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Assessing the effectiveness of foraging radius models for seabird distributions using biotelemetry and survey data

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Relatively simple foraging radius models have the potential to generate predictive distributions for a large number of species rapidly, thus providing a cost-effective alternative to large-scale surveys or complex modelling approaches. Their effectiveness, however, remains largely untested. Here we compare foraging radius distribution models for all breeding seabirds in Ireland, to distributions of empirical data collected from tracking studies and aerial surveys. At the local/colony level, we compared foraging radius distributions to GPS tracking data from seabirds with short (Atlantic puffin *Fratercula arctica,* and razorbill *Alca torda*) and long (Manx shearwater *Puffinus puffinus*, and European storm-petrel *Hydrobates pelagicus*) foraging ranges. At the regional/national level, we compared foraging radius distributions to extensive aerial surveys conducted over a two-year period. Foraging radius distributions were significantly positively correlated with tracking data for all species except Manx shearwater. Correlations between foraging radius distributions and aerial survey data were also significant, but generally weaker than those for tracking data. Correlations between foraging radius distributions and aerial survey data were benchmarked against generalised additive models (GAMs) of the aerial survey data that included a range of environmental covariates. While GAM distributions had slightly higher correlations with aerial survey data, the results highlight that the foraging radius approach can be a useful and pragmatic approach for assessing breeding distributions for many seabird species. The approach is likely to have acceptable utility in complex, temporally variable ecosystems and when logistic and financial resources are limited.

Keywords: aerial survey, biotelemetry, central place foragers, foraging radius, seabirds, species distribution modelling

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Introduction

Determining the distributions of species for conservation planning can present many challenges. In particular, it is usually time-intensive and costly to capture a representative sample of the population, especially for species with large ranges. The challenges can be even greater for marine species, where the difficulties in accessing study sites can be limiting and the dynamic nature of the environment can cause high spatio-temporal variation in distributions. Consequently, there is often insufficient data to inform conservation planning in marine systems, leading to a difficulty in defining marine protected areas for many marine top predators (Game et al. 2009, Dias et al. 2017). This is especially true for seabirds, a taxonomic group for which there remains a major gap in the level of protection afforded at sea for even the most threatened species (McGowan et al. 2017, Critchley et al. 2018) and who face significant threats when foraging at sea (Croxall et al. 2012, Dias et al. 2019).

Predictive modelling has the potential to overcome these challenges, and is less costly and time-intensive than large-scale at-sea surveys or tracking studies. Techniques available for ecological modelling have expanded rapidly (Wakefield et al. 2009, Lascelles et al. 2016), giving conservation practitioners an array of choices. However, many predictive models are still reliant on the collection of extensive data to inform inputs, for example ecological niche models (Scales et al. 2015), and the spatial resolution and temporal averaging of environmental covariates can also influence the accuracy of predictive models significantly (Pearson et al. 2006, Péron et al. 2018). Some models take a simpler and more mechanistic approach, modelling distribution based on a combination of telemetry and population data (Jones et al. 2015, Pikesley et al. 2018). This avoids any uncertainties about the relationship of observations with environmental data being propagated in the final model output.

One simple method that can be applied to any central-place forager and requires little a-priori data on at-sea distribution is the foraging radius model approach (BirdLife International 2010, Grecian et al. 2012, Critchley et al. 2018). This approach projects distributions based on a set of foraging radii, a decay function from the central place or colony, and colony size, providing a rapid and cost-effective method for assessing at-sea distribution during the breeding season. While in general the use of simplified models is thought to sacrifice species-specific accuracy (e.g. due to habitat preferences) and fails to account for local variation (e.g. spatial partitioning), there is also evidence that the foraging radius approach can be effective for individual species when compared to empirical data (Grecian et al. 2012, Ludynia et al. 2012, Soanes et al. 2016). However, the effectiveness of foraging radius models has not yet been assessed at the community level across multiple species or colonies.

Empirical methods generate essential inputs for predictive distribution models. The best method to use is dependent on the species of interest, the area to be covered, accessibility and the amount of resources available. At-sea surveys are an established approach to inform marine spatial planning at regional (Smith et al. 2014), national (Kober et al. 2012) and international (Lambert et al. 2017) scales. Aerial or ship-based surveys can target most seabird species in a community, often at large spatial scales and can also provide absolute abundance estimates if conducted following distance based methodology (Embling et al. 2010). However, such data is often obtained from surveys conducted from vessels of opportunity and tends to be spatially and temporally patchy (Stone et al. 1995, Dunn 2012) with few repeated transects that would allow an examination of temporal variation. In contrast biologging studies provide detailed information on the fine-scale distribution of seabirds, usually during the breeding season (Wakefield et al. 2013, Dean et al. 2015, Soanes et al. 2016), and on broader scale movements during the non-breeding season (Frederiksen et al. 2012, Jessopp et al. 2013, Grecian et al. 2016). However, the individuals selected may not be representative of the wider colony, other colonies in the region, or other regions, given the inevitability of only ever being able to track a small proportion of a population (Soanes et al. 2013). The temporal scale of tracking is also usually heavily restricted by resources (Wakefield et al. 2009). Furthermore, foraging areas can vary annually depending on environmental fluctuations (Robertson et al. 2014), a factor that is predicted to increase with climate change (Grémillet and Boulinier 2009, Daunt and Mitchell 2013). This source of variation is hard to capture by all empirical approaches. While foraging radius models do have limitations, the same is true for all empirical approaches, the robustness of which remains largely unknown.

Here we explore the accuracy and suitability of the foraging radius approach for assessing distributions of seabirds at sea during the breeding season. We do this by comparing foraging radius distributions to empirical data from biotelemetry and at-sea aerial surveys in Irish waters, which support diverse and internationally important numbers of breeding seabirds (Mitchell et al. 2004). At a colony level we compare foraging radius distributions to GPS tracking data obtained from four breeding seabirds (Manx shearwater, razorbill, European storm-petrel and Atlantic puffin), representing species with short and long foraging ranges. At a national level we compare foraging radius distributions for 25 breeding seabird species to extensive aerial surveys conducted over a two-year period. To provide a benchmark for the correlation values between foraging radius distributions and empirical data, we also model distributions from the aerial survey data using generalised additive models (GAMs), incorporating environmental predictors, as this approach is often considered to be the best method for modelling survey data (Booth and Hammond 2014, Potts and Rose 2018). We discuss the performance of the foraging radius model in comparison to the empirical data and the appropriateness of using this method for assessing seabird distributions under different scenarios.

Material and methods

Overview

Assessing the effectiveness of the foraging radius model for predicting seabird distributions at sea during the breeding season involved the following steps (see also Fig. 1): 1) predicting the distribution of seabirds in Irish waters using the foraging radius approach at both species and family level; 2) generating utilisation distributions from GPS tracking data for Manx shearwater *Puffinus puffinus*, razorbill *Alca torda*, European storm-petrel *Hydrobates pelagicus* and Atlantic puffin *Fratercula arctica*; 3) comparing colony level foraging radius distributions to utilisation distributions; 4) calculating density per km^2 for aerial survey data in Irish waters; 5) comparing multi-colony foraging radius distributions to fine scale aerial survey data for 20 species/groups and broad scale aerial survey data for 9 species/groups; 6) generating predicted distributions from broad scale aerial survey data using generalised additive models (GAMs) and environmental covariates; 7) comparing GAM predicted distributions to broad scale aerial data for 7 species/groups. See Supplementary material Appendix 1 Table A1 for a full list of species and data availability.

Foraging radius model

Foraging radius distributions were generated for individual colonies of all seabirds (25 species, Supplementary material Appendix 1 Table A1) across the UK and Ireland during the breeding season using the approach described in

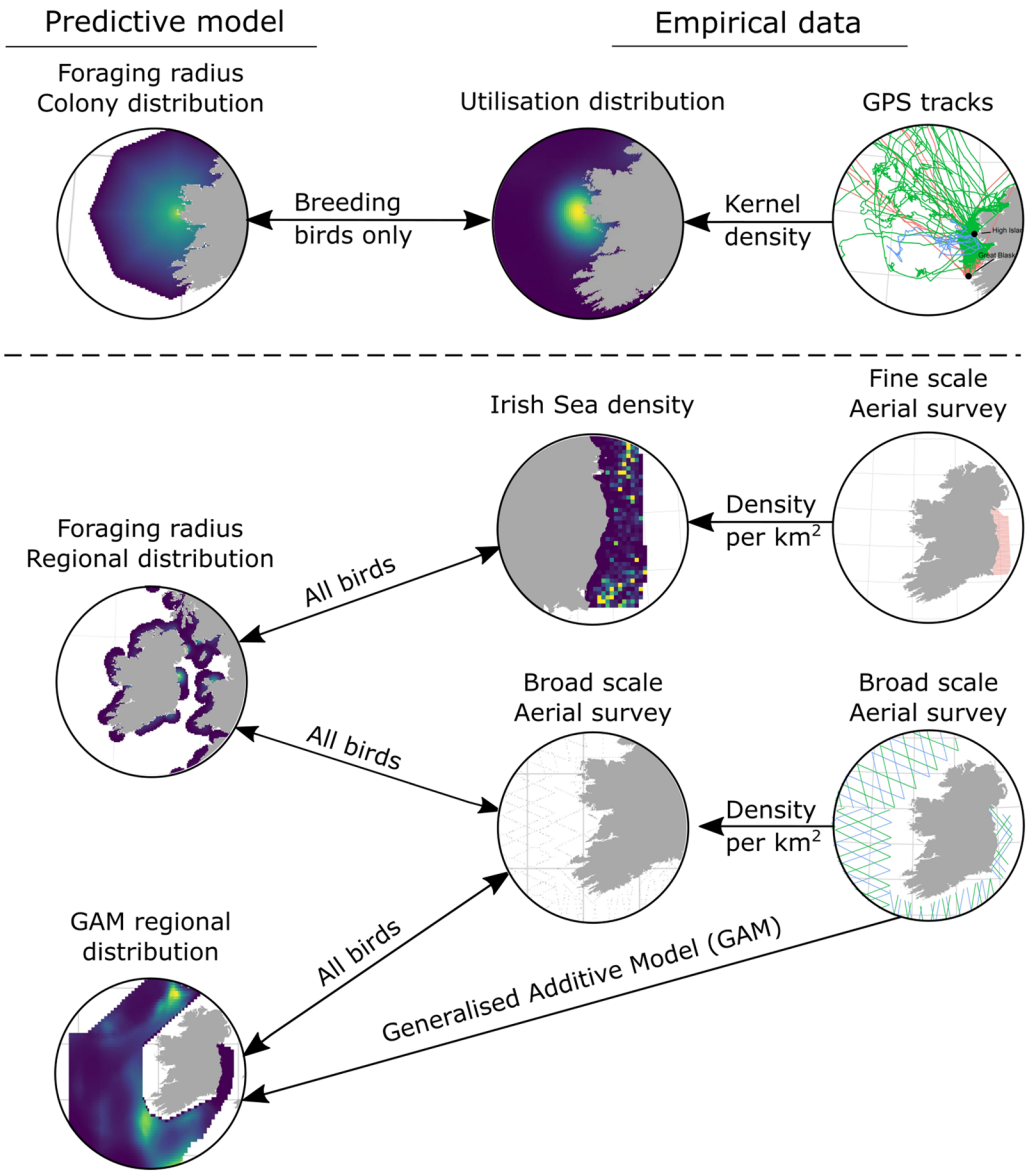


Figure 1. Schematic of methodology for data processing and distribution comparisons at colony and regional level. Double headed arrows indicate distribution comparisons and single headed arrows indicate data processing.

Critchley et al. (2018). The model predicts the occurrence of birds within the at-sea area surrounding a colony, up to a set colony-centred radius. The mean of all maximum foraging ranges (mean maximum foraging range) reported for each species was taken from the literature (Thaxter et al. 2012 and more recent studies, see Supplementary material Appendix 1 Table A2 for a list of foraging ranges and sources). A 5 × 5 km grid was generated across the study area, and the probability of occurrence within each grid square was first calculated by taking the normalised inverse distance from the grid square to the colony, so that all squares had a value of between 0 and 1 with the highest values being found closest to the colony. Distributions were then distance-weighted using a logarithmic decay function so that areas closer to the colony were of higher importance per unit area, accounting for non-foraging behaviours such as washing/preening or rafting (Wilson et al. 2009). Values were again normalised so that all grid squares summed to 100% and then multiplied by estimates of the breeding population, taken from the JNCC Seabird Monitoring Programme (SMP) Database [at <www.jncc.gov.uk/smp>] and additional colony surveys from National Parks and Wildlife Service and BirdWatch Ireland annual reports (Daly et al. 2015, Doyle et al. 2015), to estimate abundance per grid square.

The distribution maps were plotted on a 5 × 5 km grid and show the number of individuals predicted to occur in each grid square, assuming 50% of the colony is foraging at-sea at a given time. This accounts for the assumption that on average, one half of a breeding pair will remain at the nest at any one time (e.g. during incubation and early chick rearing). These steps were repeated for each individual colony in the UK and Ireland and the distributions were then summed to generate a foraging radius distribution map for each of the 25 species over the entire region. To test the sensitivity of varying foraging range on comparisons with other methods of assessing at-sea distribution, foraging radius distributions were also generated using the maximum of all recorded foraging ranges for each species (Supplementary material Appendix 1 Table A2). Foraging radius distributions were produced using R ver. 3.4.3 (R Development Core Team).

GPS tracking

GPS tracking data were collected from Manx shearwaters *Puffinus puffinus* breeding on two Islands off the west coast of Ireland, Great Blasket, Co. Kerry (2014–2015; 52.10N, 10.52W; n = 24), and High Island, Co. Galway (2014–2016; 53.55N, 10.26W; n = 65); from razorbills *Alca torda* breeding on the southeast coast of Ireland on Great Saltee, Co. Wexford (2014; 52.12N, −6.61W; n = 11); from European storm-petrels *Hydrobates pelagicus* breeding on the west coast on High Island, Co. Galway (2016; 53.55N, 10.26W; n = 8), Ireland; and from Atlantic puffins *Fratercula arctica* breeding on the southeast coast on Little Saltee, Co. Wexford (2017; 52.13N, −6.62W; n = 9) (Fig. 2). All data were collected during chick rearing, apart from for Manx shearwater for which data was also collected during the incubation stage.

All tracked birds were caught at their nest or burrow by hand, crook or purse nets. Manx shearwaters and razorbills were fitted with GPS loggers (i-gotU GT-120, Mobile Action Technology, Taiwan) attached dorsally to contour feathers using strips of waterproof Tesa tape (4651, Tesa, Germany). European storm-petrels were tracked using 0.95 g Pathtrack GPS tags attached to the tail feathers using Tesa tape (4651, Tesa, Germany). Atlantic puffins were tracked using Ecotone Uria GPS loggers attached ventrally to the lower back using Tesa tape (4651, Tesa, Germany). Deployment weight was kept below 3% (puffins, razorbills, storm-petrels) or 4% of body mass (Manx shearwater). On return to the colony, tags were recovered and downloaded from all species except puffins, where data was obtained by remote download. The use of Tesa tape as a temporary attachment method in all cases allowed for any tags not retrieved to drop off. Licenses for capture and deployment of devices were granted by National Parks and Wildlife Service, and British Trust for Ornithology.

Tags were programmed to record locations every 2–30 min depending on the tag used and the species tracked. All location fixes were included in analyses, except those generated whilst birds were within a 2 km buffer of the centre of the colony, or where recorded over land (Fig. 2 for a map of colony locations and tracks). All track processing was carried out in ArcMap 10.3.1. As there was large variation in the GPS relocation intervals across the four species (ranging from 2 to 30 min) all tracking data was also interpolated to regularised 3-min intervals, apart from the data for razorbills which was collected at 2 min intervals. Bivariate kernel utilisation distributions were generated for each species using the adehabitatHR package (Calenge 2015) in R ver. 3.4.3 (R Development Core Team). For Manx shearwaters, utilisation distributions were estimated for the two colonies separately and data for multiple years were combined. All utilisation distributions were generated using the reference smoothing parameter from the package on a 2 × 2 km grid (Supplementary material Appendix 1 Table A7 for smoothing parameter values).

Aerial surveys

Aerial survey data was obtained from the ObSERVE aerial survey programme (Jessopp et al. 2018, Rogan et al. 2018), conducted in Irish waters over the 2015 and 2016 breeding seasons. Two sets of surveys were flown, a broad-scale survey covering predominantly offshore waters, and a fine-scale survey covering the western Irish Sea, including inshore coastal waters. Broad scale survey transects were designed to provide equal coverage for the survey area and consisted of equally spaced randomly placed zig-zag lines (Fig. 3) that were positioned differently in 2015 and 2016 to allow for a more representative coverage of the study area. The fine scale survey transects consisted of 55 parallel lines spaced approximately 2 nautical miles (3.7 km) apart, and between 20–30 nautical miles in length, and were only surveyed in 2016. The parallel line design sought to cover all of the shallower sand banks on the Irish east coast which broadly run in a north-south

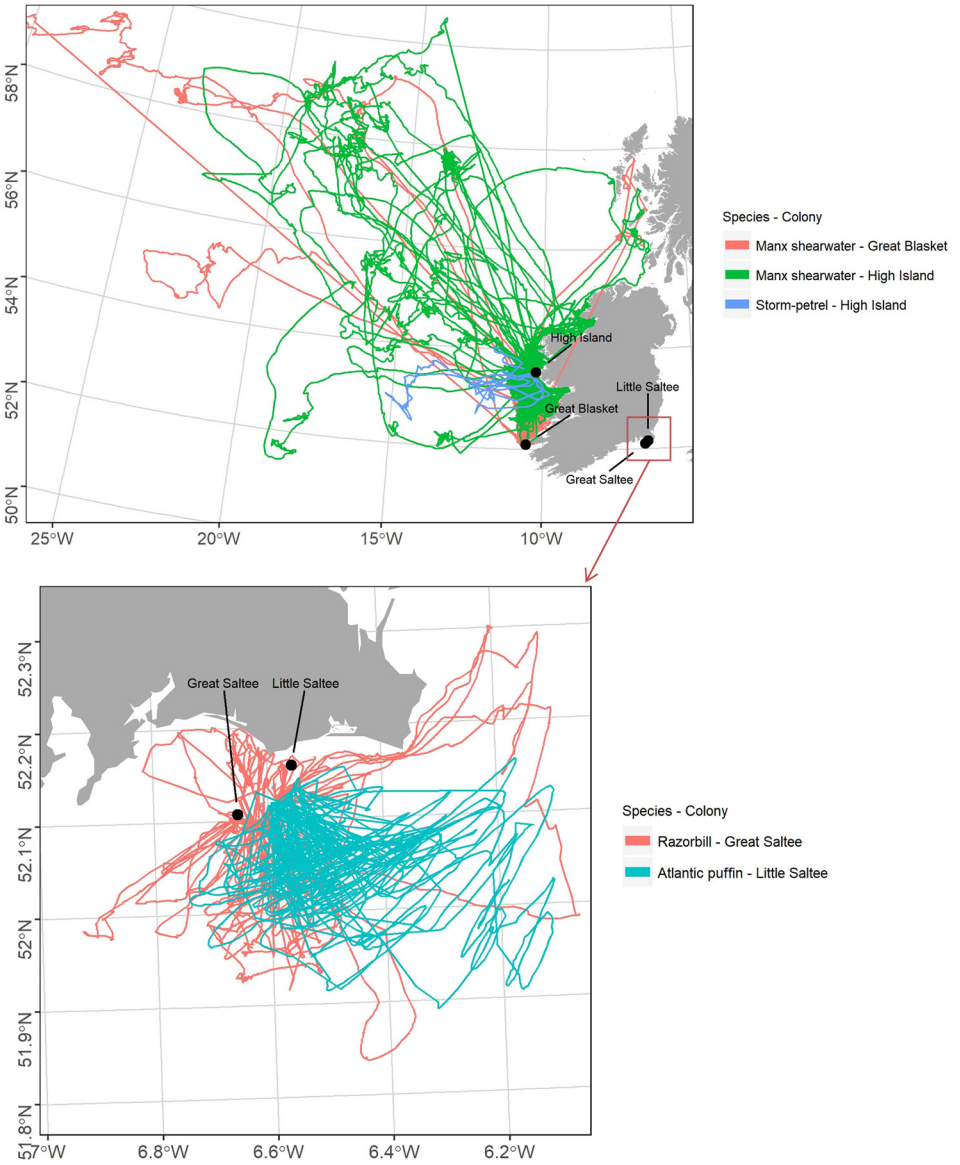


Figure 2. GPS tracks and colony locations for Manx shearwater and European storm-petrel on the west coast of Ireland and inset for razorbill and Atlantic puffin on the south east coast of Ireland.

direction, while also taking in aquatic habitat adjacent to the banks (Fig. 3).

Surveys used a fixed high-wing, twin-engine Britten-Norman (BN-2) Islander fitted with bubble-windows to afford observers unrestricted views of the transect area beneath the aircraft. Flying speed was 90 knots (167 km h^{-1}) at an altitude of 183 m on broad scale surveys, and 76 m on fine-scale surveys under target weather conditions of Beaufort Force 3 or less, with good visibility (1 km or more). The plane's geographic position was recorded every two seconds using an on-board GPS linked to a data logging computer. Two fully trained observers, one either side of the plane, employed a strip transect methodology, recording all seabirds within a 200 m distance band either side of the aircraft, determined by use of inclinometers (Camphuysen et al. 2004). When seabirds came abeam of the aircraft, a date/time stamped record was produced consisting of location (latitude, longitude), species ID and group size. Species were identified to the lowest taxonomic level whenever possible. When individuals could not be identified to species level, they were grouped into higher taxa categories.

Density of seabirds from both the fine scale and broad scale survey data was determined by dividing the number of individuals sighted by survey effort (distance travelled multiplied by strip width and corrected for observer effort), to give density per km^2 for each strip segment. The centre point for each segment was taken as the spatial point for comparison with foraging radius distributions.

In the broad scale surveys, summer seabird abundance and distribution was also modelled using generalized

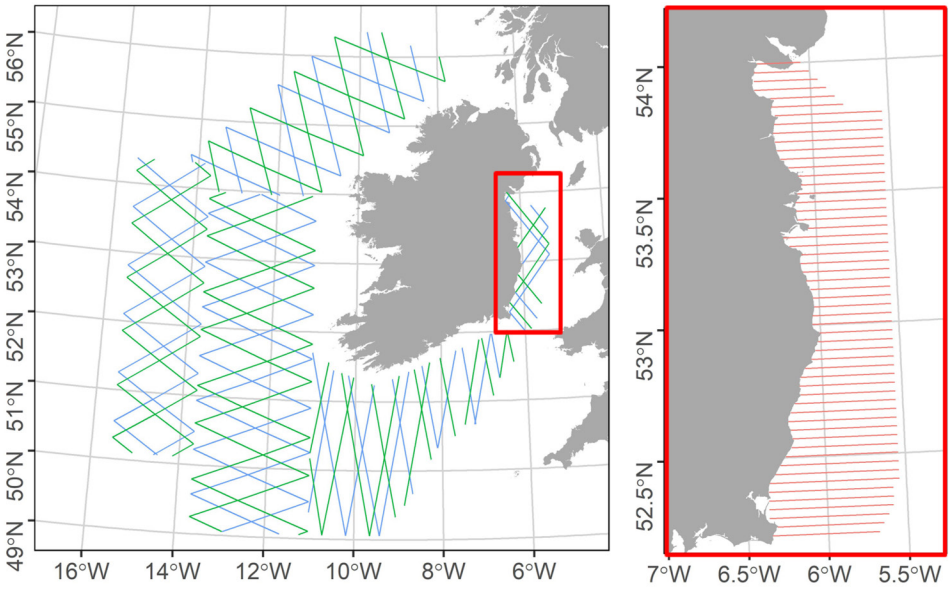


Figure 3. Broad-scale aerial survey transect lines for Irish offshore waters flown in summer 2015 (blue) and 2016 (green) and inset, fine-scale aerial survey transects in the Irish Sea flown in summer 2016 (red).

additive models (GAM) with a logarithmic link function, and a Tweedie error distribution following Cañadas and Hammond (2008). The response variable was the number of groups (or number of animals in non-gregarious species), using the effective area searched (distance travelled × 400 m strip width) as an offset. Distributions were predicted at a resolution of 0.10 × 0.06 degrees (latitude × longitude) and as a function of a wide range of environmental covariates. See Supplementary material Appendix 1 (Table A4, A5, A6) for further details of methods and environmental covariates used.

Distribution comparisons

Densities of seabirds per grid cell were compared across distributions using a Dutilleul's modified t-test of correlation (Dutilleul et al. 1993), which accounts for spatial autocorrelation within the data (Fortin and Payette 2002). Individual Dutilleul's modified t-tests for each species/family group were conducted using the 'SpatialPack' package (Osorio et al. 2014) in R. At the individual colony scale, kernel densities from GPS tracking data were compared to foraging radius distributions for the same colonies (Fig. 1). At the regional scale, aerial survey outputs for fine-scale surveys in the Irish Sea and broader offshore waters (two summer surveys combined to include any inter-annual variability in distributions) were compared to the regional foraging radius distributions for each species/family group (Fig. 1). A benchmark for the foraging radius model correlations was provided by comparing aerial survey data to modelled GAM distributions incorporating a range of environmental variables (Supplementary material Appendix 1 Table A4, A5, A6). All analysis was carried out in R ver. 3.4.3 (R Development Core Team).

Results

Example colony level and regional distribution maps, derived from both foraging radius and empirical approaches, are shown for Manx shearwater (Fig. 4) and razorbill/auks (Fig. 5).

Comparison of foraging radius distributions with GPS tracking data

Correlations of colony-level foraging radius distributions with kernel estimated utilisation distributions from GPS tracking data ranged from 0.187 to 0.621; all $p < 0.05$ apart from Manx shearwaters, (Fig. 6 and Supplementary material Appendix 1 Table A7). For all species, the use of mean maximum foraging range in the foraging radius model resulted in stronger correlations than using maximum foraging range. For three of the four species, correlations increased only marginally with the use of mean maximum foraging range; from 0.497 ($p < 0.005$) to 0.504 ($p < 0.001$) in European storm-petrel; from 0.187 ($p = 0.189$) to 0.252 ($p = 0.03$) in Manx shearwater at High Island, and 0.188 ($p = 0.3$) to 0.281($p = 0.1$) at Great Blasket for Manx shearwater; and from 0.457 ($p < 0.001$) to 0.518 ($p < 0.001$) for Atlantic puffin. For razorbill, the difference was greater changing from 0.47 ($p < 0.001$) to 0.621 ($p < 0.001$) with the use of mean maximum foraging range.

Comparison of foraging radius distributions with fine-scale Irish Sea aerial survey data

There were few significant correlations between foraging radius distributions and empirical data from fine-scale surveys, with the notable exceptions of terns (0.335–0.392,

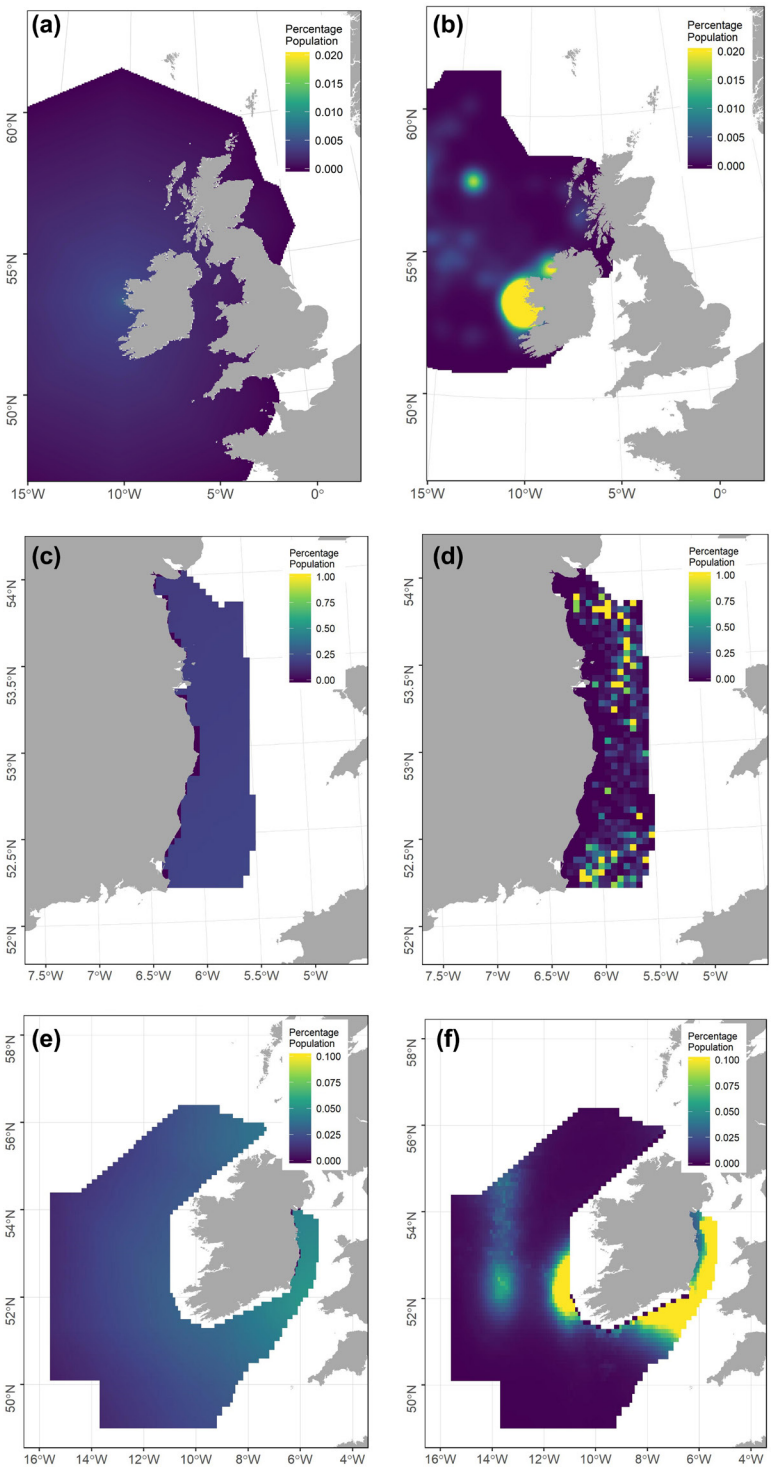


Figure 4. Maps showing (a) foraging radius distribution of Manx shearwaters from High Island colony only, generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al. 2004); (b) kernel density distribution for Manx shearwaters breeding on High Island, Co. Galway, generated from three years of summer breeding season GPS tracking data (2014–2016); (c) foraging radius distributions of Manx shearwaters in the Irish Sea generated using the mean maximum foraging radius; (d) empirical density values of Manx shearwaters in the Irish Sea from fine-scale aerial surveys (2016); (e) foraging radius distribution for all Manx shearwater colonies in Ireland and the UK generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al. 2004); and (f) GAM modelled density for Manx shearwaters in Irish waters, generated from two years of summer ObSERVE aerial survey data (2015–2016). Densities for all maps were normalised to percentage at-sea population per grid square, i.e. all grid squares in each map sum to 100%.

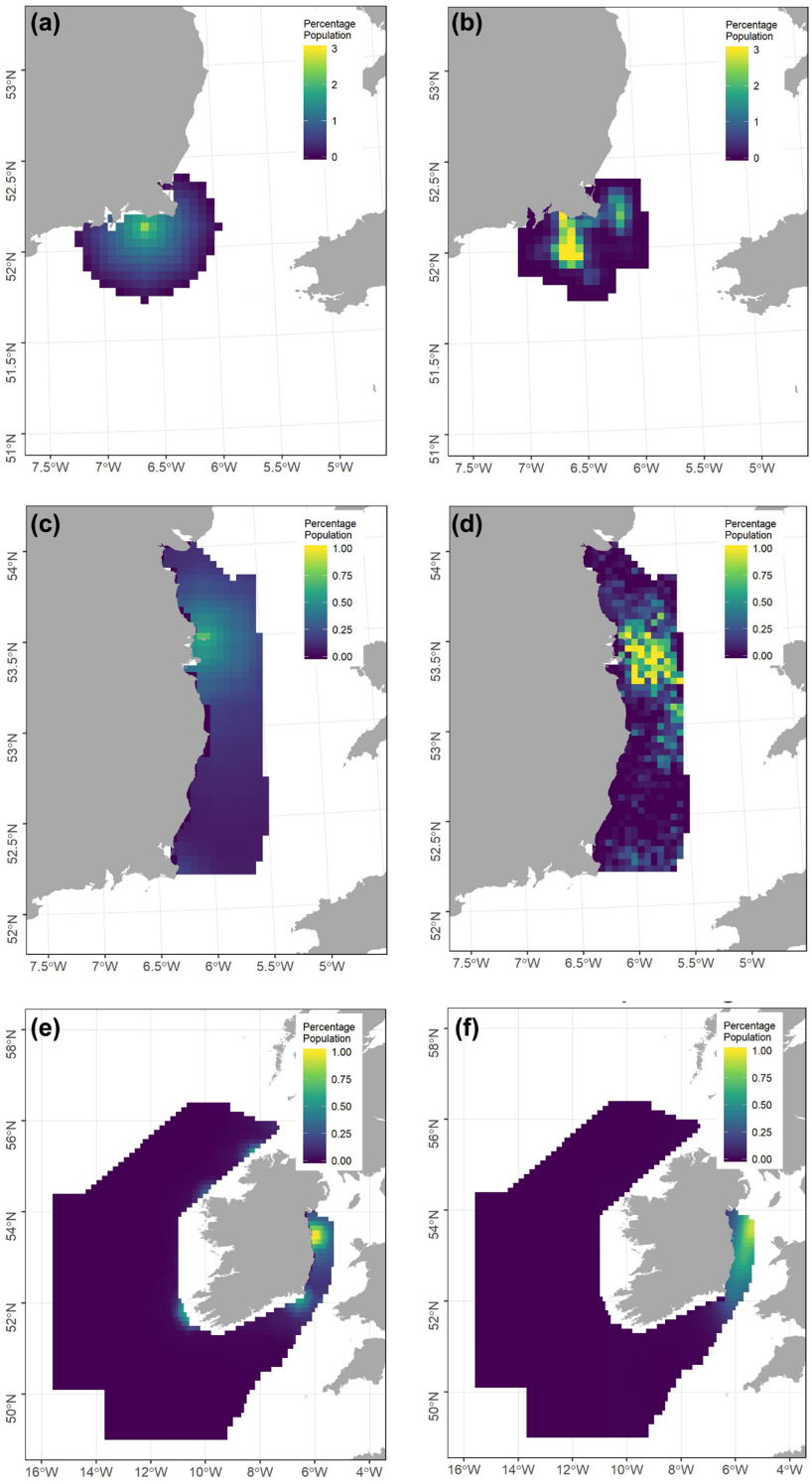


Figure 5. Maps showing (a) foraging radius distribution for razorbill from the Great Saltee colony only generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al. 2004); (b) kernel density distribution for razorbill breeding on Great Saltee, generated from summer breeding season GPS tracking data (2014); (c) foraging radius distributions in the Irish Sea generated using the mean maximum foraging radius for all auk species; (d) empirical density values in the Irish Sea from fine-scale aerial surveys (2016) for all auk species; (e) foraging radius distribution for all auk colonies in Ireland and the UK generated using the mean maximum foraging radius (population estimate from Seabird 2000 census; Mitchell et al. 2004); and (f) GAM modelled density for auks in Irish waters, generated from two years of summer ObSERVE aerial survey data (2015–2016). Densities for all maps were normalised to percentage at-sea population per grid square, i.e. all grid squares in each map sum to 100%.

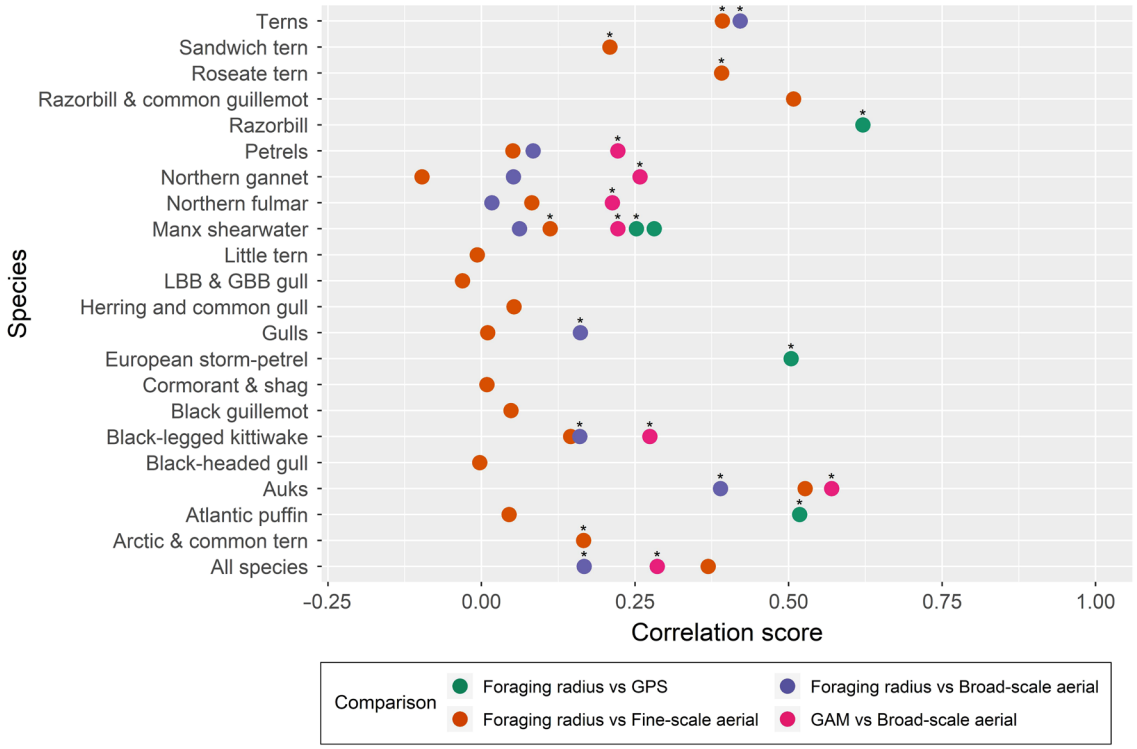


Figure 6. Pearson correlation coefficients for comparisons between (a) individual colony kernel densities (from GPS tracking data) and foraging radius distributions for that colony using mean maximum foraging range – two correlation values are shown for Manx shearwater as tracking data was collected from two colonies; (b) empirical survey data (fine-scale Irish Sea) and foraging radius distributions using mean maximum foraging range; (c) empirical survey data (broad-scale offshore) and foraging radius distributions using mean maximum foraging range; and (d) empirical survey data and predicted GAM distributions. Significant correlations ($p < 0.05$) are indicated by *. In all cases correlation coefficients and p values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method.

$p < 0.001$) and Manx shearwater (0.112, $p < 0.05$) although these correlation values were low, (Fig. 6 and Supplementary material Appendix 1 Table A8). At the species level, significant positive correlations were found for arctic and common tern (0.166–0.339, $p < 0.05$), roseate tern (0.313–0.391, $p < 0.001$) and sandwich tern (0.194–0.209, $p < 0.05$). No significant correlation was noted for all species combined, Atlantic puffin, auks, black guillemot, black-legged kittiwake, cormorant/shag, gulls, little tern, Manx shearwater, northern gannet, northern fulmar, petrels and razorbill/guillemot.

Comparison of foraging radius distributions with broad-scale offshore aerial survey data

When comparing regional foraging radius distributions to broad-scale survey data the best correlations were found for auks (0.389–0.426, $p < 0.001$) and terns (0.424–0.439, $p < 0.001$), (Fig. 6 and Supplementary material Appendix 1 Table A9). Significant correlations were also found for all species combined (0.151–0.167, $p < 0.01$), gulls (0.141–0.161, $p < 0.005$) and black-legged kittiwake (0.129–0.155, $p < 0.005$). There was no significant correlation between foraging radius distributions and broad-scale aerial survey data for petrels, Manx shearwater, northern gannet or northern fulmar. Marginal differences in correlation values were found with the use of mean maximum versus maximum foraging range for foraging radius distributions.

Benchmarking correlations

To provide a benchmark for correlations between foraging radius distributions and aerial survey data, we compared GAM modelled distributions with empirical aerial survey data. Not surprisingly GAM correlations with aerial survey data were stronger than for foraging radius distributions, but the values were still low (Fig. 6 and Supplementary material Appendix 1 Table A9). Significant correlations were detected for petrels, Manx shearwater, northern fulmar and northern gannet, whereas correlations between foraging radius distributions and aerial survey data were not significant for these species.

Discussion

Our results show good agreement (i.e. a correlation value of 0.5 or above) between a simplified foraging radius model and empirical data from GPS tracking studies across three of the four seabird species in this study. Reasonable correlations (0.389–0.439) were also found between foraging radius

distributions and broad scale aerial survey data at the family group level for both auks and terns. Other correlations between foraging radius distributions and aerial survey data were either low, although benchmark correlations against a more complex GAM approach were also low, or not significant for a number of species and family groups.

Comparison of foraging radius distributions with GPS tracking data

The good correlations found between foraging radius distributions from single colonies and GPS tracking data are promising, particularly as it holds true for both short ranging and long ranging foragers. Correlations between tracking data and foraging radius distributions for Atlantic puffin, European storm-petrel and razorbill were higher than previously found for gannets by Grecian et al. (2012), even with relatively small sample sizes for the GPS tracking data (n = 9, trips = 107; n = 8, trips = 8; n = 11, trips = 103). Given how expensive it can be to track some of these species either due to their size, e.g. European storm-petrels, or difficulty of accessing colonies, foraging radius models provide a valuable alternative to collecting additional empirical data. However, it should be noted that the relatively small sample size for tracking data is lower than that recommended by Soanes et al. (2013) and may not be fully representative of the colony level distribution. This is less likely to be the case for Manx shearwaters which had a large sample size (n = 24; 64) but the low correlations and lack of statistical significance could be explained by variation in behaviour due to their dual foraging strategy of frequent chick-provisioning trips and longer self-maintenance trips, which results in a bi-modal distribution of foraging range (Shoji et al. 2015a, Wischnewski et al. 2019). Thus a foraging radius model based on mean maximum foraging range is unlikely to be representative of their foraging distributions. The difference between the foraging radius distributions and GPS tracking data for Manx shearwaters is also notable when visually comparing Fig. 4a to 4b. In contrast, a visual comparison of the razorbill foraging radius distribution (Fig. 5a) to GPS tracking data (Fig. 5b) reflects the higher correlation value that was found for this species. Despite these promising results, it should be noted that both methods compared here only capture the distribution of breeding birds and do not account for juveniles, immature birds and non-breeding adults.

Comparison of foraging radius distributions with aerial survey data

At a regional level, correlations were low overall between foraging radius distributions and empirical data from both broad scale offshore surveys and fine scale coastal surveys. This discrepancy can be explained by a number of factors that are not accounted for in the basic foraging radius model, as well as limitations of survey data, both of which we discuss in detail below. In particular, variability in density-dependent competition (Wakefield et al. 2013) across multiple colonies and movement of non-breeders can have significant effects on regional distributions. Whereas both the foraging radius distributions and GPS distributions only account for breeding birds, survey data captures all birds observed, regardless of breeding stage. Seabird populations are composed of a significant number of juveniles, immature birds and non-breeders, which can display very different foraging behaviour compared to the colony constrained breeders (Fayet et al. 2015, Grecian et al. 2018).

Highest correlations were found for auks and terns, at both the family group and individual species level, and across both the fine scale coastal and the broad scale offshore surveys, suggesting that the foraging radius model is a suitable method for assessing their distribution. This is likely to reflect the foraging behaviour of these groups, which are restricted to smaller home ranges due to their high flight costs, in contrast with pelagic species. Terns have a high level of variability in foraging modes (Eglington et al. 2014) both within and across years, and appear to rely on trophic level segregation rather than spatial segregation to avoid competition (Robertson et al. 2014). Although foraging auks are known to associate with discrete features in the environment, such as tidal currents (Waggitt et al. 2016, Bennison et al. 2019), auk distribution is generally closely linked to distance to colony (Johnston et al. 2015). Furthermore, sympatric auk species also rely on niche segregation rather than spatial segregation during the breeding season (Linnebjerg et al. 2013, Shoji et al. 2015b). These factors probably explain why a foraging radius distribution with a uniform decay from the colony appears to be a good representation of their distribution.

Many of the species showing poor correlations have foraging behaviours that are more strongly associated with specific habitat cues or environmental conditions, which are often patchily distributed (Wakefield et al. 2009). Many gull species forage inland during the breeding season (Rock et al. 2016), while pelagic foragers, including the Manx shearwater and northern gannet, will cue to specific environmental features, such as frontal systems (Scales et al. 2014, Grecian et al. 2018) or fishing vessels (Bodey et al. 2014). Shorter ranging benthic foragers such as cormorants, shags and divers are known to have strong foraging associations with shallow sand bars and tidal streams (Waggitt et al. 2017), which will not be captured by a general foraging radius method. Modifying the foraging radius model for each species to account for known environmental features should improve the match with empirical data, as has previously been shown for gannets (Grecian et al. 2012), though doing so is likely challenging for at least two reasons. First, although primary productivity and sea surface temperature are often touted as being some of the most important, readily accessible environmental features, there is still considerable uncertainty about their utility for predicting foraging locations due to spatiotemporal and trophic lags (Grémillet et al. 2008, Wakefield et al. 2009, Oppel et al. 2012). Second, the influence of environmental features will in many cases be colony specific, and dependent

on both the location of the colony and intra- and inter-specific competition, leading to unaccounted for spatial variation (Huettmann and Diamond 2001).

The lower correlations seen between the foraging radius distributions and aerial survey data, compared to GPS tracking data, may also be due to the resolution of the underlying data. This is unlikely to be the case for spatial resolution since the Dutilleul's test groups all similar value cells into larger blocks for comparisons. Temporal resolution may be more important. Survey data is a snapshot of the distribution in a given area at a given time and will be very much dependent on the seascape (e.g. sandbanks; Fijn et al. 2016) and the environmental conditions (e.g. wind strength/direction; Gibb et al. 2017) on that day or at that time. Foraging radius models are unaffected by such variation and may represent average distributions over longer periods of time. GPS data is collected over a period of days to weeks, and therefore also likely to include more environmental variability. In cases where multi-year survey data is not available it may be more appropriate to utilise foraging radius distributions (based on robust colony size data) to inform spatial management (e.g. MPAs) as these will better reflect spatio-temporal variability in the distribution of breeding individuals. Furthermore, survey data may be less reliable for some species due to misidentification or low detectability. European storm-petrels in particular can be difficult to pick out given their small size and dark colour. Other closely related species, such as cormorants and shags, may be difficult to separate and additionally, spend much of their time underwater whilst at sea.

When benchmarking correlations between foraging radius distributions and aerial survey data against a more complex GAM approach, we noted higher correlation values for GAM outputs. This is unsurprising given that aerial survey data was also included in the GAMs along with environmental variables. However, two points are notable. The first is that correlation patterns across species for the foraging radius model/aerial survey and the GAM/aerial survey comparisons were similar. Similarly, both modelling approaches (foraging radius and GAM) performed better for auks and terns compared to the longer ranging procellariiformes and northern gannet. Correlation values higher than 0.3 were found only for auks using the GAM model, and for auks and terns using the projection model; there was insufficient empirical survey data on tern observations for use in a GAM model. The lack of a major improvement in the use of GAM models could be explained by the fact that most of the environmental variables were dropped during the model selection process, with distance to coast, latitude, longitude and an interaction between latitude and longitude often the only explanatory variables retained. Indeed, for many centrally-placed species it appears that distance to the coast or colony is one of the strongest drivers of seabird occurrence and abundance (Johnston et al. 2015, Warwick-Evans et al. 2018), emphasising further why foraging radius models may be an effective, pragmatic approach.

Finally, we found that correlation values generally increased marginally with the use of mean maximum foraging range in the foraging radius model as opposed to maximum foraging range, although not in all cases. As estimates for maximum foraging range often come from a single study, it may be more appropriate to take a conservative approach and use mean maximum foraging range, particularly if the distribution is to be used for site designation purposes. MPA designations are usually based on core foraging areas, which are often taken as the 50% utilisation distribution (Arcos et al. 2012, Lascelles et al. 2016). It should also be noted that maximum foraging range is likely to vary with colony size (Jovani et al. 2015) and where the relationship is clear, e.g. for gannets (Lewis et al. 2001), this should be accounted for in the foraging radius model.

Conclusions

Overall the foraging radius method showed a good match with empirical GPS data at the colony level, and only slightly underperformed at the regional level compared to a much more complex model requiring extensive empirical survey and environmental data. Our findings support the suggestion that foraging radius models may be a viable alternative for assessing at sea distributions rather than collecting additional empirical data (BirdLife International 2010, Grecian et al. 2012, Afán et al. 2018, Critchley et al. 2018). The foraging radius method is a far quicker and more cost-effective method for assessing at-sea distribution over a large area compared to GPS tracking studies or at-sea surveys. We suggest that further empirical research is needed over a larger number of species, colonies and regions, focusing on the ability of foraging radius models to capture average distributions over longer time periods.

Data availability statement

The seabird population data used to create the foraging radius distributions can be obtained from the JNCC Seabird Monitoring Programme: <http://jncc.defra.gov.uk/smp/>. All GPS tracking data will be made available on the Seabird Tracking Database: <www.seabirdtracking.org/>. The ObSERVE aerial survey data can be accessed at <www.dccae.gov.ie/en-ie/natural-resources/topics/Oil-Gas-Exploration-Production/observe-programme/project-data/Pages/default.aspx>.

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Author contributions – The study was designed by EJC, JLQ and MJJ. EJC, AB, AK, SW, DT, JLQ and MJJ carried out tracking and aerial survey data collection; EJC carried out the analyses, with contributions from WJG for the foraging radius method and AC who produced the GAMs; EJC led the writing of the paper with contributions from all authors.

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Supplementary material (Appendix ECOG-04653 at <www.ecography.org/appendix/ecog-04653>). Appendix 1.

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