

1 **Breeding density, fine-scale tracking and large-scale modeling reveal the regional**
2 **distribution of four seabird species**

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28

29 **Abstract**

30 Population-level estimates of species' distributions can reveal fundamental ecological processes
31 and facilitate conservation. However, these may be difficult to obtain for mobile species,
32 especially colonial central-place foragers (CCPFs; e.g. bats, corvids, social insects), because it is
33 often impractical to determine the provenance of individuals observed beyond breeding sites.
34 Moreover, some CCPFs, especially in the marine realm (e.g. pinnipeds, turtles and seabirds) are
35 difficult to observe because they range 10s to 10,000s km from their colonies. It is hypothesized
36 that the distribution of CCPFs depends largely on habitat availability and intraspecific
37 competition. Modeling these effects may therefore allow distributions to be estimated from
38 samples of individual spatial usage. Such data can be obtained for an increasing number of
39 species using tracking technology. However, techniques for estimating population-level
40 distributions using the telemetry data are poorly developed. This is of concern because many
41 marine CCPFs, such as seabirds, are threatened by anthropogenic activities. Here, we aim to
42 estimate the distribution at sea of four seabird species, foraging from approximately 5500
43 breeding sites in Britain and Ireland. To do so, we GPS-tracked a sample of 230 European shags
44 *Phalacrocorax aristotelis*, 464 black-legged kittiwakes *Rissa tridactyla*, 178 common murre
45 *Uria aalge* and 281 razorbills *Alca torda* from 13, 20, 12 and 14 colonies respectively. Using
46 Poisson point process habitat use models, we show that distribution at sea is dependent on: (i)

47 density-dependent competition among sympatric conspecifics (all species) and parapatric
48 conspecifics (kittiwakes and murre); (ii) habitat accessibility and coastal geometry, such that
49 birds travel further from colonies with limited access to the sea; and (iii) regional habitat
50 availability. Using these models, we predict space use by birds from unobserved colonies and
51 thereby map the distribution at sea of each species at both the colony and regional level. Space
52 use by all four species' British breeding populations is concentrated in the coastal waters of
53 Scotland, highlighting the need for robust conservation measures in this area. The techniques we
54 present are applicable to any CCPF.

55

56 Keywords: Central-place foraging, coloniality, animal tracking, Poisson point process, habitat
57 use, density-dependence, species distribution models.

58

59 **Introduction**

60 Accurate distribution estimates are key to effective wildlife management yet many colonial
61 central-place foragers (i.e. those that return regularly to a common breeding location or refuge)
62 are difficult to observe because they range so widely. Innovations in telemetry are increasingly
63 making it possible to track these species at the individual level (Wikelski et al. 2007, Hart and
64 Hyrenbach 2010, O'Mara et al. 2014), but both theoretical and analytical advances are needed
65 before unbiased, population-level, distribution estimates can be derived from the resulting data
66 (Aarts et al. 2008, Hebblewhite and Haydon 2010). This is of concern because many colonial
67 central-place foragers are currently suffering unsustainable declines due to human activities
68 (Mickleburgh et al. 2002, Williams and Osborne 2009, Hamann et al. 2010).

69

70 Seabirds are one of the world's most endangered avian groups (Croxall et al. 2012). This is due
71 to anthropogenic impacts including invasive species, fisheries bycatch, pollution and direct
72 exploitation. The distribution and size of seabird breeding colonies has been recorded directly in
73 many regions. In contrast, the distribution of birds at sea is generally estimated from visual
74 survey or more recently, tracking data. Systematic surveys from ships or planes, began in earnest
75 in the 1970's (Ainley et al. 2012). They provide coarse scale (1 - 10 km) Eulerian data (i.e.
76 observations at fixed points in space) but cannot reliably ascribe provenance or, in many cases,
77 life history stage. Hence, colony-level distributions cannot be estimated using this technique.
78 Since the 1990s it has also been feasible to track the movements of seabirds using bird-borne
79 devices, which are now becoming sufficiently small and cost-effective to obtain statistically
80 robust sample-sizes for a wider range of species (Burger and Shaffer 2008). Devices are usually
81 deployed at colonies so the origin and status of tracked birds are known. However, while GPS
82 tracking is now providing a wealth of fine scale (10^{-2} km) Lagrangian data (i.e. observations
83 following the animal in space) on distribution, these tend to be from a relatively small proportion
84 of colonies.

85
86 Comparatively few studies have so far tracked birds from multiple colonies within
87 metapopulations (Frederiksen et al. 2011, Wakefield et al. 2013, Dean et al. 2015) or across
88 species (Block et al. 2011, Raymond et al. 2015) and fewer still have attempted to estimate the
89 distribution of birds from unsampled colonies using such data (Wakefield et al. 2011, Raymond
90 et al. 2015, Torres et al. 2015). Hence, there is little information on the relative distributions of
91 seabirds from most colonies. This is important both because it hampers conservation (Lewison et
92 al. 2012) and because such information can reveal aspects of the ecology of colonial central-

93 place foragers that have important wildlife management implications (Wakefield et al. 2009). For
94 example, theory predicts that density-dependent competition among seabirds breeding in the
95 same colony (sympatric competition), mediated either through prey depletion or disturbance,
96 leads to a positive relationship between colony size and foraging range, ultimately regulating
97 colony growth (Ashmole 1963, Lewis et al. 2001). Similarly, density-dependent competition
98 between colonies (parapatric competition) may lead to spatial segregation of the utilization
99 distributions (UDs) of adjacent colonies (Wakefield et al. 2013) (a UD is defined as a
100 population's spatial probability distribution; Fieberg and Kochanny 2005). Evidence has been
101 advanced in support of both hypotheses (Lewis et al. 2001, Masello et al. 2010, Catry et al. 2013)
102 yet it remains uncertain how sympatric and parapatric intra-specific competition, foraging costs
103 (which increase with distance from the colony) and resource availability interact to shape the
104 UD of breeding seabirds and other colonial central-place foragers (Wakefield et al. 2013). For
105 example, the size and shape of colony UD depend on the density of conspecifics but this is a
106 function not only of colony size and resource availability but also the area of sea accessible from
107 that colony, which in turn varies with coastal morphology (Birkhead and Furness 1985). Hence,
108 we might predict birds breeding at colonies with restricted access to the sea travel further than
109 those breeding on isolated islands. Moreover, although it is clear that seabirds breed in
110 hierarchically nested aggregations (i.e. with increasing scale, nests within sub-colonies, within
111 colonies, within islands, archipelagos, etc.) it is not clear how these aggregations function as
112 groups or independently at different scales (Wakefield et al. 2014). Colonies, defined
113 subjectively during censuses, may not therefore correspond to functional units.

114

115 Despite these uncertainties, it is clear that while some threats to seabirds are widespread (e.g.
116 climate change) others, such as offshore windfarms, episodic pollution incidents, fisheries
117 bycatch and the depletion of fish stocks, may be localized, impacting colonies within wider
118 metapopulations unequally (Furness and Tasker 2000, Inchausti and Weimerskirch 2002,
119 Montevecchi et al. 2012). Hence, colony-level distribution estimates may be required in order to
120 target and monitor mitigation measures, such as Marine Protected Areas (MPAs) or fisheries
121 closures, effectively (Lascelles et al. 2012, Russell et al. 2013).

122

123 Current barriers to estimating colony-level distributions via individual tracking are both
124 logistical and analytical: for most species it would be impractical to track birds from all colonies.
125 In theory, distribution could be predicted from tracked birds from a sample of colonies by
126 modelling space use as a function of habitat, foraging costs, competition, etc. (Aarts et al. 2008,
127 Wakefield et al. 2009, Wakefield et al. 2011, Catry et al. 2013). However, statistical techniques
128 for producing unbiased estimates of distribution using tracking data are still in development
129 (Aarts et al. 2008, Patterson et al. 2008, Illian et al. 2012). This is partly because tracking data
130 violate many of the assumptions inherent to conventional parametric models (reviewed by
131 Turchin 1998, Aarts et al. 2008, Wakefield et al. 2009). Repeat observations on individuals
132 (typically 10^2 - 10^4 locations/individual in seabird studies) tend to be spatiotemporally
133 autocorrelated and the movements of individuals drawn from the same colony may be dependent
134 on one another due to public information transfer and cultural and genetic divergence (Wakefield
135 et al. 2013, Paredes et al. 2015). Furthermore, tracking data record the presence of animals but
136 not their absence (Aarts et al. 2012). In order to account for these attributes, habitat use by
137 tracked animals has been modelled using logistic mixed-effects models (Aarts et al. 2008,

138 Wakefield et al. 2011). This entails the construction of a binary response variable, which
139 comprises animal locations and randomly-generated pseudo-absence points. However, the
140 logistic model approximates an inhomogeneous Poisson point process (IPP) model (Cressie
141 1993, Aarts et al. 2012), which may be fitted more directly and efficiently by using numerical
142 quadrature to approximate the model's pseudo-likelihood (Berman and Turner 1992, Baddeley
143 and Turner 2000, Warton and Shepherd 2010) (see Methods for details). This approach may
144 therefore be more tractable for GPS tracking datasets, which typically comprise 10^3 - 10^4 locations
145 per individual. A further substantial problem is that habitat selection may vary between colonies
146 due to differences in the relative availability of prey and habitats among those colonies (e.g.
147 Chivers et al. 2012, Paredes et al. 2012), a phenomenon termed functional response in resource
148 selection (Myserud and Ims 1998). As such, habitat selection models fitted to data from one site
149 may predict poorly for others (Torres et al. 2015). Matthiopoulos et al. (2011) show that
150 Generalized Functional Response (GFR) models can interpolate usage to unsampled sites more
151 accurately than conventional habitat selection models. GFR models require that usage is sampled
152 under a range of availability regimes allowing the response to environmental covariates to be
153 conditioned on the expected site-level availability of all environmental covariates in the model.
154

155 Britain and Ireland are home to internationally important populations of breeding seabirds (Fig.
156 1). These include 34% of the world's European shags *Phalacrocorax aristotelis* (26,600 pairs),
157 20% of its razorbills *Alca torda* (93,600 pairs), 13% of its common murre *Uria aalge* (708,200
158 pairs, and 8% of its black-legged kittiwakes *Rissa tridactyla* (378,800 pairs) (Mitchell et al.
159 2004). Our study focuses on these species, referred to hereafter as shags, razorbills, murre and
160 kittiwakes. Although the foraging niches of these species partially overlap, they are differentiated

161 along several axes: In Britain and Ireland all are almost exclusively neritic while breeding,
162 feeding primarily on sandeels (*Ammodytes* spp.) and other small fish and crustaceans (Grémillet
163 et al. 1998, Watanuki et al. 2008, Thaxter et al. 2010). Shags forage either benthically or
164 pelagically (max. dive depth ~ 60 m) in coastal waters, relatively close (\leq ~ 30 km) to their
165 colonies (Grémillet et al. 1998, Watanuki et al. 2008, Bogdanova et al. 2014). Kittiwakes, murre
166 and razorbills are more wide-ranging, foraging 10s-100s km from their colonies. Kittiwakes are
167 surface feeders; murre make relatively long, deep foraging dives to the pelagic and demersal
168 zones; while razorbills make more frequent, shallow, dives to the pelagic zone (Thaxter et al.
169 2010, Linnebjerg et al. 2013). There is some evidence that kittiwakes from adjacent colonies
170 segregate in space while foraging (Ainley et al. 2003, Paredes et al. 2012) but nothing is known
171 about this phenomenon in the other species.

172

173 In a recent assessment of conservation status in the UK, shags and kittiwakes were reclassified
174 from amber to red due to 62 % and 71 % declines respectively over 25 years (Eaton et al. 2015).
175 In the UK, murre and razorbills are amber listed due to their restricted range and international
176 importance (Eaton et al. 2015), while internationally razorbills have recently been reclassified
177 from ‘Least Concern’ to ‘Globally Near-threatened’ (BirdLife International 2015). Current
178 declines are thought to be due in part to falls in prey stocks (especially sandeels in the northern
179 North Sea), due to over fishing and climate change (Frederiksen et al. 2007, Cook et al. 2014).
180 Kittiwakes are also regarded to be particularly vulnerable to wind farm developments, which are
181 burgeoning in UK waters (Furness et al. 2013). The diving species face ongoing threats from oil
182 spills (Williams et al. 1995, Votier et al. 2005) and gill nets (Žydelis et al. 2013). Domestic and
183 international legislation and agreements require countries to manage and conserve seabirds

184 (Croxall et al. 2012). Two measures adopted by governments in UK and elsewhere in the
185 European Union that contribute to seabird conservation are the extension of existing colony-
186 based Special Protection Areas (SPAs) for seabirds to adjacent waters that are used for
187 “maintenance activities” (e.g. foraging, courtship, etc.) and secondly, the establishment of
188 marine SPAs around important foraging areas (Garthe et al. 2012, Perrow et al. 2015). However,
189 both marine protected area identification and wider spatial planning at sea are being hampered by
190 a lack of colony-specific distribution estimates (Perrow et al. 2015). In the absence of such
191 information, policy-makers frequently make the unrealistic assumption that seabirds are
192 uniformly distributed out to some threshold distance from their colonies, such as their putative
193 maximum foraging range (Thaxter et al. 2012).

194

195 The main aim of our study is to estimate the coarse scale (1-10 km) metapopulation and colony-
196 level utilization distributions of four species of seabirds breeding in Britain and Ireland during
197 the late incubation and early chick-rearing periods. To do so we tracked birds from a sample of
198 colonies drawn from throughout the geographical, environmental and colony size range of our
199 study species in Britain and Ireland and modelled their distributions as functions of colony
200 distance, sympatric and parapatric intraspecific competition, coastal morphology and habitat
201 availability. In so doing we estimate the distribution of birds from > 5500 breeding sites. Further,
202 we specifically explored the marine distributions of birds from all colonies designated as SPAs,
203 in order to establish the extent, and intensity of usage, of the marine areas required by individuals
204 from these protected breeding locations.

205

206 **Materials and Methods**

207 ***Tracking data collection***

208 We carried out fieldwork at seabird colonies around the coast of Britain and Ireland during May-
209 July, 2010 – 2014, when the study species were either approaching the end of the incubation
210 period or raising small chicks. We stratified sampling effort to reflect the northwards bias in the
211 breeding distribution of seabirds in the region (Mitchell et al. 2004). We caught birds while they
212 attended their nests, either by hand or using a wire noose or crook fitted to a pole, and
213 temporarily attached a modified i-GotU GT-120 (Mobile Action Technology Inc., Taipei,
214 Taiwan) GPS logger to their backs (or rarely, in the case of kittiwakes, to their tails) with Tesa®
215 tape. Total instrument mass was $\leq 3\%$ body mass for all species, except kittiwakes, for which it
216 was $\leq 5\%$ body mass and $\leq 3\%$ if tail attachment was used. We programmed loggers to record
217 one position every 100 seconds. Handling time during capture/recapture was < 6 minutes. GPS
218 deployments were carried out following the ethical guidelines of the British Trust for
219 Ornithology, under license by Scottish Natural Heritage, Natural England, Natural Resources
220 Wales, the Northern Ireland Environment Agency and the National Parks and Wildlife Service,
221 Ireland.

222

223 ***Data preparation***

224 Diving by tagged seabirds can result in short hiatuses in tracking data. To estimate missing
225 locations, and to standardize sampling effort to exactly 100 s intervals, we resampled GPS tracks
226 data by linear interpolation prior to further analysis. Due to the need to deploy and retrieve
227 loggers at the nest, it is normal practice in tracking studies of breeding seabirds to record and
228 analyze bursts of data from one or more complete foraging trip per individual. However, this
229 usually results in individuals being observed for unequal amounts of time because trip duration

230 typically varies widely among individual seabirds. To reduce this bias we sub-sampled tracking
 231 data by randomly selecting a 24 h burst of locations from each bird (Table 1). We omitted the
 232 small number of individuals that were tracked for < 24 h from our analysis. We then selected
 233 locations recorded when birds were at sea, categorized according to distance and time from the
 234 nest (see Appendix 1 for details). Prior to analysis, we projected all spatial data in Lambert
 235 Azimuthal equal area (LAEA) coordinates.

236

237 ***Modelling approach***

238 We modeled habitat use as a function of habitat availability, accessibility and proxies of
 239 intraspecific competition. In view of the size of the dataset (55,000 – 210,000 locations per
 240 species), we fitted IPP models by numerical quadrature (Berman and Turner 1992, Baddeley and
 241 Turner 2000, Warton and Shepherd 2010) rather than approximating them using logistic
 242 regression (Aarts et al. 2012). Following Warton and Shepherd (2010), we modelled the intensity
 243 of tracking locations $\lambda(y_i)$ at the point i in space as a function of n explanatory variables:

244

$$245 \quad \log(\lambda_i) = \beta_0 + \sum_{j=1}^n c_{i,j} \beta_j, \quad (1)$$

246 where c is a vector of covariates and $\beta = (\beta_0, \beta_1, \dots, \beta_n)$ the corresponding parameters. The
 247 pseudo likelihood of IPP models can be estimated by numerical quadrature (Berman and Turner
 248 1992) as:

249

$$250 \quad l_{IPP}(\beta; y, y_0, w) \approx \sum_{i=1}^m w_i (s_i \log \lambda_i - \lambda_i), \quad (2)$$

251

252 where $y_0 = \{y_{n+1}, \dots, y_m\}$ are quadrature points (i.e. both data and dummy points),

253

254 $w = (w_1, \dots, w_m)$ is a vector of weights, $s_i = z_i/w_i$ and $z_i = \begin{cases} 1 & \text{if } y_i \text{ is a data point} \\ 0 & \text{if } y_i \text{ is a dummy point} \end{cases}$.

255

256 The right hand side of equation 2 is equivalent to the likelihood of a weighted log-linear Poisson

257 model, which can readily be estimated using conventional GLM software (Baddeley and Turner

258 2000). We assigned the centroids of the cells of a regular LAEA grid as dummy points, a

259 quadrature scheme that ensures even distribution across the study area (Warton and Shepherd

260 2010). We then assigned weights $w_i = a/n_i$ to each quadrature point, where n_i is the number of

261 points (data or dummy) in the same cell as the i th point and a is the area of that cell (Baddeley

262 and Turner 2000). Note that dummy points are not equivalent to the ‘pseudo-absence’ points

263 used in some case-control models fitted to tracking data (see Aarts et al. (2012)).

264

265 In order to account for the highest level of grouping in the tracking data (i.e. breeding colony) we

266 structured models as mixed-effects GLMs:

267

268 $\lambda_{k,i} \sim \text{Poisson}(\mu_{k,i}) \Rightarrow E(\lambda_{k,i}) \sim \mu_{k,i}$

269 $\log(\mu_{k,i}) = \text{offset}(n_k) + \beta_0 + \sum_{j=1}^m x_{i,j} \beta_j + u_k, \tag{3}$

270

271 Where $\lambda_{k,i}$ is the intensity of locations of birds from the k th colony and u_k is a random, colony-
272 level, intercept. The offset term is included to standardize model predictions because the number
273 of birds tracked n_k varied across colonies. Each bird was tracked for a period of 24 hours so the
274 response $\mu_{k,i}$ is the expected number of tracking locations at sea/bird/day/unit area from the k th
275 colony. Normalized to sum to unity over all grid cells this approximates the colony-level
276 utilization distribution UD_k . The inclusion of the colony-level random intercept necessitated a
277 separate set of dummy points for each colony: For the k th colony we therefore generated dummy
278 points and weights within the sea area accessible from each colony, which we define as that
279 lying $< d_{\max}$ from that colony, where d_{\max} is 1.1 x the maximum foraging range observed across
280 colonies in our study (shags 35 km, kittiwakes 300 km, murrees 340 km, razorbills 305 km). In
281 the absence of theoretical estimates of the maximum foraging ranges for our study species, we
282 used the maximum observed foraging range. We apply the multiplier 1.1 to ensure that the
283 quadrature grid encompasses the areas bounded by the putative maximum foraging range.
284 Models were fitted using the R package lme4 (Bates et al. 2015).
285
286 Warton and Shepherd (2010) show that the accuracy of the quadrature approximation method
287 described above increases as the ratio of dummy points to data increases. During model
288 development we investigated this effect by fitting single covariate models to datasets generated
289 using quadrature grids of varying resolutions. We found that, within the computationally
290 practicable range of scales, parameter estimates did not converge with increasingly finer scale
291 (Appendix 1: Fig. S1). Hence, following Warton and Shepherd (2010), we conducted our
292 analysis at the finest resolution practicable. This was 0.5 km for shags (55,436 tracking

293 locations; 150,557 dummy points) and 2 km for the other species (range 82,741 - 206,413
294 tracking locations; 417,578 - 806,384 dummy points

295

296 ***Model selection***

297 Eqn. 3 assumes independence among data (Baddeley and Turner 2000) yet animal tracking
298 locations are repeated measures on individuals and tend to be serially and spatially
299 autocorrelated (Aarts et al. 2008). Hence, the standard errors provided should be treated as
300 relative rather than absolute. The full likelihood of eqn. 3 is unknown, precluding the provision
301 of p values or model selection using conventional information criteria. Rather, we used k -folds
302 cross-validation to compare the out-of-sample predictive performance of models based on the
303 similarity between the observed and predicted utilization distributions (Fewster and Buckland
304 2001). To do so we calculated the observed UD of tracked birds from the k th colony (i.e. the
305 proportion of all locations of birds tracked from that colony falling in each cell in the regular
306 grids mentioned above). We then fitted the model under consideration to data from the remaining
307 colonies, predicted the UD of the k th colony from this model and calculated the Bhattacharyya
308 affinity between the observed and predicted UDs

309

$$310 \quad BA_k = \sum_{x,y} \sqrt{UD_{\text{obs},k}(x,y)UD_{\text{pred},k}(x,y)} \quad (4)$$

311

312 BA has previously been used in the contexts of UD comparison and model selection (Thacker et
313 al. 1997, Fieberg and Kochanny 2005). It ranges from 0 (no similarity) to 1 (identical UDs). We
314 calculated the weighted mean similarity across colonies:

315

316
$$\overline{BA} = \frac{\sum_{\text{All } k} n_k BA_k}{\sum_{\text{All } k} n_k}, \quad (5)$$

317

318 where n_k is the number of birds tracked from the k th colony. The contribution to \overline{BA} of colonies
 319 from which larger numbers of birds were tracked is upweighted because the UDs of colonies
 320 with small samples of tracked birds are likely to underestimate the area used by the entire colony
 321 (Soanes et al. 2013, Bogdanova et al. 2014).

322

323 In order to estimate space use from all colonies in the study area, we aimed to select the best
 324 model from a field of biologically plausible alternatives. Previous studies suggest that seabird
 325 space use may depend on numerous covariates, including colony distance, density-dependent
 326 competition and habitat (Wakefield et al. 2009, Wakefield et al. 2011). The number of plausible
 327 alternative models is therefore large. This, combined with the time taken for models to converge,
 328 precluded backwards model selection. Rather, we built usage models using a stepwise forwards
 329 selection procedure, adding candidate explanatory covariates to the intercept-only model in order
 330 of their expected effects sizes. We retained covariates if $\Delta \overline{BA}$ was positive, selecting the most
 331 parsimonious model if $\Delta \overline{BA}$ was tied. In order to compare effect sizes using standardized partial
 332 regression coefficients we standardized covariates prior to analysis (Schielzeth 2010).

333

334 ***Candidate explanatory covariates***

335 In the absence of other factors, central-place foraging theory suggests that breeding seabirds
 336 should seek prey as close to their nest sites as possible (Orians and Pearson 1979). Firstly,

337 therefore, we added distance to colony d to the model, with the expectation that usage would
338 decline with distance (Dukas and Edelman-Keshet 1998)(Matthiopoulos 2003). Our study
339 species generally avoid crossing extensive land barriers when commuting (Fig. 1) so we
340 defined $d_{k,i}$ to be the minimum distance by-sea between the k th breeding site and the i th
341 location, which we calculated on a 0.5 km (shags) or 1km (kittiwakes, murre and razorbills)
342 LAEA grid using the R package gdistance (van Etten 2012, Wakefield et al. 2013). Space use by
343 breeding seabirds is further modulated by density-dependent competition among sympatrically
344 breeding conspecifics (Wakefield et al. 2013, Jovani et al. 2015). Given that competition is
345 proportional to the density of animals we next considered whether the area of sea available to
346 birds from each breeding site, which varies with coastal geometry, affects usage (Birkhead and
347 Furness 1985). We hypothesize that density-dependent competition would be higher among birds
348 foraging from colonies with restricted access to the open sea such that they would forage further
349 from their colonies than birds from colonies surrounded by open water. To model this effect, we
350 considered the addition of $A_{k,i}$ the cumulative area at the i th location relative to the k th breeding
351 site, to our models, where:

$$352 \quad A_{k,i} = \sum_{\text{All } x} a_x \delta_{k,x}, \quad \delta_{k,x} = \begin{cases} 1 & \text{if } d_{k,x} \leq d_{k,i} \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

353
354 and a_x is the area of the x th cell of the LAEA grids mentioned above. Exploratory analysis
355 indicated that log-transforming A_k reduced colinearity with d_k , improving model stability.

356
357 We next considered the number of sympatric breeders, the other determinant of density at sea.
358 We extracted numbers of apparently occupied nests (AON) recorded during the most recent

359 complete census of seabird colonies in Britain and Ireland (Seabird 2000, carried out between
360 1998 and 2002; see Mitchell et al. (2004) for methods) from the Seabird Monitoring Programme
361 (SMP) Database www.jncc.gov.uk/smp. Defining seabird colonies objectively can be
362 problematic because the degree to which breeding seabird nests are clustered in space varies with
363 scale (Wakefield et al. 2014). During the Seabird 2000 census, AON were recorded by “subsite”
364 (for clarity, simply referred to as “sites” hereafter). These Mitchell et al. (2004) nominally
365 defined as segments of coastline <1 km long, containing clusters of breeding seabirds. However,
366 for practical reasons fieldworkers were allowed some scope to deviate from this definition. In
367 practice, sites sometimes therefore comprise isolated islands or segments of coastline >1 km
368 long. In the latter cases, we reassigned sites by splitting the coastline into the minimum possible
369 number of segments ≤ 1 km long, dividing AON equally between each. During model selection
370 we considered several potential proxies of competition from sympatric breeders: Firstly, the
371 number, N , of conspecific AONs at the home site. Secondly, because arbitrary census divisions
372 may not correspond to ecologically functional units (Wakefield et al. 2014) we considered
373 proxies that include conspecifics breeding in the vicinity of the home site of tracked birds. These
374 were the inverse-distance weighted number of breeding conspecifics:

375

$$376 \quad \theta = \sum_{\text{All } k} \frac{N_k}{d_{h,k} + 1}, \quad (7)$$

377

378 where N_k is the number of conspecific AON at the k th site of the set of all breeding sites
379 (including the home site) within the species’ maximum foraging range, and $d_{h,k}$ is the distance
380 from the home breeding site to the i th breeding site. Finally, based on exploratory analyses, we

381 also considered the square-roots of these indices, as well as (3) the inverse-distance weighted
382 square-root number of conspecific breeders:

383

$$384 \quad \theta' = \sum_{\text{All } k} \frac{\sqrt{N_k}}{d_{k,i} + 1}. \quad (8)$$

385

386 We considered each of the indices of sympatric competition as a main effect and interaction with
387 *A*, selecting that which resulted in the best improvement in model performance (step 3).

388

389 In addition to sympatric competition, breeding seabirds may be subject to competition from
390 conspecifics breeding at neighboring colonies (Furness and Birkhead 1984) (hereafter, parapatric
391 competition (Wakefield et al. 2011)). As with sympatric competition, this is thought to be
392 density-dependent (Wakefield et al. 2013). Our expectation is therefore that birds avoid locations
393 at which the null density of conspecifics from other colonies is high (Wakefield et al. 2011,
394 Catry et al. 2013, Wakefield et al. 2013). In some systems this leads to striking patterns of
395 among-colony spatial segregation (Masello et al. 2010, Wakefield et al. 2013). It has been
396 hypothesized that these are mediated by individual-level information transfer and cultural
397 divergence during colony growth (Wakefield et al. 2013). Current uncertainty about these
398 mechanisms makes this phenomenon difficult to model satisfactorily but as a first approximation
399 we considered whether birds avoided areas in which the null density of conspecifics from other
400 colonies was greater than that from their own (Catry et al. 2013). Taking the best models from
401 previous steps (hereafter models I-IV for shags, kittiwakes, murre and razorbills respectively),

402 we predicted $\rho_{h,i}$, the ratio of the expected intensity of locations $\lambda_{h,i}$ from the focal breeding site
403 h to the sum of those from all other sites in the region:

404

$$405 \quad \rho_{h,i} = \frac{\lambda_{h,i} N_h}{\sum_{k \neq h} \lambda_{k,i} N_k}, \quad (9)$$

406

407 We then determined whether adding this covariate to the usage models improved their
408 performance.

409

410 We next considered whether the addition of environmental indices describing habitat improved
411 model performance (Wakefield et al. 2009). We identified candidate biophysical covariates
412 meeting two criteria: Firstly, that data coverage was sufficient to allow seabird distributions to be
413 estimated throughout the waters of Britain and Ireland; and secondly, that previous studies had
414 established links between the covariate (or the phenomenon it quantifies) and the foraging
415 behavior or distribution of the study species or their prey. As noted above, each model level
416 requires a separate set of quadrature points. Hence, although we considered both static and
417 dynamic covariates, we averaged monthly mean dynamic covariates over the study period (May-
418 July, 2010 – 2014; Appendix 1: Fig. S2) to maintain the number of data, and thereby computing
419 time, within tractable limits. We then determined the value of environmental covariates at each
420 quadrature point. We considered (1) depth (ETOPO2 Global Relief 2v2, provided by the U.S.
421 Department of Commerce, National Oceanic and Atmospheric Administration, National
422 Geophysical Data Center, 2006); (2) seabed slope, calculated from the latter in ArcGIS 10; (3)
423 minimum distance to the coast, calculated in ArcGIS 10; (4) the proportion of gravel and (5) the

424 ratio of sand to mud in seabed sediments, derived from British Geological Survey 1:250,000
425 maps downloaded from <http://digimap.edina.ac.uk> (see Appendix 1); (6) the potential energy
426 anomaly (PEA), which quantifies the intensity of thermohaline stratification and (7) the
427 proportion of time during which the water column was stratified, both estimated using UK Met
428 Office FOAM AMM reanalysis data downloaded from <http://marine.copernicus.eu/> (see
429 Appendix 1); (8) AVHRR sea surface temperature (SST), supplied by the Natural Environment
430 Research Council Earth Observation Data Acquisition and Analysis Service (NEODAAS); (9)
431 standardized sea surface temperature (sSST), calculated on a monthly basis by subtracting the
432 mean SST in the study area and dividing by its standard deviation, which is an alternative index
433 of stratification (Wakefield et al. 2015); (10) thermal front gradient density (TFGD), estimated
434 following (Scales et al. 2014) using AVHRR SST to provide an index of the mean intensity and
435 persistence of thermal fronts (Miller and Christodoulou 2014); and (11) net primary production
436 (NPP) estimated and supplied by NEODAAS using MODIS chlorophyll and photosynthetically
437 available radiation data. For further details of candidate covariates and our rationale for their
438 consideration see Appendix 1: Table S2 and reviews by (Hunt 1997, Mann and Lazier 2006 and
439 Wakefield et al. 2009). In brief, the phenomena described by these covariates may affect our
440 study species' distributions either by modulating lower trophic level production (depth, seabed
441 slope, indices of stratification, SST, TFGD, NPP (Begg and Reid 1997, Mann and Lazier 2006,
442 Scott et al. 2010, Carroll et al. 2015)); by physically aggregating prey (indices of stratification,
443 TFGD and indirectly SST and depth) (Lefevre 1986, Begg and Reid 1997, Mann and Lazier
444 2006, Embling et al. 2012); or due to the habitat preference of prey species, especially
445 Ammodytidae and Clupeidae (depth, coast distance, sediment, indices of stratification
446 (Whitehead 1986, Holland et al. 2005, van der Kooij et al. 2008)).

447
448 In order to establish in what order to add environmental covariates to models, we first
449 determined the improvement in performance afforded by adding each singly to the best model
450 resulting from the previous steps. Based on previous work (Wakefield et al. 2011, Wakefield et
451 al. 2015) and exploratory analyses we considered log and square-root transformations of some
452 covariates (Appendix 1: Table S2). In order to model potential variation in habitat selection in
453 response to among-colony variability in habitat availability, we also considered interactions
454 between each covariate and its expected value at each colony. This we define as the covariate's
455 mean (hereafter denoted by an overbar) in waters accessible from that colony (i.e. the sea area
456 within d_{\max}). This partially implements the GFR model proposed by Matthiopoulos et al. (2011).
457 The full GFR model, in which variables interact not only with their own colony-level
458 expectations but those of all other environmental covariates, proved computationally unfeasible
459 with our dataset (see Appendix 1). We ranked environmental covariates in order of $\Delta \overline{BA}$
460 afforded by the addition of each covariate (transformed or otherwise) and its GFR equivalent.
461 We then added these terms sequentially to the model, retaining them if $\Delta \overline{BA}$ was positive (step
462 5). If two covariates were considered proxies of the same phenomenon (e.g. stratification) or
463 were otherwise colinear, we considered only that ranked highest. Finally, because relationships
464 between space use and environmental covariates may be non-linear, we also considered their
465 second degree polynomials, retaining them if their addition resulted in an increase in $\Delta \overline{BA}$ (step
466 6).

467

468 *Estimating usage*

469 For each species, we estimated λ and thereby the UD for birds from each Seabird 2000 site s
470 using the fixed-effects part of the best models (hereafter models V-VIII for shags, kittiwakes,
471 murrees and razorbills respectively). We then calculated the population-level UD across the study
472 area:

$$474 \quad UD_{P,i} = \sum_{\text{All } x} UD_{s,x} N_s \quad , \quad (10)$$

475
476 where N_s is the number of AON at the s th site. Notwithstanding the comments on standard errors
477 above, we quantified spatial variation in the relative uncertainty of our model estimates by
478 plotting the coefficient of variation (CV) of UD_p , which we calculated using parametric re-
479 sampling adapted from (Bolker 2008) and (Lande et al. 2003). Assuming that the sampling
480 distribution of $\hat{\beta}$ is multivariate normal, we generated 100 random sets of fixed-effects
481 parameters for each model, predicted the UD_p using each set of parameters and then calculated
482 its CV.

483
484 In order to illustrate how one might use these UDs to identify marine areas whose statutory
485 protection would facilitate the functional protection of the existing suite of colony SPAs,
486 following eqn. 10, we also calculated the mean UD of birds breeding at sites within each UK
487 SPA. We identified breeding sites falling within existing colony SPAs using boundaries
488 downloaded from <http://jncc.defra.gov.uk/ProtectedSites/> (accessed 24 April 2015). For each
489 SPA we then determined polygons encompassing the core 50, 75 and 90% of estimated usage as
490 well as the maximum curvature boundaries (MCBs, see Appendix 1). Whilst MCBs have no

491 ecological basis (Perrow et al. 2015), it has been suggested that they balance the proportion of a
492 population protected against the extent of the protected area and have been used by statutory
493 bodies to define boundaries for delimiting avian marine protected areas in UK (O'Brien et al.
494 2012). We then overlaid percentage UDs and MCBs of all species in order to estimate the overall
495 extent of sea area thus encompassed.

496

497 **Results**

498 *Seabird tracking*

499 We tracked 1313 birds from 29 colonies for a median of 2-3 days/bird (Fig. 1, Table 1, Appendix
500 2: Table S1). Following re-sampling to standardize the observation period to 24 h/bird, data from
501 80 % of kittiwakes and 93 – 96% of the remaining species were retained for analysis, totaling
502 1153 individuals. Full data are available for download from the BirdLife Seabird Tracking
503 Database <http://www.seabirdtracking.org>. The duration of deployment was set by the need to
504 recapture birds before tags became detached from feathers. Recapture was attempted after 24h
505 (kittiwake, where the mantle feathers are relatively weak) to 48h (other species). Median
506 foraging trip length was <24 h in all species (Table 1) so the 24 h observation window generally
507 spanned >1 trip/individual. Differences in foraging ranges were marked among species (Fig. 1):
508 Shags remained relatively close to their nest sites (median 3.4 km, IQR 1.6 - 7.5), whereas
509 kittiwakes (11.9 km, IQR 4.2 - 30.9), murrelets (10.5 km, IQR 3.2 - 19.1) and razorbills (13.2 km,
510 IQR 5.1 - 26.2) travelled further from their colonies during foraging trips.

511

512 *Explanatory covariates*

513 The addition of distance to colony d improved the performance of usage models for all species
514 (Appendix 2: Tables S2 and S3) and its effect, which was negative, was relatively large (Table
515 2). The addition of A (the cumulative area at d), interacting with indices of sympatric
516 competition, further improved model performance (Appendix 2: Table S3). In the case of
517 razorbills, square-root of the number of breeding pairs in the home site was the best index of
518 sympatric competition. For the other species, competition indices based on the summation of
519 numbers of breeders inversely weighted by distance from the focal breeding site best improved
520 model performance (Appendix 2: Table S2). Models I-IV suggest that in all species the rate of
521 decline in usage with A lessens with increasing sympatric competition (Table 2, Appendix 2:
522 Tables S2 and S3, Fig. S1). The inclusion of relative parapatric competition improved the
523 performance of kittiwake and murre usage models but not those of shags and razorbills
524 (Appendix 2: Table S2). The former species tended to avoid areas in which the potential density
525 of conspecifics from other colonies was higher than that from their own colony. The addition of
526 environmental covariates improved the performance of all models (cf. Fig. 2 and Appendix 2:
527 Fig. S3) and conditioning some but not all covariates on their regional means improved
528 performance further (Appendix 2: Table S4). Cross-validation shows that the final models for
529 shags, kittiwakes and murre all performed similarly well ($\overline{BA} \pm sd = 0.52 \pm 0.13, 0.53 \pm 0.13$
530 and 0.53 ± 0.22 respectively) but the performance of the razorbill model was somewhat poorer (
531 $\overline{BA} \pm sd = 0.34 \pm 0.11$). Spatial plots confirm our expectation that the similarity between
532 observed and predicted utilization distributions was greatest for colonies from where more birds
533 were tracked (Appendix 2: Fig. S3).

534

535 The effects of many environmental covariates were comparable in magnitude to those of colony
536 distance, cumulative area and competition (Table 2). Taking the environmental covariates
537 retained during model selection in order of their effect sizes, these suggest that shags tend to use
538 relatively mixed waters (i.e. low PEA) close to the coast. In areas where gravel is scarce, they
539 use relatively gravelly substrates but this is reversed in more gravelly areas (Appendix 2: Fig.
540 S5). Shags' usage with respect to SST was quadratic, with a tendency to visit areas where SST
541 was either warmer or cooler than the average (Table 2, Appendix 2: Fig. S5). Shags also
542 manifested a weak preference for areas of high NPP. Usage by kittiwakes with respect to seabed
543 slope and stratification was complex: In areas where the mean seabed slope was low they tended
544 to avoid steep bathymetric relief but this preference was reversed somewhat in areas where the
545 mean slope was high (Appendix 2: Fig. S5). Similarly, in areas where the mean occurrence of
546 stratification was low kittiwakes avoided stratified waters, whereas in more frequently stratified
547 areas they tended to avoid mixed waters.

548

549 In areas with low regional mean coastal distance (i.e. archipelagos) murre used areas close to
550 the coast, whereas in areas with less complex coastlines they tended to forage further from land
551 (Table 2, Appendix 2: Fig. S5). In regions with a relatively high proportion of sand in the
552 substrate murre preferred sandy areas but this preference reversed in less sandy regions. Murre
553 also showed a weak preference for frontal regions and substrates containing a relatively low
554 proportion of gravel (Table 2). Razorbills used areas with higher SSTs in regions with relatively
555 cool surface waters, whereas in warmer regions the opposite was true (Appendix 2: Fig. S5). In
556 regions with relatively low seabed relief they tended to select areas with steep relief and vice

557 versa. Razorbills' habitat preference with respect to the sand:mud ratio of the substrate was
558 quadratic, peaking just below intermediate values (Appendix 2: Fig. S5).

559

560 *Estimated population-level distributions*

561 Raster files of space use during late incubation and early chick-rearing from all of the region's
562 colonies estimated using models V-VIII are available for download from the Data Archive for
563 Marine Species and Habitats DASSH (www.dassh.ac.uk). Composite usage maps predict that
564 breeding shags, kittiwakes, murre and razorbills forage mainly within 100 km of the coast of
565 Scotland, primarily to the north and east of the mainland in the North Sea, and around the
566 Northern Isles (Fig. 3a, Appendix 2: Fig. S7). For all species, 90% of the UK regional
567 population's UDs also included waters in the southern North Sea; Dublin Bay and the North
568 Channel of the Irish Sea; as well as waters surrounding Islay; the northern Minch; and isolated
569 islands northwest of Scotland (Appendix 2: Fig. S7). The estimated distributions of shags, which
570 is the least wide-ranging of the study species, largely reflects that of its colonies (cf. Fig 1. and
571 Fig. 2). In contrast, that of kittiwakes is more pelagic, with activity more patchily distributed
572 offshore (Fig. 2). In addition to core areas mentioned above, usage hotspots included a large area
573 southeast of Flamborough Head and the northern Norfolk Banks; the central Irish Sea; and
574 Galway Bay, west of Ireland. Of the two auks, our models suggest that murre forage closer on
575 average to their colonies (Fig. 2), outnumbering razorbills in many coastal areas and in the
576 vicinity of the Celtic Sea front. In contrast, razorbills predominate in the North Channel and
577 much of the Minch (Appendix 2: Fig. S8).

578

579 **Discussion**

580 Several recent studies have assimilated tracking data from multiple colonies in order to map and
581 understand seabirds distributions (BirdLife-International 2004, Block et al. 2011, Wakefield et
582 al. 2011, Ramos et al. 2013, Wakefield et al. 2013). However, this is the first to model how
583 colony-level distributions vary due to the combined effects of sympatric and parapatric
584 conspecific interactions, coastal geomorphology, and regional habitat availability. By tracking
585 and modelling the space use of shags, kittiwakes, murrelets and razorbills from a sample of
586 colonies around Britain and Ireland, we estimated the coarse-scale (10s of km) distribution of
587 these species at sea from all of colonies in the region. Moreover, by combining these results, we
588 were able to map the at-sea distribution of each species' breeding population across a study area
589 extending over ~1.5 million km² (Fig. 2). Until recently, it was only practicable to attempt to
590 estimate the distributions of seabirds over such wide areas at comparable resolutions by
591 surveying birds from boats or planes (Stone et al. 1995, Bradbury et al. 2014). However, these
592 methods generally fail to discriminate among birds from different colonies or life history stages
593 (e.g. breeders vs. non-breeders). Our results therefore provide unprecedented insights into marine
594 distributions of breeding seabirds.

595

596 We modelled the occurrence of tracking locations as an inhomogeneous Poisson point (IPP)
597 process (Cressie 1993), which is a computationally efficient and, it has been argued, natural
598 method of treating presence-only data (Warton and Shepherd 2010, Aarts et al. 2012, Renner et
599 al. 2015). We discuss our approach in more detail in Appendices 1 and 3. However, it is
600 pertinent to highlight two caveats on our results: Firstly, due to the large volume of data involved
601 in our analysis only relatively simple models were computationally tractable and therefore not all
602 correlation structures inherent to the data (e.g. serial autocorrelation within individuals (Aarts et

603 al. 2008)) were modelled. Hence, although we presume that our parameter and usage estimates
604 are unbiased their associated uncertainty is likely to be underestimated. Secondly, the likelihood
605 estimation technique we used is approximate (Berman and Turner 1992). We therefore opted to
606 select among models by k -folds cross validation, rather than using penalized information criteria,
607 such as AIC. k -folds cross validation is robust to over-fitting when the number of data is large,
608 and the field of candidate models relatively small (Arlot 2010). However, our models are
609 optimized for prediction, rather than parsimony, so the biological inferences drawn from them
610 below are tentative.

611

612 *Distribution with respect to colony distance and competition*

613 Space use by all four study species declined with distance from the colony (Table 2), supporting
614 the hypothesis that central-place foragers minimize distance-dependent travel costs (Orians and
615 Pearson 1979). Our results also support the hypothesis that colonial central-place foragers seek to
616 minimize density-dependent intra-specific competition (Ashmole 1963, Lewis et al. 2001,
617 Wakefield et al. 2013): in all species the rate of decline in usage with cumulative area at distance
618 decreased as the number of sympatrically breeding conspecifics increased (Appendix 2: Table
619 S3, Fig. S1). Although this echoes the observation that foraging range is positively dependent on
620 colony size in many seabirds (Lewis et al. 2001, Wakefield et al. 2013), it also demonstrates that
621 conspecific density is dependent not only upon numbers of birds but the availability of suitable
622 habitat (most simply, open sea). In short, models V-VIII show that birds foraging from a colony
623 with limited access to the sea (e.g. those located in inlets) travel further on average than those
624 from a colonies of the same size surrounded by open water (i.e. on isolated islands; Appendix 2:
625 Figs. S4, S5). For the purposes of our analysis we recognized that colonies as defined in the

626 Seabird 2000 census (Mitchell et al. 2004) might not correspond to functional units. Our results
627 suggest that in all species except razorbills that this is indeed the case (Appendix 2: Table 2). For
628 the other three species, we found that sympatric competition was better quantified by the sum of
629 the inverse distance-weighted number of conspecifics breeding in the area. We hypothesize that
630 this is because the intensity of potential competition from any one conspecific declines as a
631 function of distance to its nest.

632

633 It has been hypothesized that seabirds foraging from adjacent colonies segregate in space if
634 potential density of competing conspecifics is high (Wakefield et al. 2013). Segregation among
635 the UD's of colonies has been observed in several species (Masello et al. 2010, Wakefield et al.
636 2013) but evidence for this phenomenon in our system was mixed: in accordance with the
637 density-dependence hypothesis (Wakefield et al. 2013), kittiwakes and murrelets avoided the areas
638 at which the null ratio of the density of birds from the home colony to those from other colonies
639 was low but shags and razorbills did not. Among-colony segregation is also evident in kittiwakes
640 populations geographically disparate from the UK (Ainley et al. 2003, Paredes et al. 2012) and
641 may therefore be widespread in this species but this is the first time that the phenomenon has
642 been reported in murrelets. Given the close taxonomic and functional affinities between razorbills
643 and the latter species it is perhaps surprising that terms describing among-colony segregation
644 were not retained during model selection for razorbills. This may be because a relatively large
645 proportion (48 %) of the razorbills in our study were tracked from the Northern Isles (Fig. 1,
646 Appendix 2: Table S1), where populations of this and other seabird species have been in decline
647 for the past decade (JNCC 2014) due to declines in forage fish availability (Cook et al. 2014).
648 Razorbills from this region travelled much further (median range 62.7 km, IQR 39-87) than those

649 from other areas (median 20 km, IQR 11-28), possibly due to local food shortages. It is
650 hypothesized that patterns of spatial segregation are, in part, culturally perpetuated via
651 information transfer among conspecifics (Wakefield et al. 2013). If so they may become unstable
652 in a declining population. The apparent lack of spatial segregation among shags from different
653 breeding sites is notable given that this phenomenon occurs in several other members of the
654 Phalacrocoracidae, such as *Phalacrocorax atriceps*, *P. magellanicus* and *P. georgianus* (Wanless
655 and Harris 1993, Sapoznikow and Quintana 2003). However, in comparison to these species
656 European shags breed in relatively dispersed colonies throughout much of their range in Britain
657 and Ireland so density-dependent competition among breeding aggregations may be insufficient
658 to cause segregation of foraging areas. This could be viewed as an extreme form of segregation,
659 where inter-colony spacing generally exceeds the species' maximum foraging range.

660 Additionally, in Britain and Ireland shag colonies tend to be small, further reducing inter-colony
661 competition. For example, in the Isles of Scilly, where shags breed at very low densities, birds
662 from different breeding sites forage in common areas (Evans et al. 2015), as suggested by model
663 V (Appendix Fig. S3). Notwithstanding these comments it is possible that our analysis could not
664 detect among-colony foraging segregation in razorbills and shags, for two reasons: Firstly, we
665 were unable to track these species from multiple large and closely adjacent breeding sites, where
666 theory suggests segregation is most likely to occur (Wakefield et al. 2013). Secondly, the census
667 data we used to estimate intraspecific competition was collected 8-16 years before our tracking
668 campaign. Populations of all species in our study are in a state of flux: over the past 15 years
669 shags have declined by ~ 30 % throughout the region, while razorbill have declined in the
670 Northern Isles (JNCC 2015). Further tracking from pairs of large, closely adjacent and recently

671 censused colonies would be required to conclusively establish the degree to which spatial
672 segregation occurs among colonies of shags and razorbills.

673

674 In modelling competition, we made the assumption that seabirds avoid areas of high conspecific
675 density. This is consistent established foraging theories (the ideal free distribution, optimal
676 foraging, etc.) and is supported by empirical evidence at scales of 10s of km and above (Ford et
677 al. 2007, Wakefield et al. 2013). However, at finer scales, local enhancement (when individuals
678 searching for prey are attracted to feeding conspecifics) may cause seabirds to cluster (Fauchald
679 2009). In our modelling framework, this would manifest as unexplained spatial autocorrelation.
680 Similarly, memory-based foraging or site fidelity, which cause individuals to return repeatedly to
681 the same area (Irons 1998, Wakefield et al. 2015), would result in unexplained temporal, as well
682 as, spatial autocorrelation within individuals. Techniques have been developed for modelling
683 some of these sources of autocorrelation (Marzluff et al. 2004, Aarts et al. 2008, Johnson et al.
684 2013) but as far as we are aware, no study on a colonial central-place forager to date has been
685 able to model all of these correlation structures simultaneously. This is not only because of the
686 complexity of the task but because the underlying mechanisms are still poorly understood.
687 Conversely however, modelling these dependencies in a hierarchical framework would provide
688 important insights into the foraging strategies employed by seabirds and similar taxa. Recent
689 methodological advances, especially in Integrated Nested Laplace Approximation, may soon
690 make this possible and we look forward to further development of these techniques (Blangiardo
691 et al. 2013).

692

693 *Distribution with respect to habitat*

694 Our principal aim was to estimate usage at sea, irrespective of behavior. Had we modelled
695 foraging locations only, stronger associations than we report might be expected between habitat
696 and distribution (Wakefield et al. 2009). Similarly, considering time-averaged environmental
697 covariates, though expedient, may have reduced the ability of our models to resolve dynamic
698 environmental drivers of distribution if seabirds closely track spatiotemporally unpredictable
699 prey. However, there is increasing evidence that at the coarse scale, temperate neritic seabirds
700 forage in individually consistent locations, both within and across breeding years (Irons 1998,
701 Weimerskirch 2007, Woo et al. 2008, Wakefield et al. 2015). This may be because shelf sea
702 oceanography is predictably structured by seasonal insolation and tidal stirring (Simpson et al.
703 1978), suggesting that time-averaged environmental covariates may be reasonable proxies for
704 prey distribution.

705

706 The effects of habitat on spatial usage in our models were comparable in magnitude to those of
707 foraging costs and competition (Table 2). Moreover, the habitat preferences indicated by models
708 V-VIII accord with current understanding of the foraging ecology of the study species. For
709 example, covariates describing substrate were retained only in models of habitat use for the three
710 diving species (shags, murres and razorbills). Shags and murres forage both at or near the seabed
711 and in the water column so substrate type may affect prey availability directly (Watanuki et al.
712 2008, Thaxter et al. 2010). Razorbills forage at shallower depths but in common with all species
713 in the study, prey primarily on sandeels, whose distribution varies with sediment coarseness and
714 silt content (Wright et al. 2000, Holland et al. 2005). Previous studies suggest that sympatrically
715 breeding razorbills and murres, which are closely related, do not segregate in space (Thaxter et
716 al. 2010, Linnebjerg et al. 2013). However, our results suggest some landscape scale niche

717 partitioning: murrens outnumber razorbills in inshore waters of the North Sea, the Northern Isles
718 and the Irish Sea, whereas razorbills predominate in the Western Isles. Notably, our models also
719 suggest a preponderance of murrens in the vicinity of the Celtic Sea front, which may reflect
720 divergent foraging adaptations in these species (Appendix 2: Fig. S8).

721

722 Covariates best describing the distribution of kittiwakes, which are obligate surface feeders,
723 either described properties of the water column (stratification and relative sSST) or the
724 morphology of the seabed (slope), which affects turbulent mixing. Presumably, these covariates
725 were retained because they describe physical mechanisms that affect prey availability indirectly,
726 either by enhancing production at lower trophic levels (e.g. tidal stirring resupplies nutrients to
727 the photic zone (Scott et al. 2010, Carroll et al. 2015)) or by advecting prey to the surface
728 (Embling et al. 2012, Cox et al. 2013).

729

730 Species distribution models fitted to data collected in one area may predict usage poorly in
731 another where habitat availability differs. To account for this effect we considered models in
732 which the response of birds to candidate environmental covariates was conditioned on their
733 regional means (i.e. a partial implementation of a Generalized Functional Response (GFR) to
734 resource availability (Matthiopoulos et al. 2011)). GFRs with respect to some but not all
735 covariates improved model performance, indicating that seabirds responded non-linearly to
736 changes in the availability of some environmental covariates. This is perhaps unsurprising, given
737 the oceanographically complex nature of the study area (Appendix 1: Fig. S2). For example,
738 murrens tend to forage far from the coast in areas where the mean distance to the coast was high,
739 such as the North Sea, which has a relatively simple geometry. In areas where the mean distance

740 to the coast was low, such as the geometrically complex Northern and Western Isles, this
741 relationship was reversed (Table 2; Appendix 2: Fig. S5). Presumably, this reflects differences in
742 the dominant physical drivers of prey distribution or the type of prey available to murres in these
743 areas.

744

745 *Conservation implications*

746 For conservation measures to be effective they must be evidence-based so there is an urgent need
747 to map the distributions of seabirds at sea and to understand how these are shaped by intrinsic
748 and extrinsic factors (Lewison et al. 2012). We estimated seabird distribution using data on the
749 size and location of all known colonies in Britain and Ireland. However, missing substrate data
750 meant that we did not estimate usage by shags, murres and razorbills outside the UK Exclusive
751 Economic Zone (EEZ) or for parts of the Northern and Western Isles (Fig. 2). Moreover, we did
752 not have access to contemporaneous data on conspecific colonies in countries bordering the
753 study area. Although these may interact with colonies in Britain and Ireland, their relatively
754 small size and large distance from Britain and Ireland suggest that any density-dependent
755 competition from these colonies is likely to be negligible. Notwithstanding these caveats, the
756 performance of our time-invariant models suggest that the factors determining the marine
757 distribution of breeding seabirds in Britain and Ireland are sufficiently consistent across time to
758 permit reliable estimation of area usage from biotelemetry, environmental covariates and central-
759 place foraging theory, which has important consequences for identification of priority areas for
760 conservation measures. To date, potential offshore SPAs for European seabirds have been
761 identified largely using at-sea transect survey data (Skov et al. 1995, Kober et al. 2012) and
762 progress to designate protected areas has been slow (BirdLife International 2010). Moreover,

763 because it is impossible to derive colony-specific distribution estimates from at-sea observations,
764 tracking is increasingly used to obtain the colony-level seabird distributions (Wakefield et al.
765 2011, Raymond et al. 2015) that are required for the assessment of impacts of marine industries
766 on protected breeding colonies. Unfortunately, it is neither practicable to track widespread
767 species from all their colonies, nor clear how usage can be interpolated from surveyed to
768 unsurveyed colonies (Aarts et al. 2008, Matthiopoulos et al. 2011, Torres et al. 2015). Thaxter et
769 al. (Thaxter et al. 2012) suggested that until better information becomes available, a pragmatic
770 approach (the ‘radius’ method) is to assume that seabirds are distributed uniformly out to some
771 putative maximum range from their colonies. However, as our analysis and others confirm (e.g.
772 Wakefield et al. 2011, Catry et al. 2013, Wakefield et al. 2013, Dean et al. 2015), seabird density
773 declines with distance from the colony. Moreover, density-dependent competition, coastal
774 morphology and habitat preference result in highly non-uniform distributions. We show that
775 these effects can be estimated by tracking birds from a sample of colonies and fitting IPP
776 models, structured as partial GFRs (Matthiopoulos et al. 2011), to the resulting data. The ability
777 of these models to estimate seabird distributions at un-sampled colonies is a major innovation.
778 Moreover, an advantage of IPP models over the logistic presence/pseudo-absence models latterly
779 applied to tracking data is their interpretability (Aarts et al. 2012, Renner et al. 2015). Our
780 models predict “occurrences at sea per day per individual” (i.e. incorporating information on
781 both activity budget and space use), which is directly proportional to the average amount of time
782 birds are expected to spend at a location and therefore of direct utility to conservation managers.
783 The areas of intensive usage we identified, especially those used by birds from SPA breeding
784 colonies, may warrant consideration for statutory protection following the principles recently
785 outlined by Wilson et al. (2014). Moreover, the provision of colony-level predictions allows the

786 potential impacts of anthropogenic and natural processes to be apportioned to specific colonies
787 much more accurately than is possible using the radius method. This will be of particular
788 importance in assessing potential impacts from offshore wind turbines, which are projected to
789 increase ten-fold in European shelf seas in the next decade, with the majority being constructed
790 in UK waters (Infield 2013). Current assessments of the potential displacement and collision
791 impacts, both at individual windfarm and region-wide level, rely either on data from boat or
792 aerial surveys (Furness et al. 2013, Maclean et al. 2013), tracking from very few colonies
793 (Perrow et al. 2006) or the radius method (Thaxter et al. 2012, Bradbury et al. 2014). As such,
794 potential impacts cannot be reliably apportioned to breeding colonies, hampering attempts
795 predict their demographic consequences (Bailey et al. 2014). Similarly, the impacts of oil
796 pollution and bycatch may be highly localized (Williams et al. 1995, Žydelis et al. 2013) so
797 colony-level distribution estimates will facilitate spatial planning decisions that more effectively
798 balance seabird conservation with competing interests, by linking marine aggregations of
799 seabirds to specific colonies. The methods presented here demonstrate the utility of tracking data
800 to estimate seabird distribution at national scales and further data are now required to allow the
801 application of this modelling approach to other breeding seabird species. Moreover, by
802 combining our results across species, potential areas of high conservation priority are revealed
803 (Figs. 3, Appendix 2: Fig. S7). It is clear that within Britain and Ireland the core areas of usage
804 of all four study species overlap within most of the coastal waters in Scotland. Areas of high
805 multi-species usage may warrant particular attention, since both the vulnerability to threats and
806 the potential benefits of conservation measures, are likely to be highest there. The regions
807 identified as supporting the core 90% UD of at least three of the species considered here
808 (Appendix 2: Fig. S7(b)) correspond well to those areas identified as of greatest international

809 importance for 30 seabird species in the North Sea across all seasons (Skov et al. 1995),
810 indicating the likely importance of these areas for a broad range of avian taxa.
811
812 Inclusion of density-dependent competition in our models increased their predictive
813 performance. However, this improvement over previous similar analyses (Wakefield et al. 2011,
814 Raymond et al. 2015) was only possible because the sizes of most seabird colonies in Britain and
815 Ireland are known (Mitchell et al. 2004). In contrast, seabird colonies in many regions have not
816 been censused (Croxall et al. 2012). Obtaining accurate estimates of colony size should be a
817 priority for wildlife managers intending to use tracking data to estimate the distribution of
818 seabirds from unsampled colonies. Moreover, our results suggest that distribution will change if
819 colony sizes alter. Updating colony counts periodically would allow model-based distribution
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821

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844

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1175

1176 **Table 1.** Summary of tracking data obtained during the study (see Appendix 2: Table S1 for full
 1177 details)

Species	No. sites	No. birds tracked	No. birds tracked ≥ 24 h	Median tracking duration, h (IQR)	Median trip length, h (IQR)
Shag	13	239	230	75 (55-94)	1.7 (1.0 – 2.6)
Kittiwake	20	583	464	42 (25-51)	4.0 (1.6 – 8.7)
Murre	12	192	178	54 (45-74)	7.5 (2.0 – 13.1)
Razorbill	14	299	281	70 (50-86)	6.3 (1.8 – 12.6)

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1180 **Table 2.** Summary of fixed effects in inhomogeneous Poisson point process models of the
 1181 density of seabird tracking locations as functions of colony distance, coastal geometry, intra-
 1182 specific competition and habitat.

Model (sites, birds)	Covariate [†]	Estimate	SE [‡]	z
V. Shag (13, 230)	Intercept	-6.092	0.240	-25.43
	d	-1.254	0.018	-71.52
	$\log(A)$	-1.239	0.010	-128.17
	θ'	0.353	0.250	1.41
	gravel	0.512	0.012	41.92
	$\overline{\text{gravel}}$	-0.112	0.355	-0.32
	$\sqrt{\text{PEA}}$	-1.613	0.028	-58.64
	NPP	0.048	0.011	4.22
	coast distance	-1.187	0.034	-35.28
	SST	0.797	0.046	17.37
	SST^2	0.474	0.026	18.14
	$\log(A) * \theta'$	0.110	0.005	23.02
	$\text{gravel} * \overline{\text{gravel}}$	-0.627	0.020	-30.78
VI. Kittiwake (20, 464)	Intercept	-6.375	0.175	-36.39
	d	-1.338	0.010	-140.65
	$\log(A)$	-0.486	0.005	-91.12
	θ	-0.388	0.189	-2.06
	$\log(\rho)$	1.669	0.014	118.75
	$\log(\text{seabed slope})$	-0.019	0.005	-4.15
	$\overline{\log(\text{seabed slope})}$	-1.381	0.261	-5.29
	$(\log(\text{seabed slope}))^2$	-0.161	0.003	-57.53
	sSST	-1.006	0.007	-143.32
	stratification	0.033	0.004	9.21
	$\overline{\text{stratification}}$	0.969	0.308	3.15
	$\log(A) * \theta$	0.167	0.004	46.31

	$\log(\text{seabed slope}) * \overline{\log(\text{seabed slope})}$	0.979	0.009	104.99
	$\text{stratification} * \overline{\text{stratification}}$	0.942	0.011	87.33
VII. Murre (12, 178)	Intercept	-7.294	0.177	-41.19
	d	-1.627	0.028	-57.56
	$\log(A)$	-0.862	0.007	-124.54
	$\sqrt{\theta}$	0.206	0.171	1.21
	$\log(\rho)$	0.929	0.029	32.07
	gravel	-0.223	0.005	-46.71
	$\sqrt{\text{sand : mud}}$	-0.184	0.011	-16.42
	$(\sqrt{\text{sand : mud}})^2$	-0.196	0.010	-18.80
	$\overline{\sqrt{\text{sand : mud}}}$	-2.037	0.543	-3.75
	TFGD	0.331	0.004	77.63
	coast distance	-1.709	0.032	-53.81
	$\overline{\text{coast distance}}$	3.098	0.370	8.38
	$\log(A) * \sqrt{\theta}$	0.273	0.005	54.23
	$\sqrt{\text{sand : mud}} * \overline{\sqrt{\text{sand : mud}}}$	-0.481	0.034	-14.16
	$\text{coast distance} * \overline{\text{coast distance}}$	1.760	0.057	30.68
VIII. Razorbill (14, 281)	Intercept	-4.623	0.105	-43.84
	d	-1.066	0.009	-119.85
	$\log(A)$	-1.106	0.004	-255.08
	\sqrt{N}	0.552	0.106	5.23
	SST	-0.083	0.008	-10.60
	$\overline{\text{SST}}$	0.336	0.130	2.58
	sand:mud	-0.290	0.006	-47.53
	$(\text{sand:mud})^2$	-0.266	0.005	-53.46
	$\log(\text{seabed slope})$	0.027	0.005	5.30
	$\overline{\log(\text{seabed slope})}$	-0.306	0.221	-1.38
	$\log(A) * \sqrt{N}$	0.331	0.003	123.37

SST * $\overline{\text{SST}}$	-0.882	0.010	-90.40
$\log(\text{seabed slope}) * \overline{\log(\text{seabed slope})}$	-0.525	0.015	-34.22

1183

1184 † Covariates standardised prior to model fitting; d = distance by-sea from the colony; A =
1185 cumulative area at distance d ; θ = inverse-distance weighted number of conspecifics breeders; θ'
1186 = inverse-distance weighted square-root number of conspecific breeders; N = number of
1187 conspecific breeders at the home site; ρ = density of birds from the home site relative to those
1188 from all other sites; NPP = net primary production; PEA = mean potential energy anomaly; SST
1189 = mean sea surface temperature; sSST = mean standardised SST; TFGD = thermal front gradient
1190 density. Overbars indicate the mean of the covariate in water accessible from each colony.

1191 ‡ Relative standard errors.

1192 **Figure Legends**

1193

1194 **Fig. 1.** Breeding distribution and individual movement data used to estimate the distribution at
1195 sea of seabirds foraging from UK colonies. Left-hand panels show numbers of apparently
1196 occupied nests recorded during the Seabird 2000 census (Mitchell et al. 2004) (red indicates
1197 study colonies). Right-hand panels show tracks of individual birds (colors correspond to
1198 colonies). Places mentioned in the text are shown in the upper right panel: CS Colonsy, DB
1199 Dublin Bay, FH Flamborough Head, GW Galway Bay, IL Islay, IS Isles of Scilly.

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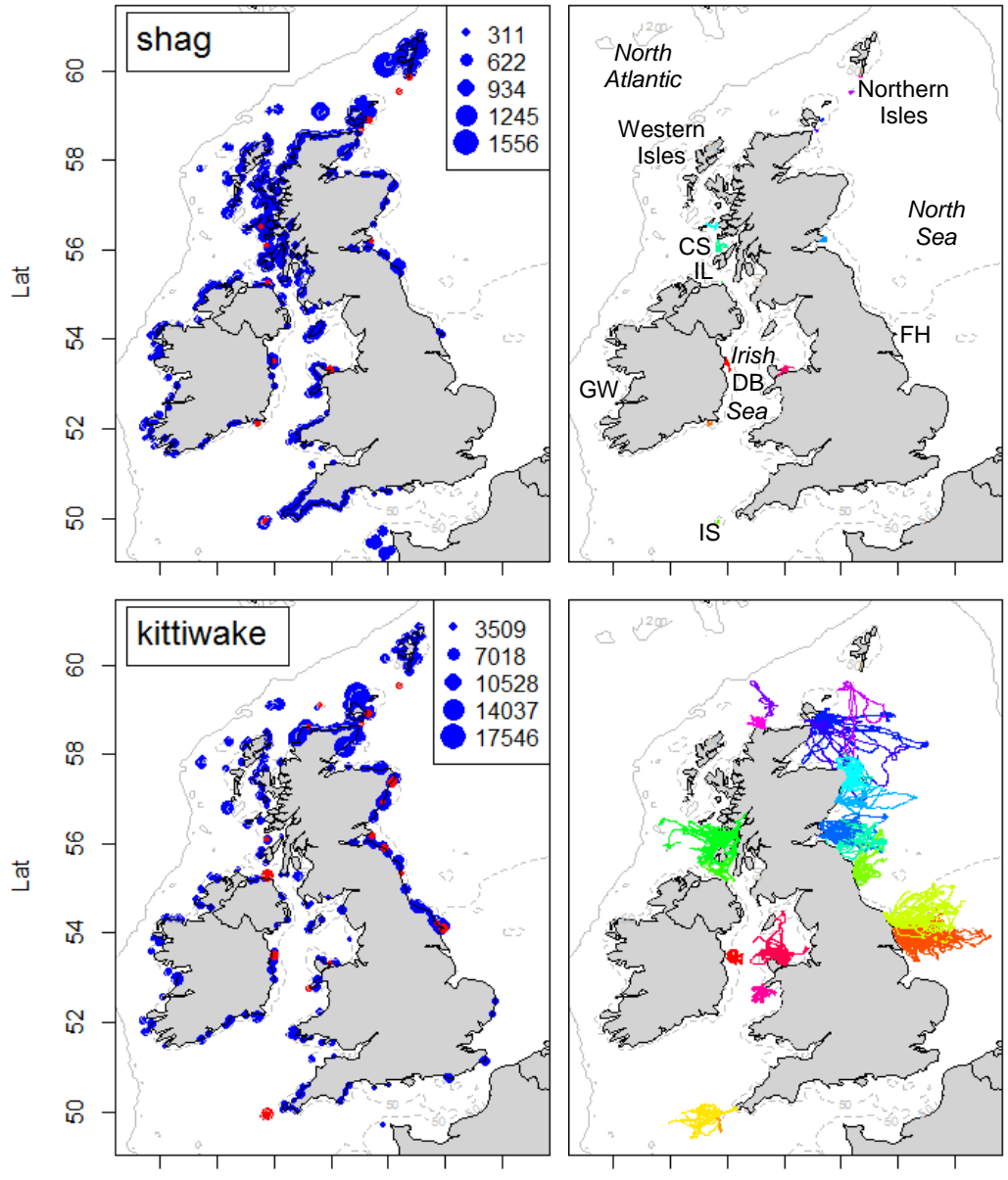
1201 **Fig. 2.** Percentage at-sea utilization distribution (UD) of seabirds breeding within Britain and
1202 Ireland during late incubation/early chick-rearing estimated as functions of colony distance, coast
1203 geometry, intra-specific competition and habitat (models V-VIII). Warmer colors indicate higher
1204 usage. Isopleths indicate relative coefficient of variation (CV) of the estimated probability
1205 density (grey = no environmental data).

1206

1207 **Fig. 3.** Predicted multi-species hotspots. (a) Overlap between estimated core areas used by the
1208 four study species during late incubation/early chick-rearing. Colors indicate number of
1209 overlapping species' core areas (75% of the species' utilization distribution, UD; see Appendix 2
1210 Fig. S7 for equivalent plots using the 50 and 90% UD). (b) Combined usage by all four study
1211 species breeding at protected SPA colonies. Colors indicate areas supporting 50, 75 and 90% of
1212 the estimated marine utilization distribution of one or more species breeding within existing
1213 colony-based SPAs. Red lines indicate areas contained within maximum curvature (MC)

1214 boundaries (O'Brien et al. 2012) for one or more species and black lines boundaries between
1215 national Exclusive Economic Zones.
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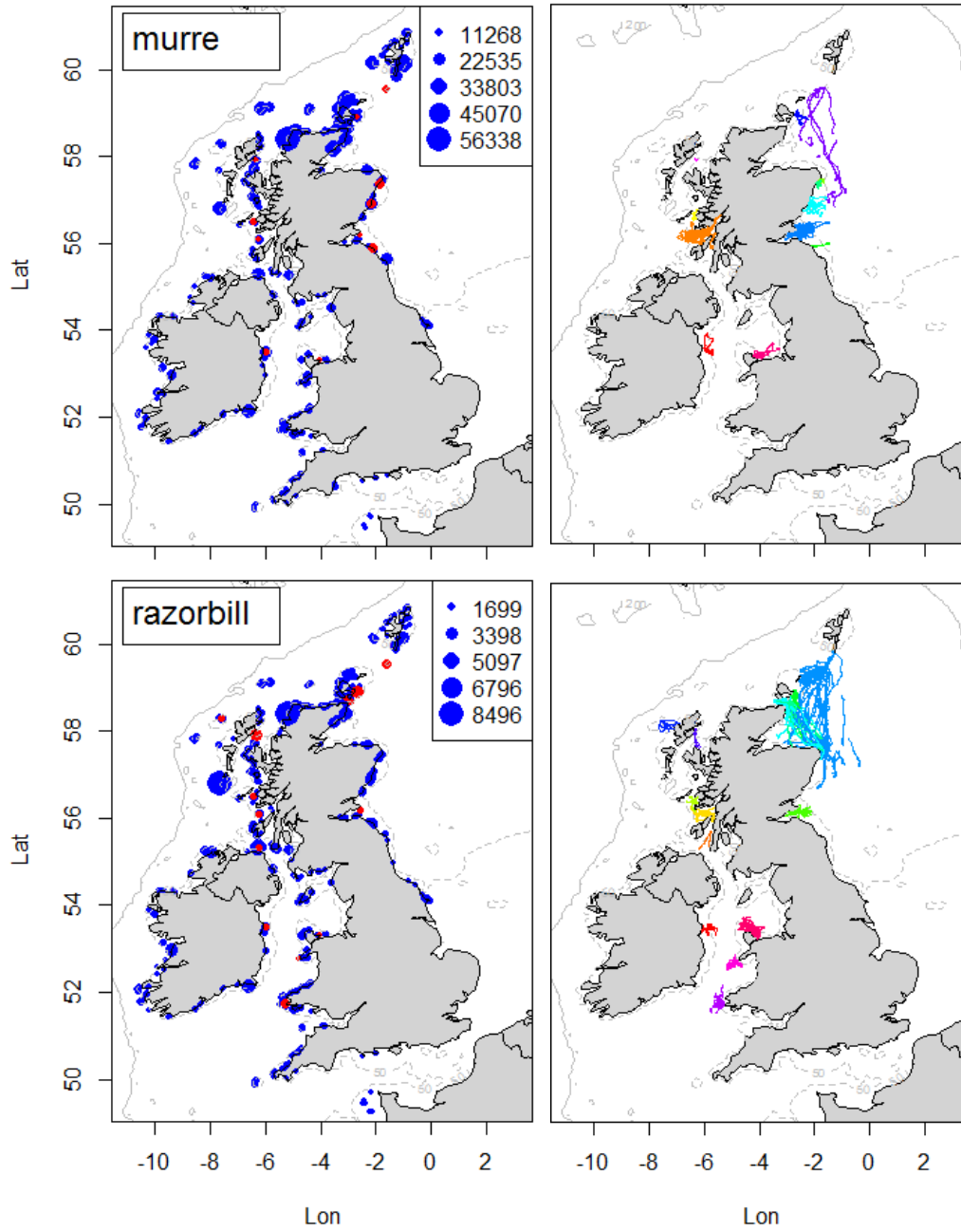
1217 **Figure 1.**



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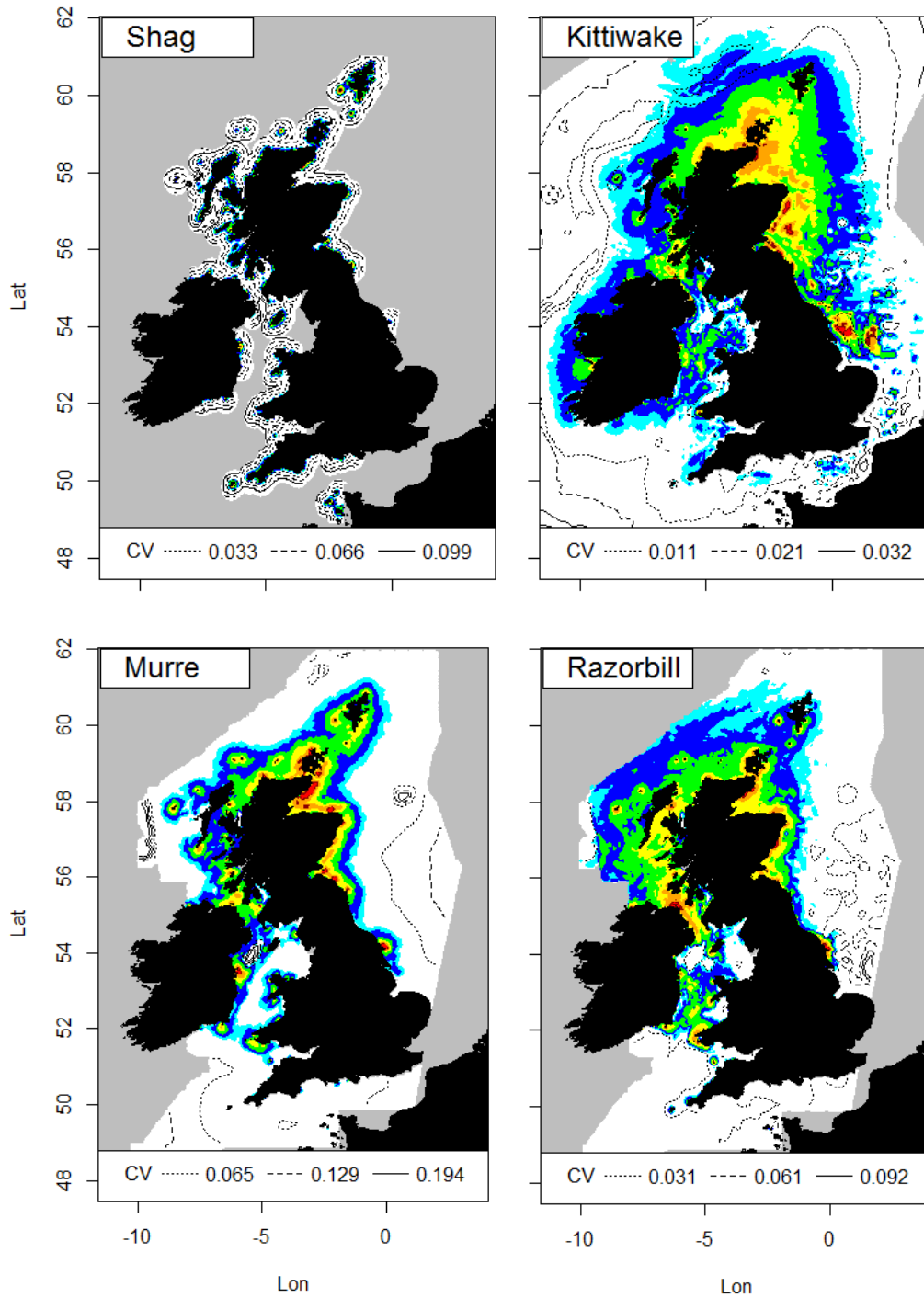
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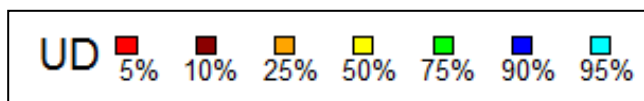
1223 **Figure 2.**



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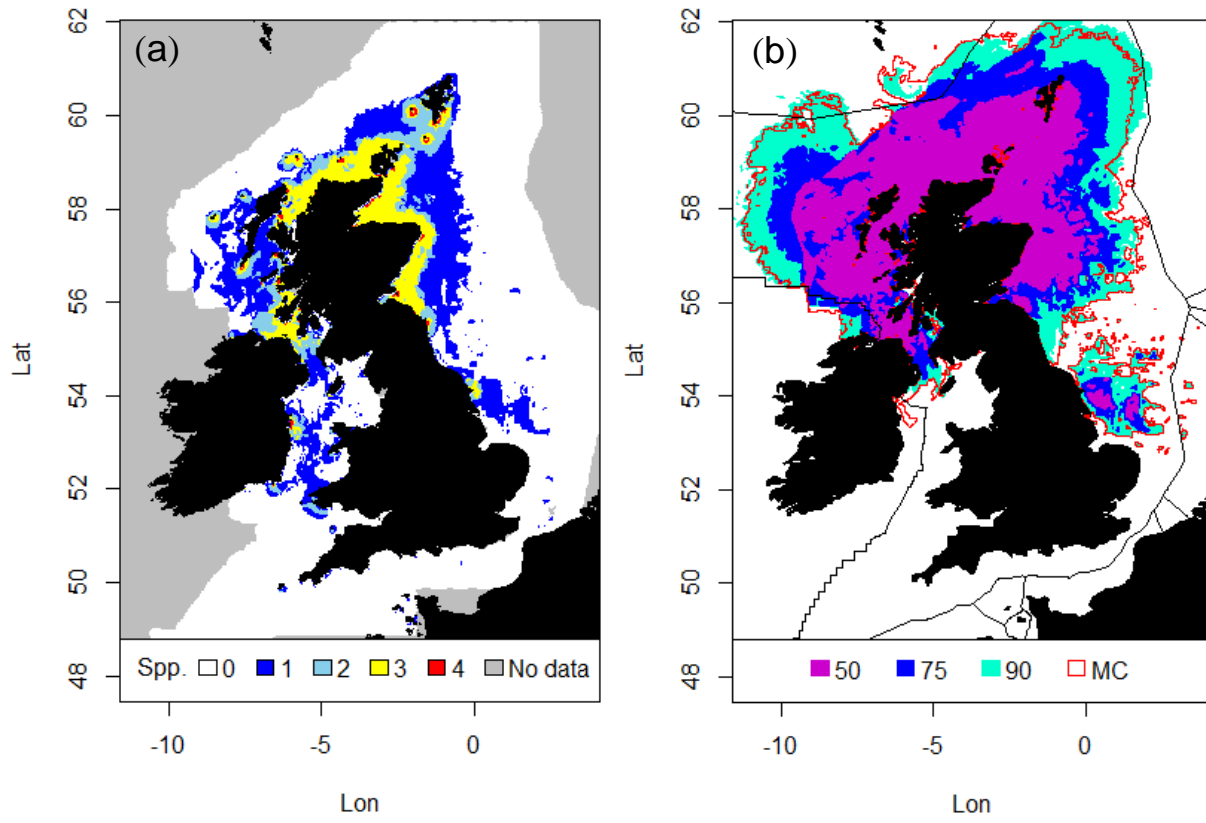
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1228 **Figure 3.**



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