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Defining marine important bird areas: *Testing the foraging radius approach*



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ABSTRACT

Recent international initiatives have promoted a number of different approaches to identify marine Important Bird and biodiversity Areas (IBAs), which are important areas for foraging, migrating or over-wintering seabirds. The 'Foraging Radius Approach' is one of these and uses known foraging range and habitat preferences to predict the size and location of foraging areas around breeding colonies. Here we assess the performance of the Foraging Radius Approach using GPS tracking data from six seabird species with a variety of foraging modes. For each species we compared the population home-range areas of our six study species with the home-range areas defined using the Foraging Radius Approach. We also assessed whether basic information on depth preferences from tracking data could improve these home-range area estimates. Foraging Radius Approach home-range areas based on maximum foraging radii encompassed the entire population home-range of five out of six of our study species but overestimated the size of the population home-range area in every case. The mean maximum foraging radius overestimated the population home-range areas by a factor of 4–14 for five of the six species whilst the mean foraging radius overestimated the population home-range area for half of the species and underestimated for the rest. In the absence of other data, the Foraging Radius Approach appears to provide a reasonable basis for preliminary marine IBA identification. We suggest that using the mean value of all previously reported maximum foraging radii, informed by basic depth preferences provides the most appropriate prediction, balancing the needs of seabirds with efficient use of marine space.

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1. Introduction

In an effort to identify sites of most value to protect and conserve avian populations, BirdLife International has defined over 12,000 Important Bird and Biodiversity Areas (IBAs) worldwide (BirdLife International 2014). These are selected based on the following criteria: (i) sites holding globally threatened species on a regular basis; (ii)

sites holding a significant component of a group of species whose breeding distributions define an Endemic Bird Area; (iii) sites holding a significant component of a group of species whose distributions are largely or wholly confined to one biome; and (iv) important sites for congregatory species, holding more than 1% of a species' global or biogeographic population or exceeding specific thresholds set for waterbirds, seabirds or migratory species. Whilst the designation of an IBA has no legal standing, they have been used to both raise the profile of a site and to provide justification for protected area management by relevant local statutory authorities and NGOs (BirdLife International, 2010, Heath et al., 2000). The identification and subsequent management of marine IBAs has been recognised as a key tool for the conservation of seabirds. Seabirds are declining at a rate faster than any other avian group (Croxall et al., 2012), but do not receive adequate protection from terrestrial IBAs alone.

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BirdLife International's marine Important Bird and Biodiversity Area programme has provided guidance and protocols for identifying priority sites for seabird conservation in a consistent manner, and a number of countries have now compiled marine IBA inventories (BirdLife International, 2010). The recommended methodologies for identifying marine IBAs include: (1) **direct tracking**, for example, the BirdLife International Marine IBA atlas (<http://maps.birdlife.org/marineIBAs/default.html>) which applies a maximum foraging radius (based on the linear distance between the colony and the position located furthest away from the colony) around a globally important breeding colony when tracking data for that colony has been submitted to them. Similarly Lascelles et al. (2016) developed a methodological approach to use seabird tracking data to identify marine Important Bird Areas around globally important breeding colonies; (2) **boat or aerial surveys**; Smith et al. (2014) used at-sea survey data spanning 30 years to identify 59 pelagic sites important to breeding seabird populations in the waters of Alaska; and (3) **the 'Foraging Radius Approach'** whereby one or more foraging radii are drawn around a breeding colony based on (i) the maximum reported distance travelled on a single trip from the same species from a different breeding colony (maximum foraging radius); (ii) a mean of all maximum foraging radii from the same species from several colonies and (iii) a mean of the total distance of all foraging trips reported from other colonies. This method was first advocated by BirdLife International (2010) in their marine Important Bird Areas toolkit and then by Thaxter et al. (2012) who compiled a dataset representing the mean, mean maximum and maximum foraging ranges reported for 25 seabird species that breed in the UK. Data used by Thaxter et al. (2012) was derived from at-sea survey data and tracking datasets (where they existed) and the authors suggest the use of these previously reported foraging radii as a good basis for defining marine Important Bird Areas for seabird breeding colonies where tracking or at-sea survey data does not exist.

To provide even more robust and valuable predictions of important foraging areas the approaches detailed above are often used in combination with modelling frameworks to account for important habitat associations which can generate predictions of likely occurrence and abundance. For example, Oppel et al. (2012) used ship-based survey data and 13 environmental variables to predict the distribution of the Balearic Shearwaters *Puffinus mauretanicus* in the Mediterranean. Grecian et al. (2012) state that the most comprehensive approach is to incorporate multiple data sources including foraging radius predictions, tracking data, habitat data, near-colony behaviour and prey data into a single modelling framework. The authors used this integrated approach for the Northern gannet *Morus bassunus* in the UK and predicted higher densities of birds closer to the breeding colonies and in areas of high copepod abundance (used as a likely indicator of prey abundance) (Grecian et al., 2012).

Limitations in capacity, logistics, data and finances mean that it is not always possible to undertake approaches (1) and (2) for all globally important seabird populations or the integrated approach recommended by Grecian et al. (2012). In the absence of such site specific data, the third "Foraging Radius Approach" is recommended as a simple, easier to apply method for defining marine Important Bird Areas with further refinement, if possible, using habitat and oceanographic preferences (BirdLife, 2010; Thaxter et al., 2012). However, when predicting the location of marine IBAs using this Foraging Radius Approach it is important to note the potential limitations. These may include an inability to account for the size of the colony, or the social aspects of seabird foraging behaviour both of which are known to affect foraging range (Gremillet et al., 2004; Wakefield et al., 2013). Furthermore the predicted foraging radii may often be too large to be easily used as a management unit in marine spatial planning and further refinement using oceanographic features such as benthic habitat and prey abundance has its complications, particularly in many parts of the world where this data does not exist or is inaccessible or hard to analyse. In addition

the Foraging Radius Approach may be more suitable/accurate for coastal rather than pelagic foragers (BirdLife, 2010).

Here we investigate the home-range areas of six seabird species representing different families and modes of foraging: (1) the European shag (*Phalacrocorax aristotelis*); (2) black-legged kittiwake (*Rissa tridactyla*); (3) masked booby (*Sula dactylactra*); (4) razorbill (*Alca torda*); (5) little penguin (*Eudyptula minor*), and (6) short-tailed shearwater (*Puffinus tenuirostris*) (Table 1). Our aim was to use these six species as test cases to assess how well the Foraging Radius Approach compares with the predicted foraging distributions derived from tracking data. To do this, sample home-range areas identified from the foraging tracks of our six study species, were combined with colony size to make population-specific predictions of home-range area. We then examined how well these estimates of population home-range area for each species fitted to the extent of areas predicted by the Foraging Radius Approach home-range areas. We also assessed whether basic information on depth preferences from tracking data could improve the foraging radius home-range area estimates.

2. Methods

2.1. Collection of tracking data

GPS tracking data was collected from European shags and black-legged kittiwakes (2010) and razorbills (2012), breeding on Puffin Island, UK (53.3°N, 4.0°W) (Soanes et al., 2013, 2014), from masked boobies (2014) breeding on Sombrero, Anguilla (Lesser Antilles) (18.6°N 63.4°W); and from little penguins (2011) and short-tailed shearwaters (2012) breeding on Gabo Island, Australia (37.55°S, 149.91°E). Birds were caught at their nests using a hand-held net or crooked pole (European shag, razorbills, masked booby, little penguin, and short-tailed shearwater) or noose pole (black-legged kittiwake and razorbills). I-gotU gt120 GPS loggers (Mobile Action Technology, Taiwan) were attached to the tail feathers (masked booby) or back feathers (all other species) using Tesa tape (Wilson et al., 1997). Loggers were set to record a location every two minutes (shags, kittiwakes, boobies and penguins), five minutes (shearwaters) or 100 s (razorbills). Differences in recording interval was due to this data being collected originally as part of other studies. Loggers were retrieved 2–10 days after deployment.

2.2. Tracking data analysis

The first three trips made by European shags, black-legged kittiwakes and masked boobies were included in the analysis to ensure that no individual was under- or over-represented in the analysis, whilst one trip per individual was used for razorbills, little penguins and short-tailed shearwaters, due to shorter logger deployment periods and fewer foraging trips recorded for these species. The GPS devices did not always record a position as programmed to do. This may provide a biased sample of the spatial distribution of foraging activity (McLeay et al., 2010), and so all GPS fixes were interpolated to every 10 s using the R statistical package *adehabitatLT* (Calenge, 2007; R Core Team, 2014). This process and interval ensured that all areas likely to have been flown over or swum through by birds were included in the spatial analysis. Tracking data used in this study were collected from chick-rearing individuals only, and compared to previously reported foraging radii from birds that were also tracked while chick-rearing. For short-tailed shearwaters which are reported to make short (1–2 day) and long trips (≥ 3 day) trips (Cleeland et al., 2014; Einoder et al., 2011) we used data from short trips only, and applied foraging radii around the colony determined from previous studies of short trips only. Long-foraging trips were not analysed in this study as there are relatively few existing data reporting the long-trips of this species, though we acknowledge that they are still an important consideration for

Table 1

Description of the foraging strategy, prey specificity and the number of previous studies that reported foraging ranges (determined by tracking data) of the six seabird species tracked in this study. References marked with * indicates primary food source** indicate the studies where foraging ranges were reported.

Species	Predominant foraging strategy	Predominately costal or offshore?	Key prey types	Max number of prey species reported in diet	Number of colonies that have previously reported foraging ranges	References
European shag	Benthic feeding	Coastal	Sparidae, Scorpaenidae, Ammodytidae, Gadidae	36	3	Al-Ismail et al., 2013; Bogdanova et al., 2014**; Fortin et al., 2013*; Wanless et al., 1991**)
Black-legged kittiwake	Surface-feeding	Offshore	*Ammodytidae Clupeidae, Osmeridae Euphausiacea	40	6	Ainley et al., 2003**; Chivers et al., 2012**; Daunt et al., 2002*; Hatch, 2013; Paredes et al. 2012**; Robertson et al., 2014**; Swann et al., 2008; Wanless et al., 2007
Razorbill	Pursuit diving	Offshore	Clupeidae, Ammodytidae	8	2	Dall'Antonia et al., 2001**; Kuepfer, 2012**; Linnebjerg et al., 2013**; Ouwehand et al., 2004; Pasquet, 1988; Thaxter et al., 2013; Wagner, 1997)
Masked booby	Plunge diving	Offshore	*Exocetidae, Ommastrephidae Hemiramphidae Coryphaenidae and	5	4	Asseid et al., 2006; Kappes et al., 2011**; Sommerfeld et al. 2013*; Weimerskirch et al., 2008; Young et al., 2010**
Little penguin	Pursuit diving	Offshore	*Engraulidae *Euphausiacea, Moridae, Loliginidae, Ommastrephidae,	6–12	4	Chiaradia et al. 2012; Flemming et al., 2013; Hoskins et al., 2008**; Preston et al., 2010**.
Short-tailed shearwater	Surface-feeding/ short dives	Dual forager (short trips coastal/nearshore, long trips offshore)	*Euphausiacea zoea (crab), larval Gadidae, and Ammodytidae	7	2	Einoder and Goldsworthy, 2005**; Einoder et al., 2011**; Hunt et al., 2002.

conservation management. However, the extensive pelagic distribution of many Procellariiformes species such as the short-tailed shearwater and albatross species means that applying any maximum foraging radii around a breeding colony would highlight a vast area of sea that is not appropriate for marine spatial planning purposes. For example, the average radius of 1284 km for the wandering albatross *Diomedea exulans* reported by Weimerskirch et al., 1993 would create a maximum foraging area of up to 5,176,779 km² around a breeding colony. This area would encompass nearly the entire Southern Indian Ocean.

2.3. Calculation of population home-range areas

The tracking data presented here and used to calculate the sample home-range areas were collected from between 8 and 30 individuals per species, and as such are highly likely to underestimate true population home-range areas for the entire population at the respective colonies (Soanes et al., 2013). For this reason, we used a bootstrap resampling approach and plotted the area (number of 1 × 1 km grid cells) used by the sample population (representing home-range area) as a function of increasing number of individuals included in a sample, then used R statistical software to apply an asymptotic model (Michaelis–Menten) to the data, which included colony size, to allow us to predict the asymptotic home-range areas used by each seabird colony (for more details on this methodology see Soanes et al., 2013). This allowed us to calculate our study populations' predicted home-range area ('population home-range area') based on our tracking data sets.

2.4. Bathymetric preferences

Further refinement of the areas defined by Foraging Radius Approach using information on bathymetric or oceanographic preferences

of seabird species may help to refine predicted foraging areas (BirdLife, 2010; Thaxter et al., 2012). For benthic feeding species (such as the European shag) this information has been frequently reported in previous studies of diving behaviour (e.g. Enstipp et al., 2005). However, for surface feeding or plunge diving species, whilst dive depths are often reported, the preferred sea depths of foraging areas (if they exist) are rarely reported. Because of the apparent lack of data on bathymetric preferences in the literature we examined the sea depths most frequented by our study species and established the maximum depth likely to be used by each population. While we recognise that this is a crude approximation, and may not be obviously relevant for all species and foraging modes, we considered it worthwhile to at least evaluate this simple addition to the approach, since it could be very readily extracted from all tracking data sets and applied to future applications of the Foraging Radius Approach. To do this, we applied kernel density analysis using BirdLife International's *marineIBA* script (Lascelles et al., 2016) in R statistical software package to create polygons that encompassed 50% of the GPS locations from each foraging trip (to represent sample core foraging areas; Soanes et al., 2013) and the range of sea depths found in these areas were used to represent potential "preferred" foraging depths for each species. To extract the depths, GPS locations that fell within these core foraging areas were extracted in Arcmap (ESRI Computing, Vienna). The depth of each GPS location was determined using the function *get.depth* in the R package *marmap* (Pante and Simon-Bouhet, 2013), which uses ETOPO1 bathymetric dataset freely downloaded at one degree resolution from NOAA (<http://www.ngdc.noaa.gov/mgg/global/global.html>). A frequency distribution of sea depths recorded in core foraging areas was plotted for each species. To assess for foraging preferences in sea depth we compared the frequency distribution of depths from the core foraging areas to the frequency distribution of all sea depths present around

the colony within the maximum foraging radius for each species using a Kolmogorov Smirnov test. ($\alpha = 0.05$).

2.5. Foraging Radius Approach home-range estimates

The Foraging Radius Approach defines the foraging area around the colony as the marine habitat (excluding land), encompassed by one of these three radii (Thaxter et al., 2012):

- Maximum foraging radius: The maximum recorded distance travelled from the colony over all previous studies,
- Mean maximum foraging radius: The mean of the maximum foraging ranges reported for each colony averaged across all colonies; and
- Mean foraging radius: The mean of the foraging range travelled from the colony each trip, averaged for all foraging trips for all colonies, weighted to reflect the number of individuals tracked from each population (Thaxter et al., 2012).

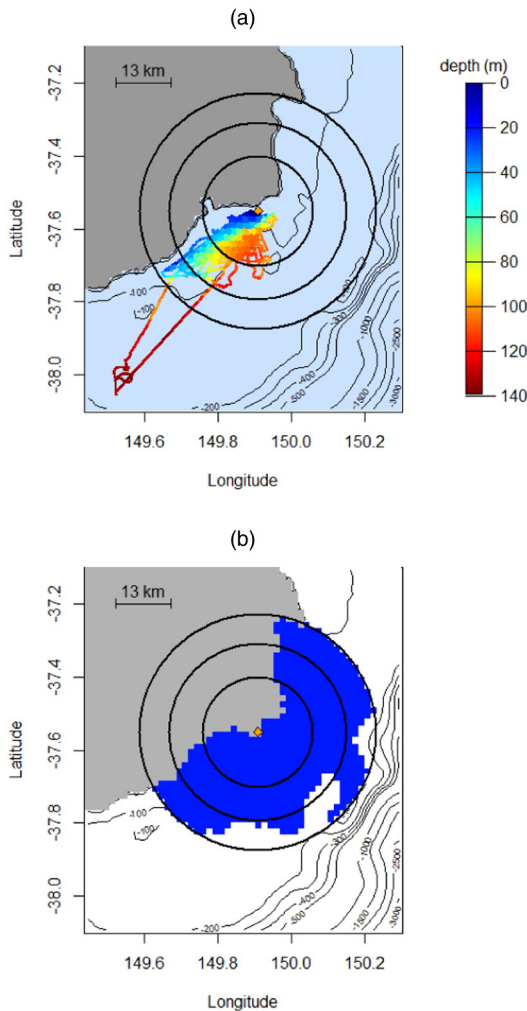


Fig. 1. Example home-range area maps for GPS tracked little penguin (a) with each GPS point coloured according to sea depth, and (b) preferred sea depths (highlighted in blue), based on the maximum depth of GPS positions recorded from our tracking data, within the maximum foraging radius for this species. In both panels the inner circle indicates the mean foraging radius, middle circle indicates the mean of all previously reported maximum distances (mean maximum radius) and outer circle indicates the maximum foraging distance reported in any previous studies (maximum radius).

These ranges were based on values reported from previous studies found on the online scientific database Web of Knowledge™ or from BirdLife International's Species Data Zone (www.birdlife.org/datazone/species) (Table 1 Fig. 1a). For those species where a significant difference in frequency was found in the sea depths of core-foraging areas and those available within the Foraging Radius Approach home-range area, we further refined the Foraging Radius Approach home-range areas by removing any sea depths that were not present in the core foraging areas of our tracking data using R package *marmap* (Fig. 1 b, Appendix 2).

2.6. Comparison of home-range areas

To compare the Foraging Radius Approach home-range areas with the predicted population home-range area, we evaluated two lines of evidence. Firstly we divided each Foraging-Radius Approach home-range area by the predicted population home-range area to compare the difference in spatial extent. We repeated this for the reduced Foraging Radius Approach home-range area for species which demonstrated a depth preference. Secondly we took into consideration that we could not make a spatially explicit prediction of the location of the population home-range area. The Foraging Radius Approach assumes that the foraging range is effectively a circular area around the colony, constrained by availability of marine habitat within this area, yet it is possible that birds will not distribute themselves in this way (Fig. 1a). To account for this we assessed the proportion of the tracking sample home-range area that fell outside of each of the three home-range areas defined by the Foraging Radius Approach, under the assumption that this proportion would be the same in the population home-range areas. Combining these two lines of evidence allowed us to evaluate which (if any) of the foraging radius home-range estimates were likely to represent both the shape and size of the population home-range area.

3. Results

3.1. Comparison of foraging ranges

Previously reported maximum, mean maximum and mean foraging radii reported for each of the study species can be seen in Table 2, along with the maximum and mean foraging radii recorded from this study. Mean foraging radii in the present study were between 61% greater and 45% lower than those reported in previous studies. However, maximum foraging radii were between 74% greater and 83% lower in this study when compared to the previously reported data, illustrating the magnitude of intra-specific variability in foraging behaviour. One species (the little penguin) in this study reported a maximum foraging radius greater than had previously been recorded.

3.2. Foraging areas and bathymetric preferences

The depth distribution within the sample core foraging areas was significantly different from the depth distribution within the area defined by the maximum foraging radius for five of the six species ($D = 0.63, 0.62, 0.27, 0.12, 0.54, 0.77$ for shag, kittiwake, masked booby, little penguin and short-tailed shearwater respectively ($p < 0.01$; Fig. 2). There was no apparent depth preference for the razorbill ($p > 0.05$); (Fig. 2).

3.3. Comparison of home-range areas

Fig. 1a shows an example of how as the size of the home-range areas from the three different foraging radii increased, then more of the sample, and hence population, home-range areas were likely to be excluded. Fig. 1a also shows how using depth preferences decreased the size of the Foraging Radius Approach home-range area estimates. Foraging Radius

Table 2

Maximum, mean maximum and mean foraging radii for each study species, as reported in previous studies compared to maximum and mean foraging radii for each species recorded in this study.

	Maximum foraging range (km)			Mean maximum foraging range (km)		Mean foraging range (km)		
	Database	This study	Difference	Database		Database	This study	Difference
European shag	25.4	10	−61%	9.21 (± 5.3)		8 (± 0.1)	5 (± 0.9)	−38%
Black-legged kittiwake	201.4	35	−83%	104.6 (± 46.7)		20 (± 1)	11 (± 2)	−45%
Razorbill	110	58	−47%	66.7 (± 23.3)		18 (± 3)	29 (± 6)	+61%
Masked booby	250	78	−69%	138.8 (± 62.8)		64 (± 30)	27 (± 3)	+58%
Little penguin	36	63	+74%	27.0 (± 4.7)		17 (± 2)	16 (± 3)	−6%
Short-tailed shearwater	97	52	−46%	83.5 (± 13.5)		61 (± 20)	38 (± 3)	−38%

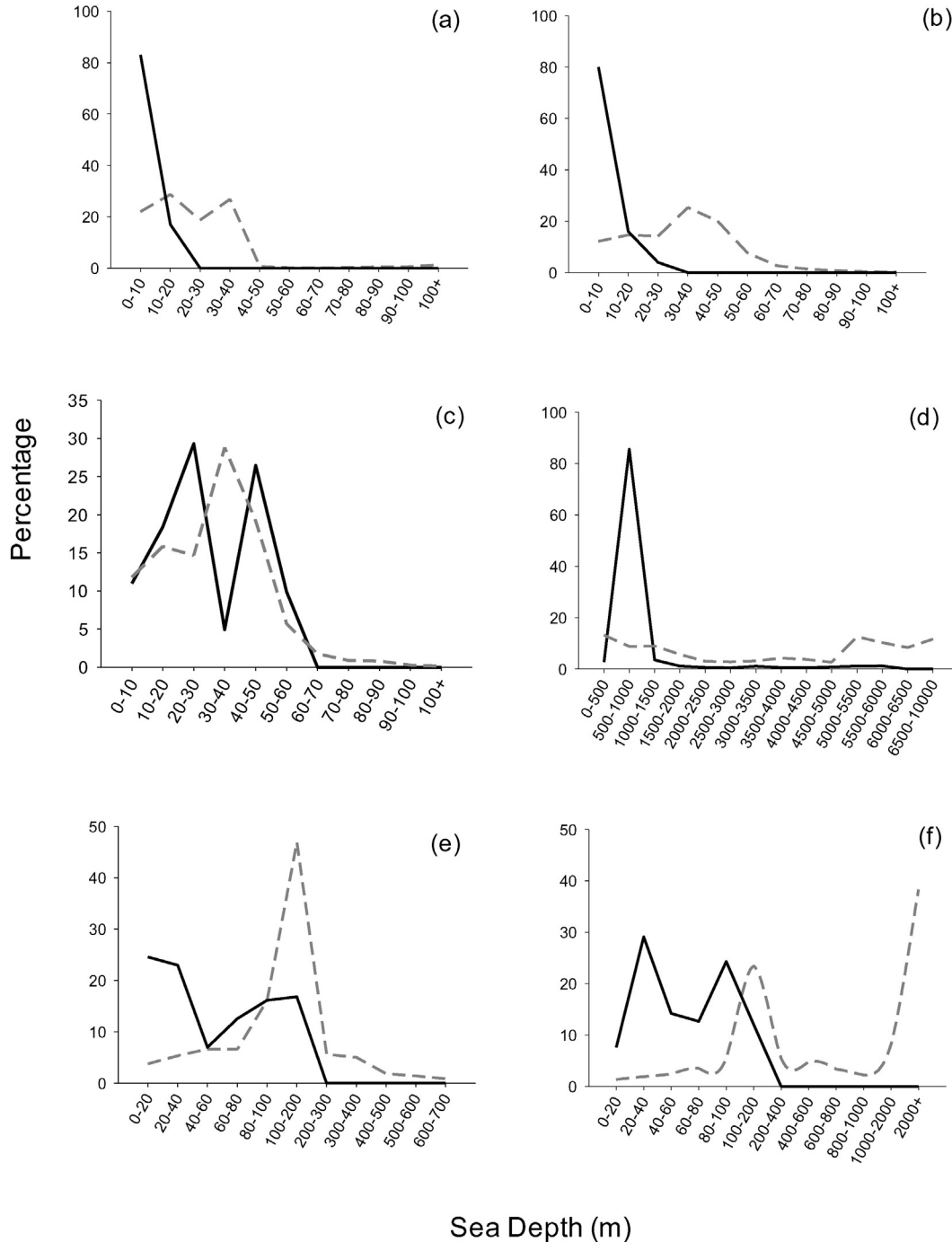


Fig. 2. Percentage of time spent at different sea depths (black solid line) and percentage of total sea depths available within the maximum foraging radius (grey dashed line) for GPS tracked (a) European shag, (b) black-legged kittiwake, (c) razorbill, (d) masked booby, (e) little penguin, (f) short-tailed shearwater.

Table 3
Size (km²) of the sample home-range areas from six populations of GPS tracked seabirds, and the extrapolated population home-range area (with 95% confidence intervals). Also shown are the percentage of each sample home-range area falling outside of the Foraging Radius Approach home-range areas defined by previously reported foraging radii.

Species	Colony size (breeding pairs)	Number of individuals tracked	Sample home-range area (km ²)	Predicted population home-range area (km ²)	Sample home-range area outside Foraging Radius Approach home-range areas (%)		
					Max. foraging radius	Mean max. Foraging radius	Mean foraging radius
European shag	178	20	82	249 (242–258)	0	12	16
Black-legged kittiwake	571	14	116	1188 (975–1672)	0	0	6
Razorbill	151	11	250	1293 (892–4089)	0	0	54
Masked booby	70	20	2882	4061 (3872–4340)	0	0	0
Little penguin	30,000	30	200	343 (328–366)	20	27	57
Short-tailed shearwater	60,000	8	543	1198 (980–1693)	0	0	8

Approach home-range areas based on maximum foraging radius always included the entire population home-range (Table 3) (with the exception of little penguins) but overestimated the size of the population home-range area in every case, by as much as a factor of 45 for masked boobies (Table 4). Incorporation of preferred diving depths led to an underestimate of the population home-range area for European shags and an overestimate for the other species, but in these cases only by a factor of around 5–10 (Table 4). Home-range areas based on the mean maximum foraging radius overestimated the predicted home-range area by a factor of 4.7–14 for five of the six species, again reduced to 2.2–4.4 by incorporating depth preferences (Table 4). The mean maximum radius home-range area underestimated the population area for European shags in part due to 12% of the population home-range area being outside of this radius (Table 3). The home-range area calculated from the mean foraging radius overestimated the predicted home-range area for half of the species, again reduced further by depth preferences (Table 4), with substantial proportions (up to 57%) of the predicted home-range areas being outside of these radii (Table 3). Fig. 3 illustrates how overall, the home-range area encompassed by the mean maximum foraging radius seems to balance the inclusion of the maximum amount of the population foraging area within the radius, but without dramatic over-estimates of the size of the area used. Including the depth preferences appears to reduce the degree of over-estimation (Fig. 3).

4. Discussion

The Foraging Radius Approach is advocated as a simple way for marine planners to predict the distribution of foraging seabirds around important colonies in the absence of tracking or at-sea survey data (BirdLife, 2010; Thaxter et al., 2012), and should avoid the need for complex modelling procedures or dependence on the availability and processing of oceanographic variables. This study tests the Foraging Radius Approach using empirical data collected from a range of seabird species and assesses its suitability in defining important foraging areas. Our results support the use of the Foraging Radius Approach.

The Foraging Radius Approach may not provide definitive areas to enable delineation of marine IBAs in all cases. Seabird foraging behaviour is complex, with spatial heterogeneity in foraging locations within a foraging range driven by patchiness in food supplies. In addition, the social behaviour of seabirds and the way that they interact with each other both within and between colonies will affect both the size and shape of foraging areas (Gremillet et al., 2004;

Wakefield et al., 2013) and 'hotspots' of use within them. Ultimately the foraging area of any given colony will be specifically dependent on the size of the population, the local environment and the presence of neighbouring colonies. As such BirdLife International advocate the use of colony-specific tracking data wherever possible (Lascelles et al., 2016). However, it is extremely unlikely that every colony will ever be tracked and many species are inaccessible, intractable or too vulnerable for this approach. As an alternative the Foraging Radius Approach can predict potential (yet broad) foraging areas around a seabird colony as a basis to which further information can be added (BirdLife, 2010; Thaxter et al., 2012). Our results suggest that applying the mean foraging radius recorded at other colonies will under-represent the actual foraging area of a new colony. Applying the maximum or mean maximum foraging radius would most likely always encompass the majority of a population's home-range area. However, using these values would increase the overall size of the predicted foraging areas around the colony, potentially making it too large to act as an IBA boundary or be a useful management tool, without further refinement using habitat and bathymetric data. We recommend the use of mean maximum foraging radius as a balance between the needs of seabirds and the desire to make efficient use of space and avoid over-designation of marine IBAs.

Further refinement of predicted foraging areas is possible with modelling techniques if the species' bathymetric and oceanographic preferences are known (Louzao et al., 2009; Oppel et al., 2012), and, importantly, if these data are freely available in user-friendly formats. Some regional marine benthic habitat mapping datasets do exist, for example the European Union's EU Sea Map project (EUSeaMap, 2014), and some more localised habitat mapping has been conducted (DeFraff and Baldwin, 2013). However, these data are generally difficult to collect and analyse, are not readily or freely available and are of varying quality and resolution across a potential range. Consequently these refinements may not be possible or readily available in many countries/territories. However, further refinement of foraging areas based on bathymetric preference may be possible in many instances, since global bathymetry data sets can be downloaded freely from NOAA, and imported straight into GIS software programs or R statistical software using the package *marmap* (Pante and Simon-Bouhet 2013). These data can then be relatively easily assessed alongside colony locations and previously reported foraging ranges and depth preferences to allow exclusion of non-preferred depths and hence produce better predictions of key foraging areas (see Appendix 1 for example code). Furthermore,

Table 4
The Foraging Radius Approach home-range areas (km²) estimated for six seabird species, based on three different foraging radii (maximum, mean maximum and mean). Also shown are these estimates divided by the population home-range estimates to illustrate whether they are likely to be over-estimates (>1) or underestimates (<1). Estimates of foraging area available and difference are also shown when only preferred sea depths were considered.

	Maximum foraging radius			Mean maximum foraging radius			Mean foraging radius		
	Preferred depths			Preferred depths			Preferred depths		
	Home-range area (km ²)	Difference (radius/pop. Hra)	Difference (radius/pop. Hra)	Home-range area (km ²)	Difference (radius/pop. Hra)	Difference (radius/pop. Hra)	Home-range area (km ²)	Difference (radius/pop. Hra)	Difference (radius/pop. Hra)
European shag	620	2.5	0.4	139	0.6	0.2	96	0.4	0.1
Black-legged kittiwake	38,739	32.6	9.7	13,261	11.2	4.4	428	0.4	0.2
Razorbill	14,582	11.2	n/a	4616	3.6	n/a	354	0.3	n/a
Masked booby	184,068	45.3	7.6	56,932	14.0	2.2	12,064	3.0	0.6
Little penguin	2111	6.2	5.3	1226	3.6	3.5	492	1.4	1.4
Short-tailed shearwater	15,888	13.3	4.8	11,699	9.8	4.1	6111	5.1	2.9

bathymetry is a physical property of the environment that does not change inter-annually (or on shorter timescales) in the way that other metrics such as sea surface temperature, wind or chlorophyll concentration do.

All diving seabirds have limits to the depths that they can dive to, with body size being a major factor that determines this (Halsey et al., 2006). For benthic feeding seabirds, such as the European shag, this then automatically excludes deeper areas of the ocean as available foraging habitat from within the area defined by the foraging radii. However, for surface feeding or plunge diving seabirds, whilst dive depths have been recorded for many species (Kappes et al., 2011; Paredes et al., 2008), preferred foraging bathymetry is often not reported. However, it is likely that most seabird species will exhibit a preferred sea depth to forage within based on the distribution of their prey (Danhardt and Becker, 2011; Pettex et al., 2010; Weimerskirch, 2005). This study reports on the range of sea depths found in the core foraging areas of our sample data. As previously reported (Watanuki et al., 2008) the benthic-diving European shags spent most time at sea depths of less than 40 m. In addition, four of the five remaining species also appeared to show preferences for a limited range of sea depths, which when applied in conjunction with the previously reported foraging radii tends to decrease the overall size of the population home-range area predicted for each species (Fig. 3). The approach to incorporate depth preferences outlined here is relatively crude and incorporates some circularity in its derivation. Yet despite this, it made an appreciable difference to the agreement between the predictions of home-range areas from the foraging radii and the tracking data, suggesting a key influence of depth, most likely on prey availability. The apparent preferences in sea depth of our study species may be useful when delineating foraging areas based on foraging radii at other colonies. As such, further routine measurement and reporting of depth use of foraging seabirds would be beneficial in future research, and improve on the initial approach outlined here.

Lascelles (2008) suggest that the Foraging Radius Approach may be more applicable to certain species based upon the species' foraging ecology. This study compared seabirds representing different foraging guilds (benthic foragers, pelagic foragers, surface feeders and plunge divers) as a first major attempt at evaluation. Thus while it is too early to assess in detail whether this approach may lend itself better to some groups than others, we note none of the species was particularly different from the others. To further test this, we urge the community to continue to test this approach on new populations and species. Globally there are around 1600 IBAs classified for their seabird breeding colonies. Whilst it is logistically impossible to collect seabird tracking data from each of these, it is still important for conservation and marine management purposes to be able to predict the foraging areas around them (Langton et al., 2011, Ronconi et al., 2012, McGowan et al., 2013). The Foraging Radius Approach can do this, but depends on tracking data to be collected in order for continued improvements to data on foraging metrics. As such, there are advantages to undertaking tracking studies and more regularly and systematically reporting details of mean, mean maximum and maximum foraging radii as well as any bathymetric and/or habitat use. We also encourage researchers to submit their data to tracking data repositories such as Movebank (www.movebank.org) (Wikelski and Kays, 2014) and BirdLife International's Seabird Tracking Database (www.seabirdtracking.org/), so as to build an even more comprehensive dataset on foraging radii and preferred foraging depths that can be applied globally for marine conservation. A more comprehensive global database will result in more accurate estimates of the mean and mean maximum foraging radii of any species and will also allow for variability around these mean values to be calculated. We urge BirdLife International and other groups interested in seabird conservation to continue to store tracking data and their metadata in accessible repositories. Thus the next iteration of guidelines for application of the Foraging Radius Approach can

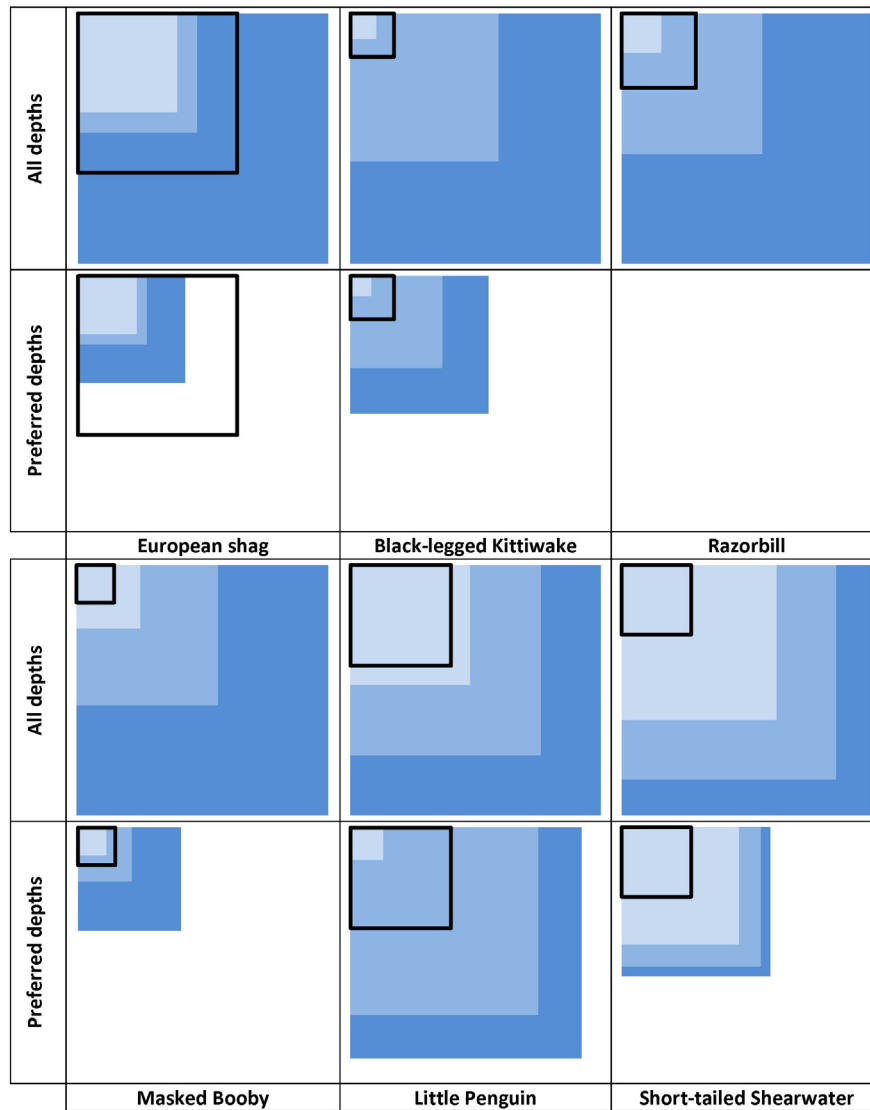


Fig. 3. Schematic diagrams showing the representativeness of foraging areas predicted using the Foraging Radius Approach for six species of seabird. In each case four foraging areas are displayed in proportion to each other, both before and after adjustment for depth preferences. Each panel shows (1) the population home-range area predicted from tracking data outlined by a black box (2) the home-range area estimated by the maximum foraging radius, in dark blue (3) the home-range area estimated by the mean maximum foraging radius, in mid blue and (4) the home-range area estimated by the mean foraging radius in light blue. Please note that scales are arbitrary and are correct between panels for a single species (i.e. without and without depth preference correction) but are not transferable between species.

both make use of and have accepted protocols for incorporation of this variability and/or the effect of colony size which is highly likely to underlie it. Indeed there are single studies which incorporate this type of best practice (e.g. Grecian et al., 2012) which demonstrate the potential of this approach when good data are available.

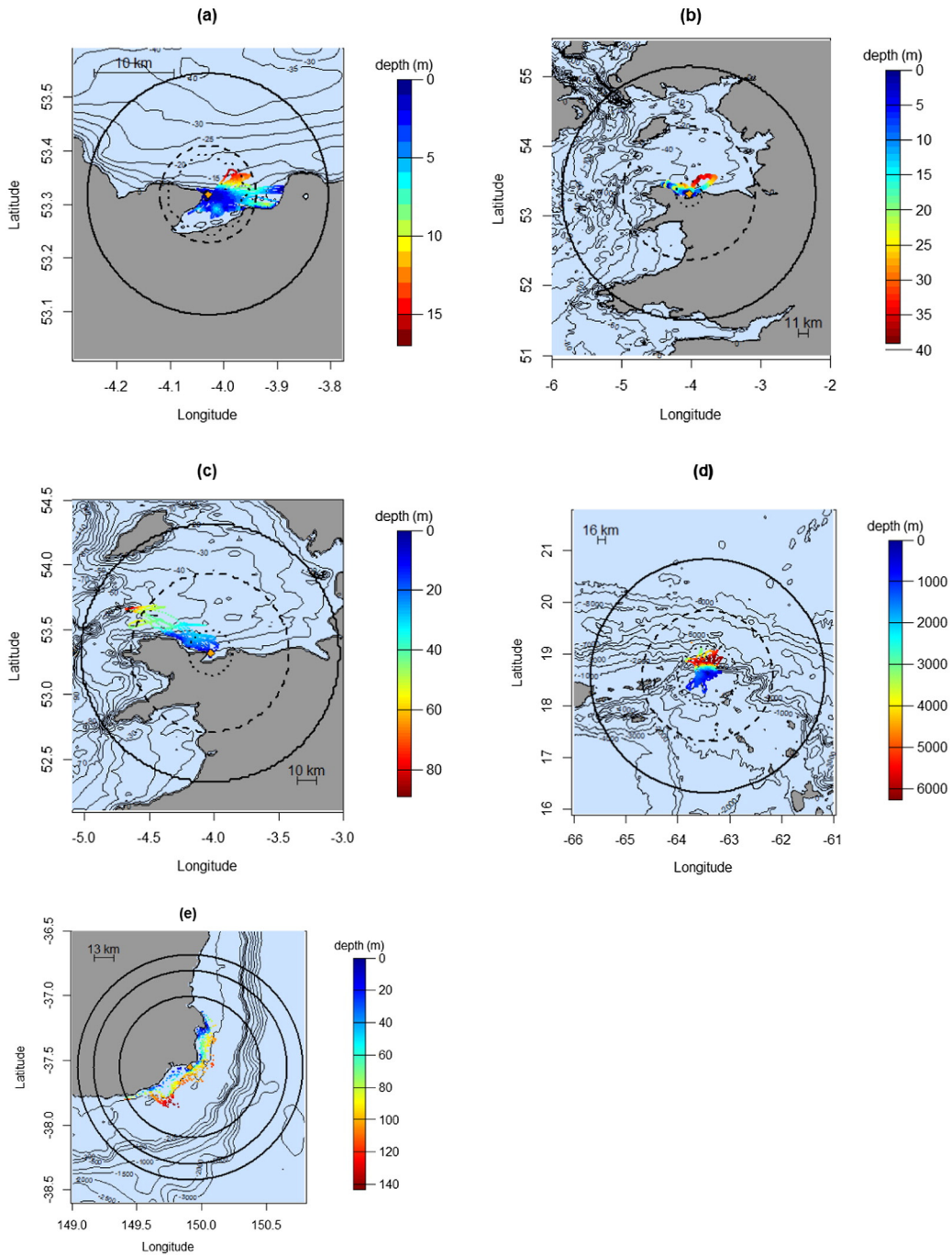
In summary, we show that the Foraging Radius Approach provides a reasonable prediction of distribution, particularly when the foraging ecology of the seabird and sea depth usage are also considered, thus providing justification for the use and further development of this approach as a potential management tool.

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Appendix 1. Home-range area maps for GPS tracked (a) European shag (b) black-legged kittiwake (c) razorbill (d) masked booby (e) short-tailed shearwater overlaid with sea depth. In all panels the inner dotted circle indicates the mean foraging radius, middle dashed circle indicates the mean of all maximum distances travelled (mean maximum radius) and outer solid circle indicates the maximum distance travelled reported by previous studies (maximum radius)



Appendix 2. R code to add a colony location, GPS data points and buffers around a colony and then to calculate/highlight specified sea depths within the buffer area. For further details on this code refer to R package marmap (Pante and Simon-Bouhet, 2013)

```
library(marmap).
library(shape) # For color legends.
library(fields).
```

```
## Get bathymetry, add latitude and longitude of study area.
bat <- getNOAA.bathy(lon1 = 150.3,lon2 = 149.44,lat1 =
-37.1,lat2 = -38.1, resolution = 1, keep = TRUE).
## Import gps tracks for species and retrieve depth from bat for each
point.
track <- read.csv("GPS locations.csv").
gps <- get.depth(bat, track, locator = FALSE).
## Location of the colony.
```

```

colony <- read.csv("colony name.csv").
# Add the foraging radii for your study species.
buf.km.max <- create.buffer(bat, colony, radius = 36, km = TRUE).
buf.km.meanmax <- create.buffer(bat, colony, radius = 27, km =
TRUE).
buf.km.mean <- create.buffer(bat, colony, radius = 16.8, km =
TRUE).
# set color palette for depth.
mx <- abs(min(gps$depth, na.rm. = TRUE)).
col.points <- femmecol(ceiling(mx)).
### Plot bathymetry.
# Prepare the plotting area for both the map and the color legend.
par(mai = c(1, 1, 1, 1.5)).
# Plot a color coded image of the bathymetry/hypsometry.
plot(bat, image = TRUE, n = 0, land = TRUE, bpal = list(c(min(bat,
na.rm. = TRUE), 0, "white"), c(0, max(bat, na.rm. = TRUE),
grey(0.6)))).
# Add contour lines with labels for marine areas.
plot(bat, deep = c(-3000, -400),
shallow = c(-500, 0),
step = c(500, 100),
lwd = c(0.05, 0.1),
lty = c(1, 1), drawlabels = TRUE, add = TRUE).
# Plot gps tracking points.
col.points[track[,1:2], col. = col.points[ceiling(abs(gps$depth))], bg =
col.points[ceiling(abs(gps$depth))], pch = 21, cex = 0.3).
# Add buffer outlines.
plot(buf.km.max, lty = 1, lwd = 2, col. = 2).
plot(buf.km.meanmax, lty = 2, lwd = 2, col. = 1).
plot(buf.km.mean, lty = 3, lwd = 2).
# To highlight different depth layers within a buffer, see? plotArea.
# To compute the area of a buffer or part of it see? get.area.
# Add colony.
points(colony[1], colony[2], pch = 23, bg = "orange").
# Add a title, kilometric scale and color depth scale for gps tracks.
title(main = "(a)").
scaleBathy(bat, deg. = 0.15, x = "topleft", inset = 10).
colorlegend(zlim = c(ceiling(mx), 0), col. = rev(col.points),
main = "depth (m)", posx = c(0.85, 0.88)).

```

References

- Ainley, D.G., Ford, R.G., Brown, E.D., Suryan, R.M., Irons, D.B., 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology* 84, 709–723.
- Al-Ismail, S., McMinn, M., Manuel Tuset, V., Lombarte, A., Antoni Alcover, J., 2013. Summer diet of European shags *Phalacrocorax aristotelis desmarestii* in southern Mallorca. *Seabird* 26, 8–23.
- Asseid, B.S., Drapeau, L., Crawford, R.J.M., Dyer, B., Hija, A., Mwinyi, A.A., Shinula, P., Upfold, L., 2006. The food of three seabirds at Latham Island, Tanzania, with observations on foraging by masked boobies *Sula dactylatra*. *Afr. J. Mar. Sci.* 28, 109–114.
- BirdLife International, 2010. Marine Important Bird Areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. BirdLife International, Cambridge, UK.
- BirdLife International, 2014. Important Bird and Biodiversity Areas: A global network for conserving nature and benefiting people. BirdLife International, Cambridge, UK.
- Bogdanova, M.L., Wanless, S., Harris, M.P., Lindstrom, J., Butler, A., Newell, M.A., Sato, K., Watanuki, Y., Parsons, M., Daunt, F., 2014. Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: implications for marine spatial planning. *Biol. Conserv.* 170, 292–299.
- Calenge, C., 2007. Exploring habitat selection by wildlife with adehabitat. *J. Stat. Softw.* 22, 1–19.
- Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R., Reid, N., 2012. Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Mar. Ecol. Prog. Ser.* 456, 267–269.
- Chiaradia, A., Forero, M.G., Hobson, K.A., Swearer, S.E., Hume, F., Renwick, L., Dann, P., 2012. Diet segregation between two colonies of little penguins *Eudyptula minor* in southeast Australia. *Austral Ecol* 37, 610–619.
- Clelland, J.B., Lea, M.A., Hindell, M.A., 2014. Use of the Southern Ocean by breeding short-tailed shearwaters (*Puffinus tenuirostris*). *J. Exp. Mar. Biol. Ecol.* 450, 109–117.
- Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22, 1–34.
- Dall'Antonia, L., Gudmundsson, G.A., Benvenuti, S., 2001. Time allocation and foraging pattern of chick-rearing razorbills in Northwest Iceland. *Condor* 103, 469–480.
- Danhardt, A., Becker, P.H., 2011. Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea? *J. Sea Res.* 65, 247–255.
- Daunt, F., Benvenuti, S., Harris, M.P., Dall'Antonia, L., Elston, D.A., Wanless, S., 2002. Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar. Ecol. Prog. Ser.* 245, 239–247.
- DeFraff, A., Baldwin, K., 2013. Expanding on the Marine Resource and Space Use Information System for the Grenadine Islands with Important Historical, Cultural and Ecological Heritage Sites. CERMES Technical Report. University of the West Indies, Barbados.
- Einoder, L.D., Goldsworthy, S.D., 2005. Foraging flights of short-tailed shearwaters (*Puffinus tenuirostris*) from Althorpe Island: assessing their use of neritic waters. *Trans. R. Soc. S. Aust.* 129, 209–216.
- Einoder, L.D., Page, B., Goldsworthy, S.D., De LITTLE, S.C., Bradshaw, C.J.A., 2011. Exploitation of distant Antarctic waters and close neritic waters by short-tailed shearwaters breeding in South Australia. *Aust. Ecol.* 36, 461–475.
- Enstipp, M.R., Gremillet, D., Lorentsen, S.F., 2005. Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*). *J. Exp. Biol.* 208, 3451–3461.
- EUSeaMap, 2014. A Broad-Scale Physical Habitat Map for European Seas (European Marine Observation and data network).
- Flemming, S.A., Lalas, C., van Heezik, Y., 2013. Little penguin (*Eudyptula minor*) diet at three breeding colonies in New Zealand. *N. Z. J. Ecol.* 37, 199–205.
- Fortin, M., Bost, C.A., Maes, P., Barbraud, C., 2013. The demography and ecology of the European shag *Phalacrocorax aristotelis* in mor braz, France. *Aquat. Living Resour.* 26, 179–185.
- Grecian, J., Witt, M., Attrill, M., Bearhop, S., Godley, B., Gremillet, D., Hamer, K., Votier, S., 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using northern gannets breeding in the North East Atlantic. *Biol. Conserv.* 156, 43–52.
- Gremillet, D., Dell'omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y., Weeks, S.J., 2004. Off-shore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of cape gannets from neighbouring colonies. *Mar. Ecol. Prog. Ser.* 268, 265–279.
- Halsey, L.G., Butler, P.J., Blackburn, T.M., 2006. A phylogenetic analysis of the allometry of diving. *Am. Nat.* 167, 276–287.
- Hatch, S.A., 2013. Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Mar. Ecol. Prog. Ser.* 477, 271.
- Heath, M.F., Evans, M.J., Hoccom, D.G., Payne, A.J., Peet, N.B., 2000. Important bird areas in Europe. Priority sites for conservation. Volume 1: Northern Europe. *BirdLife Conservation Series* 8, i–xiii. pp. 1–866.
- Hoskins, A.J., Dann, P., Ropert-Coudert, Y., Kato, A., Chiaradia, A., Costa, D.P., Arnould, J.P.Y., 2008. Foraging behaviour and habitat selection of the little penguin *Eudyptula minor* during early chick rearing in Bass Strait, Australia. *Mar. Ecol. Prog. Ser.* 366, 293–303.
- Hunt, G.L., Baduini, C., Jahncke, J., 2002. Diets of short-tailed shearwaters in the southeastern Bering sea. *Deep-Sea Res.* 49, 6147–6156.
- Kappes, M.A., Weimerskirch, H., Pinaud, D., Le Corre, M., 2011. Variability of resource partitioning in sympatric tropical boobies. *Mar. Ecol. Prog. Ser.* 441, 281–294.
- Kuepfer, A., 2012. Foraging Patterns and Home-Ranges of Breeding Razorbills (*Alca torda*) from two Colonies in North Wales, UK, as Revealed by GPS-Tracking in the Seasons of 2011 and 2012 (MSc thesis) Bangor University, Wales.
- Langton, R., Davies, I.M., Scott, B.E., 2011. Seabird conservation and tidal stream and wave power generation: information needs for predicting and managing potential impacts. *Mar. Policy* 35, 623–630.
- Lascelles, B., 2008. The BirdLife Seabird Foraging Database: guidelines and examples of its use. BirdLife International. Internal report.
- Lascelles, B.P., Taylor, P., Miller, B., Dias, M.P., O'Connell, A., Torres, L., Hedd, A., le Corre, M., Phillips, R.A., Scott, S., Weimerskirch, H., Small, C., 2016. Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions* (in press).
- Linnebjerg, J.F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., Frederiksen, M., 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS ONE* 8.
- Louzao, M., Becares, J., Rodriguez, B., Hyrenbach, K.D., Ruiz, A., Arcos, J.M., 2009. Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Mar. Ecol. Prog. Ser.* 391, 183–197.
- McGowan, J., Hines, E., Elliott, M., Howar, J., Dransfield, A., Nur, N., Jahncke, J., 2013. Using seabird habitat modeling to Inform Marine spatial planning in Central California's National Marine Sanctuaries. *PLoS ONE* 8.
- McLeay, L.J., Page, B., Goldsworthy, S.D., Paton, D.C., Teixeira, C., Burch, P., Ward, T., 2010. Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Mar. Ecol. Prog. Ser.* 411, 271–283.
- Oppel, S., Meirinho, A., Ramirez, I., Gardner, B., O'Connell, A.F., Miller, P.I., Louzao, M., 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol. Conserv.* 156, 94–104.
- Ouweland, J., Leopold, M.F., Camphuysen, K.C.J., 2004. A comparative study of the diet of guillemots *Uria aalge* and razorbills *Alca torda* killed during the tricolor oil incident in the south-eastern north sea in January 2003. *Atl. Seabirds* 6, 147–164.
- Pante, E., Simon-Bouhet, B., 2013. marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R. *PLoS ONE* 8 (9), e73051.
- Paredes, R., Jones, I.L., Boness, D.J., Tremblay, Y., Renner, M., 2008. Sex-specific differences in diving behaviour of two sympatric alcini species: thick-billed murre and razorbills. *Can. J. Zool. Revue Canadienne De Zoologie* 86, 610–622.
- Paredes, R., Harding, A.M.A., Irons, D.B., Roby, D.D., Suryan, R.M., Orben, R.A., Renner, H., Young, R., Kitaysky, A., 2012. Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. *Mar. Ecol. Prog. Ser.* 471, 253–269.

- Pasquet, E., 1988. A study of the diet of the common guillemot *Uria-aalge* and razorbill *Alca-tordau* wintering in French waters. *Alauda* 56, 8–21.
- Pettex, E., Bonadonna, F., Enstipp, M.R., Siorat, F., Gremillet, D., 2010. Northern gannets anticipate the spatio-temporal occurrence of their prey. *J. Exp. Biol.* 213, 2365–2371.
- Preston, T.J., Chiaradia, A., Caarels, S.A., Reina, R.D., 2010. Fine scale biologging of an inshore marine animal. *J. Exp. Mar. Biol. Ecol.* 390, 196–202.
- R Core Team, 2014. *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robertson, G.S., Bolton, M., Grecian, W.J., Monaghan, P., 2014. Inter- and intra-year variation in foraging areas of breeding kittiwakes (*Rissa tridactyla*). *Mar. Biol.* 161, 1973–1986.
- Ronconi, R.A., Lascelles, B.G., Longham, G.M., Reid, J.B., Oro, D., 2012. The role of seabirds in marine protected area identification, delineation, and monitoring: introduction and synthesis. *Biol. Conserv.* 156, 1–4.
- Smith, M.A., Walker, N.J., Free, C.M., Kirchoff, M.J., Drew, G.S., Warnock, N., Stenhouse, I.J., 2014. Identifying marine important bird areas using at-sea survey data. *Biol. Conserv.* 172, 180–189.
- Soanes, L., Arnould, J., Dodd, S., Sumner, M., Green, J., 2013. How many seabirds do we need to define important foraging areas. *J. Appl. Ecol.* 50 (3), 671–679.
- Soanes, L., Arnould, J., Dodd, S., Milligan, G., Green, J., 2014. Factors affecting the foraging behaviour of the European shag: implications for tracking studies. *Mar. Biol.* 161, 1335–1348.
- Sommerfeld, J., Kato, A., Ropert-Coudert, Y., Garthe, S., Hindell, M.A., 2013. Foraging Parameters Influencing the Detection and Interpretation of Area-Restricted Search Behaviour in Marine Predators. A Case Study with the Masked Booby. *PLoS ONE* 8.
- Swann, R.L., Harris, M.P., Aiton, D.G., 2008. The diet of European shag *Phalacrocorax aristotelis*, black-legged kittiwake *Rissa tridactyla* and common guillemot *Uria aalge* on canna during the chick-rearing period 1981–2007. *Seabird* 21, 44–54.
- Thaxter, C., Lascelles, B., Sugar, K., Cook, A., Roos, S., Bolton, M., Langston, R., Burton, N., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate marine protected areas. *Biol. Conserv.* 156, 53–61.
- Thaxter, C.B., Daunt, F., Gremillet, D., Harris, M.P., Benvenuti, S., Watanuki, Y., Hamer, K.C., Wanless, S., 2013. Modelling the effects of prey size and distribution on prey capture rates of Two Sympatric Marine predators. *PLoS ONE* 8.
- Wagner, R.H., 1997. Differences in prey species delivered to nestlings by male and female razorbills *Alca torda*. *Seabird* 19, 58–59.
- Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Gremillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroel, A., Murray, S., Le Nuz, M., Patrick, S.C., Peron, C., Soanes, L.M., Wanless, S., Votier, S.C., Hamer, K.C., 2013. Space partitioning without territoriality in gannets. *Science* 341, 68–70.
- Wanless, S., Harris, M.P., Morris, J.A., 1991. Foraging range and feeding locations of shags during chick-rearing. *Ibis* 133, 30–36.
- Wanless, S., Frederiksen, M., Daunt, F., Scott, B.E., Harris, M.P., 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog. Oceanogr.* 72, 30–38.
- Watanuki, Y., Daunt, F., Takahashi, A., Newei, M., Wanless, S., Sat, K., Miyazaki, N., 2008. Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. *Mar. Ecol. Prog. Ser.* 356, 283–293.
- Weimerskirch, H., 2005. Are seabirds foraging for unpredictable resources? 2nd International Conference on Bio-Logging Science. St Andrews, SCOTLAND, pp. 211–223.
- Weimerskirch, H., Salamolard, M., Sarrazin, F., Jouventin, P., 1993. Foraging strategy of wandering albatross through the breeding season – A study using satellite telemetry. *Auk* 110, 325–342.
- Weimerskirch, H., Le Corre, M., Bost, C.A., 2008. Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Mar. Ecol. Prog. Ser.* 362, 291–302.
- Wikelski, M., Kays, R., 2014. Movebank: Archive, Analysis and Sharing of Animal Movement Data. World Wide Web electronic publication (<http://www.movebank.org>).
- Wilson, R.P., Putz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B., RopertCoudert, Y., 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl. Soc. Bull.* 25, 101–106.
- Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R., Block, B.A., 2010. Resource partitioning by species but not sex in sympatric boobies in the central pacific ocean. *Mar. Ecol. Prog. Ser.* 403, 291–301.