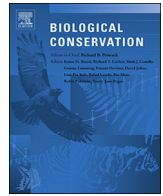




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# Identifying important at-sea areas for seabirds using species distribution models and hotspot mapping



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## ABSTRACT

Marine protected areas (MPAs) underpin the sustainable management of marine ecosystems but require accurate knowledge of species distributions. Recently, advances in tracking technology and habitat modelling have enabled the production of large-scale species distribution models (SDM), which provide the basis for hotspot mapping. In the UK, hotspot mapping to inform seabird MPA identification has involved converting observed or predicted distributions to polygons using either Maximum Curvature or Getis-Ord ( $G_i^*$ ) analysis. Here, we apply both mapping techniques to UK-wide, breeding season SDM predictions for four seabird species (Black-legged Kittiwakes *Rissa tridactyla*, Common Guillemots *Uria aalge*, Razorbills *Alca torda* and European Shags *Phalacrocorax aristotelis*) in order to compare their performance and inform seabird MPA. When using Maximum Curvature, grid cells within the identified maximum curvature boundaries were defined as hotspots. For Getis-Ord analysis, we defined hotspots as either (1) grid cells containing the top 1% or (2) the top 5%  $G_i^*$  scores or (3) cells in which  $G_i^*$  scores were statistically significant. Hotspots based upon Maximum Curvature or statistically significant  $G_i^*$  scores covered the greatest area and were generally larger than current marine Special Protection Areas. Hotspots based on the top 1% or top 5% of  $G_i^*$  scores were smaller and were concentrated around the largest breeding colonies. All hotspot methods consistently identified several high-density areas that should be prioritised for seabird conservation. Ultimately, the choice of hotspot identification method should be informed by considering species ecology alongside conservation goals to ensure hotspots are of sufficient size to protect target populations.

## 1. Introduction

Accurate species distribution estimates are key to effective wildlife management and conservation, enabling researchers to identify and prioritize geographical areas for environmental protection. However, obtaining the requisite data to assess species distributions is often challenging, particularly in the marine environment (Embling et al., 2010). Seabirds are considered important indicators of ecosystem function (Furness and Camphuysen, 1997) and are among the world's most endangered avian groups (Croxall et al., 2012). Many threats seabirds face are anthropogenic and while some are inherently wide scale and transnational (e.g. climate change, Sydeman et al., 2012; marine pollution, Wilcox et al., 2015), others such as offshore developments (Furness et al., 2012; Furness et al., 2013) or interaction with national fisheries (Žydelis et al., 2013; Bærum et al., 2019) can often be

managed effectively at the local or national scales. Marine Protected Areas (MPAs) therefore represent an important tool for the protection of marine biodiversity, including seabirds (Lascelles et al., 2012). However, the identification and protection of areas for conservation in the marine environment has generally lagged behind that in the terrestrial environment (Perrow et al., 2015). This is despite wide-spread recognition that effective conservation of seabirds and other higher marine predators requires protecting important at-sea areas (Game et al., 2009). To address this shortfall, there is a pressing need to develop effective means of mapping the at-sea distributions of seabirds and identify priority areas for conservation (Lascelles et al., 2012).

The most common methods used to estimate the distribution of seabirds at sea are systematic surveys from boats or planes (Camphuysen et al., 2004) and tracking movements of individuals using data loggers. The nature of the data collected differs between these two

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approaches and each has pros and cons (Camphuysen et al., 2012). One important advantage of electronic tracking is that the provenance of individuals is known (Perrow et al., 2015). For example, such information allows areas of high usage associated with specific colonies to be identified (Camphuysen et al., 2012) and potential impacts of localized anthropogenic and natural processes to be apportioned to specific colonies (Montevecchi et al., 2012). Unfortunately, tracking data are typically only available for a subset of tracked seabird colonies, which precludes understanding of broad-scale seabird distributions and hinders efforts to design national MPA networks. One solution is to construct species distribution models (SDM) that describe the distribution of seabirds at sampled colonies as functions of environmental and ecological indices (Aarts et al., 2008; Wakefield et al., 2011; Lascelles et al., 2012), allowing the distribution of unsampled individuals or colonies to be predicted. This approach is rapidly coming into widespread use and predictive SDMs have recently been used to determine suitable areas for protection in a variety of marine and terrestrial species (Moilanen et al., 2005; Bailey and Thompson, 2009; Wilson et al., 2014) and to aid marine MPA design (Hyrenbach et al., 2000; Embling et al., 2010).

A variety of statistical methods have been used to delineate important areas of marine animal usage objectively and repeatably from distribution data (Wilson et al., 2009; Embling et al., 2010; Garthe et al., 2012; Perrow et al., 2015). Often this involves converting a continuous, typically grid-based, measure of distribution to a categorical measure, typically defined by a spatial polygon. For example, an animal or population's utilisation distribution (UD – a probability density function describing space use (Fieberg and Kochanny, 2005), may be calculated by Kernel density estimation (van Winkle, 1975). The contours containing 95 or 50% of the UD volume may then be determined and assumed to represent the home range or core area of that animal or population (Laver and Kelly, 2008). More generally, UD contours highlight regions where higher density estimates are separated from regions of lower density (Azzalini and Torelli, 2007). As such, UDs typically make it easy to visualise areas of high abundance or intense use and benefit from widespread use among ecologists due to their ease of biological interpretation. A potential objection to using percentage UD contours to delineate higher or lower use areas is that the threshold chosen may or may not have biological relevance. On the other hand, percentage UD contours are readily interpretable and may lend themselves to target-driven management approaches. The most common methods used to delineate potential seabird MPA boundaries from continuous distribution data in the UK are Maximum Curvature (O'Brien et al., 2012) and Getis-Ord hotspot analysis (Kober et al., 2010, 2012). The Maximum Curvature method identifies the point at which the relationship between cumulative area and cumulative number of birds within that area changes most sharply. It therefore provides an objective means of balancing the proportion of the population to be protected against the size of the protected area, making it appealing to wildlife managers. The Getis-Ord ( $G_i^*$ ) statistic is a widely used local indicator of spatial association (Anselin, 1995) that identifies areas in which clusters of density or intensity are distinct from patterns in the surrounding landscape. For example, a point will be included in a hotspot only if both it and its neighbours have high utilisation values. The  $G_i^*$  statistic itself is calculated by comparing the sum of a point and its neighbours to the sum of all points across a study area. Unlike Maximum Curvature and UD contours, the significance of inclusion of locations in hotspot areas can be tested. Getis-Ord analysis is a relatively established technique (Getis and Ord, 1992) and its use for delineating important areas for conservation has grown in recent years (e.g. Sussman et al., 2019; Yurkowski et al., 2019). In contrast, use of Maximum Curvature for identification of important marine conservation areas has largely been restricted to the UK.

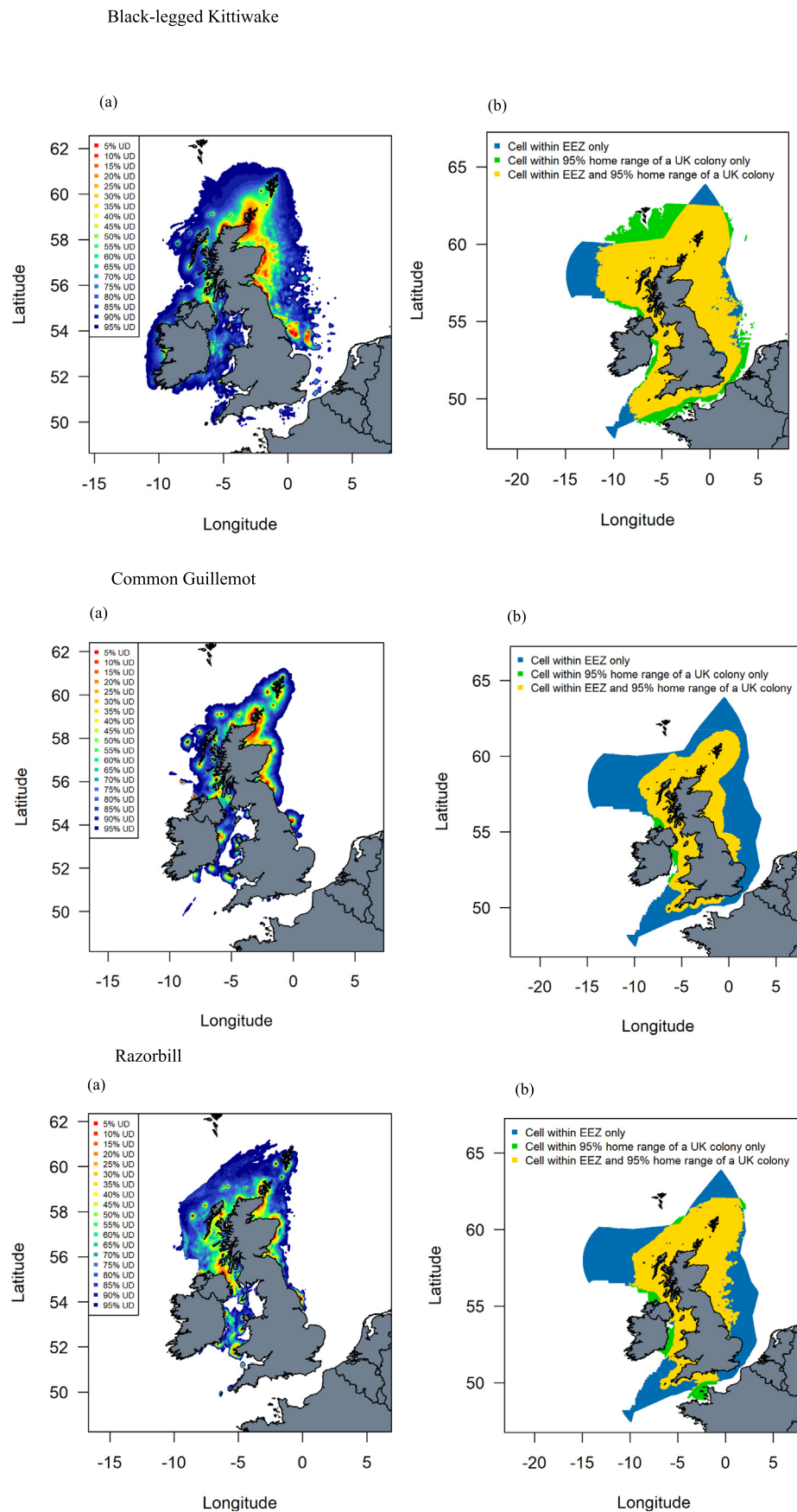
The UK is signatory to multiple international agreements that aim to protect biodiversity and ecosystem health (e.g. OSPAR Convention, 1992; Convention on Biological Diversity, 2004). In particular, the

European Union (EU) Birds Directive (Directive 2009/147/EC) requires the UK and other member states to designate a network of sites, termed Special Protection Areas (SPAs), across both the terrestrial and marine environment to protect avian species, and this requirement has been transposed into UK law. At present, many seabirds are protected by terrestrial SPAs encompassing certain breeding colonies (Stroud et al., 2001). In addition, extensive survey and data collection has been conducted over many years to identify important UK offshore areas used by seabirds (Kober et al., 2010, 2012, Fig. S1). Latterly, Wilson et al. (2014) used SDMs to identify several offshore seabird hotspots, several of which are now designated as marine SPAs (see also Fig. S1 – Supplementary material). Recently, Wakefield et al. (2017) used SDMs to model breeding seabird habitat usage from telemetry data and predict the UDs of four seabird species (European Shags *Phalacrocorax aristotelis*, Black-legged Kittiwakes *Rissa tridactyla*, Common Guillemots *Uria aalge*, and Razorbills *Alca torda*) foraging from all of their UK colonies. The predictions provide unprecedented information on the distribution and provenance of these species at the national scale and represent a valuable new resource for MPA design. Here, our objectives are: 1) to delineate important, high density sites for each of the four seabird species listed above at the UK-scale using the pre-existing SDM outputs from Wakefield et al. (2017) as the underlying distribution data on which to perform both Maximum Curvature and Getis-Ord hotspot mapping techniques; and 2) examine the performance of both Maximum Curvature and Getis-Ord techniques in terms of the location and area of the hotspots identified as well as the assessing the similarity between the location of identified hotspots and the underlying SDM predictions used to delineate such hotspots.

## 2. Materials and methods

### 2.1. Predicted utilisation distributions

All analyses are based upon the predicted seabird distributions produced by Wakefield et al. (2017), which contains a detailed description of the statistical methodology. Briefly, Wakefield et al. (2017) used telemetry data to model space use by four UK seabird species as functions of environmental covariates, intra-specific competition and accessibility. Birds were tracked using GPS loggers during the breeding season (May–July, 2010–2014) as they were approaching the end of the incubation period or raising small chicks. In total the sample sizes used in the species distribution models of Wakefield et al. (2017) were: Black-legged Kittiwake – 464 birds tracked from 20 sites, median tracking duration per individual = 42 h; Common Guillemot – 178 birds tracked from 12 sites, median tracking duration per individual = 54 h; Razorbill – 281 birds tracked from 14 sites, median tracking duration per individual = 70 h; European Shags – 230 birds tracked from 13 sites, median tracking duration per individual = 75 h. Maps showing the location of tracked colonies for each species is available in the Supplementary material, Fig. S2. The intensity of tracking locations was modelled as an Inhomogeneous Poisson Process (IPP) using numerical quadrature. Separate models were fitted for each species, but within species data from multiple colonies was included and colony was treated as a random effect. Once the best fitting models were selected, model coefficients were used to predict usage for all UK breeding sites (breeding sites were defined as those listed in the UK-wide Seabird 2000 census, Mitchell et al., 2004). Raw usage predictions were then normalized to create a Utilisation Distribution (UD, Fieberg and Kochanny, 2005) for each breeding site. Breeding site level UDs, weighted by colony size, were then combined to create a UK-wide UD map for each species (Fig. 1a). For Kittiwakes, Guillemots and Razorbills, UDs were calculated at a 1 km<sup>2</sup> resolution, whereas for Shags resolution was 0.5 km<sup>2</sup>.



**Fig. 1.** (a) Utilisation distributions separated by species for birds originating from the UK and the Republic of Ireland based on Wakefield et al. (2017). At the UK-level, Maximum Curvature and Getis-Ord analysis were based on the density estimates of birds originating from both the UK and Ireland. (b) Cells selected for UK-level hotspot mapping (UK-level analysis field) are shown in yellow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

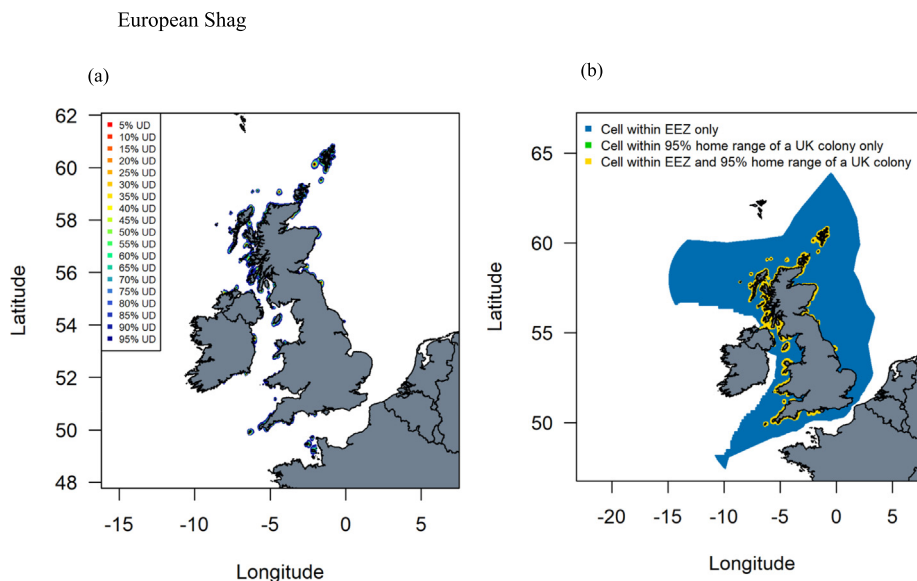


Fig. 1. (continued)

## 2.2. Estimating usage boundaries using the maximum curvature

We estimated Maximum Curvature for each species using UDs constructed by Wakefield et al., 2017. Maximum Curvature analysis starts by ordering UD grid cells  $x_i$  by decreasing probability density, selecting the highest density grid cell and plotting the probability density of birds in this cell against its area. The next highest density grid cell is then added and the cumulative probability density of birds  $\rho_i$  is plotted against cumulative area,  $A_i$  and so on. The curvature,  $k$ , of the relationship between  $\rho_i$  and  $A_i$  indicates how predicted usage increases and is defined as

$$k = \left| \frac{\frac{d^2\rho}{dA^2}}{\left[1 + \left(\frac{d\rho}{dA}\right)^2\right]^{\frac{3}{2}}}\right| \quad (1)$$

Maximum curvature identifies the point  $k_{\max}$  at which the slope of the relationship between  $A_i$  and  $\rho_i$  shows the greatest change from rapid increase to slow increase. By determining the cumulative area at this point,  $A_{\max}$ , the set of grid cells at which  $A_i < A_{\max}$  can be identified. The Maximum Curvature boundary is defined as the polygon bounding these grid cells. Note that grid cells that fall within the Maximum Curvature boundaries identified by  $A_{\max}$  are not necessarily contiguous as Maximum Curvature treats individual grid cells on a case-by-case basis and does not consider lack of independence between cells that are close neighbours.

We limited the analysis field (spatial extent of the analysis) to all those cells that satisfied two criteria: 1) Cell falls within the boundaries of the UK Exclusive Economic Zone (EEZ), 2) cell falls within the 95% home range of at least one UK colony (Fig. 1b). Definition of the analysis field is important as the size of the resulting Maximum Curvature boundaries are sensitive to its size (Webb et al., 2009). We chose the 95% home range due to its long-standing use as measure of home range within ecology (Kie et al., 2010). Moreover, use of the 95% home range ensures we do not include a large number of low density or zero density cells in the analysis which reduces computing time considerably (Kranstauber et al., 2017). In previous studies of UK seabirds, the point of maximum curvature  $k_{\max}$  was identified by fitting exponential growth models to  $A$  vs.  $\rho$  and taking the second derivative of the resulting curves (O'Brien et al., 2012). However, we found that this approach often performed poorly and occasionally identified two maxima in  $k$ , neither of which corresponded well to the point of maximum

curvature evident visually from plots of  $A$  vs.  $\rho$ . Therefore, we used Loess smoothing (Loader, 1999) to fit the more flexible model

$$\rho_i = \mu(A_i) + \varepsilon_i \quad (2)$$

to the data, where  $\mu(A_i)$  is a polynomial fitted in a sliding window. This model was fitted and its second derivatives obtained using the R locfit package (Loader, 2013). The degree of loess smoothing in (2) is determined by the bandwidth,  $h$ , which ranges from 0 to 1 and determines how much of the data is used to fit each local polynomial. Exploratory analysis showed that the location of  $k_{\max}$  (and therefore the size of  $A_{\max}$ ) was sensitive to  $h$ . A value of  $h = 0.001$  provided curves which approximated the data well in a reasonable computing time. Decreasing  $h$  below this value resulted in little change in  $A_{\max}$  but resulted in a prohibitive demand for computing power. Hence,  $h = 0.001$  was used in all analyses.

## 2.3. Estimating usage boundaries using the Getis-Ord method

Getis-Ord,  $G_i^*$  analysis compares the value of a variable in a given cell and its neighbouring cells to all cells within the analysis field in order to measure the intensity of clustering of high or low values. To generate a  $G_i^*$  score for a given cell, the sum for a cell and its neighbours (local value) is then compared proportionally to the sum of all cells (global value). The formula for the Getis-Ord,  $G_i^*$  statistic is

$$G_i^*(d) = \frac{\sum_{j=1}^N w_{ij}(d)x_j}{\sum_{j=1}^n x_j} \quad (3)$$

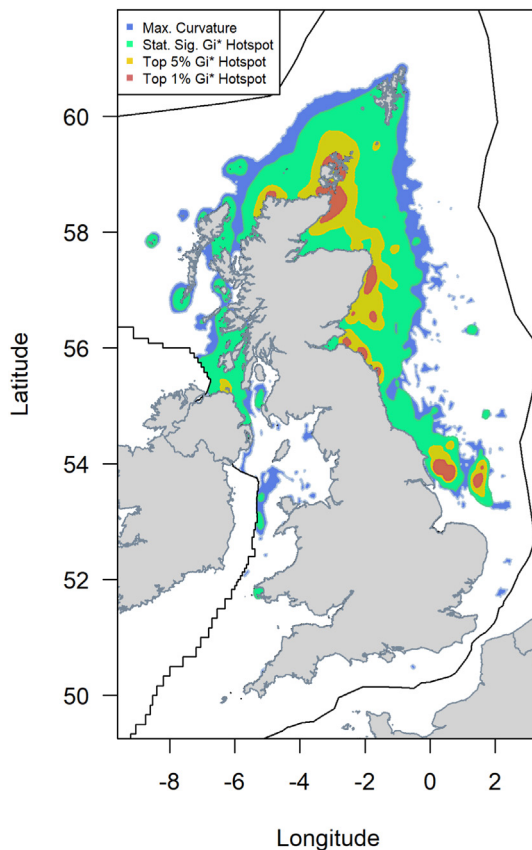
where  $w_{ij}$  denotes a spatial weights matrix with elements  $i, j$ , where

$$w_{ij}(d) = \begin{cases} 1, & \text{if } d_{ij} < d \text{ for all } i, j \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

The numerator in (3) is the local sum of the variable  $x$  within a circle of given radius ( $d$ ) from the centre of cell  $i$  and including cell  $i$  itself. The denominator in (3) is the sum of variable  $x$  across the entire region.  $G_i^*$  scores are standardized and the resulting  $G_i^*$  value reported is a standard normal deviate or  $z$ -score. Note that cells that are on land or beyond the analysis field are treated as NAs.

We conducted Getis-Ord analysis for each species in the R environment (R version 3.5.1, R Development Core Team, 2018) via the usdm package (Naimi et al., 2014) using UDs predicted by Wakefield et al. (2017) as the response variable. As with Maximum Curvature, Getis-Ord analysis is sensitive to the spatial extent of the initial analysis





**Fig. 2.** Hotspots identified at the UK-scale for Black-legged Kittiwakes using Getis-Ord hotspot analysis with a neighbourhood size of  $d = 10$  km based on FPT analysis or Maximum Curvature. Getis-Ord hotspots defined as all cells with the top 1% of calculated  $G_i^*$  scores; all cells within the top 5% of  $G_i^*$  score; all cells in which  $G_i^*$  scores were deemed statistically significant at the  $\alpha < 0.01$  level. UK EEZ also displayed.

field. Therefore, following our approach with Maximum Curvature, we limited the analysis field to cells that fell both within the boundaries of the UK EEZ and the 95% home range of at least one UK colony (Fig. 1b).

In many ecological applications, a cell's local neighbourhood is defined as all cells within a given radius  $d$  from the centre of cell  $x$ . To determine  $d$ , we performed a First-Passage Time (FPT) analysis to identify zones of area restricted search (ARS) and determine the spatial scale at which individuals interact with the environment (Fauchald and Tveraa, 2003; Lascelles et al., 2016). The scale of ARS was determined across all trips recorded within each species during the study. The average scale of ARS for a species was then estimated using an intercept-only model of ARS scale in which colony identity and individual identity were included as random effects. The average scale of ARS estimated using this analysis was 10 km for Kittiwakes, 9 km for Guillemots, 7 km for Razorbills and 4 km for Shags. The average scale of ARS was used to set  $d$  for each species when calculating  $G_i^*$  scores.

To delineate seabird hotspots using  $G_i^*$  scores, we defined hotspots in three ways as: 1) all cells within the top 1% of calculated  $G_i^*$  scores or 2) all cells within the top 5% of calculated  $G_i^*$  scores; 3) we exploited the fact that standardized  $G_i^*$  scores are  $z$ -scores and can be used for statistical testing to determine whether a cell belongs to a hotspot or not. Use of the top 1% and top 5% of  $G_i^*$  scores to delineate hotspots has previously been used to identify potential seabird MPAs in the UK by Kober et al. (2010), whereas the use of using the statistical significance of  $G_i^*$  scores to delineate hotspots is common practice and has previously been applied to other animal populations (Sussman et al., 2019; Yurkowski et al., 2019). The naive use of  $z$ -scores is problematic due to multiple statistical testing, therefore we calculated adjusted  $p$

values ( $p_{adj}$ ) using false discovery rate methods to control the error rate using the FDR methods described in Benjamini and Yekutieli, 2001 via the R stats package (R version 3.5.1, R Development Core Team, 2018). Here, we define cells as belonging to a hotspot if the probability of that cell belonging to a hotspot is  $p_{adj} < 0.01$ . One caveat to the use of standardized  $G_i^*$  scores ( $z$ -scores) for statistical testing is that typically the response variable being modelled is non-normal. However, using a conditional randomization approach Getis and Ord (1992) showed that  $G_i^*$  scores are asymptotically normal provided a cell has at least eight neighbours (see also: Ord and Getis, 1995; Nelson & Boots, 2008). The neighbourhood sizes in the current work ensure that after excluding NA cells every cell has  $\geq 8$  neighbours.

#### 2.4. Assessing the performance of different hotspot measures

We compared the resulting hotspots on the basis of: (i) The area covered ( $\text{km}^2$ ) by different hotspots; (ii) the area covered by hotspots as a percentage of the total area of the analysis field (Fig. 1b.); and (iii) the percentage of the utilisation distribution density contained within the boundaries of a given hotspot relative to total utilisation distribution density. The total utilisation distribution density is estimated as the summed density of birds at sea derived from Wakefield et al. (2017) within the selected analysis field (Fig. 1b). In addition, we used the Jaccard Index of similarity (Jaccard, 1912) to (iv) compare polygon boundaries of identified hotspots with a sequence of population-level UD contours ranging from the 5% UD to the 95% UD in 5% increments. The Jaccard index is the ratio of intersection and union areas and is scored from 0 to 1 with higher values denoting greater similarity. For each study population, the Jaccard Index was calculated based upon a comparison between the hotspots identified and the different UD contours. we also identified the % UD contour which corresponded most closely (highest Jaccard similarity) to the hotspot boundary delineation by each method. This allowed us to assess how closely the hotspots we identify align with the underlying predicted species distributions and determine how much of a species range a given hotspot is expected to cover (e.g. hotspots similar to the 50% UD will contain the majority of a species core range).

### 3. Results

#### 3.1. Black-legged Kittiwakes

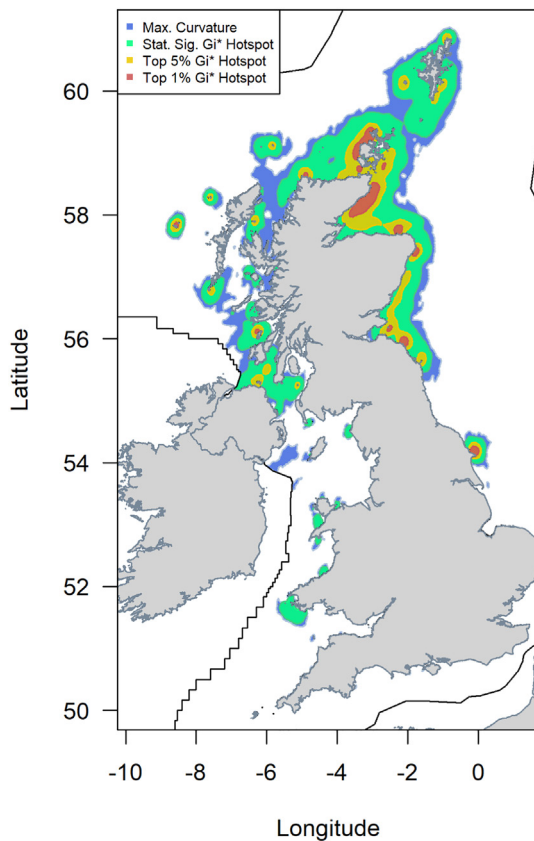
At the UK-level, the top 1% and top 5%  $G_i^*$  methods identified hotspots along the entire east coast of Scotland and off the coast of Yorkshire (Fig. 2), where some of the largest Kittiwake colonies are located. Hotspots identified using statistically significant  $G_i^*$  values or Maximum Curvature also covered these regions but included additional hotspot areas around the coast of Shetland, the Hebrides, Northern Ireland and North-East England.

#### 3.2. Common Guillemots

At the UK-level, top 1% and top 5%  $G_i^*$  hotspot methods emphasized the importance of areas along the east coast of Scotland (Fig. 3). Other hotspots were also evident around some of the larger UK colonies, e.g. Flamborough Head, Yorkshire and Rathlin Island, Northern Ireland. The larger areas identified by statistically significant  $G_i^*$  or Maximum Curvature hotspots covered these regions as well, but also encompassed almost the entirety of Scottish inshore waters. In addition, Guillemot hotspots in the Irish Sea, including areas off the Pembrokeshire coast and Anglesey, were identified by both Maximum Curvature or statistically significant  $G_i^*$ .

#### 3.3. Razorbill

At the UK-level, the top 1% and top 5%  $G_i^*$  hotspot methods



**Fig. 3.** Hotspots identified at the UK-scale for Common Guillemots using Getis-Ord hotspot analysis with a neighbourhood size of  $d = 9$  km based on FPT analysis or Maximum Curvature. UK EEZ also displayed.

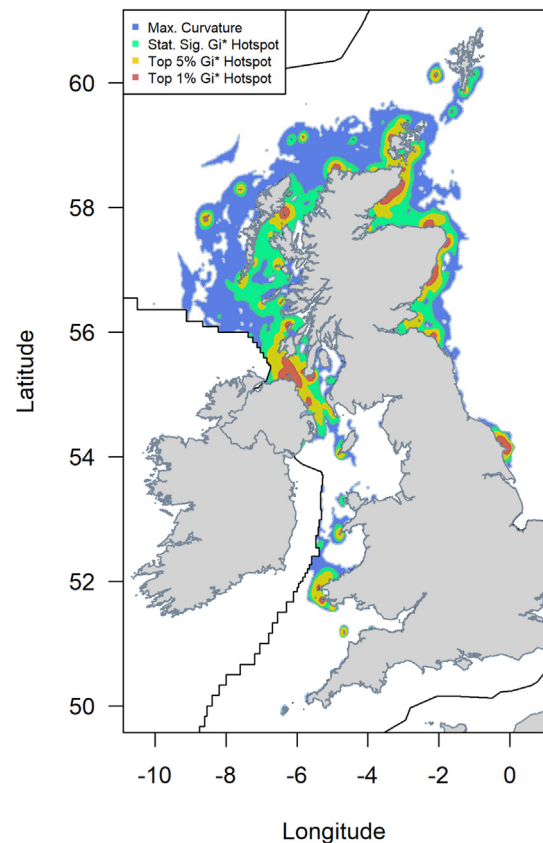
emphasized the importance of a variety of locations around the UK. Multiple hotspots were identified along the east coast of Scotland and the Orkney Islands as well as hotspots in the Hebrides and around Foula, Shetland (Fig. 4). Outside Scotland, the top 1% and top 5%  $G_i^*$  methods also identified hotspots along the Northern Irish coast, around the Yorkshire coast, England and around the Pembrokeshire coast, Wales. The hotspots identified by statistically significant  $G_i^*$  values or Maximum Curvature covered these regions as well but also extended further off-shore.

### 3.4. European Shags

At the UK-level, the top 1% and top 5%  $G_i^*$  hotspot methods emphasized the importance of a variety of locations around the UK (Fig. 5). However, the area covered by hotspots was small and the distribution of hotspots reflected the location of the larger Shag colonies. For example, top 1%  $G_i^*$  hotspots were identified around Foula and the Isle of May in Scotland as well as the Isles of Scilly and the Farne Islands in England, which represent the four largest Shag colonies counted during the Seabird 2000 census (Mitchell et al., 2004). The hotspots identified by either statistically significant  $G_i^*$  scores or Maximum Curvature covered a greater area but were still restricted to coastal locations close to larger breeding colonies.

### 3.5. Hotspot efficiency across species

For all four species, hotspots based upon Maximum Curvature encompassed the largest areas (Table 1) and were most similar to the 80%–90% UD volume contours (Table 2) demonstrating that such hotspots cover the majority of each species' foraging range. When using Getis-Ord analysis, defining hotspots as those cells within the top 1% or



**Fig. 4.** Hotspots identified at the UK-scale for Razorbills using Getis-Ord hotspot analysis with a neighbourhood size of  $d = 7$  km based on FPT analysis or Maximum Curvature. UK EEZ also displayed.

top 5% of  $G_i^*$  scores gave smaller areas than hotspots defined using the statistical significance of  $G_i^*$  scores (Table 1). Across species, the larger areas identified by Maximum Curvature or statistically significant  $G_i^*$  scores contained a higher proportion of the total utilisation distribution density ( $> 60\%$ ), but even the smallest areas, defined using the top 1% of  $G_i^*$  scores, were expected to contain  $> 10\%$  of the total utilisation distribution density (Table 1). Hotspots based upon the top 1% or top 5% of  $G_i^*$  scores for Kittiwakes, Guillemots and Razorbills were most similar to 15% - 40% UD. However, for Shags such hotspots showed greater similarity to larger UD contours (Table 2). In addition, the similarity between hotspots and the UD contours which they most closely resembled were noticeably lower in Shags than in the other species (Table 2).

## 4. Discussion

Ecologists and conservation managers often need to convert continuous measures of species distributions to categorical measures - typically polygons, delineating the extent of areas used most frequently. Our analysis demonstrates how previously established hotspot mapping techniques that have been used to identify seabird MPAs (Kober et al., 2010; O'Brien et al., 2012) can be applied to predictions from species distribution models fitted to GPS tracking data (Wakefield et al., 2017) to map seabird hotspots. We also provide the first quantitative comparison of the performance of these different hotspot mapping techniques.

Getis-Ord and Maximum Curvature methods, when applied to predicted utilisation distributions of four species of UK-breeding seabird, generally identified similar core areas but with some important differences. Across all species, Maximum Curvature boundaries consistently encompassed the largest areas and covered a greater percentage of the

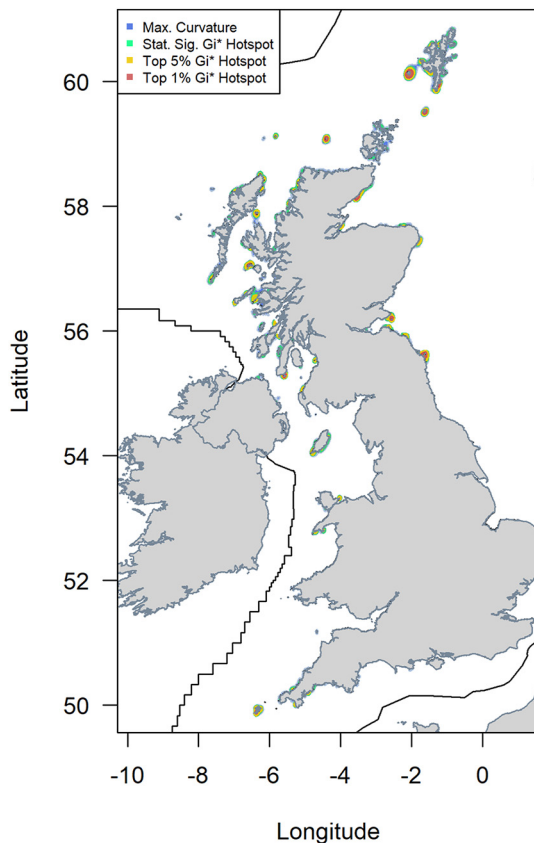


Fig. 5. Hotspots identified at the UK-scale for European Shags using Getis-Ord hotspot analysis with a neighbourhood size of  $d = 4$  km based on FPT analysis or Maximum Curvature. UK EEZ also displayed.

total utilisation distribution density. Conversely, defining hotspots using the top 1% of  $G_i^*$  scores consistently identified hotspots with the smallest areas and utilisation distribution coverage. At the UK-scale, the areas identified by the different hotspot methods were relatively large. For example, the combined area covered by currently designated UK SPAs with marine components is 22,997 km<sup>2</sup> with the largest single SPA

covering 3924 km<sup>2</sup> (data source: <http://jncc.defra.gov.uk/page-1409> - SPAs with marine components, date accessed 20/11/2018, last updated 12/10/2018). In comparison, the Maximum Curvature boundary for Kittiwakes covered 157,802 km<sup>2</sup> and the corresponding top 1%  $G_i^*$  hotspots covered 5852 km<sup>2</sup> (Table 1, Fig. 6). Results were similar for the other three species, with identified hotspots often exceeding the size of the UK's largest extant SPA and occasionally exceeding the total area covered by all current marine UK SPAs. This was particularly true of boundaries obtained using Maximum Curvature. These results highlight the importance of UK waters for breeding seabirds but also demonstrate that, alongside effectively managed MPAs, approaches that are implemented at larger scales, such as industry-level regulations, will be required to protect wide-ranging seabird species (Oppel et al., 2018).

Hotspots based on the top 1% or top 5% of  $G_i^*$  scores tended to encompass only inshore areas close to the largest colonies, whereas the larger areas identified by statistically significant  $G_i^*$  scores or Maximum Curvature extended further offshore. Maximum Curvature also produced hotspots with more complex boundaries than the simpler shapes produced by  $G_i^*$  hotspots. This arises because Getis-Ord analysis involves smoothing across local neighbourhoods whereas Maximum Curvature does not. Previously, Getis-Ord analysis has been used to assist in the design of potential SPAs by delineating hotspots as polygons that encompass a given percentage of the top  $G_i^*$  scores (Kober et al., 2010). There is no correspondence between Getis-Ord thresholds and numerical population thresholds (i.e. the top 1% Getis-Ord hotspot will not necessarily contain 1% of the population), but the hotspots identified will cover a given percentage of the analysis field (Kober et al., 2012). Therefore,  $G_i^*$  percentage thresholds are not closely linked to population-based thresholds but are more akin to area-based thresholds. Similarly, Maximum Curvature boundaries are not directly interpretable in terms of numerical population thresholds. Rather, this method balances the proportion of the population protected against the size of the protected area.

Significance testing of  $G_i^*$  scores has not previously been used to delineate seabird hotspots around the UK but has been used to identify hotspots for various marine predators (including seabirds) in polar regions (Yurkowski et al., 2019) and is also used in other fields within conservation and ecology (Ord and Getis, 1995; Harris et al., 2017; Sussman et al., 2019). When applied to our data, the hotspots identified were typically larger than those defined using the top 1% and top 5%

Table 1

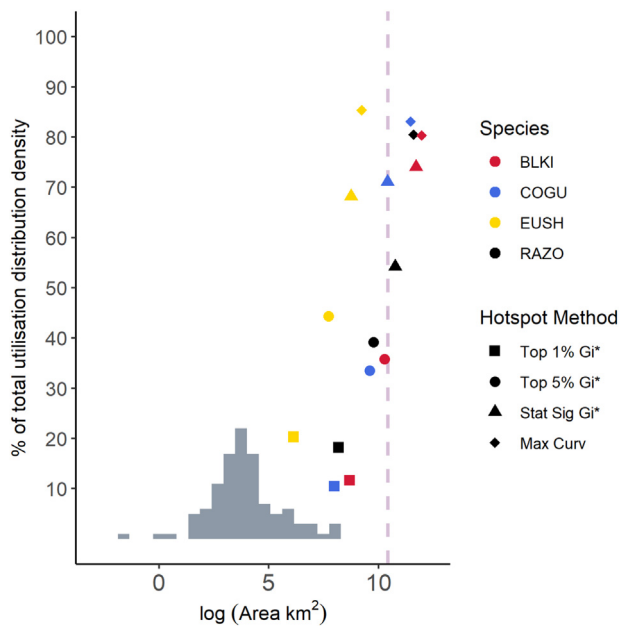
Summary of the total area of hotspots and percentage the total utilisation distribution density contained within hotspots identified by Maximum Curvature or Getis-Ord analysis for each species at the UK-scale. UK analysis field comprises all cells within the UK EEZ and within the 95% home range of at least one UK colony (Fig. 1b). Species codes: BLKI = Kittiwake, COGU = Guillemot, RAZO = Razorbill, EUSH = Shag.

Analysis	Area of hotspots identified	Hotspot area as % of UK analysis field	% of total utilisation distribution density within hotspot
<b>BLKI</b>			
Top 1% $G_i^*$ hotspot	5852 km <sup>2</sup>	1.0%	11.7%
Top 5% $G_i^*$ hotspot	29,256 km <sup>2</sup>	5.0%	35.8%
Statistically significant $G_i^*$ hotspot	122,623 km <sup>2</sup>	20.9%	74.1%
Maximum curvature	157,802 km <sup>2</sup>	26.9%	80.4%
<b>COGU</b>			
Top 1% $G_i^*$ hotspot	2933 km <sup>2</sup>	1.0%	10.5%
Top 5% $G_i^*$ hotspot	14,663 km <sup>2</sup>	5.0%	33.5%
Statistically significant $G_i^*$ hotspot	62,648 km <sup>2</sup>	21.3%	71.1%
Maximum curvature	95,093 km <sup>2</sup>	32.4%	83.1%
<b>RAZO</b>			
Top 1% $G_i^*$ hotspot	3570 km <sup>2</sup>	1.0%	18.2%
Top 5% $G_i^*$ hotspot	17,848 km <sup>2</sup>	5.0%	39.2%
Statistically significant $G_i^*$ hotspot	46,999 km <sup>2</sup>	13.2%	59.5%
Maximum curvature	108,515 km <sup>2</sup>	30.4%	80.5%
<b>EUSH</b>			
Top 1% $G_i^*$ hotspot	458 km <sup>2</sup>	1.0%	20.4%
Top 5% $G_i^*$ hotspot	2288 km <sup>2</sup>	5.0%	44.4%
Statistically significant $G_i^*$ hotspot	6235 km <sup>2</sup>	13.5%	68.2%
Maximum curvature	10,201 km <sup>2</sup>	22.1%	85.4%

**Table 2**

Summary table displaying for each hotspot method the corresponding UD contour to which it was most similar together with the calculated Jaccard similarity measure, J.

Species	Top 1% Gi*	Top 5% Gi*	Stat. sig. Gi*	Max. curvature
BLKI	20% UD, J = 0.45	40% UD, J = 0.74	80% UD, J = 0.86	85% UD, J = 0.93
COGU	15% UD, J = 0.63	35% UD, J = 0.78	70% UD, J = 0.87	80% UD, J = 0.86
RAZO	20% UD, J = 0.63	40% UD, J = 0.74	60% UD, J = 0.83	80% UD, J = 0.86
EUSH	55% UD, J = 0.12	75% UD, J = 0.12	85% UD, J = 0.21	90% UD, J = 0.38



**Fig. 6.** Log area of hotspots identified for each species vs. the percentage of the total utilisation distribution density expected to be within the hotspot. Points are colour coded by species with different symbols denoting the different hotspot delineations. The grey histogram is for reference only and shows the frequency distribution of the areas of existing SPAs with marine components within the UK. The dashed, vertical line represents the combined area of all SPAs with marine components currently designated. Thus, points to the right of this dashed vertical line represent hotspots whose total area exceeds the combined area of all current UK marine SPAs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Gi\* methods but smaller than Maximum Curvature boundaries. It should be noted that there is not necessarily a close correspondence between statistical significance and the top x% of Gi\* scores. For example, a completely random spatial pattern will still produce Gi\* scores in which it is possible to define a top 1% even though no statistically significant hotspots would be identified.

Alongside methods such as Maximum Curvature and Getis-Ord analysis, kernel density estimation of population UDs could also be used to identify important marine areas or assess overlap with existing or proposed MPAs using UD percentage volume contours. For example, followed this approach, Doherty et al. (2017) show a high degree of overlap between areas of high basking shark (*Cetorhinus maximus*) usage and the proposed Sea of the Hebrides MPA, but also identified areas of relatively high usage outside of this region. Among the advantages of UDs are their widespread use by ecologists and their ease of interpretation. In addition, UD volume contours are designed to delineate the minimum area on which the probability to relocate an animal is equal to a specified value (e.g. 0.95 for a 95% home range, Calenge, 2011). Therefore, by design, they are efficient in identifying areas that encompass a specified usage threshold within the smallest footprint. However, the choice of usage threshold is subjective and,

whereas local measures of spatial association like Gi\* are designed to test the null hypothesis that observed patterns arise by chance, UD contours are not.

Hotspots for Kittiwakes, Guillemots and Razorbills, identified through Maximum Curvature or statistically significant Gi\* scores, were most similar to larger UD contours (ranging between the 60% UD–85% UD), and would therefore be expected to encompass most of a species foraging range. Hotspots based upon the top 1% or top 5% of Gi\* scores cover a smaller area but would still be expected to approximate UD contours smaller than the 50% UD (often used to indicate core range) relatively well. Sussman et al. (2019) also noted high similarity between UD-type measures of distribution (in their case, estimated via kernel density analysis) and Getis-Ord derived hotspots in waterbirds. However, unlike the other species assessed here, Getis-Ord hotspots for Shags had lower similarity to UDs. One reason this may occur is if the local smoothing introduced by Getis-Ord analysis does not reflect the clumped and often highly localized nature of Shag distributions particularly well (Bogdanova et al., 2014). Maximum Curvature, which does not involve local smoothing, resulted in hotspots with greater similarity to estimated UD contours in Shags, but even in this case similarity was much lower than the corresponding similarity indices observed between Maximum Curvature hotspots and utilisation distributions in the other three species. One potential explanation is that because the maximum foraging range observed in Shags during the study was 35 km compared to 300 km in Kittiwakes, 340 km in Guillemots and 305 km in Razorbills the spatial scale (sensu Goodchild, 2001) of our analyses differs between the species. Specifically, due to the interaction between relatively limited foraging range of Shags and the grid resolution used for analysis, hotspots defined using Maximum Curvature or Getis-Ord hotspot boundaries tend to be coarser or blockier than the underlying utilisation distributions resulting in relatively low similarity even when high density areas are successfully identified. In the current work we were limited to a grid resolution of 0.5 km<sup>2</sup> for Shags due to constraints on the spatial resolution of the environmental data that was used for species distribution modelling (Wakefield et al., 2017). The result also highlights how approaches that may be suitable for one species may not perform as well on another species that forages at a different spatial scale (Oppel et al., 2018).

The Wakefield et al. (2017) models pool data across years primarily to ensure that model computing time remained within tractable limit. Consequently, the hotspots identified here are also calculated across years, but pooling across years in this manner does not allow us to ascertain whether a hotspot is temporally consistent from one year to the year next. Previous work has demonstrated that some temperate, neritic seabird species often forage in consistent locations and habitats within and across years (Woo et al., 2008; Wakefield et al., 2015) suggesting that, on average, the factors determining the marine distribution of breeding seabirds can be reliably estimated using biotelemetry, time-averaged environmental covariates, and central-place foraging theory (Wakefield et al., 2017). The finding that, during the breeding season, the density of breeding birds is greatest in close vicinity to the largest colonies is typical of central-place foragers (Dean et al., 2015; Briscoe et al., 2018). Comparison of seabird tracking versus at-sea transect datasets has also shown that agreement between them is greatest closest to breeding colonies (Sansom et al., 2018). However,



because seabirds are known to travel further in years of poor resource availability (Monaghan et al., 1994) there may be periods when models fitted to pooled data predict distributions poorly. In dynamic systems, temporally flexible MPA boundaries, set in response to changes in animal movements and population size may prove efficient (Lewison et al., 2015). Species distribution models can be conducted on an annual basis and techniques for calculating  $G_i^*$  hotspots that include a temporal component are available (ESRI, 2016), however, the limiting factor is likely to be obtaining enough tracking data over enough years to build such models.

The hotspots identified in the current study include all periods of breeding birds' activity budgets outside the colony (commuting, resting, foraging, etc.). Consequently, the importance of areas close to the colony that we have identified may be upweighted if birds spend a significant amount of time rafting or commuting in areas close to the colony. In addition, the distribution maps and hotspots analyses presented here only represent the behaviour of breeding birds during the late incubation and early chick rearing period of the annual cycle and may differ from patterns seen in non-breeders and immature birds (Votier et al., 2017) and at other times of the year. A further refinement of a boundary-based approach to seabird management would be to fit species distribution models to locations where birds were engaged in specific behaviours, such as foraging (Cleasby et al., 2015). This may result in stronger associations between habitat and distribution and allow identification of areas and times where birds are particularly exposed to risk from anthropogenic activities. However, the importance of areas that are used predominantly for rafting or commuting should not be under-stated (Weimerskirch et al., 2010). For example, foraging birds may be more vulnerable to bycatch, commuting birds to interactions with wind turbines, and resting birds to oil contamination. Mapping these activities in space and time would allow targeted mitigation measures, such as seasonal and locally restricted fishery closures.

Each of the methods described here defines hotspots in a subtly different way (Table 3), thus the choice of which method to use depends on the objectives of scientists and policy makers. For example, if one sought to design MPAs using numerical population thresholds, then utilisation distributions are perhaps the most directly applicable method (e.g. to protect 10% of the population at any time select the 10% utilisation distribution contour). However, in certain circumstances it may not be clear what percentage of the population should be protected, and methods such as Maximum Curvature or Getis-Ord analysis provide a means of identifying hotspots without prior specification of this value. The use of  $G_i^*$  as z-scores also provides a way to examine whether hotspots are statistically significant and is the only approach adopted here that allows for statistical testing of identified hotspots. It is also clear that the spatial scale at which seabirds forage and aggregate will also impact on how different hotspot approaches perform. For example, Maximum Curvature boundaries will tend to cover large areas unless birds have short foraging ranges (Fig. 6). In addition, the spatial smoothing required for Getis-Ord analysis can result in the loss of information on finer-scale patterns in seabird distribution for species with limited foraging ranges, especially when the underlying spatial resolution of the analysis is also relatively coarse. In contrast, for wider ranging species spatial smoothing over a local neighbourhood may be beneficial as there will typically be some uncertainty in the underlying species distributions used for hotspot mapping. For example, there may be uncertainty in transect counts, or in the habitat data used for species distribution modelling. Moreover, there is an inherent random component to animal behaviour because recorded locations are only a punctual sample of the possible locations an animal may be found within a habitat patch (Benhamou and Cornéilis, 2010).

Here, we show how a combination of GPS tracking technology and predictive species distribution modelling can be used to identify seabird hotspots using previously established techniques for informing the identification of MPAs (Kober et al., 2010; O'Brien et al., 2012). Key

features of this approach are that species distribution modelling and, hence, downstream hotspot mapping, is conditioned on species-habitat relationships and can be performed at a large scale across multiple colonies. Such features will assist in efforts to identify important at sea areas. For example, information on species-habitat relationships has proven important when designing protected areas (Hyrenbach et al., 2000) including the use of both static and/or persistent oceanographic features to define MPA boundaries (Embling et al., 2010). Within the UK, such habitat modelling has already been used as the basis for a suite of recently classified marine SPAs (e.g. Wilson et al., 2014). Wakefield et al. (2017) also demonstrates that intra- and inter-specific competition across colonies as well as coastal morphology often results in distributions radically different from those predicted using foraging range alone. Therefore, conditioning predicted seabird distributions on environmental variables to identify important seabird areas is likely to represent an improvement on previously established techniques such as those based upon foraging radii (BirdLife International, 2010; Thaxter et al., 2012; Soanes et al., 2016) for marine planning. More broadly, combining maps of identified hotspots or population UD's with other sources of marine data such as existing MPA boundaries and anthropogenic impacts will also help identify areas of high conservation priority, including within current MPAs that may not have originally been designated for the species in question (Bailey and Thompson, 2009). For instance, by combining hotspot maps with risk mapping we could target regions where management of threats would have the greatest impact on a species or colony (Bradbury et al., 2014; Wilson, 2016; Bradbury et al., 2017). The approaches outlined here could also be augmented by a more localized approach in which hotspots for important breeding colonies are identified (Cleasby et al., 2018). Ultimately, such work will contribute to our overall understanding of factors affecting seabird distributions at sea by identifying important seabird areas from local to national level spatial scales. More broadly, the use of SDM outputs to identify spatial boundaries and hotspots has wide applicability to the delineation of protected areas for other animal species in both marine and terrestrial realms. Therefore, the outputs from this work form a useful and valuable resource given the increasing political, environmental, moral and legal imperatives to identify protected areas at sea and improve the management of the marine environment.

#### Declaration of competing interest

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and submission to the journal. No part of the research has been published in any form elsewhere and the manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. The work builds upon species distribution models previously developed by the RSPB and published as Wakefield et al. (2017, *Ecological Applications*, 27, 2074-2091) which are used as the basis for hotspot modelling here. All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication. All appropriate ethics and other approvals were obtained for the research. The work has not previously been submitted to Biological Conservation.

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**Table 3**  
Summary table providing information on the application and performance of the different approaches to hotspot mapping considered in the current study.

Method	Description	Spatial smoothing?	Important parameters	Performance on current dataset	Additional details
Maximum curvature	Outlines area that best balances protecting as much as the population as possible in the most efficient (smallest) area, based on mathematical model	No, analysis done on purely grid cell by grid cell basis. However, underlying density maps may be smoothed prior to analysis.	<ul style="list-style-type: none"> <li>Size of analysis field partly determines the size of resulting hotspots.</li> <li>Choice of mathematical model to identify point of maximum curvature</li> </ul>	<ul style="list-style-type: none"> <li>Selects largest areas encompassing majority of home range unless species highly localized.</li> <li>Selected boundaries relatively complex and can be fragmented.</li> </ul>	<ul style="list-style-type: none"> <li>For widely ranging species extremely large areas (often covering areas of relatively low density) may be required before point of maximum curvature reached. For highly localized species occurring in dense clusters may select smaller areas.</li> <li>Maximum curvature boundaries not related to specific population thresholds.</li> <li>By definition will draw a boundary around x% of the analysis field being considered.</li> <li>For very localized species spatial smoothing may mask fine-scale patterns. For wider ranging species smoothing may help to incorporate spatial uncertainty in habitat and animal movement data.</li> <li>Identified boundaries not related to specific population thresholds, but more akin to user-defined area-based targets.</li> </ul>
Getis-Ord analysis: hotspots defined as cells within top x% of calculated $G_i^*$ scores.	Identify areas in which clusters of density are distinct from patterns in the surrounding landscape based on user-defined percentiles of calculated $G_i^*$ scores	Yes, local $G_i^*$ scores calculated on basis of density values in defined local neighbourhood rather than just a single, focal grid cell.	<ul style="list-style-type: none"> <li>Size of analysis field directly determines the size of resulting hotspots</li> <li>Extent of local neighbourhood size, <math>d</math>, determines degree of smoothing when calculating <math>G_i^*</math> scores</li> </ul>	<ul style="list-style-type: none"> <li>Identified the smallest hotspots of the different methods trialed, due to low value of percentage thresholds chosen.</li> <li>Selected boundaries relatively simple.</li> </ul>	<ul style="list-style-type: none"> <li>Only method trialed that provides a statistical assessment of whether a cell belongs to a hotspot.</li> <li>For very localized species spatial smoothing may mask fine-scale patterns. For wider ranging species smoothing may help to incorporate spatial uncertainty in habitat and animal movement data.</li> <li>Identified boundaries not related to specific population thresholds, but more akin to user-defined area-based targets.</li> </ul>
Getis-Ord analysis: hotspots defined as cells where $G_i^*$ scores exceed a significance threshold	Identify areas in which clusters of density are distinct from patterns in the surrounding landscape based on statistical significance of $G_i^*$ scores	Yes, local $G_i^*$ scores calculated on basis of density values in defined local neighbourhood.	<ul style="list-style-type: none"> <li>Size of analysis field partly determines the size of resulting hotspots</li> <li>Extent of local neighbourhood size, <math>d</math>, determines degree of smoothing when calculating <math>G_i^*</math> scores</li> </ul>	<ul style="list-style-type: none"> <li>Selects relatively large areas typically exceeding boundaries of 50% home range.</li> <li>Selected boundaries relatively simple.</li> <li>Sensitive to definition of analysis field and local neighbourhood size, but less so than top 1% or top 5% methods.</li> </ul>	<ul style="list-style-type: none"> <li>Only method trialed that provides a statistical assessment of whether a cell belongs to a hotspot.</li> <li>For very localized species spatial smoothing may mask fine-scale patterns. For wider ranging species smoothing may help to incorporate spatial uncertainty in habitat and animal movement data.</li> <li>Identified boundaries not related to specific population thresholds or area-based targets.</li> <li>Efficient as UD contours encompass a specified % of usage in the smallest possible area.</li> <li>Related to specific thresholds of usage and relatively easy to interpret biologically.</li> <li>Choice of appropriate UD contour directly affects area chosen and needs to be user-defined.</li> </ul>
Kernel density	Heatmap allowing visualization of high density areas. Utilisation distributions are a common approach with tracking data and UD contours delineate different levels of usage. Contour of choice is user-defined.	Yes.	<ul style="list-style-type: none"> <li>User must set a smoothing parameter and can choose to use different kernels.</li> <li>A variety of different kernel methods can be used (e.g. <a href="#">Walter et al., 2015</a>) each with different parameters so choice of underlying method also important.</li> </ul>	<ul style="list-style-type: none"> <li>Area selected depends on choice of UD contour.</li> <li>Larger UD contours result in more complex and fragmented boundaries</li> </ul>	<ul style="list-style-type: none"> <li>Identified boundaries not related to specific population thresholds or area-based targets.</li> <li>Efficient as UD contours encompass a specified % of usage in the smallest possible area.</li> <li>Related to specific thresholds of usage and relatively easy to interpret biologically.</li> <li>Choice of appropriate UD contour directly affects area chosen and needs to be user-defined.</li> </ul>

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108375>.

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