

**The effects of fixed physiographic and dynamic oceanographic conditions on the occurrence of the northern minke whale (*Balaenoptera acutorostrata*) in the southern outer Moray Firth, Scotland.**



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# 1 Abstract

- 2 1. The distribution of marine predators is strongly linked to the distribution of prey,  
3 which is influenced by combinations of fixed physiographic and dynamic  
4 oceanographic conditions. Rorqual whales in particular may use particular conditions  
5 to locate high densities of prey to optimise their foraging efficiency.
- 6 2. The Moray Firth is an important foraging ground for minke whales which feed on  
7 sandeels, herring, and sprat. A marine protected area (MPA) was designated in the  
8 Southern Trench area of the firth to increase protection for the species. However,  
9 these spatiotemporally fixed frameworks fail to account for differential importance  
10 of different areas of the MPA in relation to environmental conditions and how these  
11 may change over time due to dynamic oceanographic conditions. Therefore,  
12 improved understanding of how minke whales use these conditions is required to  
13 inform managers to consider a more dynamic approach to managing the MPA.
- 14 3. This study assesses the preferences of minke whales in the Moray Firth for  
15 physiographic (depth, seabed slope, distance to shore) and dynamic oceanographic  
16 (sea surface temperature (SST), frontal activity) using sightings data collected by the  
17 CRRU in a presence-absence generalized additive model.
- 18 4. Minke whales showed strong preference for waters deeper than 40 metres but no  
19 apparent preference for seabed slope. There was slight preference for low SST,  
20 although marginally non-significant, and low values of SST standard deviation  
21 (frontal proxy). High temporal variation in occurrence probability was observed both  
22 among months and years.
- 23 5. The observed preferences for physiographic and oceanographic conditions of minke  
24 whales are likely due to the distribution of prey. An unexpected negative relationship  
25 with frontal activity was found which indicates that minke whales do not use fronts  
26 to forage and similar results have been found in the Gulf of St Lawrence. These  
27 findings demonstrate that different areas of the survey area and MPA will be of  
28 differential importance depending on the assembly of physiographic and  
29 oceanographic conditions, and these will likely change over time. Therefore,  
30 management of the MPA would be more effective if it spatially adapts on the  
31 monthly scale to more effectively conserve the most important areas.

32

33 Keywords: adaptive management, marine protected area, minke whales, oceanographic  
34 conditions, physiographic conditions, presence-absence model

35

## 36 Introduction

37 Marine habitats are heterogenous over different spatial scales leading to non-random  
38 distribution of their inhabitants. Such fluctuations are particularly important for marine  
39 predators (Scales et al. 2014a; Scales et al. 2014b) such as cetaceans, in terms of their  
40 spatio-temporal occurrence (Robinson et al 2009; Anderwald et al. 2012) and foraging  
41 strategies (Hazen et al. 2015). The success of efforts to conserve coastally occurring  
42 cetacean populations therefore depends upon a good understanding of the environmental  
43 factors influencing their respective distribution and habitat use over spatial and temporal  
44 scales.

45

46 Marine habitat models can be used to better understand the associations between  
47 particular environmental conditions and species' distribution (Redfern et al. 2006; Mannocci  
48 et al. 2017). These models may include combinations of fixed physiographic and/or dynamic  
49 oceanographic conditions. Physiographic conditions are heterogeneous over spatial scales  
50 but remain constant over time in the marine environment and include covariates such as  
51 depth, seabed slope, and sediment type (Anderwald et al. 2012), for example. Dynamic  
52 oceanographic conditions vary over spatial scales but also change over time and include  
53 highly variable conditions such as sea-surface temperature (SST; Anderwald et al. 2012), as  
54 well as more persistent oceanographic features such as fronts (Scales et al. 2014a). Many  
55 habitat models have demonstrated that particular physiographic and oceanographic  
56 conditions are important for large marine vertebrates. For example, basking shark  
57 (*Cetorhinus maximus*) occurrence in UK coastal waters is more probable in areas of  
58 persistent frontal zones (Miller et al. 2015). For large animals such as cetaceans, modelling  
59 species distributions can inform management of the ecological requirements and  
60 preferences of the animals that may make them more susceptible to injury or disturbance  
61 from anthropogenic activities such as fishing activities or vessel traffic (Fiedler et al. 2018).

62

63 The importance of physiographic and oceanographic conditions to cetaceans is typically  
64 linked to the influence of these conditions on the distribution of their prey (Robinson et al.  
65 2007b; Segura et al. 2008; Zerbini et al. 2016; Tardin et al. 2017) so they can be used as  
66 proxies for important foraging areas. These associations can be investigated on different  
67 spatio-temporal scales. Fine-scale studies on spatiotemporal scales of hundreds of metres  
68 and several hours may seek to understand associations between predators and ephemeral  
69 prey patches (Mannocci et al. 2017). More meso/sub-mesoscale studies aim to address  
70 questions concerning associations between species and larger oceanographic features such  
71 as fronts and eddies over several kilometres and longer periods of time (e.g.,  
72 monthly/seasonal) which are potentially utilised by large mobile marine animals to locate  
73 productive regions yielding optimal foraging opportunities (Redfern et al. 2006; Mannocci et  
74 al. 2017). Mesoscale fronts (several kilometres) in particular are thought to provide  
75 excellent foraging opportunities due to their aggregatory effects upon plankton (Genin et al.  
76 2005; Scales et al. 2014a) and their tendency to persist for substantial periods making them  
77 more predictable. This ultimately encourages increased meso-predator occurrence (i.e.,  
78 fish), making them attractive foraging areas for top predators, especially those exhibiting  
79 high site fidelity (Scales et al. 2014a) such as many baleen whales (e.g., Valenzuela et al.  
80 2009; Acevedo et al. 2014; Palacios et al. 2019; Bröker et al. 2020). Monitoring dynamic  
81 oceanographic conditions such as fronts and species' presence and absence, will facilitate  
82 research into how the timing and position of fronts may change both seasonally and over  
83 the long-term due to climate change, and responses to these changes by species.

84

85 Rorqual whales (*Balaenoptera spp.*) may be especially influenced by mesoscale  
86 oceanographic conditions. These whales feed mainly using a lunge-feeding strategy  
87 involving engulfment of large volumes of seawater containing prey which is then filtered  
88 (Hazen et al. 2015). Lunge feeding is very energetically expensive, however, and high rates  
89 of lunge feeding on low-density prey patches is energetically inefficient (Hazen et al. 2015).  
90 Thus, rorquals should focus their foraging activities within areas where prey densities are  
91 high. The minke whale (*Balaenoptera acutorostrata*) whale is the smallest and most  
92 abundant of the rorquals (Horwood 1989) and approximately 8900 occur in the North Sea  
93 (Hammond et al. 2021), primarily in inshore waters less than 200 metres deep (Macleod et

94 al. 2004). As top predators (Durant et al. 2014) minke whales are an important component  
95 of the coastal marine environment (Robinson et al. 2009) and exert top-down effects on the  
96 abundance of other species through competition and predation (Durant et al. 2014), so  
97 more effective management informed by improved understanding will be relevant to the  
98 entire ecosystem as a result.

99

100 Spatiotemporal distribution in relation to physiographic and dynamic oceanographic  
101 conditions has been widely studied in other rorquals including blue (*Balaenoptera musculus*;  
102 Hazen et al. 2017; Barlow & Torres 2021) and fin (*Balaenoptera physalus*; Grossi et al. 2021;  
103 Ham et al. 2021) whales to reveal important foraging areas, and humpback whales  
104 (*Megaptera novaeangliae*; Derville et al. 2019a; Derville et al. 2019b) to identify important  
105 breeding habitat, to facilitate management bodies to make more informed decisions.  
106 Associations between minke whales and environmental conditions have been previously  
107 studied and associations have been found with depth (MacLeod et al. 2004; Ingram et al.  
108 2007; Robinson et al. 2009; Anderwald et al. 2012; Zerbini et al. 2016), SST (Tetley et al.  
109 2008; Anderwald et al. 2012), topography (Robinson et al. 2009; Anderwald et al. 2012;  
110 Correia et al. 2021), seabed slope (Ingram et al. 2007; Robinson et al. 2009) and proximity to  
111 sea ice (Kasamatsu et al. 2001). However, these associations are likely to be highly site and  
112 population specific as the comparative importance of particular environmental conditions to  
113 minke whale distribution varies across regions (MacLeod et al. 2004) and minke whales  
114 exhibit regional-specific dietary preferences (Olsen & Holst 2001). In the Norwegian Sea, for  
115 example, minke whales feed almost exclusively on herring (*Clupea harengus*; Olsen & Holst  
116 2001) whereas diet in Scottish waters comprises mostly lesser sandeel (*Ammodytes*  
117 *marinus*), herring, and sprat (*Sprattus sprattus*; Pierce et al. 2004) and about eighty-seven  
118 percent lesser sandeel with smaller amounts of mackerel (*Scomber scombrus*), whiting  
119 (*Merlangius merlangus*), and herring in the North Sea (Olsen & Holst 2001). The species,  
120 however, does show plasticity in diet, with both seasonal changes and intra-population age-  
121 class differences in prey selection being observed (Robinson et al. in press). Site-specific  
122 research into physiographic and oceanographic drivers of minke whale occurrence,  
123 therefore, is necessary to provide management with regional understanding of occurrence  
124 patterns and of which areas are of most importance.

125

126 The Moray Firth is a large inshore body of water off the northeast coast of Scotland. The  
127 area has a designated Special Area of Conservation (SAC) for the resident bottlenose dolphin  
128 (*Tursiops truncatus*) population (Thompson et al. 2006) but is important for other cetaceans  
129 including harbour porpoises (*Phocoena phocoena*) and minke whales (Robinson et al.  
130 2007b). Minke whales occur in the Moray Firth at relatively higher densities than  
131 surrounding waters and other areas around Scotland (Paxton et al. 2014) and use the area  
132 to forage throughout the summer (Robinson & Tetley 2007). The distribution of minke  
133 whales in the Moray Firth is thought to be linked to the distribution of sandeels (Robinson et  
134 al. 2007b) and previous habitat studies have tested minke whale association with a range of  
135 fixed and dynamic environmental covariates including SST, sediment type, seabed slope,  
136 *inter alia* (Tetley et al. 2008; Robinson et al. 2009). Almost 20 years of research has led to  
137 the recent designation of the Southern Trench along the southern coastline of the outer  
138 Moray Firth as a Marine Protected Area (MPA). However, as highlighted by Robinson et al.  
139 (in press) not all areas within an MPA have equal value. Since the spatiotemporal  
140 distribution of physiographic and oceanographic conditions is heterogeneous, different  
141 locations within the MPA will likely be of differential importance over space, and this  
142 importance will likely shift with time due to dynamic variables such as fronts (Miller &  
143 Christodoulou 2014), and some areas have differential importance to different demographic  
144 groups (Robinson et al. in press). Additionally, changing environmental conditions due to  
145 climate change (Mackenzie & Schiedek 2007; Belkin 2009; Lindegren et al. 2018) have  
146 already resulted in regime shifts in plankton communities (Beaugrand 2004; McQuatters-  
147 Gollop et al. 2007; Defriez et al. 2016) which has important consequences for higher trophic  
148 level predators and fisheries alike (Defriez et al. 2016). Therefore, an updated understanding  
149 of habitat preferences of minke whales to identify important foraging areas is crucial to  
150 delivering effective management.

151

152 MPAs which can adapt to dynamic oceanographic conditions have been seldom  
153 implemented but if it is demonstrated that species are utilising particular dynamic  
154 environmental conditions, then adaptive MPAs may prove more effective (Hooker et al.  
155 2011). For example, in Hawaii, loggerhead turtles (*Caretta caretta*) are known to associate  
156 with a moving temperature front feature that can be indicated by an SST isotherm. This  
157 frontal region is highlighted by managers to bring to fishers' attention and is updated

158 weekly, so that turtle bycatch is avoided, demonstrating a dynamic management approach  
159 (Howell et al. 2008). If minke whales do show particular preferences for different  
160 physiographic and dynamic oceanographic conditions, then a more adaptive management  
161 approach would be recommended (Hamazaki 2002). Adopting an adaptive approach would  
162 likely minimise the impact of anthropogenic activities, such as fishing, renewables  
163 installation, and vessel traffic, on important foraging areas by considering the changing  
164 spatiotemporal distribution of minke whales as a reaction to the availability of their prey  
165 (Tetley et al. 2008).

166

167 This study uses minke whale sightings data from boat-based surveys in a presence-absence  
168 model to assess the influence of fixed physiographic (depth, seabed slope, and distance to  
169 shore) and dynamic oceanographic (SST and frontal activity) conditions as well as monthly  
170 and interannual effects, as proxies for prey distribution, on minke whale occurrence in the  
171 southern outer Moray Firth. An increased understanding of how physiographic and dynamic  
172 oceanographic conditions affect minke whale presence will help to identify important  
173 foraging areas in the study area and inform if a more adaptive management approach is  
174 needed.

175

## 176 Methods

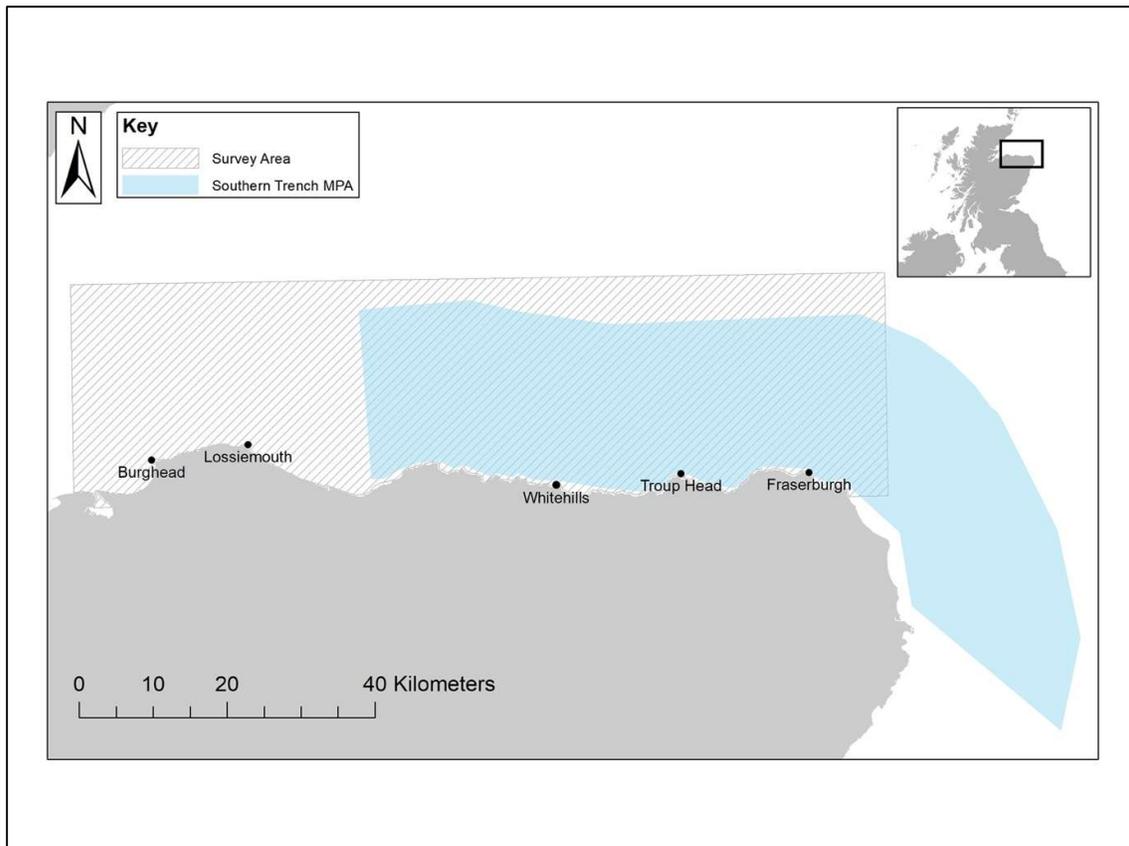
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### 178 *2019-2021 Sightings Data*

179

180 Data comprising 938 minke whale sightings were collected from dedicated boat-based  
181 survey work carried-out by the Cetacean Research and Rescue Unit (CRRU) from May –  
182 October 2001 to 2021, inclusive, within a 2987 km<sup>2</sup> area along the southern coastline of the  
183 outer Moray Firth, within and adjacent to the designated Southern Trench MPA (Fig. 1).  
184 Survey effort was available from 2009 to 2021 and 543 sightings were recorded during this  
185 period. Surveys were non-systematic in that after an animal was sighted it was typically  
186 followed to facilitate focal studies such as photo-identification, behavioural sampling, and  
187 aerial photogrammetry using an unmanned aerial vehicle (UAV). During surveys, the survey

188 vessel was typically operated at speeds of 10 to 14 km h<sup>-1</sup>. Survey tracks were recorded  
189 using a global positioning system (GPS) from which the distance travelled, and the  
190 respective positions of encounters could be extracted. When a sighting was made, the  
191 number of whales was recorded along with *in situ* environmental data such as the sea state,  
192 swell height, sea surface temperature (SST), and associated depth. Sea state corrected bias,  
193 as considered in other studies (e.g., Anderwald et al. 2012), was not implemented here as  
194 surveys were only conducted in Beaufort Sea States of <3 and swells of <3 on the Douglas  
195 Scale. Changes in detectivity at these lower sea states (0-2) are likely to be minimal with  
196 larger cetaceans such as minke whales (Hammond et al. 2002). The full methodology for  
197 these surveys is available in Robinson et al. (2009).  
198



199  
200 *Figure 1.* Map of the study area showing the position of the survey area along the southern coastline of the  
201 outer Moray Firth and the recently designated Southern Trench Marine Protected Area (MPA).  
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203  
204  
205

206 *Environmental Data Collation and Spatial analysis*

207

208 All spatial analyses were undertaken in ArcGIS Desktop v10.8.1 (Environmental Systems  
209 Research Institute 2020). Spatial layers were all projected to the British National Grid  
210 Transverse Mercator coordinate reference system so that spatial distances could be  
211 interpreted in metric units.

212

213 A rectangular grid, measuring 553 x 159 cells of 200 m<sup>2</sup> resolution was created containing  
214 mean depth values using bathymetry data derived from Admiralty charts of the Moray firth  
215 (for full description of raster creation, see Robinson et al. 2009). Another grid of the same  
216 dimensions and resolution was created containing average seabed slope (°) and this was  
217 extrapolated from the bathymetry raster using the 'Slope' tool from the Spatial Analyst  
218 extension in ArcGIS. In order for the tool to run properly, depth values had to be converted  
219 to negative values. A further grid of the same dimensions and resolution containing values  
220 of distance to shore from the centre of each grid cell was therefore determined using the  
221 'Euclidean Distance' tool from the Spatial Analyst extension.

222

223 Presence-absence grids for every surveyed month were created for the following analysis.  
224 Since the study aimed to incorporate monthly variation, this approach required up to six  
225 grids per year (May to October), and given the scope of the present study, producing grids  
226 for the full range of years there were adequate data available for (2009 to 2021) was  
227 unfeasible. Therefore, the dataset was limited to the most recent three survey years (2019  
228 to 2021) which comprised 197 sightings. For these years, no surveys were conducted in May  
229 so up to five grids (June to October) were created per year. Survey waypoints were first  
230 transformed into survey track lines using the 'Point to Line' tool, with each track line being  
231 separated by a unique survey ID number. A column was created in the sightings data  
232 indicating minke whale presence, coded for by '1', and a column created in the track line  
233 data indicating absence, coded for by '0'. This corresponds to used and available habitat,  
234 respectively, as a binary probability of occurrence response variable (Correia et al. 2021).  
235 Both vector layers were converted to raster grids using the 'Point to Raster' tool and the  
236 raster grid cell size was set as 2,000 (2 km<sup>2</sup>) to capture meso/sub-mesoscale environmental  
237 variability whilst avoiding excessive extrapolation to areas which would not be well

238 represented by this method. Derville et al. (2019a) considered waters 10 km either side of  
239 GPS tracks as surveyed to account for the maximum detection range of humpback whales  
240 from the vessel but the detection range of sightings in the CRRU dataset was lower since  
241 vessels were much lower in height, and since minke whales are considerably smaller than  
242 the other rorqual species (Horwood 1989). Accordingly, 2 km<sup>2</sup> grid cells were considered  
243 adequate. In order to produce the presence-absence grids, the tracks and sightings raster  
244 grid values for each month-year combination were added together using the 'Raster  
245 Calculator' tool from the Spatial Analyst extension.

246

247 SST data were sourced from NASA Giovanni (Acker & Leptoukh 2007) and were obtained  
248 from the Moderate Resolution Imaging Spectroradiometer instrument from the Aqua  
249 satellite (MODIS-Aqua). Monthly average daytime SST was selected at a 4 km<sup>2</sup> resolution for  
250 all surveyed months from 2019 to 2021, for an area slightly larger than the survey area. The  
251 standard deviation of SST (SST SD) can be used to quantify frontal areas since fronts typically  
252 exhibit large temperature gradients (Forney et al. 2015; Gilles et al. 2016) and so this  
253 approach was adopted in the present analysis. The 'Focal Statistics' tool from the Spatial  
254 Analyst extension was used to calculate SST SD and produce rectangular grids for each  
255 surveyed month, from 2019 to 2021, at the same spatial and temporal resolution as for SST.  
256 All environmental data grid layers were collated using the 'Sample' tool from the Spatial  
257 Analyst extension in ArcGIS.

258

### 259 *Statistical analysis*

260

261 All statistical analyses were carried out using R v4.1.2 (R Core Team 2021). Collinearity  
262 between explanatory variables, including all physiographic (depth, slope, distance from  
263 shore), oceanographic (SST, SST SD), and temporal (month, year) variables was examined  
264 using the 'pairs' function in R. From the outputs, a strong correlation was found between  
265 distance from shore and depth (0.73), and thus distance from shore was discarded from the  
266 analysis, since depth was expected to be more ecologically interpretable. All other variables  
267 were kept for the subsequent analysis.

268

269 The study aimed to evaluate the influence of environmental variables on the probability of  
270 occurrence. Whilst generalized linear models (GLMs) require linear independent variables,  
271 generalized additive models (GAMs) can utilise smooth, non-parametric functions of the  
272 independent variables, enabling GAMs to be a more flexible tool than a GLM (Forney et al.  
273 2012). A GAM was selected as the model type since the relationships between the  
274 probability of occurrence and the physiographic and oceanographic explanatory variables  
275 were not expected to be linear. GAM functions were accessed in R via the 'mgcv' package  
276 (v1.8 – 40; Wood 2011). To reduce the influence of very high values of slope and SST SD,  
277 each of these variables were transformed using the 'log10' function.

278

279 Smooth functions of SST,  $\log_{10}(\text{SST SD})$ ,  $\log_{10}(\text{slope})$ , and depth were included in the initial  
280 model selection, with the maximum number of parameters ( $k$ ) set at 4 for the depth smooth  
281 and 3 for the  $\log_{10}(\text{slope})$  smooth to avoid overfitting. Month and year were treated as  
282 factors and were included as linear predictors in the model to capture seasonal and  
283 interannual variation in the probability of minke whale occurrence. The inclusion of year  
284 prohibits predictions being made for subsequent years (Redfern et al. 2006; Wood 2006) but  
285 the additional interannual variation in occurrence incorporated by including year into the  
286 model (Becker et al. 2019; Becker et al. 2020) was prioritised since the aim was to explain  
287 variation rather than make predictions. The family was set as 'binomial' using a logit link  
288 function since the response variable for presence/absence is binary (presence or absence).  
289 Low-rank thin plate splines were the chosen smoother type for all smooth terms. Restriction  
290 maximum likelihood (REML) was used for smoothness selection to prevent overfitting. The  
291 model summary indicated that the SST and  $\log_{10}(\text{SST SD})$  effects were linear (effective  
292 degrees of freedom (EDF) = 1.0) so they were reincorporated as linear terms. Depth and  
293  $\log_{10}(\text{slope})$  were subsequently retained as smooth effects (depth smooth EDF = 2.425,  $\log_{10}$   
294 (slope) smooth EDF = 1.439). The GAM check carried out using the 'gam.check' function,  
295 indicated that  $k$  was set at an appropriate level for the depth and  $\log_{10}(\text{slope})$  smooth terms  
296 ( $P > 0.05$ ).

297

298 Sightings frequency was calculated for every year with available data (2001 to 2021) and  
299 relative abundance (sightings  $\text{km}^{-1}$ ) was estimated for each year with available survey effort

300 (2009 to 2021) and for each pooled month using data from the same period. This was done  
301 to compare with probability of occurrence results estimated by the GAM.

302

### 303 *Model validation and variable selection*

304

305 To assess whether the model met the assumptions of a GAM, model validation techniques  
306 were employed to examine the residuals. Due to the binary nature of the response variable  
307 (presence vs absence), the standard residual plots in RStudio were difficult to interpret.

308 Instead, plots of residuals *versus* explanatory variables were created and examined using  
309 the “binnedplot()” function from the ‘arm’ package (version 1.12 – 2; Gelman et al. 2021).

310 Binned plots are useful since they display the mean of residuals for discrete levels (bins) of  
311 the explanatory variables. To assess whether the model had met the assumption of

312 temporal independence, mean residuals of the final model were plotted against temporal  
313 variables (month and year). To check the assumptions of spatial independence, mean

314 residuals were plotted against spatial variables (longitude and latitude). The final

315 assumption of residual variance homogeneity was evaluated by plotting the mean residuals  
316 against all model explanatory variables.

317

318 Mean residuals increased from June to August where a peak was observed, which then fell  
319 thereafter, indicating some temporal non-independence associated with month. Against  
320 year, mean residuals were positive in 2019, negative in 2020, and positive in 2021. Residuals

321 against both temporal variables were well within the expected limits, suggesting reasonable  
322 model fit, however. Mean residuals showed no obvious patterns against either latitude or

323 longitude using a variety of bin numbers, from 10 to 150. When plotted against explanatory  
324 variables, there was some heterogeneity of variance, especially when plotted against depth,

325 SST, and  $\log_{10}$ (SST SD). Therefore, this assumption was probably not adequately met by this  
326 model, likely because there are other factors affecting minke whale presence/absence that

327 had not been considered in the model and would explain some of this variability.

328 Subsequently, these model results were interpreted with caution.

329

330 Model selection was conducted with comparison of the Akaike information criterion (AIC)

331 between the full model and alternative models, where non-significant predictor terms were

332 removed. The full model (including depth, slope, SST, SST SD, month, and year) was selected  
333 as differences in AIC, compared with alternative models, were less than 2, and the full  
334 model explained more deviance. Concurvity was assessed using the 'concurvity' function  
335 from the 'mgcv' package and looking at the worst case concurvity. Worst case concurvity  
336 was low for both smooth terms (all < 0.4) so there were no concerns with concurvity.  
337

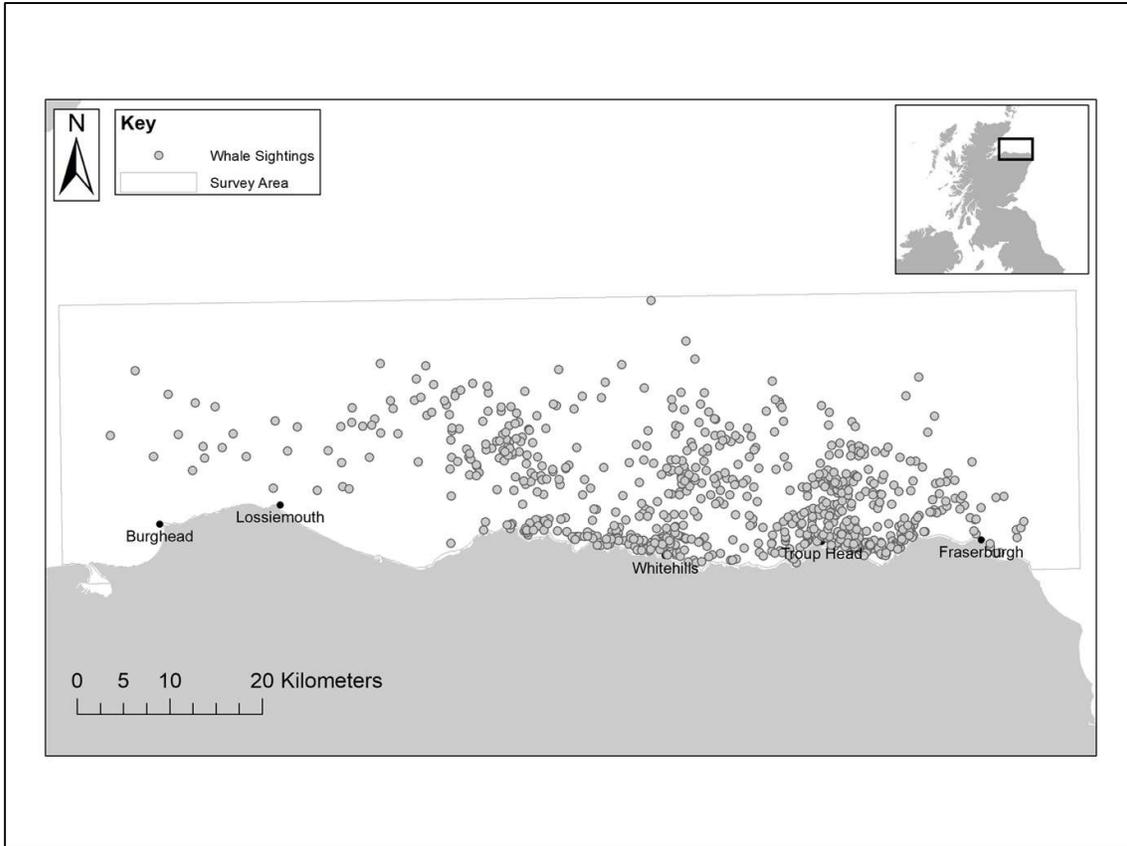
## 338 Results

339

### 340 *Sightings data*

341

342 Between May and October 2001 to 2021, 938 sightings were recorded throughout the  
343 survey area between the coastal ports of Burghead and Fraserburgh, with most sightings  
344 recorded in the eastern half of the survey area between Whitehills and Fraserburgh (Fig. 2).  
345 Sightings were recorded across a wide range of depths from 1.95 m to 211.77 m, with a  
346 mean depth of 58.70 m. Whales were further observed over a range of seabed slope  
347 gradients from gently sloping  $0.02^\circ$  seabeds to steeper  $12.2^\circ$  slopes with a mean  
348 underlying seabed slope of  $1.10^\circ$ . Mean distance from shore of sightings was approximately  
349 6 km but sightings were recorded from the immediate coast to as far off as 26.82 km (Table  
350 1). 197 sightings were recorded between 2019 and 2021, the period upon which the GAM  
351 was based.



352  
 353 *Figure 2.* Map showing the survey area and spatial distribution of minke whale sightings recorded along the  
 354 southern coastline of the outer Moray Firth from dedicated boat surveys conducted by the CRRU research  
 355 team between May and October from 2001 to 2021 (n=938).  
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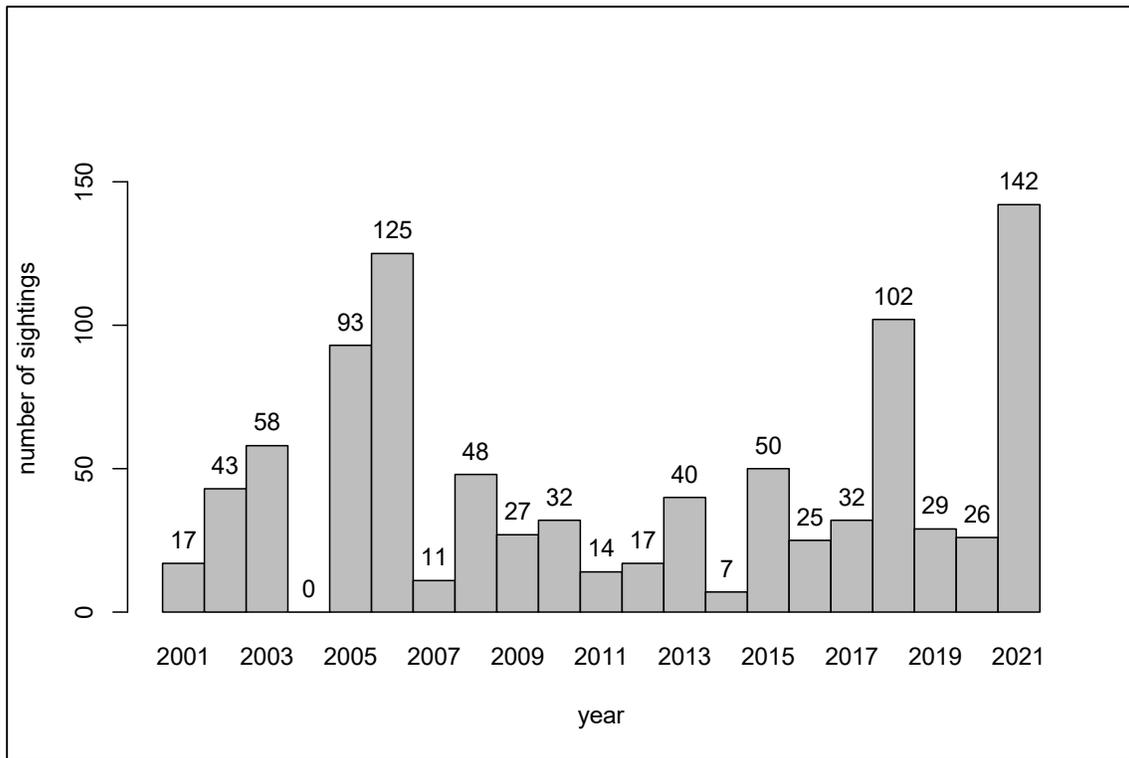
358  
 359 *Table 1.* Mean and ranges of water depth, seabed slope, and distance to shore of minke whale sightings  
 360 recorded in the southern outer Moray Firth from 2001 to 2021 (n=938).

<b>Physiographic variable</b>	<b>Mean <math>\pm</math> SD</b>	<b>Min</b>	<b>Max</b>
Depth (m)	58.70 $\pm$ 45.18	1.95	211.77
Seabed slope ( $^{\circ}$ )	1.10 $\pm$ 1.52	0.02	12.20
Distance to shore (km)	5.98 $\pm$ 4.82	0	26.82

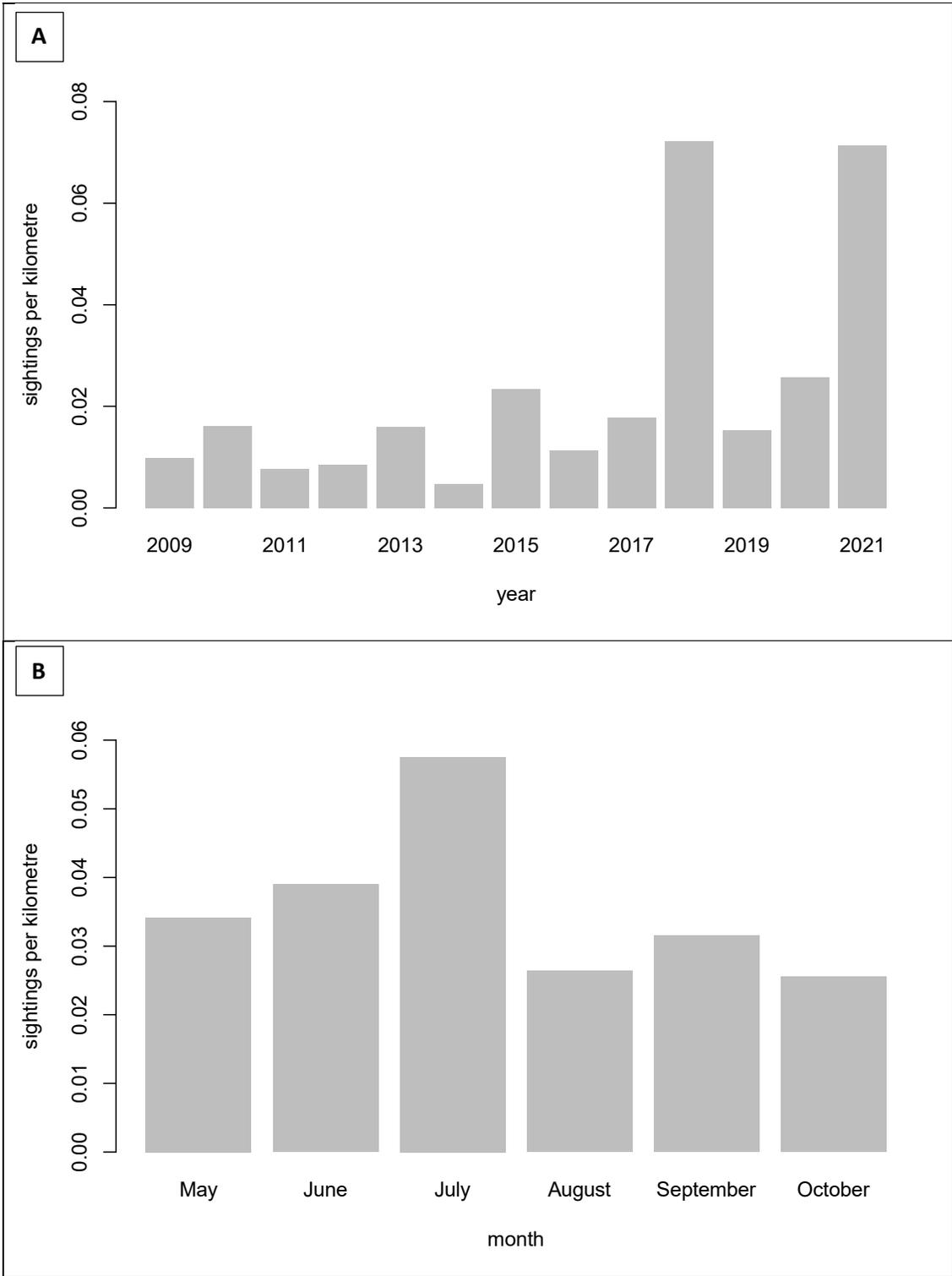
361

362 Minke whales were recorded for all years between 2001 and 2021 with the exception of  
 363 2004. Number of sightings varied considerably between years with notable peaks in 2005,  
 364 2006, 2018, and 2021 (Fig. 3). The relative abundance, number of sightings  $\text{km}^{-1}$ , from 2009

365 to 2021 varied widely but showed a slight pattern of increase (Fig. 4A). Lowest relative  
366 abundance was recorded in 2014 (0.005) whereas greatest relative abundance was  
367 observed in 2018 (0.072). From 2019 to 2021, relative abundance followed a pattern of  
368 increase where it was low in 2019 (0.015), increased in 2020 (0.026), but was much higher in  
369 2021 (0.071), comparatively (Fig. 4A). Sightings were recorded for all of the pooled months  
370 surveyed and there was variation in SPUE among months (Fig. 4B). SPUE was 0.034 in May  
371 and increased slightly in June (0.039) and peaked in July (0.058). In August, SPUE was much  
372 lower (0.026) and there was a slight increase in September (0.032) but a drop to the lowest  
373 SPUE in October (0.025). Overall, SPUE was similar from August to October (Fig. 4B).  
374  
375



376  
377 *Figure 3. Number of sightings by year, using data from all surveyed years (2001 to 2021; n=938), with annual*  
378 *count labels above bars.*  
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387 *Figure 4. Pooled relative abundance (no. sightings km<sup>-1</sup>) by year (A) and month, May to October (B), using data*  
 388 *from years with recorded survey effort (2009 to 2021; n=543).*  
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393 *Model Spatial Variation*

394

395 The selected model (Equation 1), with  $n$  denoting the probability of occurrence and  $s$  a  
396 smooth function of covariates, explained 26.8% of the deviance. Occurrence probability was  
397 low at shallow depths and quickly increased following a logistic curve where the increase  
398 slowed at approximately 30 metres (Fig. 5A). Beyond 40 to 50 metres, the occurrence  
399 probability starts to level off and at around 60 metres, it remains almost constant out to the  
400 maximum depths recorded for the 2019 to 2021 period. Data were well distributed across  
401 the range of depth values, but confidence intervals with the integrated standard error (SE)  
402 of the intercept are much wider at shallower depths and gradually become narrower with  
403 increasing depths. The depth smooth term was a significant predictor of the probability of  
404 minke whale occurrence (Chi-square = 51.41,  $P < 0.001$ ; Fig. 5A). Occurrence probability  
405 was higher at lower slope gradients and fell slightly with increasing  $\log_{10}$  (slope) until  
406 approximately  $-0.8$  where there was a slight increase in occurrence probability with  
407 increasing  $\log_{10}$  (slope) (Fig. 5B). There were fewer data at low values of  $\log_{10}$ (slope) below  
408 approximately  $-1.25$  and at very high values above  $0.25$  than at more intermediate values.  
409 Confidence intervals were approximately constant although marginally wider at the very  
410 extreme  $\log_{10}$  (slope) values. The smooth function of  $\log_{10}$  (slope) was estimated as a non-  
411 significant predictor of occurrence probability (Chi-square = 0.59,  $P > 0.05$ ; Fig. 5B).

412

413 *Equation 1.*

414  $n \sim s(\text{depth}) + s(\log_{10}(\text{slope})) + \text{SST} + \log_{10}(\text{SST SD}) \text{ month} + \text{year}$

415 The probability of occurrence declined as SST increased. This relationship was only weakly  
416 negative and marginally non-significant ( $Z = -1.95$ ,  $P = 0.051$ ). There were notably fewer  
417 data for SST values lower than  $12.5$  °C and uncertainty increased with SST (Fig. 5C),  
418 additionally. Occurrence probability also declined with  $\log_{10}$  (SST SD), used here as an  
419 indicator of frontal activity, and the relationship was significant ( $Z = -2.40$ ,  $P < 0.05$ ; Fig 5D).  
420 However, there were very few data at values above  $-0.2$  and below  $-1.0$ . Confidence  
421 intervals were wide at low values of  $\log_{10}$  (SST SD) and decreased down to high values of  
422  $\log_{10}$  (SST SD) where the intervals were very narrow (Fig. 5D).

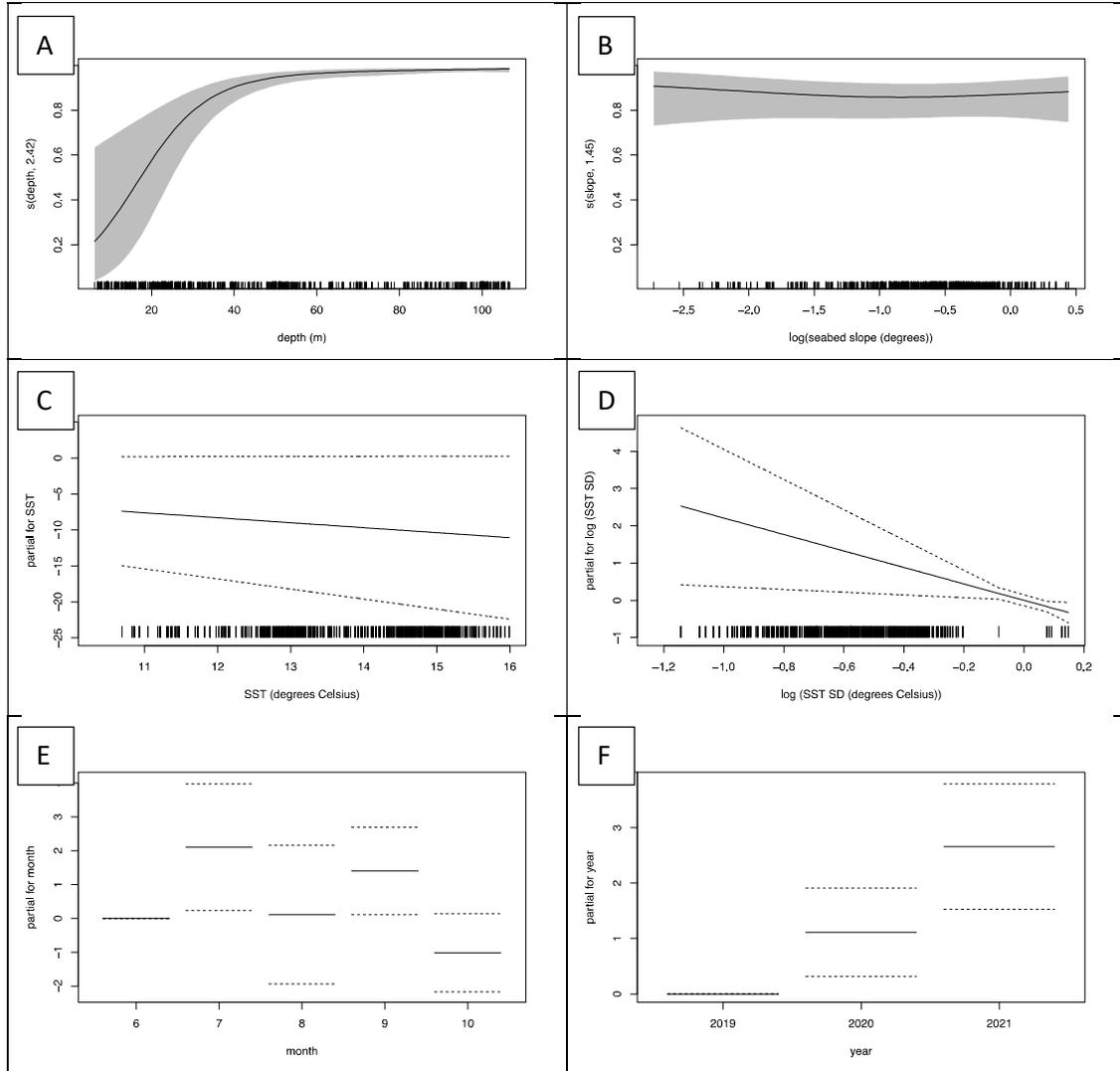
423

424 *Model Temporal Variation*

425 The probability of minke whale occurrence differed significantly between months (Fig. 5E).  
426 Occurrence probability increased from June to July ( $Z = 2.254$ ,  $P < 0.05$ ) where it peaked. In  
427 August, occurrence probability fell to a similar value to that observed in June but showed a  
428 significant increase again in September ( $Z = 2.17$ ,  $P < 0.05$ ). Probability of occurrence was  
429 lowest in October but was significantly different to that observed in June ( $Z = -1.76$ ,  $P >$   
430  $0.05$ ). There was notable interannual variation in the model intercept among years, with a  
431 pattern of increasing occurrence with year (Fig. 5F). Occurrence probability was significantly  
432 greater in 2020 than in 2019 ( $Z = 2.79$ ,  $P > 0.05$ ) and significantly greater in 2021 than in  
433 2019 ( $Z = 4.70$ ,  $P < 0.001$ ). It is worth noting, however, that the confidence intervals also  
434 increase with each progressive year (Fig. 5F).

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474 *Figure 5.* Partial effect plots showing the component effect of smooth terms including depth (A) and  $\log_{10}$   
475 seabed slope (B), and parametric terms including SST (C),  $\log_{10}$ (SST SD) (D), month (E), and year (F), on the  
476 probability of occurrence of minke whales from June to October 2019 to 2021 ( $n=197$ ). Confidence intervals  
477 take account for error in the intercept estimation, additionally.  
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## 483 Discussion

484 Minke whales exhibit habitat preferences in their feeding grounds related to the distribution  
485 of their prey (Robinson et al. 2009; Anderwald et al. 2012; Zerbini et al. 2016; Robinson et  
486 al. in press). The results of the present study demonstrate that the minke whales in the  
487 study area show specific preferences for a variety of fixed, physiographic and dynamic,  
488 oceanographic conditions that vary across space and time, and can be used to provide a  
489 better understanding of the spatial and temporal habitat use of the species to inform  
490 management for their protection.

491

### 492 *Physiographic Preferences*

493

494 Minke whale occurrence in the Moray Firth study area increased with depth and showed a  
495 preference for deeper waters beyond 40 m in the model (Fig. 3A) as intimated by Robinson  
496 et al. (2009). Such preferences for deeper coastal waters have been previously observed for  
497 the species in the Bering Sea (Zerbini et al. 2016), the Bay of Fundy (Ingram et al. 2007), and  
498 along the west coast of Scotland (MacLeod et al. 2004; Anderwald et al. 2012) and has been  
499 indirectly linked to the distribution of targeted prey (MacLeod et al. 2004; Ingram et al.  
500 2007; Robinson et al. 2009; Anderwald et al. 2012; Zerbini et al. 2016). Sandeels are  
501 evidently an important prey species for these coastally-occurring whales (Robinson & Tetley  
502 2007; Pierce et al. 2004) and are thought to occur at highest densities in water depths of 30  
503 to 70 m (Wright et al. 2000). However, minke whales show seasonal and demographic  
504 dietary plasticity, and ongoing studies in the Moray Firth by Robinson et al. (in press) have  
505 shown that adult minke whales primarily target juvenile herring and sprat in deeper  
506 offshore waters, whilst juveniles preferentially target sandeels in shallower inshore waters.

507

508 In contrast to previous studies (e.g., Robinson et al. 2009; Anderwald et al. 2012; Ingram et  
509 al. 2007), no significant relationship with slope was observed in the GAM. Steep slopes  
510 correspond to large depth gradients, which may result in fine-scale upwellings and fronts  
511 which aggregate plankton (Ingram et al. 2007). However, the importance of slope may  
512 change throughout the year (Anderwald et al. 2012) and this may have resulted in the lack  
513 of relationship observed when only considered using spatial sightings alone. Additionally,

514 adults and juveniles may use slopes differently in view of the dietary differences highlighted  
515 above. Indeed, Robinson et al. (in press) found no preference for slope in juvenile minke  
516 whales. Since over 60% of the sightings data used in the present study were juveniles, this  
517 might conceivably explain why no such correlation was observed herein.

518

519 Preferences for fixed physiographic features, such as depth and slope, will correspond to  
520 preferences for particular areas with the adequate underlying conditions remaining stable  
521 over time (Anderwald et al. 2012). Understanding the preferences of minke whales for these  
522 conditions subsequently allows the identification of particular areas that may be important  
523 for management. Thus, waters beyond 40 m within the designated Southern Trench MPA  
524 may constitute important foraging areas for minke whales which might be subjected to  
525 considerable anthropogenic disturbance. The differences in preferences for certain  
526 physiographic conditions between age classes within the MPA as highlighted by Robinson et  
527 al. (in press), suggest that the adaptive management process may be optimised by  
528 considering these differences. For example, alternative management regulations in inshore  
529 waters may also be important for the protection of juvenile foraging habitat from fisheries  
530 and other activities, especially since inshore waters may bear greater anthropogenic activity  
531 (Robinson et al. in press).

532

### 533 *Dynamic Oceanographic Preferences*

534

535 In the present study, the weak negative relationship observed between the probability of  
536 minke whale occurrence and sea surface temperature (SST) detected in the GAM, suggests a  
537 preference by the species for lower water temperatures, although this relationship was  
538 marginally non-significant. This is a similar trend to that observed in other rorqual species.  
539 For example, fin and blue whales around the Azores are associated with lower sea  
540 temperatures which correspond to higher primary production (Prieto et al. 2017). Thus,  
541 lower water temperatures may be associated with better foraging opportunities for minke  
542 whales. North Sea herring occurrence, for example, is greater at lower temperatures of 11  
543 to 12 °C (Maravelias 1997), which may attract greater numbers of foraging minke whales  
544 targeting these prey items. Other filter-feeding large marine vertebrates such as basking  
545 sharks are also known to associate with areas of lower temperature, which are thought to

546 be linked to local upwellings of nutrient-rich waters and mixing providing good  
547 opportunities for feeding (Miller et al. 2015). It is likely that such relationships may vary  
548 seasonally and interannually, as well. Around the Inner Hebrides on the west coast of  
549 Scotland, for example, minke whales show temperature preferences that change  
550 throughout the summer months, with whales preferring higher seasonal temperatures of  
551 11.5 to 12 °C in June and more average seasonal temperatures of 13 to 14 °C in August and  
552 September (Anderwald et al. 2012).

553

554 Contrary to expectations, however, the probability of whale occurrence declined with SST  
555 SD (frontal activity), in the GAM suggesting no preference in the study area for frontal  
556 regions or a preference for fronts with a lower temperature gradient. A similar relationship  
557 was observed for sei whales (*Balaenoptera borealis*) in the Azores, where occurrence  
558 declined with night-time SST SD, which suggested sei whales did not associate with local SST  
559 gradients (Prieto et al. 2017). This is likely due to the fact that sei whales use the Azores as a  
560 migratory path, rather than a foraging location *per se* (Prieto et al. 2017; Pérez-Jorge et al.  
561 2020). However, this is evidently not the case in the Moray Firth, since the highly productive  
562 waters provide rich feeding grounds for minke whales (Robinson et al. 2007b). It may be  
563 that minke whales are not as reliant on fronts to concentrate their prey as other baleen  
564 whales, and in the Gulf of St Lawrence minke whales have been found to occur further from  
565 frontal locations than blue, humpback, and fin whales, with distances to fronts not being a  
566 significant predictor of occurrence (Doniol-Valcroze et al. 2007). Differences in diet between  
567 adults and juveniles may also result in differential use of frontal areas according to prey  
568 preference. For example, adults feeding on herring in late summer (Robinson et al. in press)  
569 may associate with fronts as herring distribution is strongly influenced by these areas  
570 (Maravelias 1997) whereas juveniles feeding on sandeels may not rely on fronts since  
571 sandeels may be more limited by other variables (van der Kooij et al. 2008). The weak  
572 relationship observed in the present study may have been skewed by the large proportion  
573 of juveniles in the study area (Robinson et al. 2009). Additionally, seasonal prey switching in  
574 adults (Robinson et al. in press) may result in the reliance on fronts changing over the  
575 course of the year in adults.

576

577 Dynamic oceanographic conditions are heterogeneous over space and time (Anderwald et  
578 al. 2012). Therefore, management considering preferences of a species for particular  
579 dynamic conditions must adapt to these temporal changes to optimise the effectiveness of  
580 measures (Hooker et al. 2011). The results from the present study indicate that areas  
581 forecasted to have cooler SST may be important to inform the management process. Since  
582 the importance of and preferences for SST may change over the course of a year  
583 (Anderwald et al. 2012) and may differ by age classes, however, these seasonal changes and  
584 demographic differences need to be addressed in future research and management  
585 decisions.

586

587 North Sea annual water temperatures have been rising for several decades (Mackenzie &  
588 Schiedek 2007; Belkin 2009) and such climatic changes will likely affect the distribution of  
589 prey species and predators alike. Many fish species inhabit surface waters as eggs, juveniles  
590 or adults (Mackenzie & Schiedek 2007), and so climate change will not only directly affect  
591 the surface temperatures experienced by minke whales but may further result in changes to  
592 targeted prey through physiological or ecological (e.g., competition and predation) impacts  
593 (Mackenzie & Schiedek 2007; Lindegren et al. 2018).

594

595 One impact affecting minke whales could be upon the availability of passive feeding  
596 opportunities. Passive or bird-associated feeding opportunities are generally schools of  
597 small fish that have been already concentrated by feeding seabirds from above and  
598 predatory fish such as mackerel from below (Hoelzel et al. 1989), which juvenile minke  
599 whales in particular are thought to associate with (Robinson et al. in press). Individuals  
600 exploiting these opportunities are thought to use less energy compared with those using  
601 more energetically costly active lunge-feeding techniques (Hoelzel et al. 1989; Kuker et al.  
602 2005). However, temperature changes have been observed to influence mackerel school  
603 structure resulting in changes to migratory speed and behaviour, and even, in extreme  
604 changes, causing migration termination and dispersal (Reid et al. 1997). Due to the  
605 importance of mackerel in creating these passive foraging opportunities by corralling the  
606 targeted baitfish prey to the surface (Robinson & Tetley 2007), the inferred climatic changes  
607 may have adverse effects upon juvenile foraging opportunities in the study area.

608

609 *Temporal Variation*

610

611 There was significant interannual variation in occurrence probability over the three-year  
612 period, with a general pattern of increase indicated by the model (Fig. 5F), and relative  
613 abundance varied widely between years but showed an overall pattern of increase from  
614 2009 to 2021 (Fig. 4A). Year can be incorporated into habitat models to account for  
615 population trends (Becker et al. 2019; Becker et al. 2020) but analysis of minke whale  
616 population trends for the wider North Sea have found no evidence for significant population  
617 changes over the past few decades (Hammond et al. 2021). The increasing trend over years  
618 may correspond to increasing usage of the Moray Firth by North Sea minke whales in years  
619 with higher occurrence or relative abundance, due to increases in prey availability. This  
620 would be in line with previous observations where patterns of minke whale numbers in the  
621 Moray Firth appear inverse to patterns observed on the west coast of Scotland (e.g., period  
622 from 2001 to 2005). It is thought these inverse patterns are due to foraging habitat  
623 switching by minke whales (Robinson et al. 2007a), reaffirming that minke whales  
624 throughout Scottish waters come from a wider single population and that foraging  
625 opportunities are the principal driver of minke whale distribution in the study area.

626

627 Minke whales occurred across all surveyed months but there was notable variation between  
628 months in occurrence probability (Fig. 5E) detected in the model. Pooled monthly data show  
629 fairly high relative abundance for the entire study period (Fig. 2B), supporting that presence  
630 is sustained in the region, as also confirmed from consistent recaptures of the same animals  
631 during the same year and between years (Baumgartner 2008), indicating not only that  
632 whales remain in the immediate study area but also reaffirming that some individuals return  
633 in consecutive years. In June, sandeels are especially important and other studies have  
634 found minke whale distribution in June to be linked to sandeel distribution (MacLeod et al.  
635 2004; Anderwald et al. 2012). Both occurrence probability and relative abundance was  
636 greatest in July, indicating that this is when the optimum foraging conditions are available.  
637 This may also indicate the minke whales are less preferential in their habitat selection due  
638 to higher availability of prey and wider prey options. Indeed, reduced habitat selectivity in  
639 July has been observed on the west coast of Scotland, for example, thought to be due to  
640 increases in abundance of several prey species (MacLeod et al. 2004). The reduction in

641 occurrence probability and relative abundance in August may be due to minke whales  
642 becoming more selective of their foraging habitat as pre-spawning herring becomes more  
643 abundant during this month. Thus, the overall spatial distribution may become more  
644 localised compared with July, perhaps causing the reductions in relative abundance and  
645 occurrence probability. The following increase in relative abundance and occurrence in  
646 September is probably linked to increasing abundance of herring which may result in  
647 increases in feeding aggregation numbers, as observed by MacLeod et al. (2004), on the  
648 west coast of Scotland. Indeed, the changing availability of different prey species over the  
649 season may be the underlying reason for the different preferences for different  
650 environmental covariates for different months observed in other studies (MacLeod et al.  
651 2004; Anderwald et al. 2012).

652

653 With such seasonal and interannual temporal variation, combined with the preferences for  
654 fixed physiographic and dynamic oceanographic covariates observed, a more adaptive  
655 approach to management of the Southern Trench MPA would optimise the effectiveness of  
656 management measures (Tetley et al. 2008). Since minke whale occurrence probability is  
657 variable at least on the monthly scale, adaptive approaches should consider updating  
658 restrictions and mitigation measures by month. Previous adaptive management approaches  
659 have updated restrictions on weekly scales (Howell et al. 2008), so monthly updates are  
660 likely feasible.

661

#### 662 *Future Recommendations*

663

664 To better inform the adaptive management process, predictions for future months would be  
665 a logical extension to the study. This would require discarding the year variable, as including  
666 year only permits predictions within the study period and not for subsequent years (Redfern  
667 et al. 2006; Wood 2006). The model from the present study explained 26.8 % of the  
668 deviance which is in line with other cetacean habitat models (e.g., Becker et al. 2014;  
669 Tepsich et al. 2014, Gilles et al. 2016). However, the model residuals suffer from temporal  
670 and spatial non-independence and variance heterogeneity so addressing these issues in  
671 future models would make model interpretation more reliable.

672

673 A large proportion of variation remains unaccounted for by the model. Incorporating  
674 sediment type would likely improve the model's explanatory power, since sandeels occur  
675 where there are coarse, sandy sediments (Wright et al. 2000) and minke whale occurrence  
676 has previously been found to be influenced by seabed type in the study area (Robinson et al.  
677 2009; Robinson et al. in press). Differences between adult and juvenile preferences have  
678 been observed in the study area for sediment type, depth, and slope (Robinson et al. in  
679 press) suggesting that inclusion of an age-class variable and interaction would reaffirm  
680 existing demographic differences in these preferences and improve explanatory power.  
681 Inclusion of an interaction between month and the selected environmental variables may  
682 further aid in the identification of monthly changes in the preferences of whales as  
683 previously observed in other studies (e.g., MacLeod et al. 2004; Doniol-Valcroze et al. 2007;  
684 Anderwald et al. 2012). Additionally, individuals are often sighted travelling to foraging  
685 locations through potentially poorer habitat, and therefore incorporating a behavioural  
686 model term (e.g., foraging/travelling) could enable better identification of foraging habitat  
687 preferences (Hooker et al. 2011). To facilitate effective long-term management of the  
688 designated MPA, consideration of climate change effects would be a current research  
689 priority, requiring analysis of a longer-term dataset (Redfern et al. 2006). The scope of the  
690 present study meant that only a three-year dataset could be analysed but future research  
691 utilising the full 20-year CRRU dataset would enable the long-term effects of climate change  
692 to be considered to inform the adaptive MPA management process.

693

694 The unexpected relationship observed between occurrence and SST SD was likely influenced  
695 by limited data at the high and low values of SST SD, even after the  $\log_{10}$  transformation. An  
696 alternative method would be to use threshold values to firstly define what strength of  
697 gradient is considered as a 'front', and to then calculate the Euclidean distance for each  
698 sighting. Scales et al. (2014a) considered thresholds of 0.4 and 1.0 °C to compare the effects  
699 on their modelling outcomes, whereas Doniol-Valcroze et al. (2007) used a 2 °C km<sup>-1</sup>  
700 threshold to consider only the strongest temperature gradients. However, the latter method  
701 fails to capture the continuously varying frontal gradient, which is likely to be ecologically  
702 important, since greater temperature gradient fronts will persist for longer periods and thus  
703 be more attractive to marine predators (Miller et al. 2015).

704

705 Monthly-averaged composite images are a common data source in habitat models.  
706 However, the temporal variability in SST or fronts over averaged periods is concealed with  
707 temporally averaged data (Miller 2009; Scales et al. 2014a) which may result in  
708 misalignment between animals and conditions they are associated with, which may be  
709 different to conditions actually experienced (Zerbini et al. 2016). A key advantage of  
710 monthly-average composites is that they allow retention of adequate sample sizes rather  
711 than limiting data to days or weeks where SST is available (Prieto et al. 2017), as SST outputs  
712 are typically limited by cloud cover, for example. Environmental data gaps will likely reduce  
713 model accuracy, and thus, broader temporal resolutions may be more useful (Scales et al.  
714 2017). Additionally, fine-scale temporal data can be problematic in that animals may not  
715 respond to very short-term oceanographic changes (Hamazaki 2002). A lag may also occur  
716 when using fine-scale temporal data between the response and the oceanographic change,  
717 as the oceanographic change must first alter the productivity which may then influence the  
718 availability of prey species, and subsequently the predator presence leading to no  
719 relationship being detected (Hamazaki 2002). Consequently, for investigating the meso/sub-  
720 mesoscale preferences of minke whales in the study area, the temporal resolution used was  
721 considered to be adequate for this study.

722

723 Some improvements to future models could be made to minimise the effects of differing  
724 survey effort in each defined grid cell. For instance, Ingram et al. (2007) removed grid cells  
725 from the analysis which had been surveyed on less than three occasions to minimise bias  
726 stemming from these potentially under-sampled areas. Another issue often encountered in  
727 presence-absence approaches is that the high number of absence cells compared to  
728 presence cells, can result in poor model fits (Segura et al. 2008). By increasing the cell size  
729 (e.g., to 4 km<sup>2</sup>), the relative number of absence cells will also be reduced (Segura et al.  
730 2008). Additionally, methodological absences, caused by biases in the collection and/or  
731 scarcity of presence data, are more likely in areas of suitable habitat situated near recorded  
732 presences (Lobo et al. 2010) such that increasing the cell size will reduce the impact of  
733 methodological absences by expanding the recorded presence into adjacent areas.

734

735 Since cetaceans can remain underwater for long durations and make inconspicuous surfaces  
736 (Praca et al. 2009), obtaining true absence data is challenging (Praca et al. 2009; Tepsich et

737 al. 2014). ‘False absences’, where animals are not detected but may have been present  
738 (Praca et al. 2009; Tepsich et al. 2014), will often bias models. However, minke whales  
739 typically take 1.5 to 3 breaths per minute (Christiansen et al. 2015) which should increase  
740 the likelihood of detection compared with those species spending longer periods  
741 underwater. Additionally, data collection surveys in this study were conducted exclusively in  
742 ‘good’ sea conditions, greatly reducing the likelihood of failed detection (Hammond et al.  
743 2002).

744

#### 745 *Conclusions*

746

747 This study builds on research previously conducted in the study area resulting in the present  
748 designation of the Southern Trench MPA and has demonstrated that minke whales in the  
749 study area exhibit preferences for both fixed physiographic and dynamic oceanographic  
750 conditions that vary across space and time. This reinforces the idea that different areas of  
751 the study area and MPA will be of differential importance, and these will likely vary over  
752 time. To fully inform an adaptive management process, predictions for future months and  
753 years may be useful to identify which areas within the MPA will be most important and how  
754 these areas will change over time. Evidently, not all areas within an MPA will have equal  
755 value (Robinson et al. in press) and so determining those areas of high importance will be  
756 highly informative for management and the effective conservation of these coastal  
757 cetaceans within the MPA and adjacent UK waters.

758

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760

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773

774

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