

Marine Protected Areas show low overlap with projected distributions of seabird populations in Britain and Ireland

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Abstract

Marine Protected Areas (MPAs) are an important tool for the conservation of seabirds. However, mapping seabird distributions using at-sea surveys or tracking data to inform the designation of MPAs is costly and time-consuming, particularly for far-ranging pelagic species. Here we explore the potential for using predictive distribution models to examine the effectiveness of current MPAs for the conservation of seabirds, using Britain and Ireland as a case study. A distance-weighted foraging radius approach was used to project distributions at sea for an entire seabird community during the breeding season, identifying hotspots of highest density and species richness. The percentage overlap between distributions at sea and MPAs was calculated at the level of individual species, family group, foraging range group (coastal or pelagic foragers), and conservation status. On average, 32.5% of coastal populations and 13.2% of pelagic populations overlapped with MPAs, indicating that pelagic species (many of which are threatened) are likely to have significantly less coverage from protected areas. We suggest that a foraging radius approach provides a pragmatic and rapid method of assessing overlap with MPA networks for central place foragers. It can also act as an initial tool to identify important areas for potential designation. This would be particularly useful for regions throughout the world with limited data on seabird distributions at sea and limited resources to collect this data. Future assessment for marine conservation management should account for the disparity between coastal and pelagic foraging species to ensure that wider-ranging seabirds are afforded adequate levels of protection.

Keywords:

Seabirds, Protected areas, Predictive modelling, Hotspots, Foraging, Ecosystem approach

33 1. Introduction

34 Even though most of the world's oceans continue to be impacted by humans (Game et al., 2009;
35 Halpern, 2008), just over 4% of their area is currently protected (UNEP-WCMC and IUCN, 2016).
36 There is an urgent need to speed up the identification and designation of Marine Protected Areas
37 (MPAs) given that one of the Aichi targets is to protect 10% of the oceans by 2020 (Secretariat of the
38 Convention on Biological Diversity, 2014; Watson et al. 2014). Seabirds provide an important focus
39 for the development of protected areas. As is true for all marine top-predators, they are threatened by
40 a suite of impacts, particularly from fisheries and pollution, and are in urgent need of protection in
41 many parts of the world (Croxall et al., 2012). The use of Important Bird Areas (IBAs) to delineate
42 candidate MPAs for the conservation of seabirds globally has been encouraged by conservation
43 bodies (BirdLife International, 2010; Lascelles et al., 2012). In the European Union (EU), as of 2014,
44 59% of areas identified as marine IBAs have been designated as either Special Protected Areas
45 (SPAs) or Special Areas of Conservation (SACs) (BirdLife International, 2014). However, only 3.9%
46 of the total EU marine area is designated for marine SPAs, similar to global levels of coverage, and
47 much lower than the 12.5% designated for terrestrial SPAs (Ramirez et al., 2017). One of the reasons
48 that designation of MPAs in Europe and elsewhere has been slow is that the costs and challenges of
49 identifying biodiversity hotspots are prohibitive for many marine regions. In this paper we develop a
50 simple modelling approach that can be used to quickly identify areas of importance for seabird
51 communities, and assess coverage by existing protected areas.

52 Protected areas for seabirds usually focus on the locations of important breeding colonies, either at the
53 nesting sites themselves or through seaward extensions in the waters immediately surrounding the
54 colony (BirdLife International, 2010). The use of IBAs based on short-range colony extensions works
55 well for coastal foragers (McSorley et al., 2003; Wilson et al., 2009) – especially when individual
56 colonies hold a high proportion of the total population – as the designated protected areas often
57 encompass the majority of the colony's range. These coastal MPAs, however, are less effective for
58 protecting pelagic species, whose ranges cover large areas, often crossing national boundaries (Game
59 et al., 2009; Grémillet and Boulinier, 2009; Hyrenbach et al., 2000). At the same time, pelagic species
60 are more threatened than coastal species, and many of the greatest threats, such as by-catch, occur in
61 feeding grounds offshore (Croxall et al., 2012). Designation of MPAs in these areas, using a multi-
62 species and multi-colony approach, can help ensure appropriate conservation management practices
63 are put in place (Ballard et al., 2012; Nur et al., 2011; Ronconi et al., 2012).

64 Ideally identifying important areas for seabirds should be done with empirical data since foraging
65 areas are patchy and difficult to locate, especially for pelagic species. For example, recent work has
66 identified multiple global hotspots for pelagic species using existing tracking data (Lascelles et al.,
67 2016). In general, however, tagging studies rarely collect information from more than one or two

68 colonies or species at a time (but see Dean et al., 2015 and Wakefield et al., 2017), and data is
69 generally only collected for a limited time span within seasons, across seasons, and across years.
70 Large-scale studies of multiple species from multiple colonies take a long time and enormous
71 resources (Block et al., 2011; Grecian et al., 2016). Furthermore, although empirical data from aerial
72 and ship surveys are highly valuable, even the European Seabirds at Sea database (amassing data from
73 over 35 years) contains large gaps in coverage (Dunn, 2012; Stone et al., 1995). Replication within
74 areas over time is limited and yet foraging areas can shift from year to year (Robertson et al., 2014),
75 variability that is likely to increase with climate change (Grémillet and Boulinier, 2009). In many
76 circumstances, therefore, predictive distribution modelling is likely to be a more cost effective and
77 realistic approach for identifying biodiversity hotspots at an ecosystem level.

78 In recent years, an approach using colony census data together with foraging ranges of seabirds, who
79 are central place foragers during the breeding season, has been used to identify hotspots for individual
80 species (Grecian et al., 2012; Soanes et al., 2016; Thaxter et al., 2012). Predicted distributions from
81 these models correlate well with GPS tracking and at-sea survey data for northern gannets (*Morus*
82 *bassanus*) in Britain and Ireland (Grecian et al., 2012), and six other species globally (Soanes et al.,
83 2016). Use of the method led to designation of the first MPA in Namibia for African penguins
84 (*Spheniscus demersus*) (Ludynia et al., 2012). The foraging range approach is one of the
85 recommended methods for identifying marine IBAs (BirdLife International, 2010), and may be
86 particularly useful in regions where distribution data is lacking and the cost of at-sea surveys would
87 be prohibitive, such as the South East Atlantic or South West Pacific (Kot et al., 2010). This relatively
88 simple method predicts a baseline distribution which can then be further refined using data on species
89 specific foraging behaviours or other ecological factors to identify concentrated patches. However, it
90 has yet to be applied on a large regional scale, for multiple colonies or for multiple species.

91 In this study we use the foraging range approach to produce projected distributions for all seabird
92 species breeding in Britain and Ireland, identifying potential hotspots of high abundance. We then
93 assess overlap with marine protected areas at a species, family and foraging range group (coastal or
94 pelagic foragers) level. The location of at-sea distribution hotspots will vary according to colony
95 location and we hypothesise that the level of coverage by protected areas will be higher for coastal
96 species, which would be better covered by seaward colony extensions than pelagic species. Finally,
97 we discuss the validity and potential for using the foraging range approach globally.

98 **2. Methods**

99 *2.1. Data collation*

100 Open-access data for all seabird species breeding in Britain and Ireland were used to generate
101 projected distributions (see Table 1). Data on colony locations and population sizes were extracted
102 from the JNCC Seabird Monitoring Programme (SMP) Database [at www.jncc.gov.uk/smp] to create

103 individual data sets for the 25 species that breed in Britain and Ireland. Most colonies have been
104 counted at least as recently as the Seabird 2000 survey (Mitchell et al., 2004), however colony counts
105 for some species were incomplete and were supplemented with information from BirdWatch Ireland
106 and RSPB annual reports where available (Doyle et al., 2015; Daly et al., 2015; Burke et al., 2015). In
107 the final dataset used for this study ~3% of colonies have not been censused in the last 30 years, these
108 are all mainly colonies in remote regions. Additional colony data for locally threatened species (e.g.
109 roseate tern) were provided with the permission of RSPB, however these distributions are not
110 included here due to the sensitive nature of the data.

111 Maximum foraging range estimates were taken from reviews (Thaxter et al., 2012 and Jovani et al.,
112 2015), and more recent studies (Kane, A. Pers. Comm.; Thaxter et al., 2013; Wakefield et al., 2013)
113 (see Table 1). The best available estimate was taken for each species, either from direct (e.g. GPS
114 tracking), indirect (e.g. time-activity data loggers) or survey data (boat, aerial, or land-based). In
115 general, values for foraging range obtained from direct and indirect estimates do not vary significantly
116 (Camphuysen et al., 2006; Thaxter et al., 2012) suggesting that where tracking data is not available
117 other methods can provide useful estimates of foraging ranges. Maximum foraging range was used to
118 ensure that all potential usage areas were accounted for, even though densities of birds at the edge of
119 the ranges would be very low. Whilst some studies using the foraging radius approach have used the
120 mean of all maximum foraging ranges, maximum foraging ranges from multiple colonies are not
121 available for all species in Britain and Ireland. In reality maximum distances are likely to vary quite a
122 lot around the coasts and the use of the maximum recorded foraging range here is a conservative way
123 to incorporate all of this variation. The validity of this approach is considered further in the
124 discussion, including selected post hoc analyses using mean maximum foraging ranges.

125 *2.2. Generating projected distributions*

126 Using the steps below, and as set out in Figure A.1 in the supplementary information, projected at-sea
127 distributions for individual colonies were generated following a similar process to Grecian et al.
128 (2012). Maps of colony locations and population size can be seen in Figure 1a for sample coastal and
129 pelagic species, and in the supplementary information for all species. The distribution maps are
130 plotted on a 5 x 5 km grid and show the number of individuals predicted to occur in each grid square,
131 if 50% of the colony is foraging at-sea at a given time. This accounts for the assumption that on
132 average, one half of a breeding pair will remain at the nest at any one time (e.g. during incubation and
133 early chick rearing). The proportion of the population at sea (and subsequent numbers of birds in each
134 grid square) at any one time will vary with both time of day and season. However, the relative
135 importance of each grid square will remain the same and the same hotspots will be identified.

136 Step 1: Create a grid surface (5 x 5km grid) where values in each grid square represent the distance
137 from the focal colony.

138 Step 2: Plot colony centred radii based on maximum foraging range for each species. Any land
139 occurring within the foraging area is excluded to define the total available foraging area for the
140 colony. Birds were assumed to only travel over sea, and therefore land was made too expensive to
141 cross in the model. Maximum foraging range was used to ensure coverage of the majority of a
142 colony's foraging area. However, it can be assumed that due to additional behaviours the individuals
143 from a colony will not be spread evenly across this area, and steps 3 and 4 correct for this.

144 Step 3: Invert and normalise the grid square values, so that they all have a value of between 0 and 1
145 with the highest values being found closest to the colony. These values are now the probability of a
146 bird occurring in a given grid square, with probability decreasing linearly as distance from colony
147 increases.

148 Step 4: Weight values in each grid square by the inverse log distance from the colony. This weights
149 the areas closer to the colony of higher importance to account for non-foraging behaviours such as
150 washing/preening or rafting (Wilson et al., 2009).

151 Step 5: Normalise values so that the sum of all grid squares is equal to 1 i.e. 100 % of the at-sea
152 population.

153 Step 6: Multiply proportions in each grid square by the total at-sea population (e.g. 50% of the
154 breeding population). This generates the predicted number of individuals occurring per grid square.

155 These steps were repeated for each individual colony and the distributions were then summed to
156 generate a projected distribution map for the entire region (e.g. Britain and Ireland). A number of
157 colonies in the dataset were located at a further distance inland than the reported maximum foraging
158 range, therefore at-sea distributions were not created for these colonies. Most of these colonies were
159 gulls (see Table 1 for specifics) and can be presumed to be mainly foraging over land (Rock 2016).
160 Table 1 contains details of all of the coastal colonies included in the analysis.

161 Distributions were summed across species to assess the overall distribution of all species collectively,
162 as well as eight family groups (e.g. terns, gulls, see Appendix B for full list) and two foraging range
163 groups (coastal vs. pelagic foragers). For the purpose of this study species with a maximum foraging
164 range of less than 75 km were defined as coastal and those with a maximum foraging range of 75 km
165 or greater were defined as pelagic. There is no clear bimodal distinction between the two groups,
166 however a cut off of 75 km generates groups of comparable size (Coastal = 12; Pelagic = 13). The
167 groupings also reflect the foraging ecology of the species, with Terns, Cormorants and most Gulls in
168 the coastal group and species such as gannet and Manx shearwater that are known to occur well off-
169 shore in the pelagic group.

170 In order to assess species richness from the grouped distribution, the number of species occurring
171 within each grid square was calculated.

172 *2.3. Calculating protected area overlap*

173 Coverage of protected areas for individual species was quantified by calculating the percentage of the
174 at-sea population estimated to occur within the spatial boundaries of a protected area. Spatial data for
175 the boundaries of all protected areas with marine components in Britain and Ireland were obtained
176 from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2016). These were then split
177 into three types: (1) Special Protected Areas (SPAs); (2) OSPAR convention (Convention for the
178 Protection of the Marine Environment of the Marine Environment of the North-East Atlantic) MPAs;
179 and (3) all protected areas (PAs) combined (also including SPAs and OSPAR MPAs). This allowed a
180 comparison between protected area types which often include seabirds as their designation criteria to
181 meet EU requirements (SPAs which are specifically for protection of birds and OSPAR MPAs which
182 are designated for a wider range of taxa) and all other protected area types recognised in Britain and
183 Ireland. All individual protected area polygons were merged to generate one polygon for each type
184 (e.g. one polygon for all SPAs) to avoid double-counting birds that occurred in grid squares where
185 protected areas overlap.

186 A Wilcoxon rank sum test was used to assess the difference in percentage overlap for (1) foraging
187 group (coastal or pelagic) and (2) conservation status (Least Concern or Near Threatened and above).
188 These comparisons were carried out for percentage overlap of SPAs, OSPAR MPAs and all PAs
189 combined. All analyses were carried out in R version 3.2.1 (R Development Core Team, 2016). Maps
190 of the distributions were created using the R package ‘ggplot2’ version 2.00 (Wickham 2009).

191 **3. Results**

192 Projected distributions for all seabird species breeding in the UK and Ireland individually (Figure 1b
193 for a sample of species, and supplementary information for all species) and in family groups (Figure
194 1c for a sample of family groups, and supplementary information for all family groups) were
195 generated. The distributions generated show the average number of individuals per 5 x 5 km grid cell
196 predicted to be at-sea during the breeding season.

197 Grouped distributions were produced for all coastal species (Figure 2a), all pelagic species (Figure 2b)
198 and all species combined (Figure A.5, supplementary information). Hotspots of abundance for coastal
199 species are spread around Britain and Ireland, with the east coast of Ireland, the south-east coast of
200 England and the Shetland Islands shown as being particularly important. Conversely, for pelagic
201 species, Scotland is of greatest importance. At the family level, considerable variation also occurs. For
202 example, most tern hotspots are spread around the east coasts of Britain and Ireland whereas

203 Procellariidae hotspots are clumped on the west coasts where they have easy access to distant foraging
204 areas. A map of species richness was produced showing the potential number of species occurring
205 within each grid square based on the projected distribution for all species combined (Figure 3).

206 Overlap between projected seabird distributions and currently designated protected areas (SPAs,
207 OSPAR MPAs, and all PAs) ranged from under 7% of the at-sea population contained in all protected
208 areas (European storm-petrel) to over 70% of the at-sea population (Mediterranean gull) (Figure 4).
209 See Table B.1 in the supplementary material for a breakdown of overlap by species and family group.
210 Values are likely to vary with the time of day, but remain representative for the time period when the
211 majority of foraging takes place.

212 Overall, the percentage of a population covered by a protected area was significantly higher for
213 coastal species (mean = 32.5%) than for pelagic species (mean = 13.2%) ($p < 0.001$, Table 2). This
214 difference was also significant when considering SPAs (mean coastal = 18.1% and mean pelagic =
215 2.4%, $p < 0.001$), or OPSAR MPAs (mean coastal = 25.5% and mean pelagic = 11.9%, $p = 0.001$)
216 individually. Non-threatened species had a higher coverage from protected areas than threatened
217 species (mean non-threatened = 25.0% and mean threatened = 14.3%). This relationship was
218 significant for overlap with SPAs ($p = 0.01$), but just fell short of significance at the $\alpha = 0.05$ level for
219 overlap with OSPAR MPAs ($p = 0.09$) or all PAs combined ($p = 0.07$) (Table 2).

220

221 **4. Discussion**

222 *4.1 General patterns of distribution*

223 Projection based models using foraging ranges and colony sizes have previously been used to estimate
224 and map densities of seabirds at sea for single or small numbers of species (Grecian et al., 2012;
225 Ludynia et al., 2012; Soanes et al., 2016). Here we applied this approach for an entire seabird
226 community in a major area for seabirds in Europe. Patterns of distribution varied remarkably between
227 species. In particular a clear distinction is seen between hotspots for coastal versus pelagic species,
228 which are reflected in the distribution of breeding colonies (Mitchell et al., 2004). Naturally the
229 models show that abundance hotspots are located nearest the colonies or groups of colonies with the
230 largest population sizes. Even though some seabirds will travel long distances away from the colony
231 to forage, it should still follow that the largest colonies will be located where access to resources
232 minimizes the cost of travel to reach resources (e.g. Sandvik et al., 2016), and where direct
233 competition from other colonies is low (Furness & Birkhead, 1984). This basic principle of optimal
234 foraging means that a projection based model such as ours is well suited for capturing the majority of
235 space use by central place foragers (Ashmole 1963).

236 *4.2 Protected area overlap*

237 The analysis of overlap between protected areas and projected at-sea distributions found large
238 variation in coverage amongst species, ranging from 7% (European storm-petrel) to 70%
239 (Mediterranean gull) of at-sea population contained in protected areas. In particular, we found a
240 significantly higher proportion of coastal birds were covered by protected areas compared to pelagic
241 birds, many of which are threatened globally, suggesting that they are afforded better protection from
242 designated MPAs. This result is explained by the fact that most MPAs (particularly marine
243 components of SPAs) are developed as extensions from the coast, often surrounding an important
244 colony for a particular seabird species. This pattern occurred even though the projected distributions
245 are weighted so that proportionally more birds are found closer to the colony than at the edge of their
246 foraging ranges, which will affect pelagic foragers more heavily. It is clear that due to the large
247 foraging ranges of pelagic species, coastal colony-centred marine protected areas will not provide
248 sufficient coverage to adequately protect them (see Game et al. 2009 on the lack of pelagic protected
249 areas). While OSPAR MPAs seem to afford better protection to pelagic species than SPAs, the
250 percentage overlap is still significantly lower than for coastal species.

251 Our analyses also suggest that current marine SPAs afford better protection to species with a
252 conservation status of 'Least Concern' compared to those ranked as 'Near Threatened' or above. The
253 level of coverage is also higher for 'Least Concern' species in OSPAR MPAs and all MPAs
254 combined, but not significantly so. This reflects the fact that all species ranked 'Near Threatened' or
255 above are also pelagic foragers, which have lower coverage by MPAs. For example, the Atlantic
256 puffin is listed as a species of conservation priority in Europe (European Commission, 2010) and is
257 categorised as Endangered on the European Red List (BirdLife International, 2015); however, our
258 results show that it has less protection than many species of Least Concern. Less than 20% of the at-
259 sea population is covered by protected areas, with only a small fraction of this contributed by SPAs.
260 Thus, these analyses highlight the limitations of assuming that protected areas near colonies are
261 necessarily going to serve the species that need most protection, particularly as the majority of
262 foraging by pelagic species will occur in offshore areas (Game et al., 2009; McGowan et al., 2017).
263 An important next step would be to assess which type of protected area (e.g. fixed or dynamic pelagic
264 MPAs) would be more effective for these species, using additional information on foraging behaviour
265 on a species by species basis and spatial prioritisation tools to inform future planning.

266 *4.3 Predictive models of seabird biodiversity*

267 A range of methods have been used to predict seabird distribution at sea, but all show that distance to
268 colony is usually the most important factor (Chivers et al., 2013; Ford et al., 2007; Louzao et al.,
269 2012; Skov et al., 2008). Some studies (see below) have explored how the use of different foraging
270 ranges (e.g. maximum, mean maximum or mean) affects the potential accuracy of the predicted

271 distributions. For gannets, Grecian et al. (2012) found that varying the foraging range used in models
272 by $\pm 25\%$ had no effect on how well the projected distributions correlated with at-sea survey data, and
273 elected to use maximum foraging range in the final model. Studies by Perrow et al. (2015) and Soanes
274 et al. (2016) suggest that the use of the mean of all maximum foraging range estimates may be more
275 appropriate to ensure that an area proposed for conservation is not unfeasibly large. This may be true
276 when the foraging radius approach is used to delineate a home range area (km^2) for protection,
277 whereas for this study the final projected distributions are expressed in density of birds per grid
278 square. The use of maximum foraging radius here allows the hotspots of highest abundance to be
279 highlighted without completely discarding areas at the extremes of a species range where birds may
280 still be foraging. Applying a log decay weighting to the distributions, as in step 4 of the methods,
281 results in low densities of birds at the edge of the distributions, approaching zero individuals.
282 Furthermore we conducted a posthoc analysis of MPA overlap using mean maximum foraging range
283 for a short-, mid- and long-range forager, with values taken from Thaxter et al. (2012). The maximum
284 and mean maximum overlaps were as follows: (northern gannet, 709 km range = 9.56% overlap and
285 229.4 km range = 12.55% overlap; black-legged kittiwake, 120 km range = 12.51% overlap and 60
286 km range = 13.86% overlap; common tern, 30 km range = 34.21% overlap and 15.2 km range =
287 27.55% overlap). Thus use of maximum versus mean maximum made little difference and use of
288 maximum values in this approach is justified.

289 One limitation of projection models is that they cannot account for all factors that explain where
290 animals are found, and inevitably the predicted and true distributions will diverge. For example,
291 density dependent segregation is likely to occur between colonies for all species (Furness & Birkhead,
292 1984; Wakefield et al., 2013), and within-colony segregation between breeders, non-breeders, and
293 juveniles, or by sex may also occur (Fayet et al., 2015; Stauss et al., 2012; Votier et al., 2017). More
294 importantly, however, spatio-temporal variation in oceanic, meteorological, and ecological factors
295 leads to patchy resource distribution and variable prey availability (Scales et al., 2014; Schneider,
296 1990; Gibb et al., 2017). These factors are likely to be especially important since they can vary within
297 (Grémillet et al., 2008) and across (Robertson et al., 2014) years, and over long periods of time
298 (Behrenfeld et al., 2006), issues that will also confound empirical data. Despite these limitations,
299 however, simple projection models could be an important tool in seabird conservation for several
300 reasons. First, dynamic oceanic and ecological factors cannot easily be included in a universal model
301 of seabird distribution because such information is lacking for most species in most areas, even in our
302 study area where seabirds have been studied relatively intensively. Moreover, in most cases it is
303 unrealistic to expect these data to become available in the near future, because spatio-temporal
304 variation is so difficult and costly to capture at any spatial scale, let alone at the scale of the marine
305 environment for an entire community of species. Second, modifications to the model on a species-
306 specific basis would need to greatly improve accuracy to be considered useful, at the cost of

307 sacrificing general applicability for all species. Work to date suggests that model performance is not
308 improved dramatically when additional data on resource abundance (Grecian et al., 2012) or
309 bathymetric preference (Soanes et al., 2016) have been included. Third, the approach has already been
310 shown to produce good correlations with distributions obtained from at-sea surveys or GPS tracking
311 in a number of species in different regions (Grecian et al., 2012; Ludynia et al., 2012). Although we
312 are only just beginning to validate our model using a variety of different kinds of empirical data
313 (Critchley et al. in prep), visual comparison of our predictive distributions with the European Seabirds
314 at Sea (ESAS) database outputs (Dunn, 2012; Stone et al., 1995) shows good agreement where there
315 is sufficient coverage by ESAS. At the very least, this suggests that the foraging radius approach can
316 be used to provide an important baseline distribution in poorly surveyed regions of the world, with the
317 potential to include additional ecological factors where available to further refine distributions on a
318 species by species basis. Finally, for a tool to be effective across multiple species and utilised by
319 regulatory bodies, it should be simple to use and implement, which is true of the projection model
320 approach.

321 **Conclusion**

322 The projected distribution maps generated in this study have identified both the species and areas that
323 are currently lacking sufficient protection through establishment of protected areas during the
324 breeding season, using a simple but universally applicable method. In particular, the combined species
325 distributions allow us to see where hotspots with a large number of species are found, highlighting
326 sites for further investigation. Although pelagic species are the most threatened group of seabirds
327 globally, they were also the least well protected in our study area, where most MPAs are in coastal
328 locations. Future assessment for marine conservation planning should account for at-sea distribution
329 to ensure that wider-ranging seabirds are afforded sufficient levels of protection. Designation of
330 MPAs does not per se confer protection, but appropriate management of activities within them, e.g.
331 regulation of fisheries/petroleum exploration, can result in positive conservation outcomes at the
332 broader ecosystem level. Utilisation of distribution maps that show hotspots of both bird density and
333 species richness in offshore waters should enable effective conservation measures to be put in place
334 that benefit multiple species, either through fixed or dynamic MPAs (Game et al., 2009; Hays et al.,
335 2016). Our approach relies on good abundance estimates for individual colonies, which themselves
336 can be extremely challenging and costly to generate. However, these challenges are likely to be
337 considerably less than those for collecting detailed tracking or at-sea survey data, though naturally
338 both approaches are valuable and complementary. The foraging radius method used here is therefore
339 likely to be particularly useful in regions around the world where little data on at-sea distributions
340 currently exist.

341

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357

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544

Tables & figures

Table 1

Summary for each species of the number of colonies in Britain and Ireland; total population size (individuals) from most recent colony counts; European conservation status; proportion of the European population contained in Britain and Ireland; maximum foraging range (km); and foraging range group (pelagic or coastal). European conservation status is taken from the IUCN Red List of Threatened Species (Choudhury et al., 2016). European population size was taken as the maximum estimate from the IUCN (Choudhury et al., 2016). The proportion estimated is therefore the minimum potential percentage of the biogeographical population contained in Britain and Ireland. Maximum foraging range was taken from a review by Thaxter et al. (2012) with a few exceptions, see table footnotes. Species with a maximum foraging range of less than 75 km were defined as coastal and those with a maximum foraging range of 75km or greater were defined as pelagic.

Species	Number of colonies	Population size (individuals)	European conservation status	Proportion of European population (%)	Maximum foraging range (km)	Foraging range group
Arctic skua <i>Stercorarius parasiticus</i>	643	4740	Least concern	4.23	75	Pelagic
Arctic tern <i>Sterna paradisaea</i>	959	116472	Least concern	6.43	30	Coastal
Atlantic puffin <i>Fratercula arctica</i>	405	869690	Endangered	7.50	200	Pelagic
Black guillemot <i>Cephus grylle</i>	1323	38529	Least concern	5.19	15 ^c	Coastal
Black-headed gull ^a <i>Larus ridibundus</i>	415	184240	Least concern	7.44	40	Coastal
Black-legged kittiwake <i>Rissa tridactyla</i>	538	704028	Vulnerable	15.96	120	Pelagic
Common guillemot <i>Uria aalge</i>	506	1271624	Near threatened	41.56	135	Pelagic
Common gull ^a <i>Larus canus</i>	1330	48110	Least concern	4.76	50	Coastal
Common tern ^b <i>Sterna hirundo</i>	376	35468	Least concern	3.11	30	Coastal
European shag <i>Phalacrocorax aristotelis</i>	1238	61798	Least concern	39.36	17	Coastal
European storm-petrel <i>Hydrobates pelagicus</i>	107	178138	Least concern	17.29	336 ^d	Pelagic
Great black-backed gull <i>Larus marinus</i>	2010	36528	Least concern	13.73	60 ^c	Coastal
Great cormorant ^b <i>Phalacrocorax carbo</i>	290	27084	Least concern	3.00	35	Coastal

Great skua <i>Stercorarius skua</i>	700	16016	Least concern	46.42	219	Pelagic
Herring gull ^a <i>Larus argentatus</i>	2633	278340	Near threatened	17.82	92	Pelagic
Leach's storm-petrel <i>Oceanodroma leucorhoa</i>	16	96714	Least concern	17.68	120	Pelagic
Lesser black-backed gull ^a <i>Larus fuscus</i>	907	180790	Least concern	26.79	181	Pelagic
Little tern <i>Sterna albifrons</i>	63	3424	Least concern	3.23	11	Coastal
Manx shearwater <i>Puffinus puffinus</i>	43	658798	Least concern	83.92	330	Pelagic
Mediterranean gull ^a <i>Larus melanocephalus</i>	16	1026	Least concern	0.16	20	Coastal
Northern fulmar <i>Fulmarus glacialis</i>	2643	1075514	Endangered	15.36	580	Pelagic
Northern gannet <i>Morus bassanus</i>	27	576088	Least concern	42.05	709 ^e	Pelagic
Razorbill <i>Alca torda</i>	679	178773	Near threatened	17.53	95	Pelagic
Roseate tern <i>Sterna dougallii</i>	5	3060	Least concern	52.76	30	Coastal
Sandwich tern <i>Sterna sandvicensis</i>	64	34166	Least concern	11.58	54	Coastal

^a Gull colonies that were located at a distance of greater than 5 km from the coast were classified as inland, following criteria set out by Mitchell et al. (2004) and excluded from analysis.

^b For common tern and great cormorant a number of colonies were located at a distance greater than the maximum foraging range; these were excluded from analysis.

^c Maximum foraging range taken from review by Jovani et al. (2015)

^d Maximum foraging range taken from unpublished GPS tracking data from High Island, Co. Galway, Ireland (Kane, A., Pers. Comm.)

^e Maximum foraging range taken from Wakefield et al. (2013)

Table 2 Results of Wilcoxon rank sum tests to assess differences in percentage overlap for (1) foraging group (Coastal or Pelagic) and (2) conservation status (Least Concern or Near Threatened and above). Significant results are shown in **bold**. Mean percentage overlap contained within SPAs, OSPAR MPAs and all PAs combined is shown for each group.

Foraging group	% overlap with predicted distributions			Conservation status	% overlap with predicted distributions		
	SPAs	OSPAR MPAs	All PAs		SPAs	OSPAR MPAs	All PAs
Coastal	18.13%	25.45%	32.49%	Least Concern	12.45%	20.27%	25.04%
Pelagic	2.43%	11.89%	13.21%	Threatened	2.11%	12.48%	14.29%
	Result of Wilcoxon Rank Sum test (p-value)				Result of Wilcoxon Rank Sum test (p-value)		
coastal > pelagic	<0.001	0.0012	<0.001	least concern > threatened	0.01	0.09	0.07

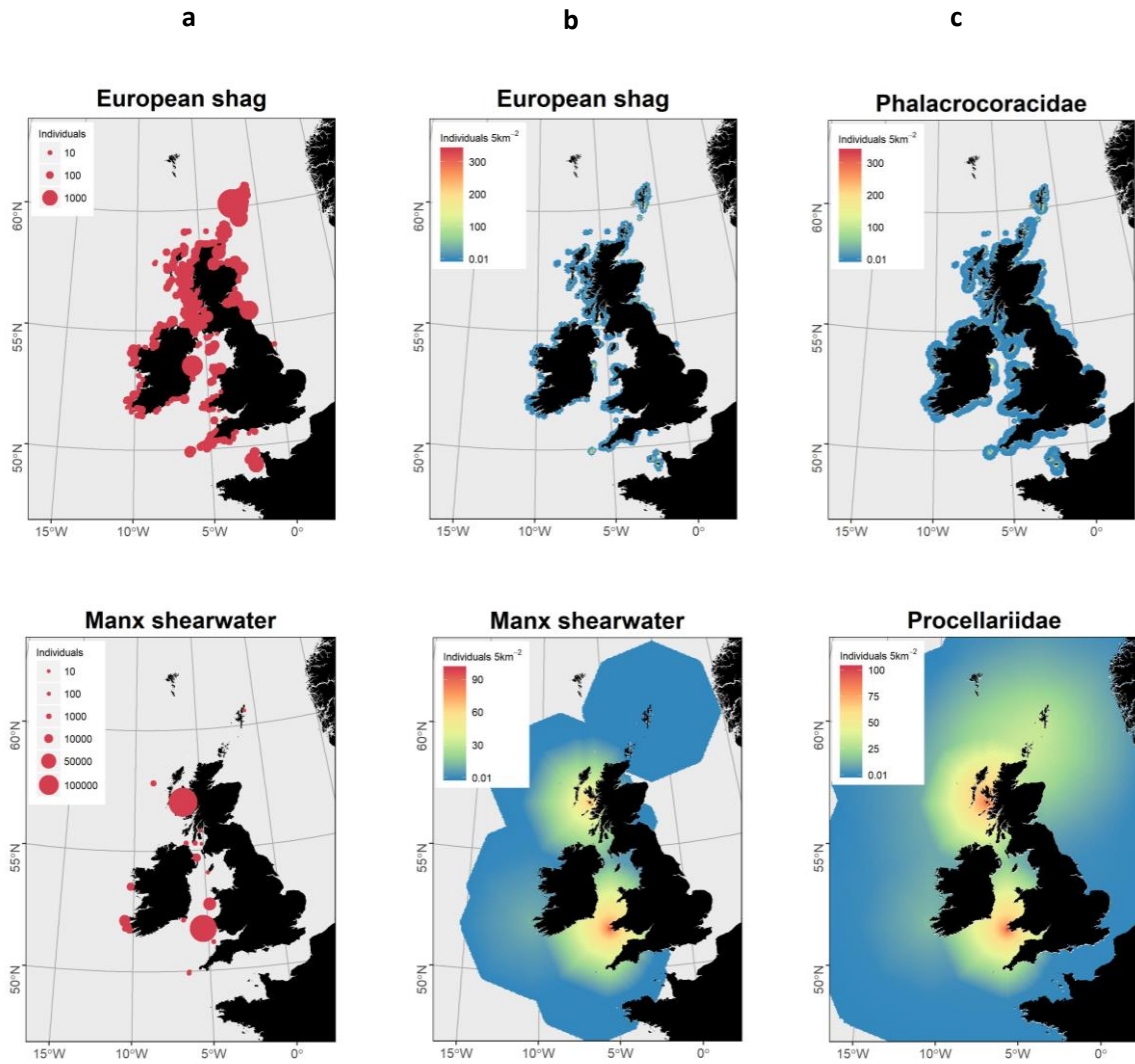


Figure 1 Maps for example coastal (Phalacrocoracidae) and pelagic (Procellariidae) family groups occurring in Britain and Ireland showing a) colony location and population size for a sample species, b) projected at-sea distributions for a sample species, and c) projected at-sea distribution for the family group. Maps for all species and groups can be found in Figures A.1, A.2 and A.3 in the supplementary material. Details of the species contained within each family group can be found in Table B.2

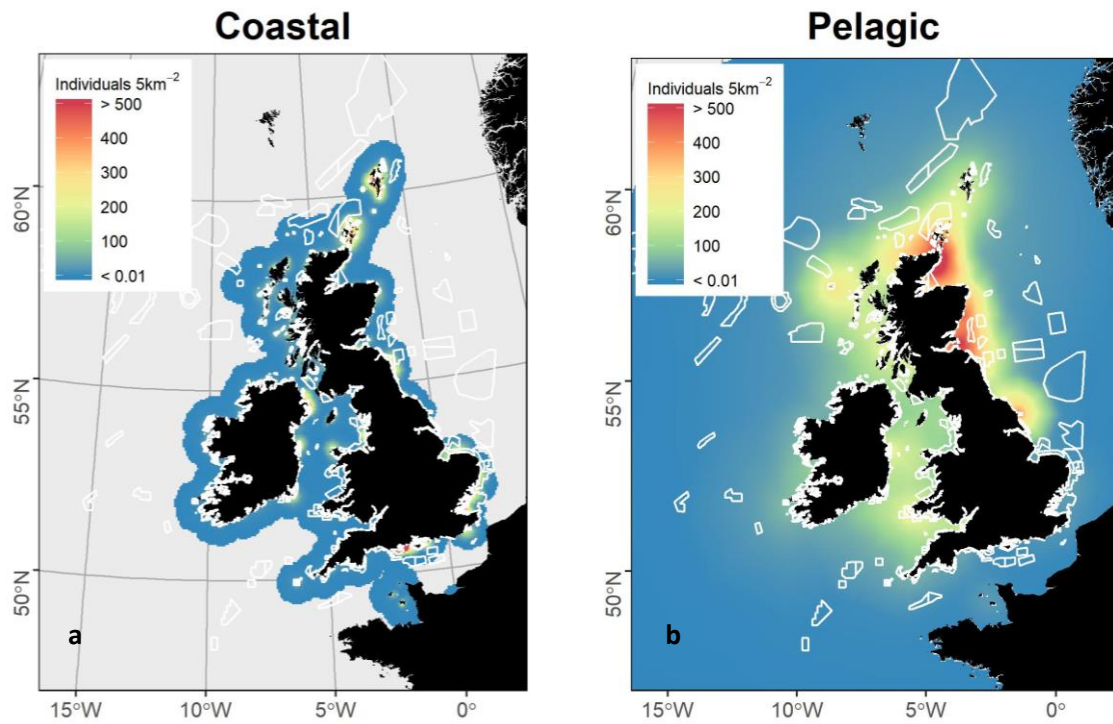


Figure 2 Maps showing the projected distributions for a) all coastal species and b) all pelagic species, with protected areas overlaid (white polygons). The colour scale shows predicted density (individuals per 5 x 5 km square) if 50% of the colony is at-sea at a given time, and values are consistent across both maps. Grid squares with over 500 individuals are red and grid squares containing less than 0.01 are blue.

Species richness

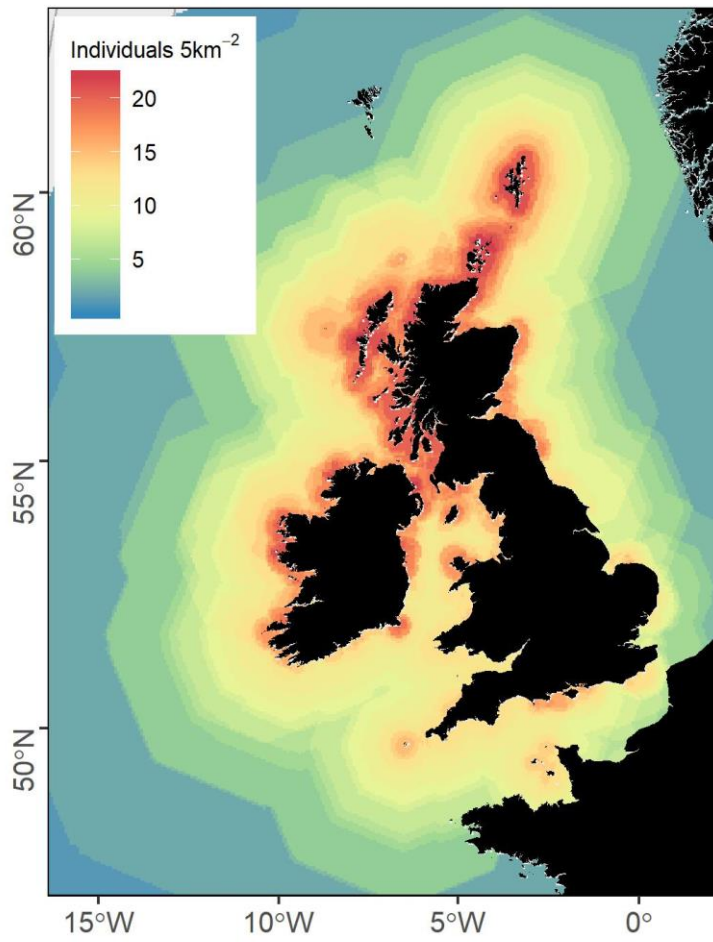


Figure 3 A map of species richness showing the potential number of species occurring within each 5 x 5 km grid square based on the projected distribution for all species combined.

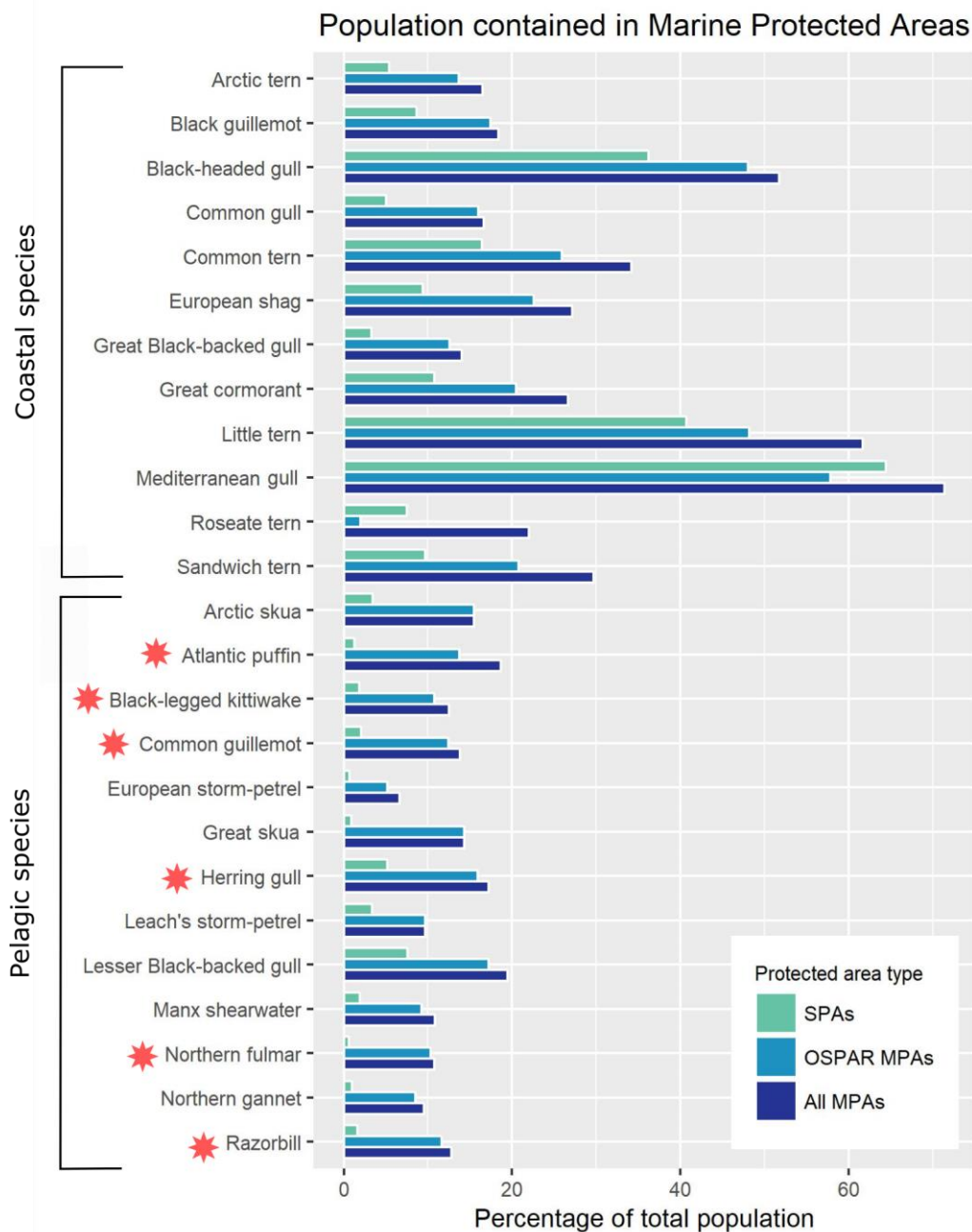


Figure 4 Percentage of predicted at-sea population contained within a currently designated protected area for: green = Special Protected Areas (SPAs); light blue = OSPAR Marine Protected Areas; and navy blue = All protected areas combined. Red stars indicate species that have a European Conservation status of ‘Near threatened’ or higher. Percentage values are not additive as there is spatial overlap between the different protected area types. See Table B.1 in the supplementary material for a complete list of the percentage values.