accounted for the variability in species–habitat associations that is a typical feature within the annual life cycle of migratory marine birds. Breeding niches were quantified for fulmar, Cory's shearwater, Manx shearwater and

storm petrel, and non-breeding niches were quantified for fulmar, great shearwater and sooty shearwater in the North Atlantic. The breeding niche (and subsequent modelled range) describes the habitat associations of breeding adults while occupying nest sites; the non-breeding niche is that occupied by non-breeding adults, and the subsequent modelled range comprises both 'wintering' areas and migratory range. Note that non-breeding birds may be present within the non-breeding range throughout the year.

Environmental data

The study area covered the North Atlantic, bounded by the coordinates 68.0°N 85.0°W, 0.0°S 12.0°E. A regular grid with the cell dimensions 0.25 × 0.25° was constructed in ArcGIS 9.2 (Environmental Systems Research Institute) and displayed using the WGS-1984 coordinate system. A landmask was applied using ArcWorld Supplement's 'continents' layer. Bathymetric data were obtained from GEBCO (IOC et al. 2003), providing elevation in 1 min (0.016°) intervals, and interpolated using inverse distance weighting at a scale of 0.25°. SST and chl *a* data were provided by the NERC Earth Observation Data Acquisition and Analysis Service. SST data were collected by the Advanced Very High Resolution Radiometer (AVHRR) and have a resolution of 4 km (0.036°). Chl *a* data were collected by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and have a resolution of 9 km (0.081°).

Seasonal averages were derived for dynamic parameters (i.e. SST and chl *a*) from data collected between 1995 and 2005, corresponding with the period over which the test data were collected. 'Summer' (April–September) and 'winter' (October–March) seasons were defined to correspond with species' phenology. 'Summer' corresponds closely with the breeding season of fulmar, Cory's shearwater, Manx shearwater and storm petrel and the non-breeding season of great shearwater and sooty shearwater, which breed in the Southern Hemisphere. 'Winter' corresponds with the non-breeding season of fulmar. Seasonal averages of SST and chl *a* were subsequently imported and averaged across grid cells within the raster using bilinear interpolation. The shortest distance to land was calculated for each grid cell using the Euclidean Distance function in ArcGIS.

Model structure

An index of RES was derived for each grid cell depending on how the environmental attributes of a cell corresponded with the parameters quantitatively defining a species' ecological niche. After Kaschner et al. (2006), RES was measured on a scale from 0 to 1 and

was based on a product of the suitability of the environment in relation to each individual EGV. Each EGV was afforded equal weighting in models. The overall RES for each cell was calculated using the formula:

$$RES_{overall} = RES_{depth} \times RES_{SST} \times RES_{distance} \times RES_{chl} \qquad (1)$$

The multiplicative approach means that if any one variable within a cell fell outside of a species' absolute range, the overall suitability was equal to 0. This is based on the assumption that an animal would not be expected to occur within an environment that is unsuitable in respect of one or more variables that are key determinants of distribution. RES values were imported into the GIS grid and displayed using a continuous colour scale. Model outputs delineate a species' predicted geographic range and illustrate the relative suitability of the environment (equating to likelihood of occurrence) throughout that range.

Observation data

MARINElife provided point data collected from monthly seabird surveys carried out in the English Channel and Bay of Biscay (Fig. 2) between 1995 and 2005 (though data from 2003 and 2004 were not available). Surveys were carried out aboard a commercial ferry liner within a restricted transect route involving repeated sampling of grid cells. A total of 2696 h of observations, collected across 156 grid cells, provided data for the model evaluation. The data set comprises a large number of observations, representing a high diversity of species, collected over a decade and employing consistent methodology across space and time. The sampling area covers a wide spectrum of environmental strata. Observations were binned within grid cells (0.25 × 0.25°) to match the spatial resolution of environmental data. Cells were assigned a binary value of 1 or 0, indicating 'presence' and 'background', respectively.

Species occurrence data typically exhibit spatial autocorrelation, which arises when the probability of occurrence in one sampling unit is not independent of the probability of occurrence in neighbouring units (Legendre 1993, Dormann et al. 2007). If unaccounted for, spatial autocorrelation can increase the frequency of Type I errors (i.e. identifying a non-significant relationship as significant; Dormann et al. 2007). We checked for spatial autocorrelation in species' observations data and residuals of generalised linear models (with Poisson error structures) fitted to data on the number of observations as a function of RES. Clustering of observations may be driven by spatially autocorrelated environmental variables; if predictors (here, RES) explain most of the variation in species occurrences (i.e. a model is correctly specified), there should be minimal spatial autocorrelation in the residuals

(Dormann et al. 2007, Elith & Leathwick 2009). We calculated Moran's *I* values for the 50 nearest neighbouring grid cells using the function moran.test in the *spdep* package in R. Moran's *I* values range from –1 (negative autocorrelation) to +1 (positive autocorrelation), with values around 0 indicative of a completely random spatial pattern. Small positive values of Moran's *I* were yielded from species observation data (range: 0.004–0.254) and model residuals (range: 0.012–0.024), indicating weak spatial clustering at the spatial scale of models (0.25 × 0.25°). Analysis of correlograms showed no significant spatial autocorrelation in either observations data or residuals and revealed irregular patchiness. Subsequently, we did not incorporate measures to account for spatial autocorrelation into models.

Model evaluation

Using independent point data collected by MARINElife in a subset of the model area (Fig. 2), we tested the predictive performance of models using receiver-operating characteristic (ROC) plots and comparing the resulting area under the curve (AUC) against that of a null model (see Olden et al. 2002, Raes & ter Steege 2007). ROC analyses offer a method of assessing model accuracy that is threshold-independent, by evaluating the proportion of correctly and incorrectly classified predictions across a continuous range of threshold values (Fielding & Bell 1997). The ROC plot is obtained by plotting sensitivity (the true positive rate) as a function of 1-specificity (the false positive rate) at every possible threshold value. The resulting AUC provides a measure of predictive ability; the higher the AUC, the greater the predictive accuracy of a model. An AUC value of 1.0 indicates a perfect model, while a value of 0.5 is usually considered to be equivalent to performing no better than random (Fielding & Bell 1997).

The use of null models has been demonstrated for improving testing for statistical significance in AUC values (Raes & ter Steege 2007) and addressing the issue of spatial sorting bias (Hijmans 2012). Spatial sorting bias can inflate AUC values of both empirical and null models, meaning an AUC of 0.5 might not necessarily be indicative of random performance (Hijmans 2012). Predictions of RES models were tested by comparing the AUC value of actual models against a null distribution (a 'null model') of AUC values derived from randomised data. This tested whether model predictive performance was significantly different from what would be expected by chance alone. We generated a null distribution of AUC values, corresponding with each RES model, by randomly distributing the species' observations (presence/background) amongst the grid cells covered by survey effort. By

generating random data only from the survey area, we aim to minimise spatial sorting bias by ensuring that the null model only reflects the environmental conditions where sampling was carried out (Hijmans 2012). The resulting ROC plot was generated and the AUC was calculated using the ROCR package in R 2.14.0. This procedure was repeated 10,000 times to generate a random frequency distribution of AUC values that would be expected if the RES model did not perform better than expected due to chance. If the AUC of the empirical model exceeded the 95% quantile of the ranked AUC values of the corresponding null model, the model was considered to perform significantly better than chance would dictate (Olden et al. 2002) and the relationship between RES and species' presence can be considered to be stronger than would be expected by chance. We used 1-sided testing, since it was only of interest whether models performed significantly better than expected by chance, not whether they performed significantly worse. The significance level was calculated as the proportion of random AUCs that were equal to or greater than the observed AUC.

The model evaluation has 2 main assumptions: (1) there are sufficient records within the test data set to accurately describe a species' distribution within the survey area; and (2) the range of possible RES values is represented within the survey area (i.e. there is heterogeneity of habitat suitability). To assess these assumptions, we calculated and considered the total number of species' observations, number of 'presence' cells, and percentiles of the ranked RES values within the survey area for each model.

Model outputs were also visually compared with published range maps (del Hoyo et al. 1992, Onley & Schofield 2007), allowing detection of any large-scale geographical discrepancies in the predictions of models. While qualitative in nature, this comparison provides a useful additional evaluation of the models at a much larger geographical scale than the more quantitative evaluation described above.

RESULTS

Quantifying and modelling species' ecological niches

Ecological niches of 6 seabird species – fulmar, Cory's shearwater, great shearwater, sooty shearwater, Manx shearwater and storm petrel – were quantified in relation to 4 EGVs – depth, SST, chl *a* concentration and distance to land – and are described in Table 2. The 6 species all occupy different ecological niches, with varying degrees of overlap. Niches were subsequently modelled using the RES approach, which resulted in a spatial visualisation of

niches into potential distributions (Fig. 3) and illustrated the relative suitability of the environment throughout ranges. Manx shearwater and storm petrel share similar niches during their concurrent breeding seasons; both species occur in cold temperate to subtropical waters (5–25°C) and primarily range within a few hundred kilometres of land. However, while the Manx shearwater prefers depths of less than 200 m – from coastal waters to the edge of the continental shelf – the storm petrel prefers deeper waters between 100 and 1000 m. Breeding seabirds occur closer to land (all MinP = 0 km) than non-breeding birds (MinP ranges from 6 to 50 km).

The fulmar occupies a similar niche in the breeding and non-breeding seasons; the absolute minimum and maximum values of each EGV do not change between the 2 seasons, but the preferred range of all environmental variables (except chl *a*) differs. During the non-breeding season, the fulmar's preferred niche encompasses cooler deeper waters further from land, compared with when breeding. Non-breeding great shearwater and sooty shearwater occupy the widest niches with respect to SST, spanning a range of 37 and 30°C, respectively. The preferred niche of great shearwater extends further offshore (<2000 km) than that of sooty shearwater, which tends to range closer to land (<200 km).

Qualitative comparison with published range maps

From visual qualitative assessment, it can be seen that model outputs (Fig. 3) illustrate variability in predicted range extents of the 6 seabird species in the North Atlantic. Relative environmental suitability varies throughout ranges, reflecting niche segregation between species. Predicted range extents vary in total surface area and geographical coverage. Comparing between species, non-breeding birds (with the exception of fulmar) occupy a larger range and latitudinal extent than breeding birds.

Predicted range extents closely corresponded with published distribution maps for all species. However, all ranges comprised a wider extent than maps in the literature. A common discrepancy was the prediction of suitable habitat in enclosed seas, when such areas are excluded from published ranges for several species, for example, the inclusion of the Mediterranean Sea in model outputs for great shearwater and Manx shearwater, the Caribbean Sea and Gulf of Mexico for great shearwater and sooty shearwater, and Hudson Bay for great shearwater. Elsewhere, models captured areas of known absence well, for example, the absence of breeding Manx shearwater from the western central Atlantic and

Caribbean Sea, the absence of sooty shearwater from Hudson Bay, and the low habitat suitability in the central Atlantic for the sooty shearwater.

The model output for storm petrel predicted a much wider range across the North Atlantic than published range maps; the latter define the species' range as restricted to the northeast Atlantic, extending no further west than 30°W. Areas of high environmental suitability were separated by a large area of low RES in the central Atlantic. Similarly, a small area of suitable habitat was predicted for fulmar in the north Mediterranean Sea but separated from the core range by a large area of unsuitable habitat.

Statistical model evaluation

RES models for 5 out of 6 species performed significantly better than expected by chance when tested with independent observation data from the Bay of Biscay ($p < 0.05$; Table 3). The AUC of empirical models was significantly higher than that of corresponding null models, revealing a significant relationship between RES and species' occurrences for 6 out of 7 models. In the case of 4 out of a total of 7 models, less than 0.1% of random samples had a higher AUC than the actual model ($p < 0.001$). The model for sooty shearwater did not perform significantly better than random ($p = 0.260$), with 26% of random AUCs exceeding the observed AUC. While the model for great shearwater performed significantly better than expected by chance ($p = 0.041$), the model AUC was only very slightly higher than the 95% quantile of the ranked null AUC values, indicating that the model did not perform much better than random.

The number of species' encounters ranged from 115 to 590 (mean 353.1 ± 65.3; Table 4). The range and frequency distribution of habitat suitability across the model evaluation area for each species is illustrated by percentiles of ranked RES values (Table 4). The distribution of RES in the survey area varies between species and is strongly skewed – indicating reduced heterogeneity of habitat suitability – for 3 models: fulmar (breeding), sooty shearwater and Manx shearwater. The majority of habitat within the sampling area is of low suitability for breeding fulmars but of homogenously high suitability for sooty and Manx shearwaters.

DISCUSSION

RES predictions

When compared with simulated random data, RES models performed significantly better for 5 out of 6 seabird species (and 6 out of 7 models) at predicting relative likelihood of occurrence in a subset of the study area. Model outputs provide more information on species' distributions than published range maps since they provide indices of relative environmental suitability throughout a species' range. RES predictions represent simple, testable hypotheses concerning a species' potential niche in respect of a few environmental predictors. Visualisation of hypotheses in a spatial context facilitates our understanding of species–habitat relationships, inference of areas of potentially high seabird abundance and identification of regions to be targeted for future research and conservation planning.

Observed versus predicted distributions

RES modelling of the potential niche resulted in predictions of occurrence outside of known (or observed) ranges for several species, when compared with published range maps, indicating that distributions are influenced by additional biological and/or physical parameters, besides those included in models. Indeed, modelling of the realised niche – the part of the potential niche that a species actually uses – requires the incorporation of biotic interactions (Soberón & Nakamura 2009) and physiological constraints (Kearney & Porter 2009). Qualitative comparison of RES model outputs with observed distributions thus allows the assessment of the importance of other factors that may influence the at-sea distribution of seabirds.

Distributions of pelagic animals are ultimately constrained by the abundance and distribution of prey (Pahl-Wostl 1997), but scales of association between mobile predators and prey are highly variable (Schneider & Piatt 1986) and prey indices are considered inappropriate for predicting global distributions of many highly mobile marine organisms (Torres et al. 2008). Karpouzi et al. (2007) incorporated information on prey distributions in mapping at-sea foraging distributions of seabirds; however, they found little or no information concerning the diet of many seabirds and detected high spatial variability in associations between seabirds and prey. Habitat modelling is, therefore, largely reliant on predictor variables that indirectly affect species distribution.

Evidence from energetic and physiological studies highlights the significance of wind speed (Furness & Bryant 1996) and area of available ocean extent (Davies et al. 2010) in influencing the foraging behaviour and life-history strategies of procellariiform seabirds. The Strait of Gibraltar (Friesen et al. 2007) and the Almeria-Oran Oceanographic Front (Gómez-

Díaz et al. 2006) have both been proposed as barriers limiting dispersal of, and genetic exchange between, seabirds in the Atlantic Ocean and the Mediterranean Sea. Such physical and geographical factors may explain why, despite the prediction of suitable habitat, the observed distributions of some species do not extend into enclosed seas, e.g. the absence of great shearwater from the Mediterranean Sea and Hudson Bay.

Biotic interactions may play a significant role in determining distribution across smaller spatial and temporal scales (Furness & Birkhead 1984), and their incorporation into SDMs is widely recognised as a key challenge in both terrestrial (Araújo & Guisan 2006) and marine environments (Robinson et al. 2011). Shearwaters do not typically form mixed-species colonies (Warham 1990), suggesting that interspecific competition and niche segregation may influence the breeding distributions of some procellariiform seabirds. While the observed range of Manx shearwater does not extend into the Mediterranean Sea, the breeding ranges of the Balearic shearwater *Puffinus mauretanicu*s and the Yelkoaun shearwater *P. yelkoauni*, which occupy similar ecological niches to the Manx shearwater (and were, until recently, considered to be subspecies of Manx shearwater; Sangster et al. 2002), are restricted to the Mediterranean Sea (Onley & Schofield 2007). A combination of evolutionary history and biotic interactions may explain the reduced niche overlap that is observed (compared with predicted overlap) between these 3 ecologically similar species. Depending on the objectives, it may be a more useful approach to apply niche modelling to a species complex when there are several closely related species.

Despite their ability to traverse large sections of ocean, many procellariiform seabirds show limited dispersal (the 'seabird paradox' proposed by Milot et al. 2008). Their philopatric habits are expected to limit colonisation by long-distance dispersal and subsequent range expansion (Matthiopoulos et al. 2005, Brown et al. 2010). Despite the prediction of high RES in the northwest Atlantic for the storm petrel, high breeding-site fidelity and the large area of predicted low habitat suitability in the central Atlantic may explain why the species' observed distribution (from published range maps) is restricted to the northeast Atlantic (del Hoyo et al. 1992). Additionally, the niche is already filled by another pelagic seabird, Leach's petrel *Oceanodroma leucorhoa*, in the northwest Atlantic (del Hoyo et al. 1992). In the interpretation of RES model outputs, consideration should thus be afforded to a species' evolutionary history as well as areas of low RES separating areas of high environmental suitability, both of which may act to restrict ranges.

The availability of suitable nest sites is a fundamental constraint on the current breeding distribution of seabirds (Brown et al. 2010). Procellariiform seabirds are largely restricted to remote islands, free of mammalian predators, which are within range of suitable foraging areas (Warham 1990). If all occupied breeding colonies could be accurately identified and niche envelopes constrained by maximum foraging range from colonies, models could yield more accurate predictions of range extent during the breeding season. However, given the difficulties of surveying and monitoring remote locations, our knowledge of breeding sites is likely to be incomplete, particularly for less well-studied species. Restricting distribution to within species-specific foraging range of all land, therefore, represents a more conservative approach.

Where suitable habitat is predicted outside of current observed distributions, this may indicate areas that are used by a species, but for which there are no data, or areas that could be suitable for colonisation. Future colonisation or range shifts could be driven by changes in environmental suitability as a result of natural changes (e.g. Gaston & Woo 2008) and/or anthropogenic-induced changes, such as by means of active conservation management (Miskelly et al. 2009). By identifying areas of potentially suitable at-sea habitat, the RES modelling approach may thus offer insight into the effects of future changes in climate and anthropogenic activities on species' distributions. Further model development could be based on different scenarios for climate or nest-site availability to generate predictions of future changes in distributions.

Model evaluation

Statistical evaluation demonstrates that the generic approach of RES modelling can accurately describe habitat suitability for wide-ranging seabirds. RES predictions were more strongly related to species' presence for 6 out of 7 models than expected due to chance. While qualitative assessment of the model output for non-breeding sooty shearwater suggested reasonable consistency with published distribution data, the model did not perform significantly better than a null model. Poor model performance could be explained by the low quality of data used for model parameterisation (see Table S1), resulting in an inaccurate description of a species' ecological niche. It is well established that species–environment relationships can change with scale (Manly et al. 2002), and there is evidence for intraspecific spatial variation in species–habitat relationships in seabirds (Huettmann & Diamond 2001). Most information on the at-sea habitat associations of the sooty shearwater comes from

studies in the Pacific Ocean (Briggs & Chu 1986, Vermeer et al. 1989, but see Hedd et al. 2012). Therefore, we cannot be certain of the spatial stability of the species' niche across distinct ocean basins. The availability and quality of ecological data may limit the wider application of RES modelling to other species of seabird, if insufficient data are available to accurately quantify species' ecological niches.

Rigorous evaluation of models requires that the test data set accurately reflects the distribution and occurrence of a species within the evaluation area. The test data comprised far fewer observations of sooty shearwater than the other study species and the sampling area was characterised by low variation in RES, i.e. highly homogeneous habitat suitability (Table 4). However, despite highly skewed distributions of RES, the models for fulmar (breeding) and Manx shearwater showed highly significant predictive accuracy, when compared to null-models. This indicates these models must be performing very well, if they can perform significantly better than random, even under less favourable conditions for the evaluation. Rigorous model evaluation relies on representative observation data collected across broad spatial and temporal scales to compliment the macro-scale modelling approach. While 'regular' and 'equal-stratified' sampling strategies are the most accurate and robust (Hirzel & Guisan 2002), these are not typically features of opportunistically collected data – the source of most at-sea seabird observations. The increasing availability of large-scale point data (e.g. OBIS, GBIF) and range maps, such as those available through the IUCN Red List (www.iucnredlist.org), presents opportunities for further testing of RES models. However, the availability of representative test data may limit the application of RES modelling for scarcer and under-recorded species.

Biases in model parameters

A frequent obstacle encountered in predictive distribution modelling of marine animals is the lack of reliable and comprehensive occurrence data from which to define species-habitat relationships (Robinson et al. 2011). The issue of environmental bias – spatial and/or temporal bias in collection of occurrence data – is widely recognised in species distribution modelling (Araújo & Guisan 2006, Phillips et al. 2009, Ready et al. 2010). It mainly arises from limitations in data accessibility and sampling strategies, preventing representative coverage of the entire environmental range of species (Phillips et al. 2009). The biases inherent to most observation data can easily lead to incorrect interpretation of habitat preferences of wide-ranging species (Hirzel & Guisan 2002).

RES modelling provides a technique for predicting large-scale distributions which does not rely on point data. The niche hypotheses underlying RES models still ultimately depend on the quality and amount of available ecological information. Quantitative data on the relationships between seabirds and ocean productivity are lacking and large areas of the oceans remain under-studied, e.g. the central Atlantic (but see Skov et al. 1994). However, the ability for RES modelling to incorporate a range of qualitative and quantitative data, collected from different parts of species' ranges at different times of year, broadens the scope of environmental coverage. Consequently, the outputs may represent more balanced and robust predictions, for many marine animals, than the more commonly used predictive modelling techniques. When previously tested against a range of marine taxa, RES modelling was shown to perform very well compared with traditional presence-only modelling methods (Ready et al. 2010).

Accounting for temporal variability

Temporal variability in ecological niches and environmental parameters is frequently overlooked in species distribution modelling (Dambach & Rödder 2011). Previous applications of RES modelling to marine top predators did not account for temporal variability in species–habitat relationships or EGVs (Kaschner et al. 2006, Ready et al. 2010). In this study, we have accounted for the seasonal shifts in habitat associations that occur within the annual life cycle by distinguishing between a species' breeding and non-breeding niche and subsequently relating niches to seasonally averaged data for dynamic EGVs. Accounting for temporal variation in both species–environment relationships and dynamic environmental variables is expected to increase the reliability of RES predictions, particularly in areas where environmental conditions fluctuate greatly between seasons. Consequently, our seasonal RES predictions can provide greater insight into species' behaviour and ecology than those based on an annual average niche envelope.

Applications and recommendations for future research

RES modelling could prove a valuable tool for informing the development and implementation of effective conservation and management practices. In the absence of comprehensive occurrence data for wide-ranging species, RES models can identify critically important areas and biodiversity hotspots in pelagic marine ecosystems. This is of direct relevance to the development of quantifiable criteria for the designation of marine Important

Bird Areas (IBAs; BirdLife International 2004). The modelling approach could be used to direct observation effort to areas where under-recorded seabirds are predicted to occur and inform sampling strategies to incorporate a range of environmental suitability. Matching data on seabird distribution, as revealed by RES model outputs, with data on fishing effort could inform the responsibilities of Regional Fisheries Management Organisations (RFMOs) and the development of suitable monitoring and mitigation measures to reduce negative interactions between seabirds and fisheries (e.g. Le Corre et al. 2012).

Application of RES modelling to a greater variety of species, demonstrating variable niche characteristics, will allow further examination of the broad-scale applicability of the approach. Expanding the RES approach to wider geographic areas, incorporating all of a species' range, would offer greater insight into understanding distribution, dispersal and migratory behaviour. An iterative approach to the development of models (as recommended by Elith et al. 2006) will improve the robustness of predictions, by considering the effects of a wider range of predictor variables on model performance. Additional factors that have been shown to influence the at-sea distribution of seabirds, and could be incorporated into future models, include sea-surface salinity (e.g. Huettmann & Diamond 2001), horizontal (e.g. Louzao et al. 2009) and vertical gradients in SST (e.g. Spear et al. 2001), and fishing effort (e.g. Karpouzi et al. 2007).

Wider application of RES modelling requires simultaneous developments in at-sea sampling and large-scale studies of species–habitat relationships, which inform one another and offer direction for future research. The increasing use of tracking devices for recording movements of seabirds provides opportunities for quantification of habitat use and preference (Wakefield et al. 2009, Le Corre et al. 2012). Increasing the public availability of tracking data will facilitate further development of SDMs (Skov et al. 2008). Further studies are required to improve quantitative understanding of species–habitat relationships across a variety of spatio-temporal scales and integration of data across scales is necessary to enhance the predictive ability of RES models. Having demonstrated RES is a robust modelling approach, predictions could be improved by the use of ensemble model averaging (Araújo & New 2007).

CONCLUSIONS

Based on quantitative definitions of species' ecological requirements, RES maps offer a robust alternative to subjectively generated traditional range maps. We have shown that RES modelling can adequately describe habitat suitability across large scales for wide-ranging

pelagic seabirds. RES modelling presents a generic and objective approach for predicting distributions of wide-ranging marine animals across large spatial scales, when the absence of representative point data precludes the application of traditional modelling techniques. Model outputs represent an alternative to the conventional and subjective approach of delineating range extents based on limited records of occurrence. The approach is based on clear assumptions concerning species' habitat preferences, which can be easily modified and tested.

RES predictions are limited by the extent of published data and the subsequent ability to accurately quantify species' ecological niches. While some gaps in the literature are evident, the synthesis of knowledge concerning species–habitat relationships can adequately describe ecological niches for the purposes of building predictive distribution models. This offers a more robust approach for answering broad-scale questions about species' distributions than deriving niches from limited and biased sampling data. Of greater significance is the limited availability of representative at-sea observations data to rigorously evaluate models, which may prove to be the key limiting factor in the wider application of RES modelling for wide-ranging marine animals.

Acknowledgements. Thanks to the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS) for supplying data for this study. MARINElife's contribution to this research was part-funded by the EU as part of the Channel Integrated Approach for Marine Resource Management (CHARM) Phase 3 project. We thank MARINElife volunteers for collection of observation data and P&O Ferries for sponsoring surveys aboard the Pride of Bilbao.

LITERATURE CITED

Airamé S, Dugan JE, Lafferty KD, Leslie H, McArdle DA, Warner RR (2003) Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. Ecol Appl 13:170–184

Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. J Biogeogr 33:1677–1688

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–7

Ashmole N (1971) Sea bird ecology and the marine environment. In: Farner DS, King, JR (eds) Avian Biology, Vol.1. Academic Press, New York, 223–286

BirdLife International (2004) Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop, 1-5 September, 2003, Gordon's Bay, South Africa. Birdlife International, Cambridge

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Briggs KT, Chu EW (1986) Sooty shearwaters off California: distribution, abundance and habitat use. Condor 88:355–364

Brown RM, Nichols RA, Faulkes CG, Jones CG, Bugoni L, Tatayah V, Gottelli D, Jordan WC (2010) Range expansion and hybridization in Round Island petrels (*Pterodroma* spp.): evidence from microsatellite genotypes. Mol Ecol 19:3157–3170

Corre M Le, Jaeger A, Pinet P, Kappes MA, Weimerskirch H, Catry T, Ramos JA, Russell JC, Shah N, Jaquemet S (2012) Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. Biol Conserv In press

Cramp S, Simmons K (1980) Handbook of the birds of Europe, the Middle East and north Africa. The birds of the western Palearctic. Volume 1. Ostrich to Ducks. Oxford University Press, Oxford

Dambach J, Rödder D (2011) Applications and future challenges in marine species distribution modeling. Aquat Conserv: Mar Freshwat Ecosyst 21:92–100

Davies RG, Irlich UM, Chown SL, Gaston KJ (2010) Ambient, productive and wind energy, and ocean extent predict global species richness of procellariiform seabirds. Global Ecol Biogeogr 19:98–110

Dormann CM, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

Elith J, Graham H, Anderson P, Dudík M, Ferrier S, Guisan A, Hijmans J, Huettmann F, Leathwick R, Lehmann A, Li J, Lohmann G, Loiselle A, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton CM, Townsend Peterson A, Phillips J, Richardson K, Scachetti-

Pereira R, Schapire E, Soberón J, Williams S, Wisz S, Zimmermann E (2006) Novel methods improve prediction of species distributions from occurrence data. Ecography 29:129–151

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Friesen VL, Burg TM, McCoy KD (2007) Mechanisms of population differentiation in seabirds. Mol Ecol 16:1765-1785

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding-season. Nature 311:655–656

Furness RW, Bryant DM (1996) Effect of wind on field metabolic rates of breeding northern fulmars. Ecology 77:1181–1188

Gaston AJ, Woo K (2008) Razorbills (*Alca Torda*) follow subarctic prey into the Canadian Arctic: colonization results from climate change? Auk 125:939–942

Gregr EJ, Trites AW (2008) A novel presence-only validation technique for improved Steller sea lion *Eumetopias jubatus* critical habitat descriptions. Mar Ecol Prog Ser 365:247–261

Guinotte JM, Bartley JD, Iqbal A, Fautin DG, Buddemeier RW (2006) Modeling habitat distribution from organism occurrences and environmental data: case study using anemonefishes and their sea anemone hosts. Mar Ecol Prog Ser 316:269–283

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Model 157:89–100

Gómez-Díaz E, González-Solís J, Peinado MA, Page RDM (2006) Phylogeography of the *Calonectris* shearwaters using molecular and morphometric data. Mol Phylogenet Evol 41:322–332

Hardy SM, Lindgren M, Konakanchi H, Huettmann F (2011) Predicting the distribution and ecological niche of unexploited snow crab (*Chionoecetes opilio*) populations in Alaskan waters: a first open-access ensemble model. Integr Comp Biol 51:608–22

Hedd A, Montevecchi WA, Otley H, Phillips RA, Fifield DA (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. Mar Ecol Prog Ser 449:277–290

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688

Hirzel AH, Guisan A (2002) Which is the optimal sampling strategy for habitat suitability modelling? Ecol Model 157:331–341

Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-Niche Factor Analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2027–2036

Hobbs M, Brereton T, Weir C, Williams A (2003) Baseline monitoring data on Procellariformes [Procellariiformes] (shearwaters) in the Bay of Biscay. Ornis Hungarica 12-13:115–125

Hoyo J del, Elliott A, Sargatal J (1992) Handbook of the birds of the world. Volume 1: ostrich to ducks. Lynx Edicions, Barcelona

Huettmann F, Diamond AW (2001) Seabird colony locations and environmental determination of seabird distribution: a spatially explicit breeding seabird model for the Northwest Atlantic. Ecol Model 141:261–298

Huettmann F, Artukhin Y, Gilg O, Humphries G (2011) Predictions of 27 Arctic pelagic seabird distributions using public environmental variables, assessed with colony data: a first digital IPY and GBIF open access synthesis platform. Marine Biodiversity 41:141–179

IOC, IHO, BODC (2003) Centenary edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans.

Karpouzi VS, Watson R, Pauly D (2007) Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment Mar Ecol Prog Ser 343:87–99

Kaschner K, Watson R, Trites AW, Pauly D (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. Mar Ecol Prog Ser 316:285–310

Kaschner K, Tittensor DP, Ready J, Gerrodette T, Worm B (2010) Current and future patterns of global marine mammal biodiversity. PLoS ONE 6:e19653–

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12:334–350

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673

Louzao M, Hyrenbach KD, Arcos JM, Abelló P, Sola LG De, Oro D (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. Ecol Appl 16:1683–1695

Louzao M, Bécares J, Rodríguez B, Hyrenbach KD, Ruiz A, Arcos JM (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Mar Ecol Prog Ser 391:183–197

Manly BF, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Springer, New York

Matthiopoulos J, Harwood J, Thomas L (2005) Metapopulation consequences of site fidelity for colonially breeding mammals and birds. J Anim Ecol 74:716–727

Maxwell DL, Stelzenmüller V, Eastwood PD, Rogers SI (2009) Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. J Sea Res 61:258–267

Milot E, Weimerskirch H, Bernatchez L (2008) The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. Mol Ecol 17:1658–1673

Miskelly CM, Taylor GA, Gummer H, Williams R (2009) Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*: Family Procellariidae). Biol Conserv 142:1965–1980

Nur N, Jahncke J, Herzog MP, Howar J, Hyrenbach KD, Zamon JE, Ainley DG, Wiens JA, Morgan K, Ballance LT, Stralberg D (2011) Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. Ecol Appl 21:2241–2257

Oedekoven CS, Ainley DG, Spear LB (2001) Variable responses of seabirds to change in marine climate: California Current, 1985-1994. Mar Ecol Prog Ser 212:265–281

Olden JD, Jackson DA, Peres-Neto PR (2002) Predictive models of fish species distributions: a note on proper validation and chance predictions. T Am Fish Soc 131:329–336

Olivier F, Wotherspoon SJ (2006) Modelling habitat selection using presence-only data: case study of a colonial hollow nesting bird, the snow petrel. Ecol Model 195:187–204

Onley D, Schofield P (2007) Field guide to the albatrosses, petrels and shearwaters of the world. Christopher Helm, London

Oppel S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, Louzao M (2011) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biol Conserv In press

Ostrand WD, Drew GS, Suryan RM, McDonald LL (1998) Evaluation of radio-tracking and strip transect methods for determining foraging ranges of black-legged kittiwakes. Condor 100:709–718

Pahl-Wostl C (1997) Dynamic structure of a food web model: comparison with a food chain model. Ecol Model 100:103–123

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197

Raes N, Steege H ter (2007) A null-model for significance testing of presence-only species distribution models. Ecography 30:727–736

Raymond B, Woehler EJ (2003) Predicting seabirds at sea in the Southern Indian Ocean. Mar Ecol Prog Ser 263:275–285

Ready J, Kaschner K, South AB, Eastwood PD, Rees T, Rius J, Agbayani E, Kullander S, Froese R (2010) Predicting the distributions of marine organisms at the global scale. Ecol Model 221:467–478

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torres L, Werner F (2006) Techniques for cetacean-habitat modeling. Mar Ecol Prog Ser 310:271–295

Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, Possingham HP, Richardson AJ (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global Ecol Biogeogr 20:789–802

Ross DA (1988) An introduction to oceanography. Prentice Hall, Englewood Cliffs

Sangster G, Knox AG, Helbig AJ, Parkin DT (2002) Taxonomic recommendations for European birds. Ibis 144:153–159

Schneider DC (1997) Habitat selection by marine birds in relation to water depth. Ibis 139:175–178

Schneider DC, Piatt JF (1986) Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Mar Ecol Prog Ser 32:237–246

Skov H, Durinck J, Danielsen F, Bloch D (1994) The summer distribution of Procellariiformes in the central North Atlantic Ocean. Vogelwarte 37:270–289

Skov H, Humphreys E, Garthe S, Geitner K, Grémillet D, Hamer KC, Hennicke J, Parner H, Wanless S (2008) Application of habitat suitability modelling to tracking data of marine animals as a means of analyzing their feeding habitats. Ecol Model 212:504–512

Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. P Natl Acad Sci USA 106:19644–19650

Spear LB, Ballance LT, Ainley DG (2001) Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. Mar Ecol Prog Ser 219:275–289

Strauss B, Biedermann R (2007) Evaluating temporal and spatial generality: How valid are species-habitat relationship models? Ecol Model 204:104–114

Sverdrup H, Johnston MW, Fleming RH (1942) The oceans: their physics, chemistry, and general biology. Prentice Hall, New York

Tasker ML, Reid JB (1997) Seabirds in the marine environment - Introduction. Ices J Mar Sci 54:505–506

Torres LG, Read AJ, Halpin P (2008) Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? Ecol Appl 18:1702–1717

Vermeer K, Morgan KH, Smith GEJ, Hay R (1989) Fall distribution of pelagic birds over the shelf off SW Vancouver Island. Colon Waterbirds 12:207–214

Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar Ecol Prog Ser 391:165–182

Warham J (1990) The petrels: their ecology and breeding systems. Academic Press, New York

Yen PPW, Huettmann F, Cooke F (2004) A large-scale model for the at-sea distribution and abundance of marbled murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada. Ecol Model 171:395–413

Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning JC (2010) New trends in species distribution modelling. Ecography 33:985–989

Table 1. Quantitative and qualitative definitions of habitat categories in respect of 4 ecogeographical variables (depth, sea-surface temperature, distance to land and chlorophyll *a* concentration) used to quantify species' ecological niches

Variable	Habitat category
Depth (m) (after Ross 1988)	
0–10	Coastal waters
11–200	Coastal waters to edge of continental shelf
201–1000	Edge of continental shelf to upper continental slope
1001–2000	Continental slope
2001–6000	Abyssal plains
6001–8000	Very deep waters
Sea-surface temperature (°C) (adapted from Sverdrup et al. 1942, Ashmole 1971)	
–2–5	Polar
0–10	Sub-polar
5–15	Cold temperate
10–20	Warm temperate
15–25	Subtropical
25–35	Tropical
Distance to land (km) (after Ashmole 1971)	
0–6	Inshore waters
6–50	Offshore
50+	Pelagic
Chlorophyll *a* (mg m^{-3}) (after Louzao et al. 2006)	
<0.1	Oligotrophic
0.1–0.3	Mesotrophic
0.3–1	Eutrophic
>1	Enriched waters

Table 2. Quantitative descriptions of species' ecological niches in respect of 4 ecogeographical variables: depth, sea-surface temperature (SST), distance to land and chlorophyll *a* concentration. Niches were defined for 6 procellariiform seabirds during the breeding and/or non-breeding season. MinA and MaxA refer to absolute minimum and maximum values of the resource selection function; MinP and MaxP: preferred minimum and maximum values (see Fig. 1). Chl *a* (mg m^{-3}; identical for each species and status): MinA, MinP = 0, 0.3; Max P, MaxA = 60, 60. Status: B = breeding, N = non-breeding. See Table S1 in Supplement 1 (www.int-res.com/articles/suppl/mXXXpXXX_suppl.pdf) for data sources

Species	Status	Depth (m)		SST (°C)		Distance (m)	
		MinA, MinP	MaxP, MaxA	MinA, MinP	MaxP, MaxA	MinA, MinP	Max P, MaxA
Northern fulmar	B	0, 100	1000, 8000	–2, 0	15, 15	0, 0	320, 2364
	N	0, 100	2000, 8000	–2, 0	10, 15	0, 50	2364, 2364
Cory's shearwater	B	0, 100	1000, 8000	10, 20	20, 25	0, 0	200, 2364
Great shearwater	N	0,100	200, 8000	–2, 0	20, 35	0, 6	2000, 2364
Sooty shearwater	N	0, 10	1000, 8000	5, 10	20, 35	0, 15	200, 2364
Manx shearwater	B	0, 10	200, 8000	5, 10	20, 25	0, 0	360, 2364
European storm petrel	B	0, 100	2000, 8000	5, 10	20, 25	0, 0	200, 2364

Table 3. Evaluation of predictive performance of relative environmental suitability (RES) models for 6 procellariiform seabirds. A model was considered to perform significantly better than chance if the area under the curve of the empirical model (AUC_m) exceeded the 95% quantile of the ranked AUC values of a null model (AUC_n). p-values indicate the proportion of random AUCs that were equal to or greater than AUC_m

	AUC_m	AUC_n	p
Northern fulmar			
Breeding	0.735	0.568	<0.001
Non-breeding	0.774	0.583	<0.001
Cory's shearwater			
Breeding	0.712	0.580	<0.001
Great shearwater			
Non-breeding	0.587	0.583	0.041
Sooty shearwater			
Non-breeding	0.530	0.575	0.260
Manx shearwater			
Breeding	0.614	0.572	0.004
European storm petrel			
Breeding	0.704	0.582	<0.001

Table 4. Summary of test data used for evaluating the predictive performance of relative environmental suitability (RES) models. Independent observation data were collected from repeated sampling of 156 grid cells (0.25 × 0.25°) by MARINElife in the Bay of Biscay (Fig. 2). The number of species' records, number of 'presence' cells and variation in RES within the model evaluation area (percentiles of ranked RES) are presented

Species	No. of records	No. of 'presence' cells	Percentiles of ranked RES in survey area		
			10%	50%	90%
Northern fulmar					
Breeding	590	71	0.0	0.0	1.0
Non-breeding	248	45	0.12	0.36	0.56
Cory's shearwater					
Breeding	527	51	0.15	0.43	0.62
Great shearwater					
Non-breeding	452	48	0.37	0.69	1.0
Sooty shearwater					
Non-breeding	115	46	0.55	1.0	1.0
Manx shearwater					
Breeding	245	60	0.50	1.0	1.0
European storm petrel					
Breeding	295	46	0.45	0.86	1.0

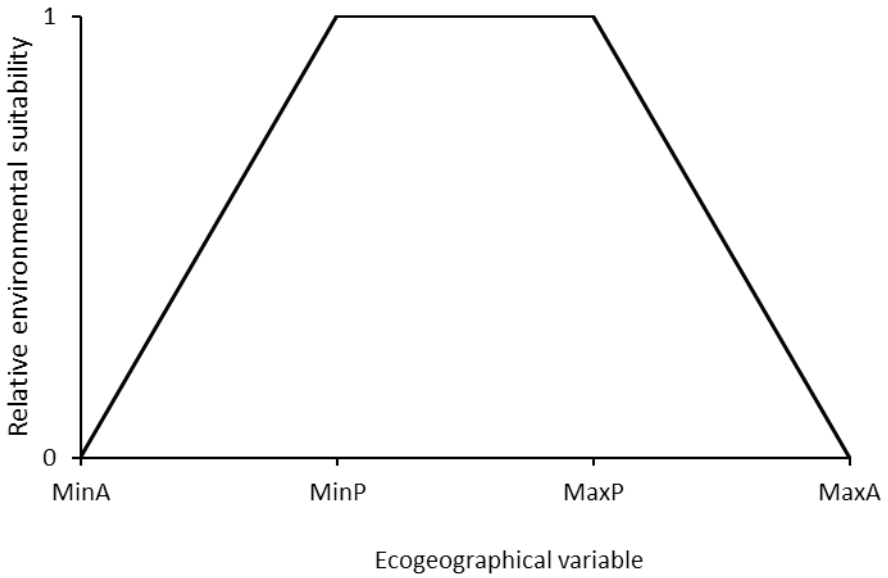


Fig. 1. Resource selection function describing a species' ecological niche as a function of likelihood of relative environmental suitability throughout the range of an ecogeographical variable. MinA and MaxA: absolute minimum and maximum values; MinP and MaxP: preferred minimum and maximum values of individual niche parameters

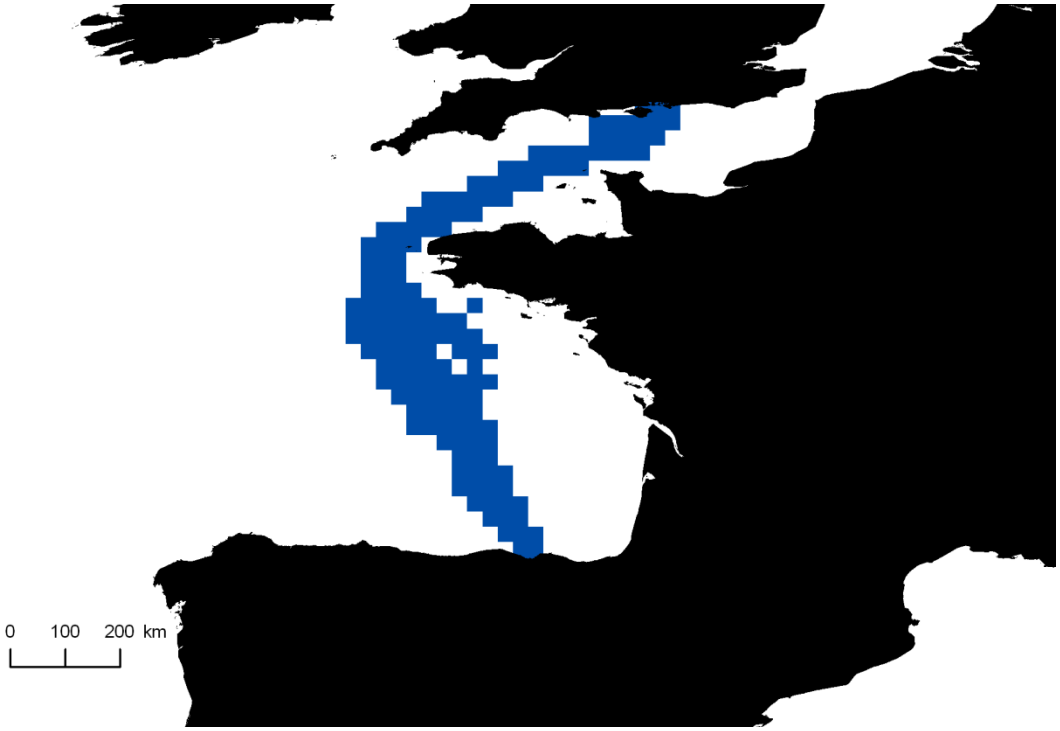
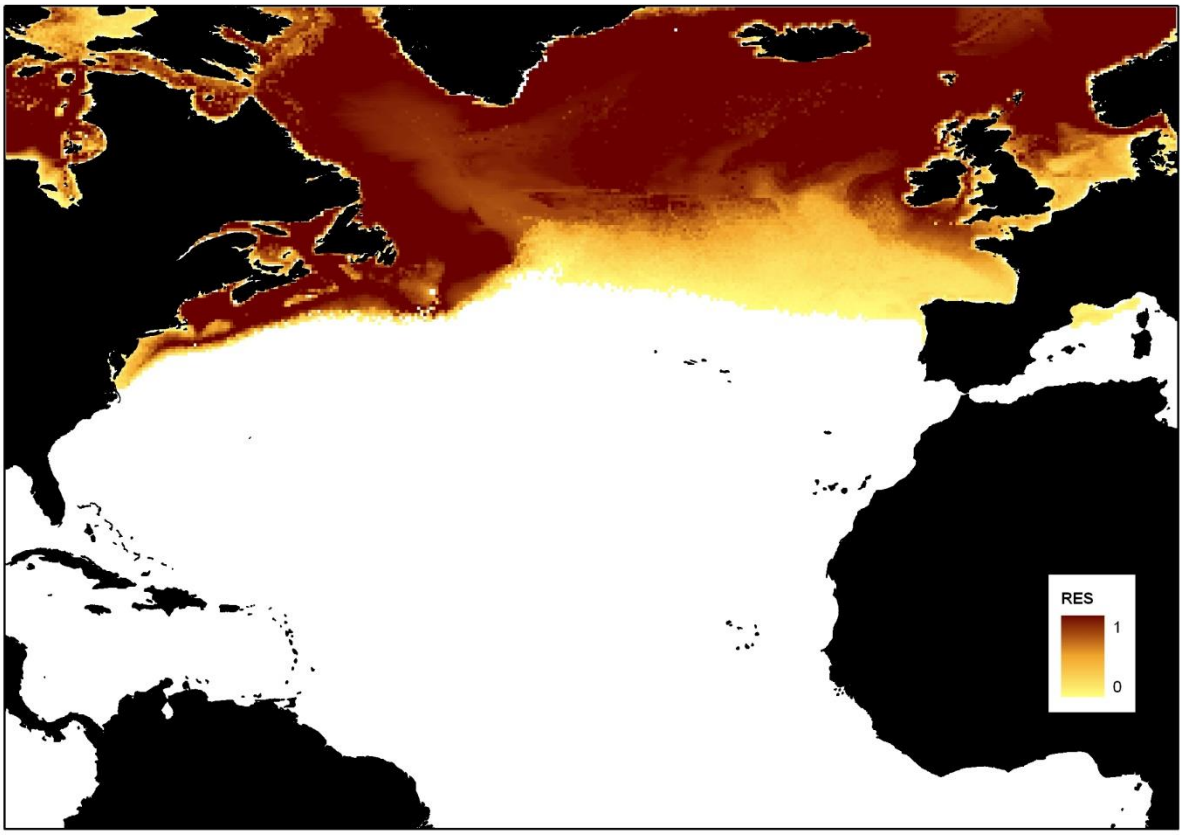
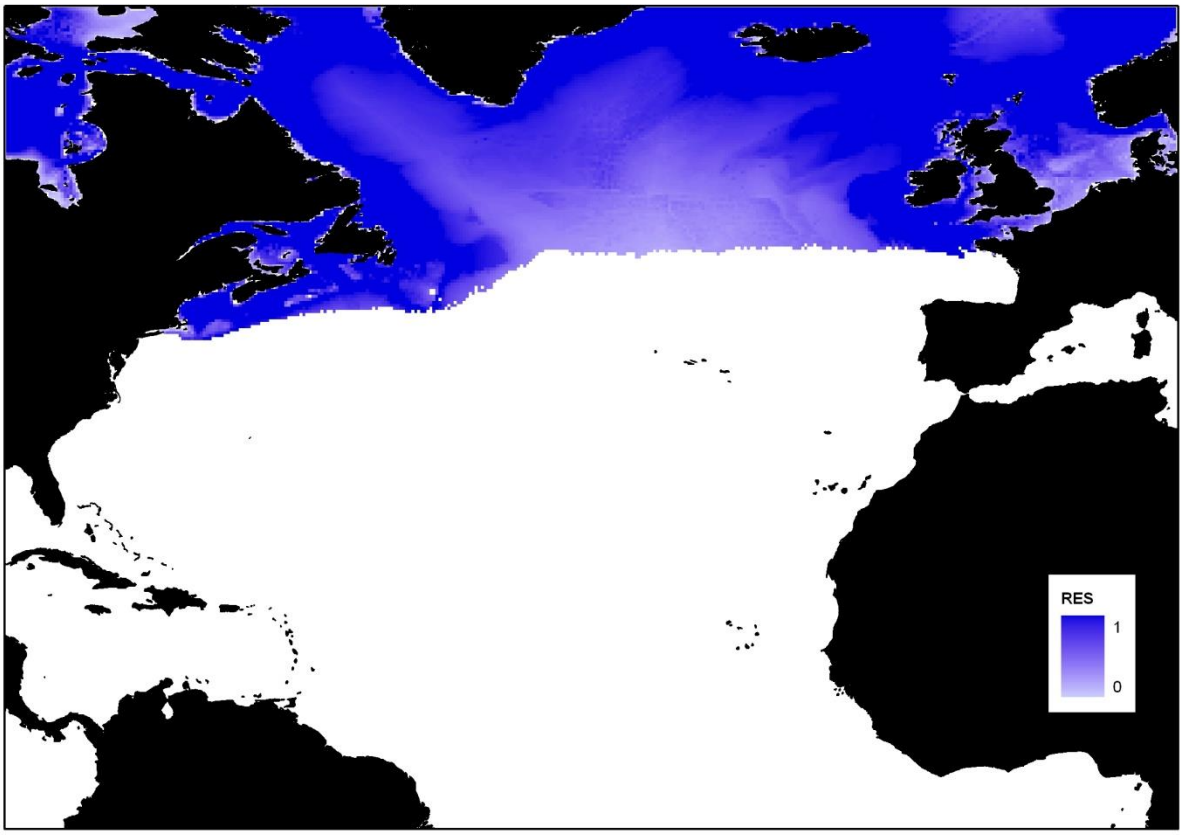


Fig. 2. Area where MARINElife conducted monthly seabird surveys between 1995 and 2005 in the English Channel and Bay of Biscay. Data collected served as independent observation data for evaluation of relative environmental suitability (RES) models. Blue squares delineate grid cells (0.25 × 0.25°) covered by sampling effort

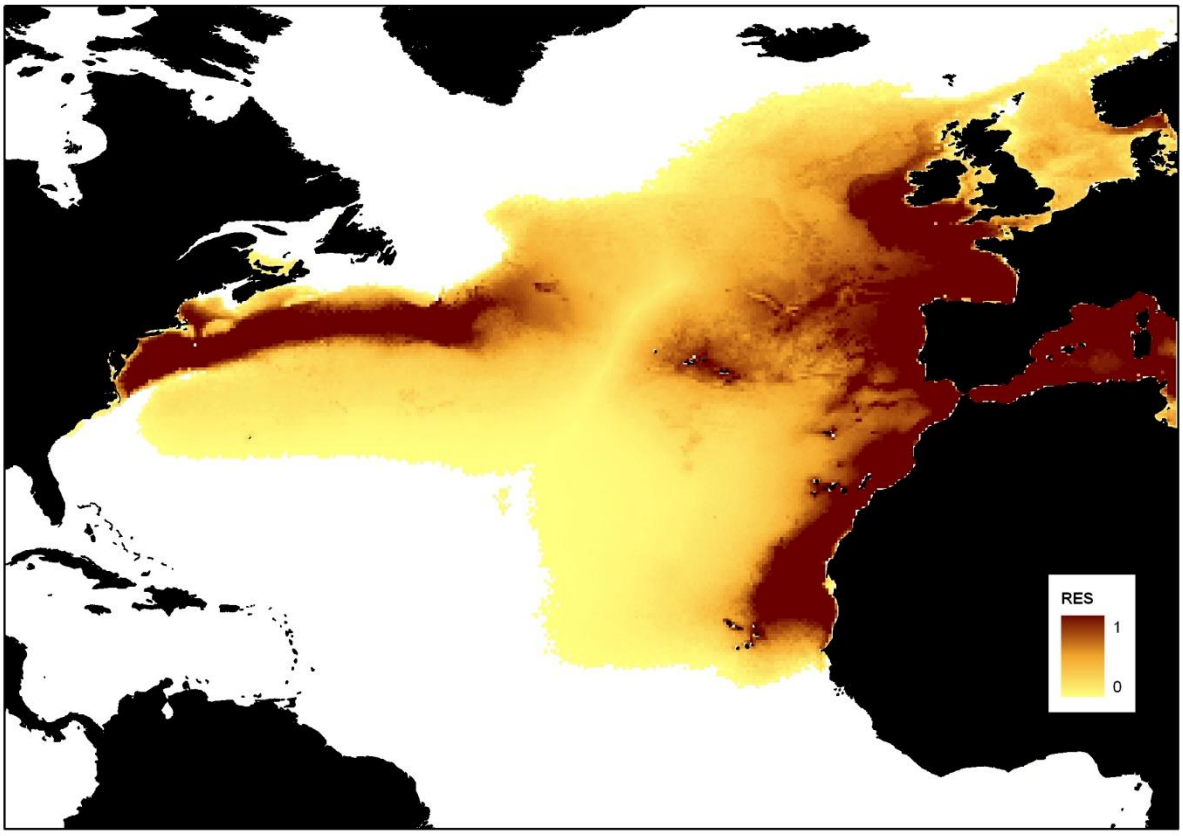
(a) Northern fulmar *Fulmarus glacialis*, breeding



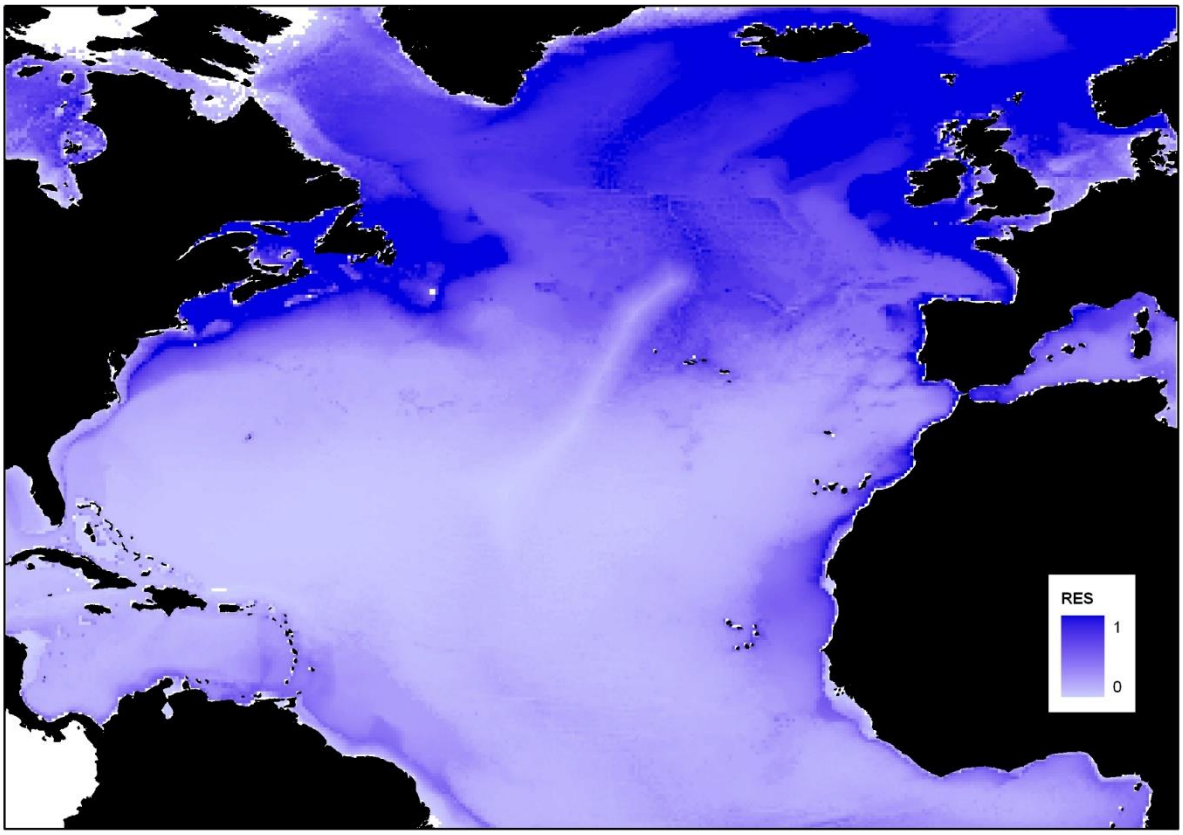
(B)



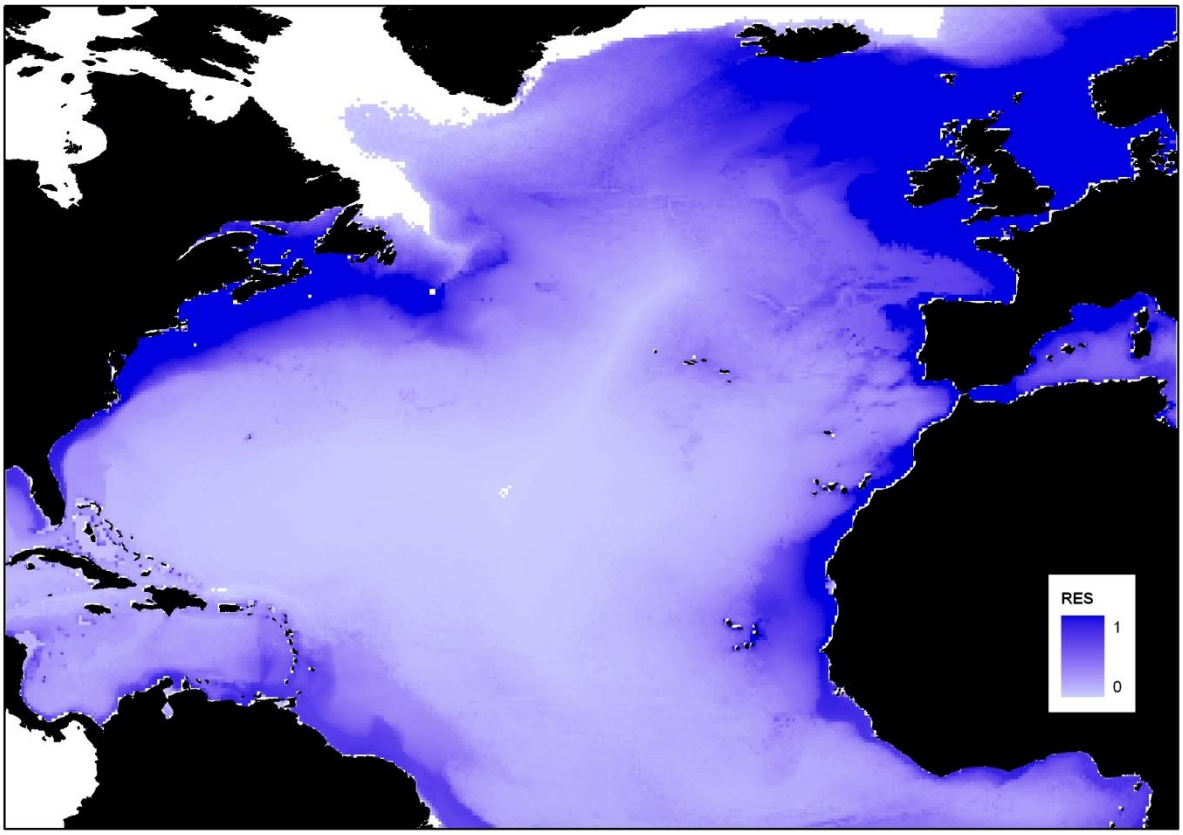
(C)



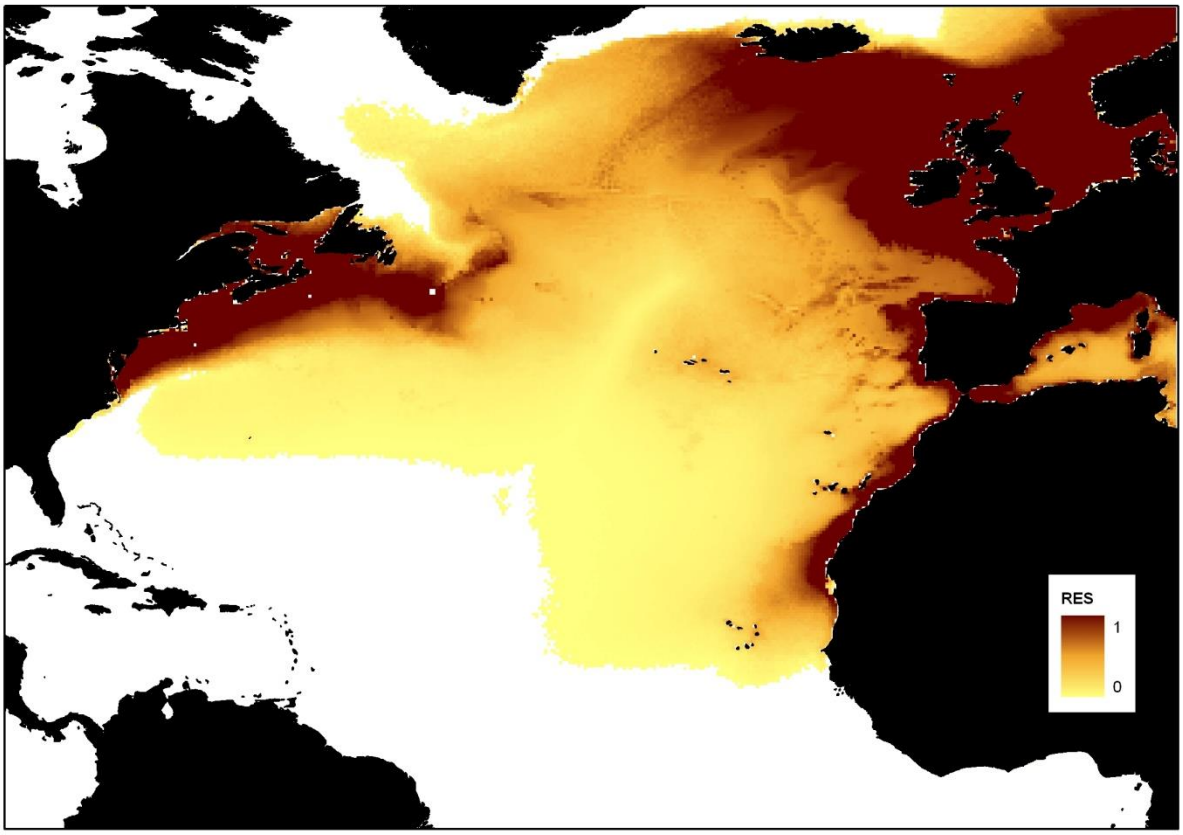
(D)



(E)



(F)



(G)

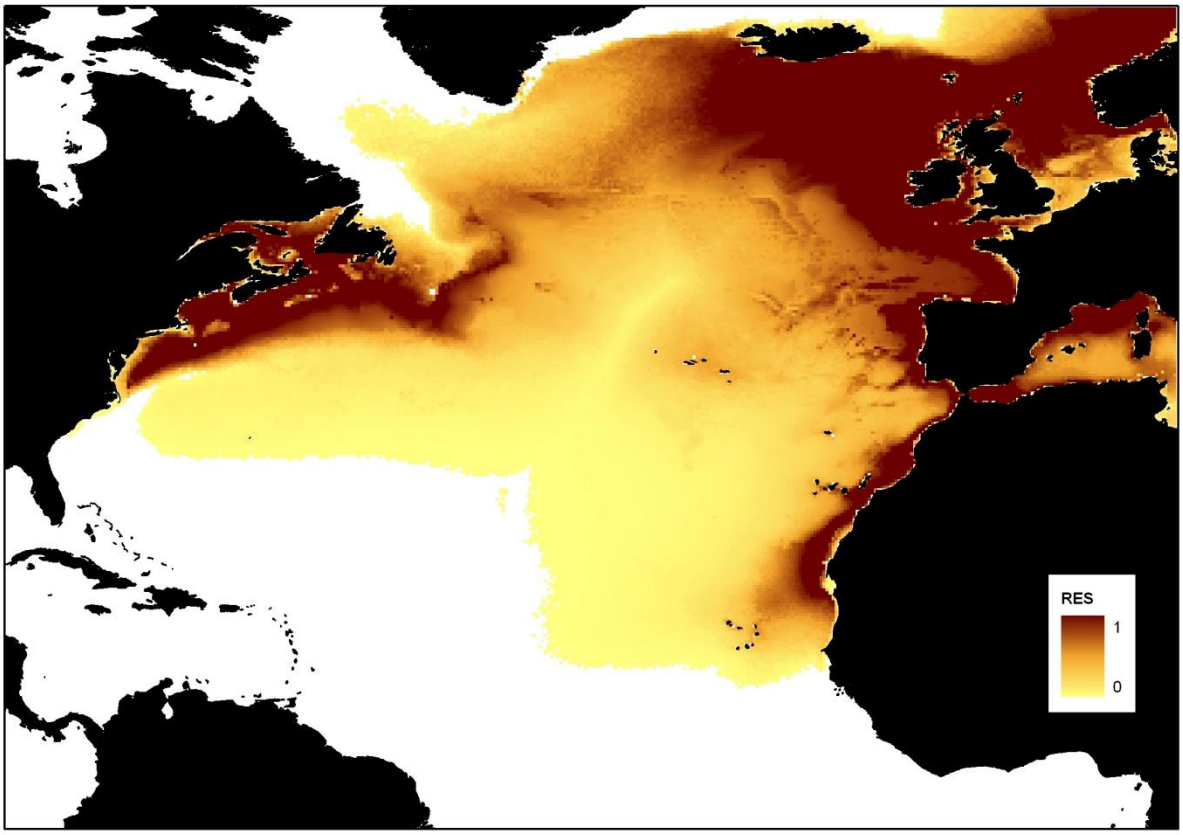


Fig. 3. Model outputs illustrating predicted geographic range and relative environmental suitability (RES) for 6 procellariiform seabirds in the North Atlantic during their breeding (yellow–brown) and/or non-breeding seasons (blue): (A) northern fulmar *Fulmarus glacialis*, breeding; (B) northern fulmar, non-breeding; (C) Cory's shearwater *Calonectris diomedea*, breeding; (D) great shearwater *Puffinus gravis*, non-breeding; (E) sooty shearwater *P. griseus*, non-breeding; (F) Manx shearwater *P. puffinus*, breeding; and (G) European storm petrel *Hydrobates pelagicus*, breeding. Predicted RES is on a scale from 0 (least suitable, white) to 1 (highly suitable, dark).