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Abstract

The Antarctic Peninsula is one of the most rapidly warming regions on earth, and it is likely that the abundance and distribution of marine predators in this region will change as a result. Additionally, other anthropogenically induced factors, such as competition with commercial fisheries, may result in changes to the availability of prey for marine predators. Procellariiform seabirds are highly mobile marine predators, which target specific habitat characteristics associated with the underlying distribution of prey and areas of increased prey availability. We use surveys conducted from ship transects and hurdle models, to estimate the summer distribution and relative density of 11 seabird species within the northern Antarctic Peninsula marine ecosystem. Covariates included in hurdle models differed among species, however sea surface temperature and depth were frequently associated with seabird occurrence and had the greatest explanatory power across many species. Null models based on observation data were always better at predicting seabird density than models which included environmental covariates. This suggests that the main driver of distribution patterns is the broad-scale habitat features, and more fine scale aggregations within these broad-scale ranges are harder to predict. Our seabird distribution models reflect previously known habitat associations, species hotspots, and community organization relative to oceanic and coastal marine processes. Application of species distribution models will benefit the assessments of critical habitat and also potential responses to climate change and anthropogenic disturbance, which will provide insight into how these species may change in polar ecosystems.

Key words: Climate change, ecosystem oceanography, Fisheries management, Species Distribution modelling,

Introduction

40 The Antarctic Peninsula region is one of the most-rapidly changing parts of our planet with a rise in
41 atmospheric temperature of nearly 3°C since 1951, coinciding with a decrease in winter sea-ice
42 duration (Meredith and King 2005, Stammerjohn et al. 2008, Cook et al. 2016). Such large-scale
43 physical changes have the potential to cause alteration to the marine ecosystem across a range of
44 trophic levels (Loeb et al. 2009, Ducklow et al. 2013). Indeed, changes in sea surface temperature as
45 a result of climate change, are sometimes associated with demographic changes, and in some cases
46 population collapse (Morrison et al. 2015, Rilov 2016). This may be a result of underlying changes in
47 the distribution of prey, resulting in reduced prey availability to predators. Alternatively, some species
48 may shift their distributions in response to a changing environment (Parmesan and Yohe 2003). For
49 an area that is changing rapidly, documenting such processes will be important when evaluating how
50 Antarctic and other geographic regions may change in the future. Long-term declines are hard to
51 detect and the key to our understanding will be the establishment of baseline data describing the at-
52 sea distribution of all species. For some groups, seabirds in particular, information about the location
53 and size of breeding colonies in the region is sparse, leading to gaps in our baseline understanding of
54 their distribution and abundance.

55

56 As the environment continues to change along the Antarctic Peninsula region, some species of seabird
57 may decline. For example, Hinke et al. (2017b) predict continued declines in Adélie penguin (*Pygoscelis*
58 *adeliae)* populations at the northern extent of their range. For many species, it is likely that regional
59 warming will result in population range shifts (Grémillet and Boulinier 2009). In addition to warming,
60 other anthropogenically induced factors, such as competition with commercial fisheries, can also
61 result in changes to prey availability for marine predators, leading to changes in their foraging ecology
62 (Bertrand et al. 2012), which can then lead to subsequent population change (Bost et al. 2015). In the
63 Antarctic Peninsula region, there is concern regarding the commercial harvest of Antarctic krill
64 *Euphausia superba,* the main prey item for many Southern Ocean seabirds (Trathan et al. 2018). Krill
65 biomass in this region may already be in decline (Atkinson et al. 2004, Atkinson et al. 2008, , but see
66 Cox et al. 2018a). Although many species in this study have much broader diets that include squid and
67 mesopelagic fish, many of these mid-trophic dietary items also consume krill (Nemoto et al. 1988,
68 Barrera-Oro 2002). Indeed, there is concern that krill depletion in key foraging areas for krill-
69 dependent predators may cause population-level impacts (Mangel and Switzer 1998, Hinke et al.
70 2017a).

71

72 Seabirds are considered indicators of the status of the marine environment (Parsons et al. 2008). For
73 example, demographic traits of seabird populations can be used to improve understanding about

74   ocean climate variability (Jenouvrier et al. 2003), the localised abundance of prey items (McLeay et al.

75   2009) and to detect illegal fisheries (Weimerskirch et al. 2020). Procellariiforms are pelagic seabirds

76   comprising albatrosses, petrels, shearwaters and storm-petrels, and are the most abundant flying

77   seabird group in Antarctica. They are colonial breeders and usually return to the same breeding site

78   annually. One egg is laid annually (or every two years for some species of albatross), and parents

79   alternate nest attendance during egg incubation and chick provisioning. Many procellariiforms employ

80   a dual foraging strategy of interspersed long (6 – 29 days) and short (1 – 5 days) foraging trips providing

81   for their young whilst maintaining adult body condition during the chick-rearing period (e.g.

82   Weimerskirch et al. 1994, Granadeiro et al. 1998, Baduini and Hyrenbach 2003). Procellariiform

83   seabirds are highly mobile, frequently associated with specific habitat characteristics, and forage

84   across a range of spatio-temporal scales (Hunt Jr and Schneider 1987). Broad-scale habitat

85   characteristics such as sea surface temperature may restrict the wider distribution of seabirds, whilst

86   high density aggregations may occur at a finer scale within a species' broad range (Becker and

87   Beissinger 2003, Waggitt et al. 2020). For example, sea surface temperature limits the broad-scale

88   distribution of short-tailed albatrosses (*Phoebastria albatrus*), whilst their fine- and meso-scale

89   foraging behaviour coincides with proxies of prey availability such as chlorophyll-a and topography

90   (Suryan et al. 2006). These multi-scale distribution patterns are a result of prey patchiness, which is

91   often associated with fine- (< 10 kms) or meso- scale (10s to ~100 kms) oceanographic features

92   including eddies and fronts (van Franeker et al. 2002, Bost et al. 2015). The distribution of breeding

93   seabirds is also limited by the distance from the breeding site, given that breeding individuals must

94   return frequently to incubate eggs or provision chicks. Finally, both inter- and intra- specific

95   competition for prey may help to shape seabird distribution at-sea (Wakefield et al. 2011, Trathan et

96   al. 2018).

97

98   Areas of increased species abundance, diversity or trophic transfer can be referred to as biological

99   hotspots (Santora et al. 2017a). By identifying seabird hotspots, we can provide information on the

100   size, persistence, and distribution of areas that are key to trophic coupling in the marine ecosystem

101   (Santora et al. 2017b). The use of animal-borne biologging devices such as GPS has improved our

102   understanding of the at-sea distribution of some species of seabirds in the region, but does not provide

103   information about relative density (animals km^{-2}), community or population structure. The assessment

104   of ecosystem and climate dynamics would benefit from an improved understanding about the at-sea

105   density and distribution patterns of other seabird species, as well as species associations and

106   interactions. Shipboard surveys provide a means to improve our understanding but are expensive and

107   are on the decline compared to biologging studies. Thus, the gaps in our knowledge of seabird

108 abundance and distribution in the Antarctic Peninsula region leads to challenges when trying to

109 quantify the impacts of disturbance or change within the area.

110

111 To better understand the implications of environmental change and anthropogenic disturbances, such

112 as the commercial krill harvest in the Antarctic Peninsula region on seabirds, we can apply species

113 distribution models to quantify habitat use. As such, observations of at-sea seabird distribution and

114 abundance, derived from ship-based surveys, can be used to estimate species density and distribution

115 (e.g. Oppel et al. 2012, Santora et al. 2017b, Waggitt et al. 2020). Ecological models that link seabird

116 observations to environmental characteristics are frequently used to describe the distribution within,

117 and predict the distribution beyond, the survey region (e.g. Clarke et al. 2003, Oppel et al. 2012),

118 although extrapolations outside of the survey region will provide less robust estimations, and thus

119 should be interpreted with caution (Yates et al. 2018). Here, we use seabird surveys conducted from

120 extensively replicated ship transects, and multi-scale ecological models, to estimate the summer

121 distribution and relative density of procellariformes in the northern Antarctic Peninsula marine

122 ecosystem. We use presence/absence models to estimate the broad-scale range of each species and

123 to gain a baseline understanding about how their distributions are limited by broad-scale

124 environmental characteristics. We then use density models to estimate the mesoscale areas within

125 these broad species ranges where increased abundance of individuals are observed. These relative

126 density models highlight the areas which may provide improved foraging habitats within the broader

127 species range. The implications of these distribution patterns may be used for future assessments

128 including understanding important areas for krill consumption or evaluating the potential impacts of

129 the krill fishery.

130

131 **Materials and methods**

132 Data collection

133 The U.S. Antarctic Marine Living Resources (AMLR) Program conducted annual ecosystem monitoring

134 surveys throughout the northern Antarctic Peninsula region during summer (January-March) from

135 2003 to 2011. A fixed grid of stations and transects were sampled (average spacing of 20 nm) to assess

136 physical and biological oceanographic conditions and to map the distribution and abundance of krill

137 and air-breathing predators. The survey area was partitioned by the South Shetland Islands, with

138 oceanic waters to the north, and coastal waters to the south towards the Antarctic Peninsula. Ocean

139 circulation in this region reflects inputs from the Antarctic Circumpolar Current (ACC), outflow from

140 the Weddell Sea Gyre, and inflow from coastal upstream regions along the western Antarctic

141 Peninsula that enter through western Bransfield Strait (Amos 2001, Moffat and Meredith 2018,

4

142 Trathan et al. 2018). Rugged bathymetry, including the peri-insular shelf around islands, deep basins

143 of the Bransfield Strait, and the South Shetland Trench and the Shackleton Fracture Zone ridge in

144 Drake Passage, are important drivers of hydrographic variability in the region (Figure. 1; Orsi et al.

145 1995; Thompson et al. 2009; Moffat and Meredith 2018). The southern ACC front (SACCF) is the

146 southernmost deep-reaching front of the ACC, while the southern ACC Boundary (SACCB) defines the

147 southernmost limit of ACC-derived waters (Orsi et al 1995). Additionally, the southern SACCF and

148 SACCB are important hydrographic features that concentrate primary production, krill and top

149 predators (Santora and Veit 2013, Force et al. 2015, Loeb and Santora 2015).

150

151 Standardized visual surveys of seabirds were conducted on 14 shipboard surveys during 2003-2011.

152 The extensive shipboard tracklines covered open water, bays, inlets and passages between islands.

153 Nine surveys were conducted in mid-summer (early January to early February) and 5 were in late-

154 summer (mid-February to mid-March; Santora et al. (2009), Santora and Veit (2013), Santora et al.

155 (2017b)). Strip-transect methods were used to estimate relative seabird abundance and counts were

156 made within a 90° arc out to 300 m on the side of the trackline with the best visibility (i.e. no glare). A

157 rangefinder was used to identify the 300m transect width (Heinemann 1981). All birds were counted

158 whether flying or resting on the water. Strip-transect methods assume that all seabirds up to a pre-

159 defined distance are detected because observers concentrate on a small area. All of the species

160 included in these analyses, aside from storm-petrels which would not be sitting on the water, are

161 relatively large and distinctively marked. As such, it is likely that almost all birds within the area were

162 sighted and distance sampling and associated detection functions were not performed (Buckland et

163 al. 2001). Therefore no distance or bearing data were collected for seabirds. Sea-surface conditions

164 and visibility were continuously monitored and survey effort was ceased in poor conditions (e.g.

165 Beaufort sea state >6; heavy fog impacting visibility of the 300 m strip transect, and storms). However,

166 because we cannot guarantee that birds were not missed, or account for these, we present relative

167 rather than absolute densities. Ship speed during transits between sampling stations was generally 10

168 knots (18.6 km hr^{-1}) and observers used hand-held binoculars (10x50 and 20x60) to scan from a height

169 of 13 m above sea level. Birds were detected with binoculars and by eye, and binoculars were used

170 when necessary for identification. Each sighting was assigned a time and spatial position (of the vessel)

171 and entered into a computer synchronized with the ship's navigational and acoustic system.

172

173 Data analysis

174 The purpose of our analysis was to estimate a spatio-temporal average of seabird distributions, and

175 to identify which habitats were consistently targeted. As such, we did not investigate inter-annual

176   variation in habitat use. To remove issues with unequal survey effort ship transects were divided into

177   3 km segments (n(3km segments) = 8,019), and for each species the number of sightings and the

178   number of individuals observed along each segment were summed. Segments which were not 3 km

179   in length (i.e. the end of transects where the remaining length is < 3 km) were removed from the

180   dataset, as is commonly done in these analyses (removing < 3% of all sightings). The position of the

181   midpoint of each segment was recorded along with the corresponding time that the ship reached this

182   location. For each species, the frequency of individuals sighted each year was plotted and examined

183   visually to ensure that there was no major trend in abundance across the survey years. Species which

184   were observed only in one or two years, or for which there were few sightings, were excluded from

185   the analysis. Species which were observed but excluded from the analyses comprise: Antarctic petrel

186   (*Thalassoica antarctica*), common diving petrel (*Pelecanoides urinatrix*), Kerguelen petrel

187   (*Aphrodroma brevirostris*), light-mantled sooty albatross (*Phoebetria palpebrata*), northern giant

188   petrel (*Macronectes halli*), royal albatross (*Diomedea epomophora*), snow petrel (*Pagodroma nivea*),

189   sooty shearwater (*Ardenna grisea*) and soft-plumaged petrel (*Pterodroma mollis*). Almost all observed

190   individuals were identified to species level. However, 49 % of prions were unidentified, and thus

191   Antarctic (*Pachyptila desolata,* n=3,345), thin-billed (*Pachyptila belcheri*, n=125) and unidentified

192   (n=3,401) prions were grouped together.

193

194   *Covariate data*

195   Both static and dynamic environmental variables were used in our analysis (Table 1, Figure S1). The

196   distance from the breeding colony may limit the foraging range of breeding seabirds during the

197   breeding season when birds are constrained to return to the nest frequently to incubate eggs or

198   provision young (e.g. Wakefield et al. 2011, Warwick-Evans et al. 2018). This variable was calculated

199   using R package *gDistance* (van Etten 2012) for species documented to breed on the Antarctic

200   Peninsula or South Shetland Islands, comprising: Wilson's storm-petrel *Oceanites oceanicus*, southern

201   fulmar *Fulmarus glacialoides*, Southern giant petrel *Macronectes giganteus* and cape petrel *Daption*

202   *capense*. Breeding locations were obtained from the Agreement on the Conservation of Albatrosses

203   and Petrels (ACAP), Harris et al. (2015) and (Creuwels et al. 2007). It was not possible to weight the

204   distance from the breeding colony by population size because population counts for most of these

205   species are not available for this region. Chlorophyll-a (Chl) provides a proxy for primary productivity,

206   which is frequently used to indicate areas of increased prey biomass (Suryan et al. 2012). Sea Surface

207   Temperature (SST) may limit the broad-scale distribution of seabirds as a result of the underlying

208   distribution of prey (e.g. Hunt et al. 1992). Seabed depth (Depth) may shape the distribution of some

209   species as a result of variation in prey availability (Paiva et al. 2010). For instance, interactions between

210   rough seabeds and currents in shallow water create flows which entrain and aggregate prey (Hunt

211   1999, Benjamins et al. 2015). Current speed (C) was included to identify areas where such flows are

212   particularly prevalent (Waggitt et al. 2016). Eddy kinetic energy (EKE) and sea level anomalies (MSLA)

213   provide measures of the relative intensity of mesoscale ocean circulation and are indicators of

214   dynamic oceanic features such as eddies and large-scale fronts. Fronts and eddies can be associated

215   with regions of strong upwelling, increasing the availability of nutrients in surface waters and

216   consequently increasing phytoplankton production, and prey abundance (Owen 1981, Martin et al.

217   2002). Additionally, the convergent currents associated with frontal jets can concentrate prey,

218   increasing its availability for foraging seabirds (e.g. Becker and Beissinger 2003, Sokolov et al. 2006,

219   Santora et al. 2017b). Wind speed was included to account for variation in detectability due to weather

220   conditions. High wind speeds create greater sea-surface featuring which may impact the detection

221   rate for seabirds (Camphuysen et al. 2004). Wind speed was recorded throughout the survey

222   transects, and thus represents real-time conditions. The remotely sensed dynamic covariates were

223   based on daily or monthly mean values. Remote sensing data may be subject to data gaps from cloud

224   cover. In cases where daily values were subject to missing data, monthly mean values were used. In

225   addition, environmental climatologies were calculated for each of the dynamic covariates

226   independently, by calculating the average value across January to March from 2003 to 2011.

227   Contemporaneous and climatological values for each dynamic covariate, were extracted for each data

228   point during the corresponding time period, and each of these were evaluated as described below.

229   Covariates which were correlated by > 0.7 were not included in the same models. Instead, the variable

230   which improved model performance the most (as described below) was included.

231

232   *Species distribution modelling*

233   Hurdle models were used to model the relationship between seabird sightings and environmental

234   covariates, for each species independently. Hurdle models comprise two component models; firstly

235   the probability of occurrence is modelled using a presence-absence General Linear Model (GLM) with

236   a binomial error structure, and secondly the relative density of individuals, conditional on their

237   presence, is modelled using a GLM with a zero truncated negative binomial error structure (Zuur et al.

238   2009). The hurdle approach helps to overcome the statistical challenges associated with zero-inflation

239   and overdispersion of data, as well as providing multi-scale estimates of habitat use (e.g. Goetz et al.

240   2012, Sveegaard et al. 2012, Waggitt et al. 2020): This approach provides two descriptors of habitat

241   use, discriminating between persistent presence of small groups and occasional presence of large

242   groups (Waggitt et al. 2020). The biogeographical range of most seabird species may reflect the

243   environmental conditions which influence the distribution of their prey, such as temperature and

244 depth, and this is represented by the presence-absence model. The clusters of animals within this

245 range may be associated with the environmental conditions which aggregate prey, such as eddies and

246 fronts, represented by MSLA, EKE and C, and modelled using the density model (Waggitt et al. 2020).

247 To account for non-linear relationships between the environmental predictors and the response

248 variables the second order polynomial of the values of environmental covariates were evaluated in

249 addition to the linear value. Second order polynomials were chosen rather than polynomials of a

250 higher order, or General Additive Models, to ensure ecologically plausible relationships and reduce

251 the likelihood of overfitting models (Waggitt et al. 2020). Model residuals were checked for spatial

252 and temporal autocorrelation using Morans-I tests and Auto Correlation Function (ACF) plots.

253 Uncertainty in model predictions was calculated for the final models using a non-parametric

254 bootstrapping approach (Davison and Hinkley 1997, Fieberg et al. 2020). For each species in turn, the

255 data were resampled with replacement, selecting the same number of data points as in the original

256 data frame. The resampled data were input into the final hurdle model, and the model was then used

257 to predict the relative density of individuals across the study area, and the predicted density in each

258 grid cell was stored. This was repeated 1000 times for each species and the difference between the

259 5% and 95% quantiles of predicted density in each grid cell was calculated. This provides a

260 measurement of absolute uncertainty i.e. the absolute difference between upper and lower

261 boundaries. For comparisons between species, this was standardised by dividing by the maximum

262 value. In order to identify the covariates which provided the highest predictive power for the final

263 hurdle model, we evaluated each component of the hurdle model independently (i.e. the presence-

264 absence and the density models), before combining the two models.

265

266 <u>Presence-absence models</u>

267 The presence or absence of a species in each cell was modelled as a function of each of the specified

268 broad-scale covariates independently (distance to colony, SST, Depth, Chl, Wind speed) using GLMs

269 with a binomial error structure. As all data points represented 3 km of transect, there was no need to

270 account for variation in effort between data points.

271

272 Model performance was evaluated using six-fold cross validation (Wood 2006). Data were split into

273 six equal groups randomly and models were developed using five of the six groups. The models were

274 then used to predict presence or absence of the excluded group, and predictions were evaluated to

275 determine the predictive power of the model. This process was carried out six times to ensure that all

276 groups were used for model evaluation, and the mean Area Under the Curve (AUC) value across groups

277 was taken. AUC was generated by producing a ROC curve using R package *pROC* (Robin et al. 2011)

278   and used to evaluate the predictive power of the models. AUC values may range from 0.5 to 1.0, where

279   a value of 0.5 is no different than random and 1.0 indicates a perfect model (Fielding and Bell 1997).

280   AUC values of 0.5–0.7 are often taken to indicate low accuracy, values of 0.7–0.9 indicate useful

281   applications and values of > 0.9 indicate high accuracy (Swets 1988). Model selection followed the

282   forwards stepwise selection approach. Each of the covariates was ranked according to the AUC value,

283   and the highest-ranking covariate was selected. Each of the remaining covariates was added in turn,

284   to the best model, and the covariate was retained in the model if the AUC value increased. This process

285   continued, adding more covariates until the AUC value no longer increased (Wakefield et al. 2017).

286

287   <u>Density models</u>

288   The relative density of individuals (individuals m^{-2}) when encountered was modelled as a function of

289   each of the specified mesoscale variables (MSLA, EKE, Currents, Wind speed) using GLMs with a

290   truncated negative binomial error structure in R package *countreg* (Zeileis and Kleiber 2008). We also

291   evaluated null models (i.e. no covariate) to ensure that no incorrect associations were identified for

292   species where there was low variation in the relative density of individuals. All points where no

293   individuals were observed were removed from this part of the analysis as this part of the model deals

294   with the density of individuals where they do occur (both models are combined when calculating the

295   final predictions). As with presence-absence models, six-fold cross validation was used for model

296   selection and forward stepwise selection was used to find the best model. Covariate models were

297   compared to null models to identify whether adding an environmental covariate provided a better fit.

298   Density models were evaluated using normalised root mean square error (instead of AUC) where

299   lower values indicate less residual variance.

300

301   Once the presence-absence model and the density model with the highest predictive power had been

302   identified, they were combined into a hurdle model using the *hurdle* function in package *pscl* (Zeileis

303   et al. 2008). These models were then applied to predict the distribution of each species across the

304   survey area at a scale of 1 km^2. Areas in the southern Drake Passage where SST exceeded 2.5 ^{o}C (the

305   maximum value in the sampled area) were excluded from the prediction data frame to avoid

306   predicting beyond the range of the sampled data, and potentially inflating predictions in this area. The

307   maximum values in the prediction data for all other covariates did not exceed those in the sampled

308   area, negating concerns associated with extrapolating outside of the environmental conditions

309   surveyed. For species where wind speed was included, the mean value was used for predictions, to

310   represent typical survey conditions. The predictions were cropped to exclude areas covered by the

311   mean summer sea-ice extent (> 15% concentration, generally to the north east of the peninsula)

9

312   across the survey years, given that some of these species will be unable to forage in these conditions

313   (Ainley et al. 1993). Finally, in order to identify areas with higher densities of seabirds in the region,

314   we combined the predicted relative densities for each species: Firstly, the predicted relative densities

315   were normalised by dividing the value for each grid cell by the sum of all grid cells for that species.

316   Subsequently, the normalised predictions for each species were summed together to produce an

317   overall plot of seabird density in the region.

318

319   **Results**

320   Sightings of 11 species of procellariiform seabird occurred frequently across the survey years (Table

321   2, Figure 2). An average of 3,575 km (sd: 1,483 km) of surveys occurred each year with a maximum of

322   6,246 km of survey effort during 2011, and a total of 32,181 km across the nine years (this includes

323   repeats of transects surveyed across multiple years). Survey effort occurred between seabed depths

324   of ~20 m and ~5000 m, and sampling effort was highest in areas < 1 km deep (Figure S2). Surveys

325   occurred in areas with SST between -0.05 ^{o}C and 2.5 ^{o}C, reflecting offshore ACC water and coastal

326   Antarctic current and Weddell Sea surface water, and was highest in areas where temperature was ~2

327   ^{o} C (Figure S3). The frequencies of each species sighted across these temperature, depth and wind

328   speed ranges are shown in Figures S2, S3 and S4. Although all species showed inter-annual variation

329   in abundance, there appeared to be no major trend in abundance across survey years, except perhaps

330   for wandering albatross and black-bellied storm petrel for which there appeared to be fewer sightings

331   in recent years (Figure 2). For all species the majority of observations occurred during January, with

332   considerably fewer individuals observed during February and March. This likely reflects the increased

333   survey effort in January (ship transects across all years = 24,399 km) compared with February (5,577

334   km) and March (2,205 km).

335

336   The models which predict the presence-absence of seabirds performed moderately to well, with AUC

337   values ranging from 0.60 to 0.80 (Table 3).   There was little evidence of spatial or temporal

338   autocorrelation in model residuals for most species, although negligible levels were detected for some

339   species (southern fulmar, prions, Wilson's storm-petrel, black-bellied storm-petrel, Table S1, Figure

340   S5). The models which predicted the relative density of individuals within this region were more

341   variable, with NRMSE values ranging from 0.06 (good) to 0.26 (less good). In all cases the null models

342   provided lower NRMSE values than the covariate models. MSLA and current speed were correlated

343   (0.92) and thus only the highest scoring covariate was included in our final models. The best predictors

344   for the presence-absence models varied among species (Table 3, Figure S6), however SST and depth

345   were the covariates most frequently associated with seabird occurrence.

346

347   The distribution of species within the survey area was highly variable within and among seabird groups

348   (Figure 3). However, the distribution of seabirds reflected two ecoregions: the southern Drake Passage

349   (oceanic), and coastal Antarctic waters (coastal). Depth, SST and distance to breeding sites increase

350   with distance from the Peninsula with highest values in the southern Drake Passage. When all species

351   were standardised and combined the areas of highest density were in oceanic areas and in the mid

352   Bransfield Strait (Figure 4). The uncertainty in model predictions were species specific, with blue

353   petrels showing the highest uncertainty. For most species areas of highest uncertainty generally

354   coincided with areas of highest density. For some species (e.g. southern giant petrel, southern fulmar

355   and black-bellied storm-petrel) uncertainty was also high in areas where predicted density was lowest.

356

357   *Albatrosses*

358   Wandering and grey-headed albatross both showed an oceanic distribution (Figure 3) and were

359   associated with increased SST, Chlorophyll (wandering and grey-headed) and depth (grey-headed,

360   Figure S6), with the highest probability of occurrence over deeper, warmer water with higher

361   chlorophyll concentration. Black-browed albatrosses showed a more widespread distribution,

362   concentrated around the South Shetland Islands as well as further offshore, and associated with

363   increased SST and shallower water (Figure S6).

364

365   *Petrels*

366   Southern giant petrels and southern fulmars showed a coastal distribution whereas prions, blue

367   petrels, cape petrels and white-chinned petrels had an oceanic distribution (Figure 3). For southern

368   giant petrels the probability of occurrence was highest in shallower waters with low chlorophyll-a

369   concentrations near the colony (Figure S6). Fulmars had a quadratic association with depth and SST,

370   peaking at depths of 2 – 3 km and SST ~ 0.5^o – 1° C (Figure S6) with peak concentrations within the

371   Bransfield Strait, over deep basins. Prions and cape petrels both had a quadratic relationship with

372   depth, peaking ~3 km deep, and were negatively associated with chlorophyll-a concentration. Prions

373   were also associated with wind speed, peaking around 25 knots. Blue petrels preferred warm waters

374   > 2° C with wind speeds of 20-30 knots, and white-chinned petrels preferred deeper waters with SST

375   ~ 2° C (Figure S6).

376

377   *Storm-petrels*

378   Wilson's storm-petrel showed a highly coastal distribution (Figure 3) with probability of occurrence

379   highest in areas closer to the colony, with SST of ~1 ^{o} C and low chlorophyll concentration and wind

380   speed (Figure S6). Conversely, black-bellied storm-petrels showed a more heterogenous distribution

381   (Figure 3), with higher abundance in the Bransfield Strait and further offshore, yet very low abundance

382   in areas close to the coast. Black-bellied storm-petrels showed an increased probability of occurrence

383   at depths of ~3 km and in areas with low chlorophyll-a concentration and high wind speed (Figure S6).

384

385   **Discussion**

386   Seabirds are an important component of the marine ecosystem, and without a better understanding

387   of their baseline distributions in remote locations, we are limited in our ability to understand the

388   impacts of anthropogenic disturbance and environmental change on their abundance and

389   distribution. Specifically, relative seabird density can inform reference points in fishery management

390   plans as well as scoping planning of Marine Protected Areas. In general, our models performed well in

391   describing seabird distributions, although we noted some model limitations discussed below.

392

393   *Seabird habitat associations*

394   The models highlighted two distinct patterns of species distribution; oceanic - concentrated in the

395   southern Drake Passage and coastal – concentrated around the Peninsula and South Shetland Islands.

396   Seabirds in the Southern Ocean feed predominantly on squid, fish and krill (Croxall et al. 1985), and

397   the availability of species-specific key prey items is likely to drive the distribution of seabirds. As such,

398   it might be expected that species with similar dietary preferences could utilise habitats with similar

399   characteristics. This was observed to some extent in this study. For example, grey-headed and

400   wandering albatrosses both feed on a variety of prey items, including a high proportion of squid

401   (Croxall et al. 1985), also consuming a small proportion of krill in their diet. These species showed

402   similar distributions, with higher concentrations predicted in the southern Drake Passage region than

403   in the coastal Antarctic waters. Conversely, the predicted distribution of black-browed albatrosses,

404   which generally consume a higher proportion of fish and krill and fewer squid, was more widely

405   distributed occurring in both the oceanic and coastal Antarctic region (Santora et al. 2017b).

406   Traditionally, black-browed albatrosses are considered a shelf-feeding species, often found in neritic

407   or upper-shelf waters (Burg and Croxall 2001, Wakefield et al. 2011), and grey-headed and wandering

408   albatrosses have a more oceanic distribution (Wood et al. 2000). It has been well documented that

409   segregation of diet and foraging locations between these species provides a means of resource

410   partitioning to reduce competition (Weimerskirch et al. 1988).

411

412   Another example is for the Wilson's and black-bellied storm-petrel, which are morphometrically

413   similar, yet the Wilson's storm-petrel has a diet higher in krill, whereas the black-bellied storm petrel

414 consumes a larger amount of fish (Hahn 1998, Quillfeldt 2002). Our models indicate that Wilson's
415 storm-petrel remain in coastal regions, whereas black-bellied storm petrels are also abundant further
416 offshore and into the Drake Passage region. Whilst both species breed across the South Shetland
417 Islands, previous studies have shown little overlap in their foraging distributions and abundance
418 hotspots (Santora and Veit 2013). It is likely that these sympatrically breeding species are also resource
419 partitioning in order to reduce competition. However, in other cases where one might expect to see
420 similarities in the distribution of species with similar diets, this is not the case. For example, southern
421 fulmars, blue petrels and cape petrels all consume 80 – 85 % krill in their diet (Croxall et al. 1985). Yet,
422 observations and models suggest that fulmars remain in coastal waters, in areas with lower SST
423 whereas blue petrels and cape petrels were concentrated in the Drake Passage region in areas of
424 higher SST. Both cape petrels and fulmars breed in the region, and this may be constraining the
425 distribution of fulmar to more coastal regions, although it is unclear why this constraint does not apply
426 to cape petrels. It is plausible that species that consume high proportions of krill may prefer foraging
427 further offshore, yet in some cases may be constrained to coastal areas during the breeding season.
428 Since 87 % of krill has been estimated to be distributed in oceanic environments (Atkinson et al. 2008),
429 this could explain the preferences we found for seabirds with a high proportion of krill in their diet.
430 We recognise that species distributions change during the course of breeding, with brood or early
431 chick-rearing being particularly constrained. For some management applications understanding how
432 distributions differ during these periods will be important. Nevertheless, our analyses included data
433 across different periods of breeding, enabling us to capture important generalities about species
434 distributions.
435
436 *Broad scale presence-absence models*
437 SST and depth were the covariates in the most parsimonious models describing the broad-scale
438 distribution of flying seabirds in this region, and at least one of these covariates was included in models
439 for all species (Table 3, Figure S6). All models for species for which SST was important and with an
440 oceanic distribution showed a positive or quadratic relationship between seabird occurrence and SST
441 peaking at 2° C or above. For coastal species, this relationship peaked below 1° C. The relationship
442 between oceanic species and depth was always positive or quadratic peaking at ~3 km or above. For
443 coastal species this was more variable. Adding chlorophyll or distance to breeding colony into the
444 models improved the predictive power of some models from both groups. Black-browed albatrosses
445 did not clearly fit either group, instead showing more heterogenous distributions across both habitat
446 types. Some of the covariates selected in the final models showed some level of correlation (Table S2),
447 so it is challenging to disentangle the exact effect each has on species distributions. However, the

448   addition of each variable in the final models improved their predictive power and as such we can be

449   confident that they can be associated with the distribution of these species. Previous studies (e.g.

450   Weimerskirch et al. 1997, Wakefield et al. 2011, Scales et al. 2016) provide strong evidence that all of

451   these variables can influence the at-sea distribution of seabirds. We discuss how each of the variables

452   in our final models may be associated with the distribution of seabirds.

453

454   SST is frequently associated with the preferred foraging habitats of many species of seabirds (e.g

455   Wakefield et al. 2011, Scales et al. 2016, Dehnhard et al. 2019), with birds generally showing a

456   preference for a specific thermal range within their available habitat. This may be associated with the

457   thermal requirements of the prey items sought, and the availability of lower trophic level species for

458   consumption by these prey items. Alternatively, SST may indicate different water masses, for example

459   oceanic versus regions of coastal influences. The broad scale variation of SST within the NAP reflects

460   water masses among ACC, coastal currents in Bransfield Strait and Weddell Sea that are critical for

461   zooplankton communities and krill species distribution (Loeb and Santora 2015).

462

463   Seabird foraging areas are often associated with bathymetric aspects, with many species showing

464   clear preferences for neritic, shelf-break or upper shelf-slope waters (e.g Weimerskirch et al. 1997,

465   Warwick-Evans et al. 2016, Santora et al. 2017b), and others showing a preference for deeper oceanic

466   waters (Hunt Jr et al. 1990). Upwelling associated with shelf edges and bathymetric features transport

467   nutrients to the surface (Bakun 1996), increasing phytoplankton growth, and consequently

468   concentration of higher trophic level species (Prézelin et al. 2000, Croxall and Wood 2002, Cox et al.

469   2018b). Additionally bathymetric features such as canyons, in nearshore areas may aggregate prey, or

470   interact with mesoscale features leading to prey retention, increasing its availability to seabirds

471   (Lavoie et al. 2000, Embling et al. 2012). In deeper waters mesoscale ocean dynamics may be

472   enhancing biological processes, and aggregating prey. For example, mesoscale fronts and eddies such

473   as the SACCF occur in the deeper oceanic waters, and it is likely that seabirds foraging in the oceanic

474   environment are targeting such features. Indeed, models suggest that krill is advected in the ACC

475   (Atkinson et al. 2008), with most of the population further offshore.

476

477   Chlorophyll concentration is frequently used to provide a measure of phytoplankton in the water

478   column. Phytoplankton provides a key food supply for many prey species and, as such, chlorophyll

479   concentration is frequently used as a proxy for prey availability. Relationships between chlorophyll

480   concentration and the abundance of marine predators have been observed (e.g. Scott et al. 2010,

14

481 Santora et al. 2017a, Cox et al. 2018b), however, these relationships are complex for a number of
482 reasons.

483

484 Firstly, it is likely that a time-lag exists between elevated chlorophyll concentration and elevated
485 predator abundance, given that predators do not feed directly on phytoplankton, but on the small fish
486 and krill which consume phytoplankton. As such it has been suggested that chlorophyll concentration
487 may not adequately reflect prey abundance (Santora et al 2012). A time-lag between the abundance
488 of predators and prey may also exist if prey move away from areas as predators arrive (Fauchald 2009).
489 Additionally, areas of increased prey abundance may be less important to predators than areas of
490 predictable prey availability (e.g. Boyd et al. 2015, Boyd et al. 2017, Waggitt et al. 2018), particularly
491 for those species considered in this study, which generally forage in the upper water column and
492 surface waters. Seabirds may also show hierarchical foraging behaviour between prey patches of
493 varying spatial scales (Fauchald et al. 2000, Fauchald and Erikstad 2002), which may further explain
494 why prey abundance does not always correspond with predator abundance at some spatial scales.
495 Additionally, in some cases sub-surface maximum chlorophyll values (the maximum chlorophyll
496 recorded at any depth across the water column) provides a better indication of increased prey
497 abundance, than near-surface measurements (Scott et al. 2010, Embling et al. 2012). Finally,
498 uncertainty in estimations of chlorophyll concentration using remote sensing approaches is often high
499 in turbid waters, particularly in coastal areas (Cui et al. 2020), potentially biasing inferred relationships.

500

501 In this study the relationship between chlorophyll concentration and seabird density for those species
502 for which chlorophyll was included in the final model, was negative. The majority of these species
503 were those whose distribution was concentrated offshore in the ACC, and not in the coastal waters of
504 the Bransfield Strait where chlorophyll concentrations were higher, due to spring ice break up. It is
505 plausible that by including sub-surface chlorophyll concentration in these models, these relationships
506 may be different, however we highlight the complexity in relating predator abundance with
507 chlorophyll concentration.

508

509 Distance to the breeding colony was included in the final models for two of the five species breeding
510 in this location and for which breeding locations are known. The probability of occurrence was
511 negatively associated with distance to the colony for all models in which it was included. This covariate
512 is frequently associated with distributions of central place foragers, including seabirds, which are
513 constrained to return frequently to the breeding site to provision offspring (e.g. Wakefield et al. 2011,
514 Warwick-Evans et al. 2018). As such, they are limited in the distance they may travel during foraging

515   trips, and it is not surprising that distance to the breeding colony is included in the models for some
516   of these species. For three of the five species which breed in the region no association with distance
517   to the colony were observed. This may be because not all Antarctic colony locations are known for
518   many species, and species which are particularly wide ranging and oceanic are unlikely to remain near
519   breeding colonies.

520

521   Wind speed showed variable relationships with the presence of four species of seabirds. Prions and
522   blue petrels were associated with wind speed with peak relative density at wind speeds of 20 – 30
523   knots, whereas for Wilson's storm-petrel this association was negative, and for black-bellied storm-
524   petrel was positive. Peaks in relative density at mid-range wind speeds (non-linear) do not imply that
525   wind speed is a significant driver as it is likely to be a result of interactions with habitat and location
526   within the study area. Additionally, birds may be more flighty as wind speed increases, but this may
527   be masked by waves at higher wind-speeds. The variation between two similar storm-petrel species,
528   with varying distributions (oceanic and coastal), is an indication that it is indeed a result of interactions
529   between habitat and location within the study area. It remains plausible that the association between
530   Wilson's storm-petrel and wind speed is related to detectability. This highlights the difficulty of
531   accounting for detection when it naturally varies across environmental gradients of interest.

532

533   *Mesoscale density models*
534   In all of the density models the null model provided an equally good predictive power as the covariate
535   model, and thus null models for density were used in the final hurdle models for all species. It is likely
536   that different environmental drivers operate within coastal and oceanic domains given the complex
537   bathymetry in coastal areas. Pelagic ecosystems are highly dynamic systems, and it is likely that the
538   influence of ocean dynamics is variable across habitat types. Finer-scale and species-specific models
539   may enable the detection of associations within one of these two habitats (coastal versus oceanic).
540   This requires knowledge of the foraging behaviour and prey of the species, and the key physical
541   processes in the region. The dynamic aggregation and dispersion of birds means that group size can
542   be highly variable. As such, perhaps presence/absence is then driving distributions given that a species
543   range is more or less consistent.

544

545   ***Model performance and limitations***
546   Our AUC values indicate that the models generally performed moderately to well in their power to
547   predict the presence or absence of seabirds within the study area. AUC values for covariate models
548   for all species were higher than the null models, which supports the inclusion of these covariates in

549 the models. There was more variation in the NRMSE values, indicating that the density of individuals
550 was more predicable in some species than others. The inclusion of null models instead of covariate
551 models for density suggests that variations in aggregation size for many species are not linked to
552 prominent environmental variations (that we have identified and included) in the region, and the main
553 driver of distribution patterns is the variation in the presence-absence of a species rather than
554 variations in their numbers. There may also be mismatch in scale between the fine-scale aggregations
555 of birds, and the mesoscale biophysical variables that were included in the models, and as such, these
556 may not accurately reflect prey distributions at smaller scales (e.g Santora et al. 2009, Santora and
557 Reiss 2011, Abrahms et al. 2018). Given the AUC values associated with the models we can be
558 confident that the broad-scale prediction of the distributions of most species are indicative of their
559 overall distributions. However, for species with a higher NRMSE value we should be cautious of over-
560 interpreting the finer-scale densities within the broad species range.

561

562 The uncertainty in model predictions were highly species specific, although the highest uncertainty
563 generally coincided with areas of highest density. This is likely to be a result of high variability in the
564 abundance of individuals in each grid cell. For example, if the data selected in some model iterations
565 included cells with high abundance, the predicted distributions in these areas would be large,
566 however, if in other iterations cells with much lower abundance were sampled, these predictions
567 would be lower. As a result the uncertainty would be higher in habitat types where these high
568 abundances were observed. For some species (e.g. southern giant petrel, southern fulmar and black-
569 bellied storm-petrel) uncertainty was also high in areas where predicted density was lowest. This may
570 be because species which aggregate may have greater uncertainty due to variable group size, whereas
571 solitary animals may have greater uncertainty in presence/absence.

572

573

574 Biases may be introduced into ecological models in a variety of ways, and we highlight two potential
575 causes of bias in this study. Firstly, strip-transect methods assume that all seabirds up to a pre-defined
576 distance are detected because observers concentrate on a small area. However, there is a chance that
577 during some weather conditions birds may be missed. In this study, the majority of species are large
578 and distinctly marked, and we believe that it is unlikely that many were missed. However, because we
579 cannot guarantee this, we present relative rather than absolute densities. Additionally, in order to
580 account for variation in detection rates between species as a result of weather conditions we have
581 included wind speed as a sample covariate. As such we do not believe that our models are biased in
582 this way. Secondly, there is potential inflation or deflation of apparent abundance due to movement

583   of flying birds relative to the survey platform. Seabirds may be attracted or repelled by the presence

584   of the vessel (Bailey and Bourne 1972), with some species, including some albatross species being

585   persistent ship-followers (Tasker et al. 1984). Additionally, the majority of flying birds travel faster

586   than ship speed, and thus the chance of them entering the observers field is a function of their speed

587   relative to the ship (Gaston et al. 1987). As such, Tasker et al. (1984), suggest a snapshot method is

588   used to correct for bird movement, whereby a series of instantaneous counts of all flying birds occur

589   regularly throughout the transect. In this study we used a continuous method to count flying seabirds

590   and thus there is a chance that ship attraction or flux may introduce bias in our results. Accounting for

591   all biases and errors remains challenging given that individuals cannot be uniquely identified. There

592   was some evidence of autocorrelation in model residuals for four species, although this was deemed

593   negligible (Diniz-Filho et al. 2003, Hawkins et al. 2007, Gaspard et al. 2019).

594

595   In order to conduct robust analyses with large sample sizes we included all seabird sightings in the

596   analyses, including both flying and resting individuals. As such, we may have inadvertently included

597   individuals that were commuting through a particular habitat type and not foraging. However, given

598   that the majority of sightings recorded during transects were of individuals in flight, it was necessary

599   to include all sightings. Many of these species are visual pursuit foragers, which forage after spotting

600   prey items from the air, and thus an individual observed flying seabird is considered foraging.

601   Additionally, previous studies show that time spent in an area can be used to infer foraging behaviour

602   (Warwick-Evans et al. 2015), and it is likely that species were observed in areas where they were

603   spending more time, and thus are likely to have been foraging.

604

605   For all species, using climatological values for SST and contemporaneous values for Chlorophyll-a

606   concentration provided the best model fit. Mannocci et al. (2017) provide a detailed evaluation of the

607   appropriate scales of environmental covariates for species distribution models. They conclude that

608   associations with large scale and persistent oceanographic features are best modelled with

609   climatological covariates. However, for mesoscale features where ephemeral processes are present

610   or interannual variability occurs, contemporaneous covariates should be used, whereas if seasonal

611   processes dominate and interannual variability is weak then climatologies are best (Mannocci et al.

612   2017). Given that all models that we evaluated which included SST provided the highest predictive

613   power when climatological covariates were included, it is likely that SST is persistent across years, and

614   represents different water masses. Conversely, contemporaneous values were the better predictors

615   for all models which included chlorophyll-a concentration, which is likely to represent seasonality in

616 productivity, and be more variable. However, as previously discussed, relationships with chlorophyll
617 are complex and not always intuitive.

618

619 One of the limitations of this type of survey is that it is not possible to determine the life history stage
620 (sex or breeding status) of individuals observed, and for many species the distribution of non-breeders
621 or failed breeders can vary greatly from that of breeding individuals (Phillips et al. 2005). Thus, these
622 distributions may represent breeders from some species and non-breeders from others, and it is
623 plausible that these broad scale habitat preferences may vary if models were conducted
624 independently for specific life-history stages.

625

626 **Conclusion**

627

628 Our models provide a baseline understanding of important habitat characteristics for Southern Ocean
629 seabirds. This study describes how seabirds generally show either coastal or oceanic distributions, and
630 that patterns are driven by presence/absence, with large scale climatic variables. Finer-scale
631 processes, such as those at fronts or within submarine canyons, not associated with prominent
632 environmental gradients could influence aggregations within these species' ranges. By gaining this
633 baseline understanding, we can further enhance understanding about the impacts that environmental
634 change and anthropogenic disturbance may have on ecologically important species in this remote and
635 iconic environment. Understanding which species are likely to overlap with fisheries, and where these
636 overlaps may occur, is an important consideration when establishing fisheries management
637 frameworks. Baseline estimates of species distributions will be particularly important as the Antarctic
638 marine ecosystem changes in the future, particularly in the context of ongoing climate change, but
639 also with increased competition from recovering marine mammal populations, and as the potential
640 impacts of krill harvesting are realised.

641

642 Data Availability
643 All seabird sightings data are available upon request from Dr. Jarrod Santora at the National Oceanic
644 and Atmospheric Administration, National Marine Fisheries Services, Southwest Fisheries Science
645 Center; e-mail: jarrod.santora@noaa.gov.

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650

651 **References**

652 Abrahms, B., K. L. Scales, E. L. Hazen, S. J. Bograd, R. S. Schick, P. W. Robinson, and D. P. Costa. 2018.
653   Mesoscale activity facilitates energy gain in a top predator. Proceedings of the Royal Society
654   B: Biological Sciences **285**:20181101.

655 Ainley, D. G., C. A. Ribic, and L. B. Spear. 1993. Species-habitat relationships among Antarctic
656   seabirds: a function of physical or biological factors? The Condor **95**:806-816.

657 Amos, A. F. 2001. A decade of oceanographic variability in summertime near Elephant Island,
658   Antarctica. Journal of Geophysical Research: Oceans **106**:22401-22423.

659 Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and
660   increase in salps within the Southern Ocean. Nature **432**:100-103.

661 Atkinson, A., V. Siegel, E. Pakhomov, P. Rothery, V. Loeb, R. Ross, L. Quetin, K. Schmidt, P. Fretwell,
662   and E. Murphy. 2008. Oceanic circumpolar habitats of Antarctic krill. Marine Ecology
663   Progress Series **362**:1-23.

664 Baduini, S., and K. Hyrenbach, D. 2003. Biogeography of procellariiform foraging strategies: does
665   ocean productivity influence provisioning? Marine Ornithology **31**:101-112.

666 Bailey, R., and W. Bourne. 1972. Counting birds at sea. Pages 124-&. NEDERLANDSE
667   ORNITHOLOGISCHE UNIE C/O PAUL STARMANS, OUDE ARNHEMSEWEG 261 ….

668 Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. California
669   Sea Grant, in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz,
670   Mexico.

671 Barrera-Oro, E. 2002. The role of fish in the Antarctic marine food web: differences between inshore
672   and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. Antarctic
673   Science **14**:293-309.

674 Becker, B. H., and S. R. Beissinger. 2003. Scale-dependent habitat selection by a nearshore seabird,
675   the marbled murrelet, in a highly dynamic upwelling system. Marine Ecology Progress Series
676   **256**:243-255.

677 Benjamins, S., A. Dale, G. Hastie, M. Lea, B. Scott, J. Waggitt, and B. Wilson. 2015. Confusion reigns?
678   A review of marine megafauna interactions with energetic tidal features. Oceanography and
679   Marine Biology: An Annual Review **53**:1-54.

680 Bertrand, S., R. Joo, C. Arbulu Smet, Y. Tremblay, C. Barbraud, and H. Weimerskirch. 2012. Local
681   depletion by a fishery can affect seabird foraging. Journal of Applied Ecology **49**:1168-1177.

682 Bost, C. A., C. Cotté, P. Terray, C. Barbraud, C. Bon, K. Delord, O. Gimenez, Y. Handrich, Y. Naito, and
683   C. Guinet. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour
684   and demography. Nature Communications **6**:1-9.

685 Boyd, C., R. Castillo, G. L. Hunt, A. E. Punt, G. R. VanBlaricom, H. Weimerskirch, and S. Bertrand.
686   2015. Predictive modelling of habitat selection by marine predators with respect to the
687   abundance and depth distribution of pelagic prey. Journal of Animal Ecology **84**:1575-1588.

688 Boyd, C., D. Grünbaum, G. L. Hunt Jr, A. E. Punt, H. Weimerskirch, and S. Bertrand. 2017. Effects of
689   variation in the abundance and distribution of prey on the foraging success of central place
690   foragers. Journal of Applied Ecology **54**:1362-1372.

691 Buckland, S., D. Anderson, K. Burnham, J. Laake, D. Borchers, and L. Thomas. 2001. Introduction to
692   Distance Sampling Oxford University Press, Oxford, UK.

693 Burg, T., and J. Croxall. 2001. Global relationships amongst black-browed and grey-headed
694   albatrosses: analysis of population structure using mitochondrial DNA and microsatellites.
695   Molecular Ecology **10**:2647-2660.

696 Camphuysen, C., A. Fox, M. Leopold, and I. K. Petersen. 2004. Towards Standardised Seabirds at Sea
697   Census Techniques in Connection with Environmental Impact Assessments for Offshore
698   Wind Farms in the UK: a comparison of ship and aerial sampling methods for marine birds
699   and their applicability to offshore wind farm assessments. Report commissioned by COWRIE
700   Ltd., London. www. offshorewindfarms. co. uk.

701   Clarke, E., L. Spear, M. McCracken, F. Marques, D. Borchers, S. Buckland, and D. Ainley. 2003.
702   Validating the use of generalized additive models and at-sea surveys to estimate size and
703   temporal trends of seabird populations. Journal of Applied Ecology **40**:278-292.
704   Cook, A. J., P. Holland, M. Meredith, T. Murray, A. Luckman, and D. G. Vaughan. 2016. Ocean forcing
705   of glacier retreat in the western Antarctic Peninsula. Science **353**:283-286.
706   Cox, M. J., S. Candy, W. K. de la Mare, S. Nicol, S. Kawaguchi, and N. Gales. 2018a. No evidence for a
707   decline in the density of Antarctic krill Euphausia superba Dana, 1850, in the Southwest
708   Atlantic sector between 1976 and 2016. Journal of Crustacean Biology **38**:656-661.
709   Cox, S., C. Embling, P. Hosegood, S. Votier, and S. Ingram. 2018b. Oceanographic drivers of marine
710   mammal and seabird habitat-use across shelf-seas: a guide to key features and
711   recommendations for future research and conservation management. Estuarine, Coastal and
712   Shelf Science **212**:294-310.
713   Creuwels, J. C., S. Poncet, P. J. Hodum, and J. A. van Franeker. 2007. Distribution and abundance of
714   the Southern Fulmar Fulmarus glacialoides. Polar biology **30**:1083-1097.
715   Croxall, J., and A. Wood. 2002. The importance of the Patagonian Shelf for top predator species
716   breeding at South Georgia. Aquatic Conservation: Marine Freshwater Ecosystems **12**:101-
717   118.
718   Croxall, J. P., P. Prince, and C. Ricketts. 1985. Relationships between prey life-cycles and the extent,
719   nature and timing of seal and seabird predation in the Scotia Sea. Pages 516-533 Antarctic
720   nutrient cycles and food webs. Springer.
721   Cui, T., J. Zhang, K. Wang, J. Wei, B. Mu, Y. Ma, J. Zhu, R. Liu, and X. Chen. 2020. Remote sensing of
722   chlorophyll a concentration in turbid coastal waters based on a global optical water
723   classification system. ISPRS Journal of Photogrammetry and Remote Sensing **163**:187-201.
724   Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their application. Cambridge
725   university press.
726   Dehnhard, N., H. Achurch, J. Clarke, L. N. Michel, C. Southwell, M. D. Sumner, M. Eens, and L.
727   Emmerson. 2019. High inter-and intraspecific niche overlap among three sympatrically
728   breeding, closely related seabird species: Generalist foraging as an adaptation to a highly
729   variable environment? Journal of Animal Ecology.
730   Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in
731   geographical ecology. Global ecology and Biogeography **12**:53-64.
732   Ducklow, H. W., W. R. Fraser, M. P. Meredith, S. E. Stammerjohn, S. C. Doney, D. G. Martinson, S. F.
733   Sailley, O. M. Schofield, D. K. Steinberg, and H. J. Venables. 2013. West Antarctic Peninsula:
734   an ice-dependent coastal marine ecosystem in transition. Oceanography **26**:190-203.
735   Embling, C. B., J. Illian, E. Armstrong, J. van der Kooij, J. Sharples, K. C. Camphuysen, and B. E. Scott.
736   2012. Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine
737   ecosystems: a functional data analysis approach. Journal of Applied Ecology **49**:481-492.
738   Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. Marine
739   Ecology Progress Series **391**:139-151.
740   Fauchald, P., and K. E. Erikstad. 2002. Scale-dependent predator-prey interactions: the aggregative
741   response of seabirds to prey under variable prey abundance and patchiness. Marine Ecology
742   Progress Series **231**:279-291.
743   Fauchald, P., K. E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator–prey interactions: the
744   hierarchical spatial distribution of seabirds and prey. Ecology **81**:773-783.
745   Fieberg, J. R., K. Vitense, and D. H. Johnson. 2020. Resampling-based methods for biologists. PeerJ
746   **8**:e9089.
747   Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in
748   conservation presence/absence models. Environmental conservation **24**:38-49.
749   Force, M. P., J. A. Santora, C. S. Reiss, and V. J. Loeb. 2015. Seabird species assemblages reflect
750   hydrographic and biogeographic zones within Drake Passage. Polar biology **38**:381-392.

751   Gaspard, G., D. Kim, and Y. Chun. 2019. Residual spatial autocorrelation in macroecological and
752   biogeographical modeling: a review. Journal of Ecology and Environment **43**:19.
753   Gaston, A., B. Collins, and A. Diamond. 1987. The" snapshot" count for estimating densities of flying
754   seabirds during boat transects: a cautionary comment. The Auk:336-338.
755   Goetz, K. T., R. A. Montgomery, J. M. Ver Hoef, R. C. Hobbs, and D. S. Johnson. 2012. Identifying
756   essential summer habitat of the endangered beluga whale Delphinapterus leucas in Cook
757   Inlet, Alaska. Endangered Species Research **16**:135-147.
758   Granadeiro, J. P., M. Nunes, M. C. Silva, and R. W. J. A. B. Furness. 1998. Flexible foraging strategy of
759   Cory's shearwater, Calonectris diomedea, during the chick-rearing period. **56**:1169-1176.
760   Grémillet, D., and T. Boulinier. 2009. Spatial ecology and conservation of seabirds facing global
761   climate change: a review. Marine Ecology Progress Series **391**:121-137.
762   Hahn, S. 1998. The food and chick feeding of blackbellied stormpetrel (Fregetta tropica) at King
763   George Island, South Shetlands. Polar biology **19**:354-357.
764   Harris, C., K. Lorenz, and J. van Franeker. 2015. Important bird areas in Antarctica 2015. BirdLife Int.
765   and Env. Research & Assessment.
766   Hawkins, B. A., J. A. F. Diniz-Filho, L. Mauricio Bini, P. De Marco, and T. M. Blackburn. 2007. Red
767   herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology.
768   Ecography **30**:375-384.
769   Heinemann, D. 1981. A range finder for pelagic bird censusing.
770   Hinke, J. T., A. M. Cossio, M. E. Goebel, C. S. Reiss, W. Z. Trivelpiece, and G. M. Watters. 2017a.
771   Identifying risk: concurrent overlap of the Antarctic krill fishery with krill-dependent
772   predators in the Scotia Sea. PLoS One **12**:e0170132.
773   Hinke, J. T., S. G. Trivelpiece, and W. Z. Trivelpiece. 2017b. Variable vital rates and the risk of
774   population declines in Adélie penguins from the Antarctic Peninsula region. Ecosphere
775   **8**:e01666.
776   Hunt, G., J. Priddle, M. Whitehouse, R. Veit, and R. Heywood. 1992. Changes in seabird species
777   abundance near South Georgia during a period of rapid change in sea surface temperature.
778   Antarctic Science **4**:15-22.
779   Hunt, G. L. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds.*in*
780   Proceedings of the 22nd International Ornithological Congress, 16-22 August 1998, Durban.
781   BirdLife South Africa.
782   Hunt Jr, G., D. Heinemann, R. Veit, R. Heywood, and I. Everson. 1990. The distribution, abundance
783   and community structure of marine birds in southern Drake Passage and Bransfield Strait,
784   Antarctica. Continental Shelf Research **10**:243-257.
785   Hunt Jr, G., and D. Schneider. 1987. Scale-dependent processes in the physical and biological
786   environment of marine birds. Seabirds: feeding biology and role in marine ecosystems.
787   Cambridge University Press, Cambridge:7-41.
788   Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal
789   population dynamics of southern fulmars. Journal of Animal Ecology **72**:576-587.
790   Lavoie, D., Y. Simard, and F. J. Saucier. 2000. Aggregation and dispersion of krill at channel heads and
791   shelf edges: the dynamics in the Saguenay-St. Lawrence Marine Park. Canadian Journal of
792   Fisheries and Aquatic Sciences **57**:1853-1869.
793   Loeb, V. J., E. E. Hofmann, J. M. Klinck, O. Holm-Hansen, and W. B. White. 2009. ENSO and variability
794   of the Antarctic Peninsula pelagic marine ecosystem. Antarctic Science **21**:135-148.
795   Loeb, V. J., and J. A. Santora. 2015. Climate variability and spatiotemporal dynamics of five Southern
796   Ocean krill species. Progress in Oceanography **134**:93-122.
797   Mangel, M., and P. Switzer. 1998. A model at the level of the foraging trip for the indirect effects of
798   krill (Euphausia superba) fisheries on krill predators. Ecological Modelling **105**:235-256.
799   Mannocci, L., A. M. Boustany, J. J. Roberts, D. M. Palacios, D. C. Dunn, P. N. Halpin, S. Viehman, J.
800   Moxley, J. Cleary, and H. Bailey. 2017. Temporal resolutions in species distribution models of

801   highly mobile marine animals: Recommendations for ecologists and managers. Diversity and
802   Distributions **23**:1098-1109.
803 Martin, A. P., K. J. Richards, A. Bracco, and A. Provenzale. 2002. Patchy productivity in the open
804   ocean. Global Biogeochemical Cycles **16**:9-1-9-9.
805 McLeay, L., B. Page, S. Goldsworthy, T. Ward, D. Paton, M. Waterman, and M. Murray. 2009.
806   Demographic and morphological responses to prey depletion in a crested tern (Sterna bergii)
807   population: can fish mortality events highlight performance indicators for fisheries
808   management? ICES Journal of Marine Science **66**:237-247.
809 Meredith, M. P., and J. C. King. 2005. Rapid climate change in the ocean west of the Antarctic
810   Peninsula during the second half of the 20th century. Geophysical Research Letters **32**.
811 Moffat, C., and M. Meredith. 2018. Shelf–ocean exchange and hydrography west of the Antarctic
812   Peninsula: a review. Philosophical Transactions of the Royal Society A: Mathematical,
813   Physical and Engineering Sciences **376**:20170164.
814 Morrison, K. W., P. F. Battley, P. M. Sagar, and D. R. Thompson. 2015. Population dynamics of
815   Eastern Rockhopper Penguins on Campbell Island in relation to sea surface temperature
816   1942–2012: current warming hiatus pauses a long-term decline. Polar biology **38**:163-177.
817 Nemoto, T., M. Okiyama, N. Iwasaki, and T. Kikuchi. 1988. Squid as predators on krill (Euphausia
818   superba) and prey for sperm whales in the Southern Ocean. Pages 292-296 Antarctic Ocean
819   and resources variability. Springer.
820 Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A. F. O'Connell, P. I. Miller, and M. Louzao. 2012.
821   Comparison of five modelling techniques to predict the spatial distribution and abundance
822   of seabirds. Biological Conservation **156**:94-104.
823 Owen, R. W. 1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects.
824   Analysis of marine ecosystems:197-233.
825 Paiva, V. H., P. Geraldes, I. Ramírez, S. Garthe, and J. A. Ramos. 2010. How area restricted search of a
826   pelagic seabird changes while performing a dual foraging strategy. Oikos **119**:1423-1434.
827 Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across
828   natural systems. Nature **421**:37-42.
829 Parsons, M., I. Mitchell, A. Butler, N. Ratcliffe, M. Frederiksen, S. Foster, and J. B. Reid. 2008.
830   Seabirds as indicators of the marine environment. ICES Journal of Marine Science **65**:1520-
831   1526.
832 Phillips, R. A., J. R. Silk, J. P. Croxall, V. Afanasyev, and V. J. Bennett. 2005. Summer distribution and
833   migration of nonbreeding albatrosses: individual consistencies and implications for
834   conservation. Ecology **86**:2386-2396.
835 Prézelin, B. B., E. E. Hofmann, C. Mengelt, and J. M. Klinck. 2000. The linkage between Upper
836   Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic
837   Peninsula continental shelf. Journal of Marine Research **58**:165-202.
838 Quillfeldt, P. 2002. Seasonal and annual variation in the diet of breeding and non-breeding Wilson's
839   storm-petrels on King George Island, South Shetland Islands. Polar biology **25**:216-221.
840 Rilov, G. 2016. Multi-species collapses at the warm edge of a warming sea. Scientific reports
841   **6**:36897.
842 Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J.-C. Sanchez, and M. Müller. 2011. pROC: an
843   open-source package for R and S+ to analyze and compare ROC curves. BMC bioinformatics
844   **12**:77.
845 Santora, J. A., and C. S. Reiss. 2011. Geospatial variability of krill and top predators within an
846   Antarctic submarine canyon system. Marine Biology **158**:2527-2540.
847 Santora, J. A., C. S. Reiss, A. M. Cossio, and R. R. Veit. 2009. Interannual spatial variability of krill
848   (Euphausia superba) influences seabird foraging behavior near Elephant Island, Antarctica.
849   Fisheries Oceanography **18**:20-35.

850 Santora, J. A., W. J. Sydeman, I. D. Schroeder, J. C. Field, R. R. Miller, and B. K. Wells. 2017a.
851   Persistence of trophic hotspots and relation to human impacts within an upwelling marine
852   ecosystem. Ecological Applications **27**:560-574.
853 Santora, J. A., and R. R. Veit. 2013. Spatio-temporal persistence of top predator hotspots near the
854   Antarctic Peninsula. Marine Ecology Progress Series **487**:287-304.
855 Santora, J. A., R. R. Veit, C. S. Reiss, I. D. Schroeder, and M. Mangel. 2017b. Ecosystem Oceanography
856   of Seabird Hotspots: Environmental Determinants and Relationship with Antarctic Krill
857   Within an Important Fishing Ground. Ecosystems **20**:885-903.
858 Scales, K. L., P. I. Miller, S. N. Ingram, E. L. Hazen, S. J. Bograd, and R. A. Phillips. 2016. Identifying
859   predictable foraging habitats for a wide-ranging marine predator using ensemble ecological
860   niche models. Diversity and Distributions **22**:212-224.
861 Scott, B., J. Sharples, O. N. Ross, J. Wang, G. J. Pierce, and C. Camphuysen. 2010. Sub-surface
862   hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat
863   indicated by tidal mixing and sub-surface chlorophyll. Marine Ecology Progress Series
864   **408**:207-226.
865 Sokolov, S., S. R. Rintoul, and B. Wienecke. 2006. Tracking the Polar Front south of New Zealand
866   using penguin dive data. Deep Sea Research Part I: Oceanographic Research Papers **53**:591-
867   607.
868 Stammerjohn, S., D. Martinson, R. Smith, X. Yuan, and D. Rind. 2008. Trends in Antarctic annual sea
869   ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern
870   Annular Mode variability. Journal of Geophysical Research: Oceans **113**.
871 Suryan, R. M., J. A. Santora, and W. J. Sydeman. 2012. New approach for using remotely sensed
872   chlorophyll a to identify seabird hotspots. Marine Ecology Progress Series **451**:213-225.
873 Suryan, R. M., F. Sato, G. R. Balogh, K. D. Hyrenbach, P. R. Sievert, and K. Ozaki. 2006. Foraging
874   destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using
875   first-passage time analysis. Deep Sea Research Part II: Topical Studies in Oceanography
876   **53**:370-386.
877 Sveegaard, S., J. Nabe-Nielsen, K.-J. Stæhr, T. F. Jensen, K. N. Mouritsen, and J. Teilmann. 2012.
878   Spatial interactions between marine predators and their prey: herring abundance as a driver
879   for the distributions of mackerel and harbour porpoise. Marine Ecology Progress Series
880   **468**:245-253.
881 Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285-1293.
882 Tasker, M. L., P. H. Jones, T. Dixon, and B. F. Blake. 1984. Counting seabirds at sea from ships: a
883   review of methods employed and a suggestion for a standardized approach. The Auk
884   **101**:567-577.
885 Trathan, P. N., V. Warwick-Evans, J. Hinke, E. F. Young, E. J. Murphy, A. Carneiro, M. Dias, K. Kovacs,
886   A. Lowther, and O. Godø. 2018. Managing fishery development in sensitive ecosystems:
887   identifying penguin habitat use to direct management in Antarctica. Ecosphere **9**.
888 van Etten, J. 2012. gdistance: Distances and routes on geographical grids. R package version 1.1–4.
889   Available a t CRAN. R-project. org/package= gdistance.
890 van Franeker, J. A., N. W. van den Brink, U. V. Bathmann, R. T. Pollard, H. J. de Baar, and W. J. Wolff.
891   2002. Responses of seabirds, in particular prions (Pachyptila sp.), to small-scale processes in
892   the Antarctic Polar Front. Deep Sea Research Part II: Topical Studies in Oceanography
893   **49**:3931-3950.
894 Waggitt, J. J., P. W. Cazenave, L. M. Howarth, P. G. Evans, J. van der Kooij, and J. G. Hiddink. 2018.
895   Combined measurements of prey availability explain habitat selection in foraging seabirds.
896   Biology letters **14**:20180348.
897 Waggitt, J. J., P. W. Cazenave, R. Torres, B. J. Williamson, and B. E. Scott. 2016. Quantifying pursuit-
898   diving seabirds' associations with fine-scale physical features in tidal stream environments.
899   Journal of Applied Ecology **53**:1653-1666.

900   Waggitt, J. J., P. G. Evans, J. Andrade, A. N. Banks, O. Boisseau, M. Bolton, G. Bradbury, T. Brereton,
901   C. J. Camphuysen, and J. Durinck. 2020. Distribution maps of cetacean and seabird
902   populations in the North-East Atlantic. Journal of Applied Ecology **57**:253-269.
903   Wakefield, E. D., E. Owen, J. Baer, M. J. Carroll, F. Daunt, S. G. Dodd, J. A. Green, T. Guilford, R. A.
904   Mavor, and P. I. Miller. 2017. Breeding density, fine-scale tracking and large-scale modeling
905   reveal the regional distribution of four seabird species. Ecological Applications.
906   Wakefield, E. D., R. A. Phillips, P. N. Trathan, J. Arata, R. Gales, N. Huin, G. Robertson, S. M. Waugh,
907   H. Weimerskirch, and J. Matthiopoulos. 2011. Habitat preference, accessibility, and
908   competition limit the global distribution of breeding Black-browed Albatrosses. Ecological
909   Monographs **81**:141-167.
910   Warwick-Evans, V., P. Atkinson, R. Gauvain, L. Robinson, J. Arnould, and J. Green. 2015. Time-in-area
911   represents foraging activity in a wide-ranging pelagic forager. Marine Ecology Progress Series
912   **527**:233-246.
913   Warwick-Evans, V. C., P. W. Atkinson, L. A. Robinson, and J. A. Green. 2016. Predictive modelling to
914   identify near-shore, fine-scale seabird distributions during the breeding season. PLoS One
915   **11**.
916   Warwick-Evans, V., N. Ratcliffe, A. D. Lowther, F. Manco, L. Ireland, H. L. Clewlow, and P. N. Trathan.
917   2018. Using habitat models for chinstrap penguins Pygoscelis antarctica to advise krill
918   fisheries management during the penguin breeding season. Diversity and Distributions.
919   Weimerskirch, H., J. A. Bartle, P. Jouventin, and J. C. Stahl. 1988. Foraging ranges and partitioning of
920   feeding zones in three species of southern albatrosses. The Condor **90**:214-219.
921   Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer, and J.
922   Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. Animal
923   Behaviour.
924   Weimerskirch, H., J. Collet, A. Corbeau, A. Pajot, F. Hoarau, C. Marteau, D. Filippi, and S. C. Patrick.
925   2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the
926   extent of nondeclared fishing. Proceedings of the National Academy of Sciences **117**:3006-
927   3014.
928   Weimerskirch, H., T. Mougey, and X. Hindermeyer. 1997. Foraging and provisioning strategies of
929   black-browed albatrosses in relation to the requirements of the chick: natural variation and
930   experimental study. Behavioral Ecology **8**:635-643.
931   Wood, A., B. Naef-Daenzer, P. Prince, and J. Croxall. 2000. Quantifying habitat use in satellite-tracked
932   pelagic seabirds: application of kernel estimation to albatross locations. Journal of Avian
933   Biology **31**:278-286.
934   Wood, S. N. 2006. Generalized additive models: an introduction with R. CRC press.
935   Yates, K. L., P. J. Bouchet, M. J. Caley, K. Mengersen, C. F. Randin, S. Parnell, A. H. Fielding, A. J.
936   Bamford, S. Ban, and A. M. Barbosa. 2018. Outstanding challenges in the transferability of
937   ecological models. Trends in ecology & evolution **33**:790-802.
938   Zeileis, A., and C. Kleiber. 2008. countreg: Count Data Regression.
939   Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression Models for Count Data in R. Journal of
940   Statistical Software **27(8)**.
941   Zuur, A., E. Ieno, N. Walker, A. Saveliev, and G. Smith. 2009. Mixed effects models and extensions in
942   ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. New York, NY:
943   Spring Science and Business Media.

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Figure legends

947 Figure 1. Seabed depths and some of the key bathymetric features in the study area. Survey
948 transects are indicated in white.

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950 Figure 2. The number of individuals observed per km of effort during seabird observations
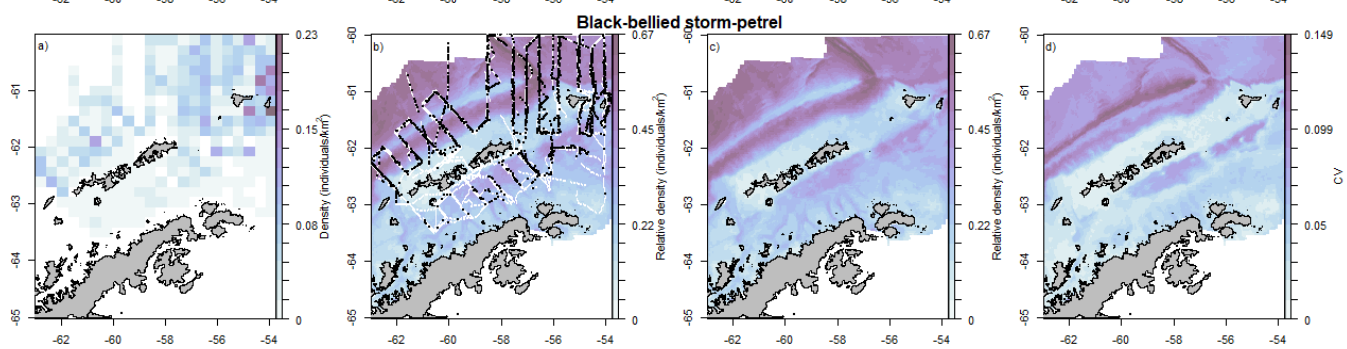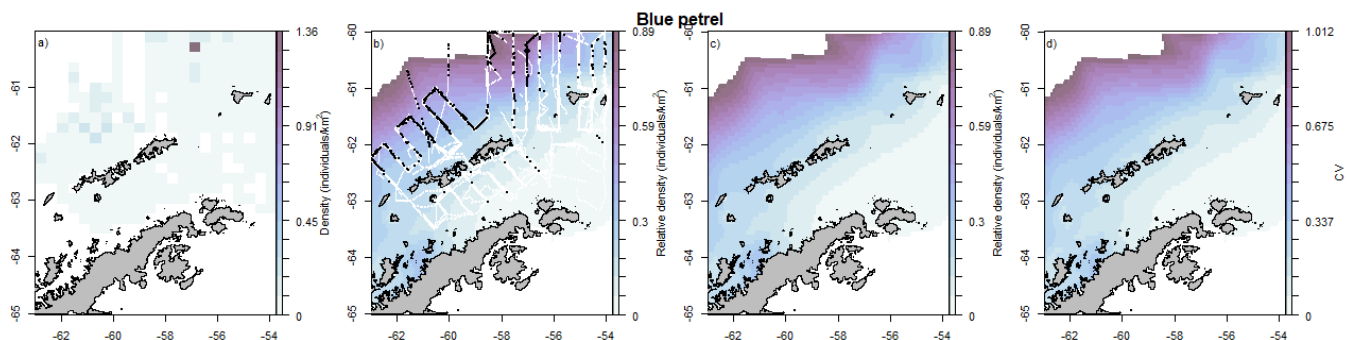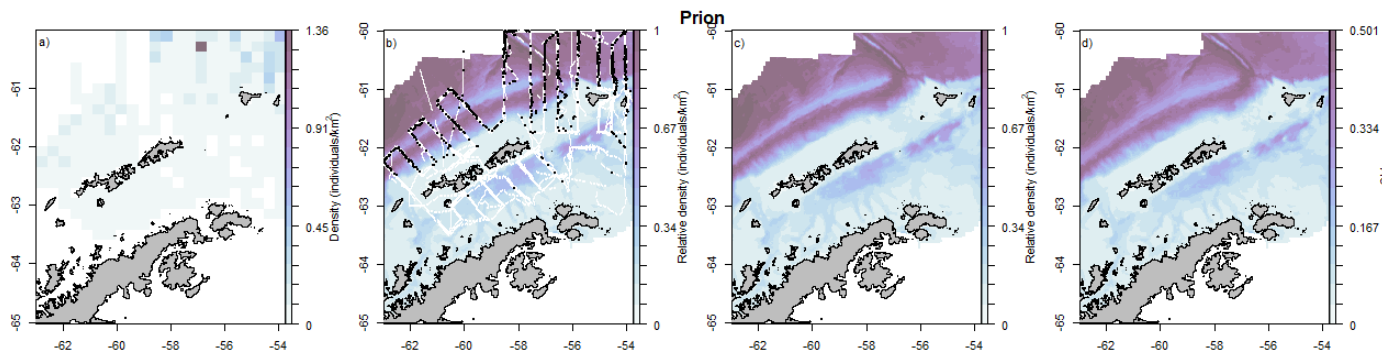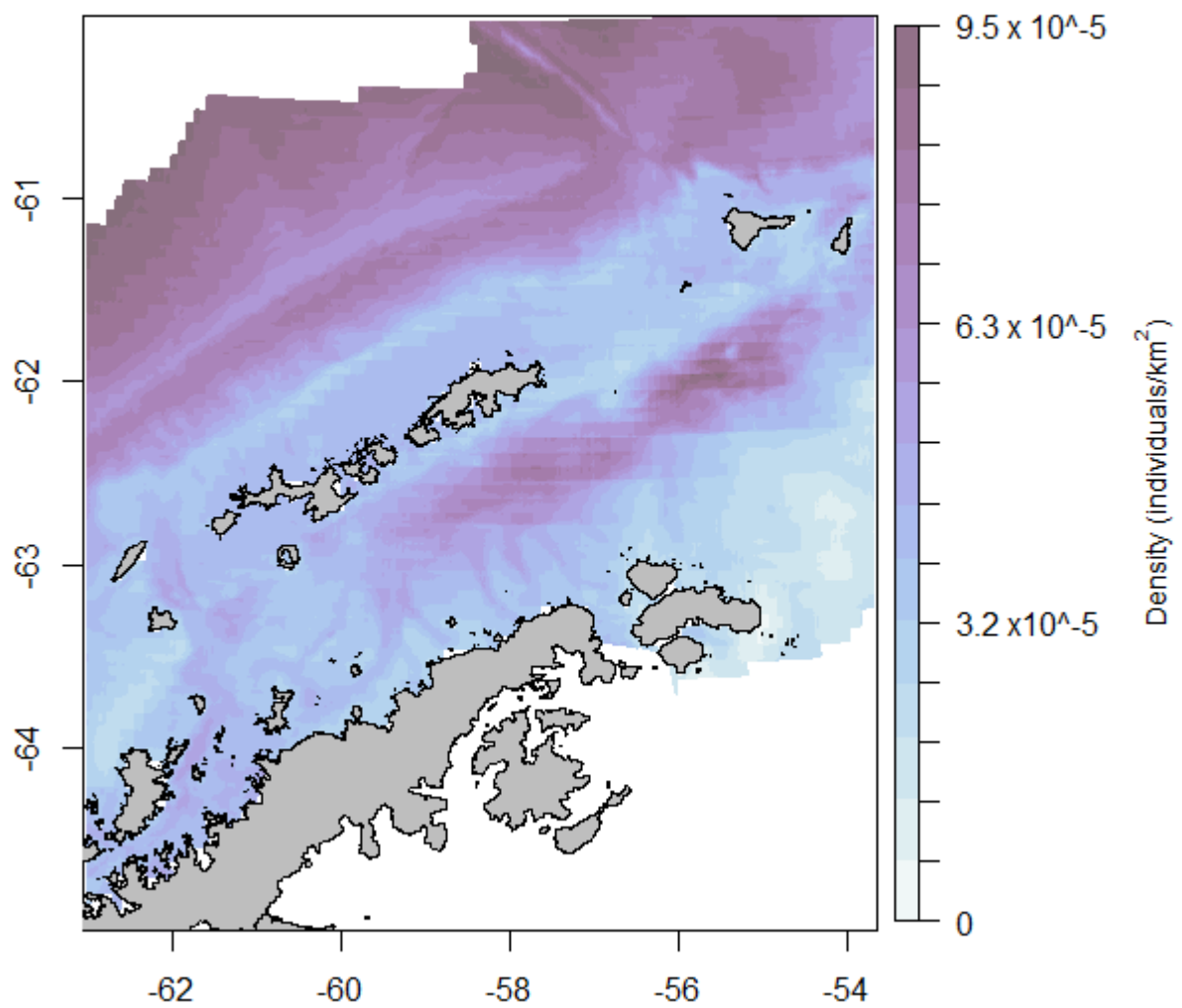951 throughout the survey period.

952

953 Figure 3. Observed and predicted distributions of flying seabirds around the western Antarctic
954 Peninsula and South Shetland Islands; a) gridded observations of species density obtained from ship
955 surveys, aggregated across all years of the survey (models were fitted to data for each year
956 independently) b) number of individuals observed in each grid cell obtained from ship surveys and
957 overlaid on predicted distributions of the relative density of species from model predictions. White
958 dots indicate cells surveyed, black dots indicate observed individuals, increasing in size with the
959 number of individuals observed c) predicted distributions of the relative density of species from
960 models, d) Uncertainty in model predictions, calculated using a non-parametric bootstrapping
961 approach.

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963 Figure 4. The combined predicted distributions of eleven species of procellariform around the
964 northern Antarctic Peninsula and South Shetland Islands. Predicted relative densities for each species
965 were normalised prior to summing all species.

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Figures

Figure 1. Seabed depths and some of the key bathymetric features in the study area. Survey transects are indicated in white.

Wandering albatross

Grey-headed albatross

Black-browed albatross

Southern giant petrel

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Fulmar

Antarctic prion

Blue petrel

White-chinned petrel

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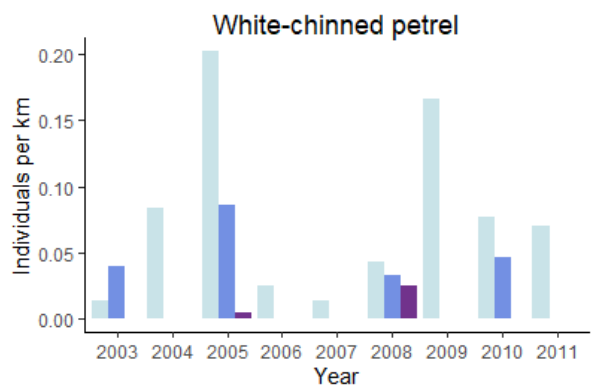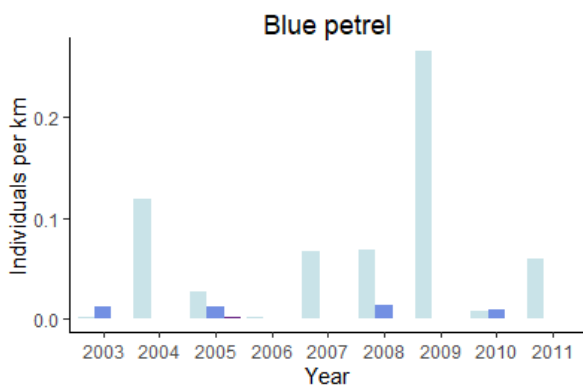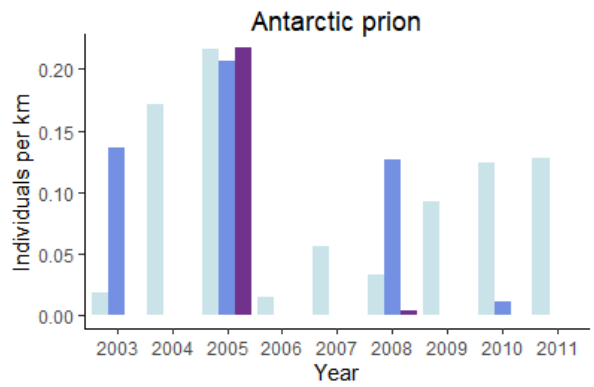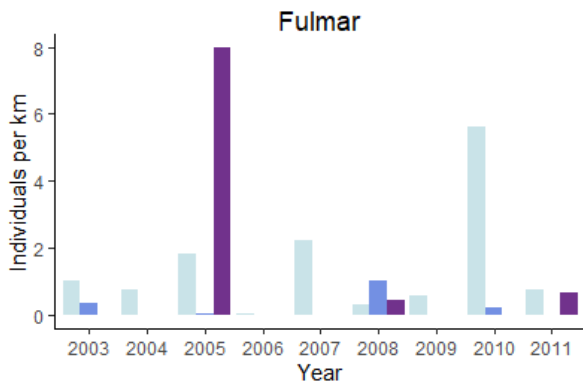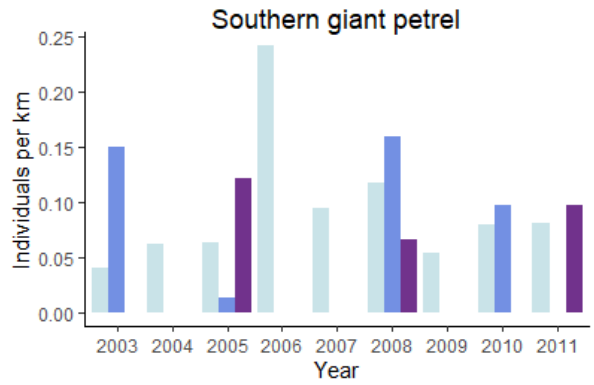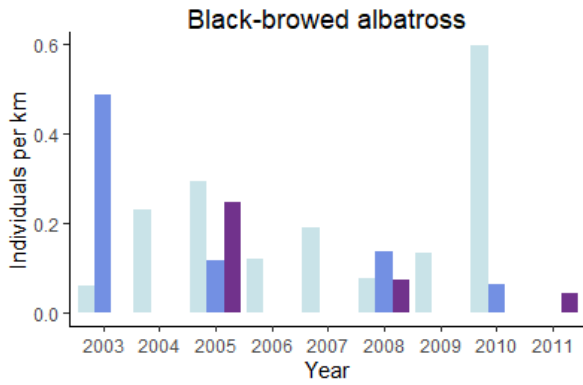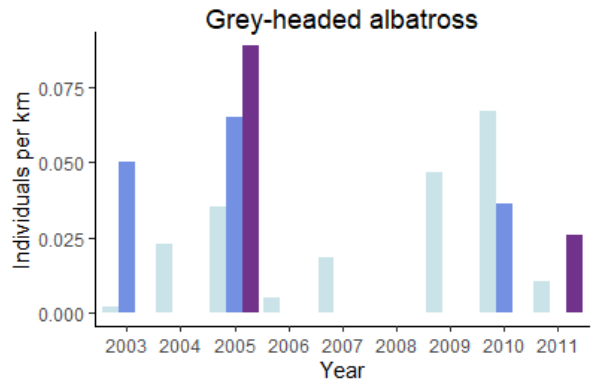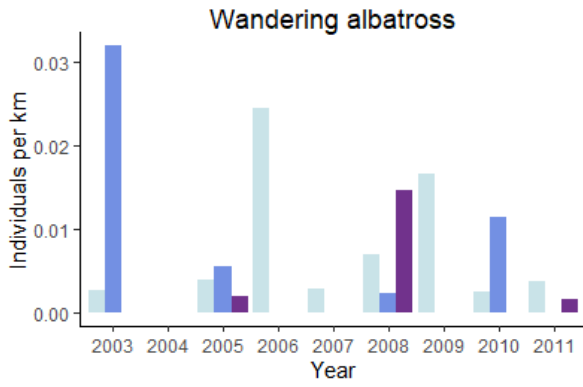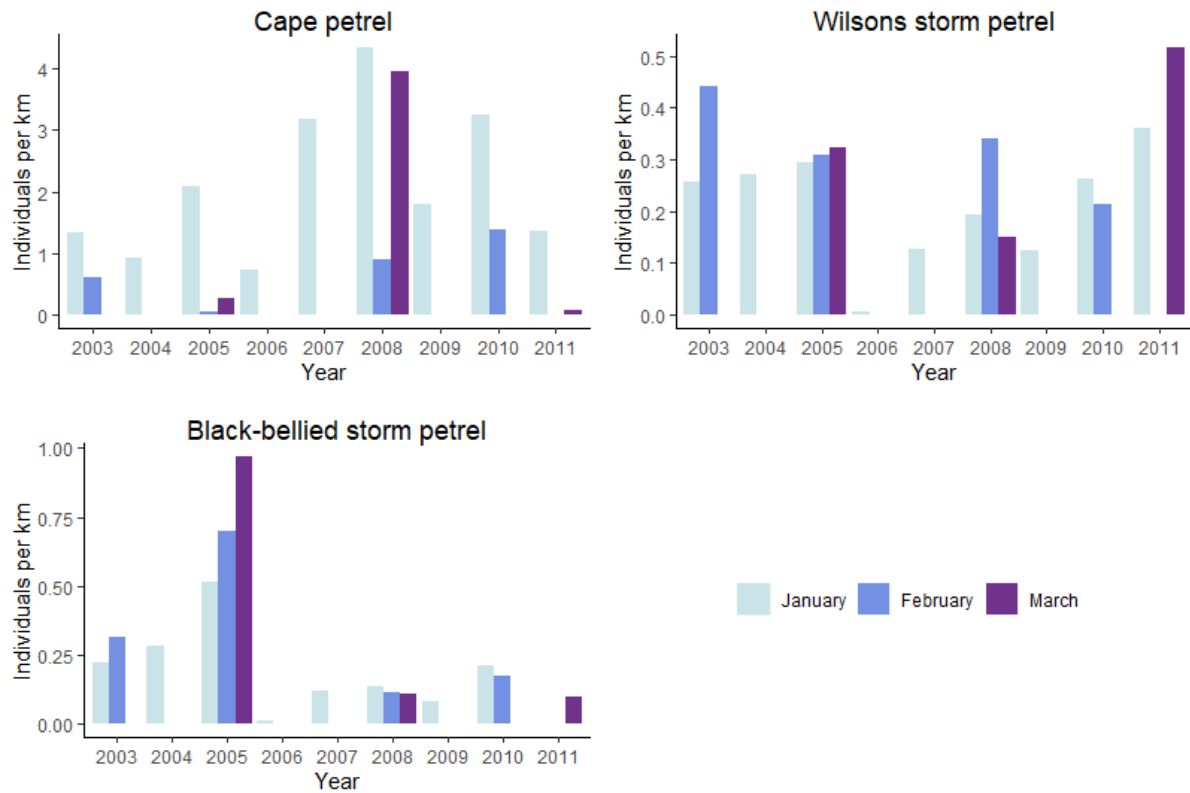
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975 Figure 2. The number of individuals observed per km of effort during seabird observations

976 throughout the survey period.

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995   Figure 3. Observed and predicted distributions of flying seabirds around the western Antarctic
996   Peninsula and South Shetland Islands; a) gridded observations of species density obtained from ship
997   surveys, aggregated across all years of the survey (models were fitted to data for each year
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1007 Figure 4. The combined predicted distributions of eleven species of procellariform around the

1008 northern Antarctic Peninsula and South Shetland Islands. Predicted relative densities for each species

1009 were normalised prior to summing all species.

1010 **Tables**

1011

1012 **Table 1.** The explanatory variables used in statistical models to predict the at-sea distribution of

1013 seabirds

Model	Covariate	Spatial resolution	Temporal resolution	Source
Presence-absence	Distance from colony (D_{col})	0.3 (km)	NA	Calculated using R package *Raster*
	Bathymetry (Depth)	0.3 (km)	NA	www.marine.copernicus.eu
	Chlorophyll-a (Chl)	4.0 (km)	Monthly	www.marine.copernicus.eu
	Sea Surface Temperature (SST)	0.083 degree	Daily	www.marine.copernicus.eu
	Wind Speed (W)		Continuous	Collected throughout transects
Density model	Mean Sea Level Anomaly (MSLA)	0.25 degree	Daily	www.marine.copernicus.eu
	Eddy Kinetic Energy (EKE)	0.083 degree	Daily	Calculated in R using data from www.marine.copernicus.eu
	Current Speed (C)	0.083 degree	Daily	Calculated in R using data from www.marine.copernicus.eu
	Wind Speed (W)		Continuous	Collected throughout transects

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1016 **Table 2.** A summary of the number of sightings and individuals observed during ship surveys of

1017 seabirds in the west Antarctic Peninsula, and South Shetland Island region.

Species	Number of individuals observed	Number of sightings observed	Mean (sd) flock size	Median (Interquartile range) flock size	Max flock size
Wandering albatross	260	208	1.1 (0.5)	1 (0)	6
Black-browed albatross	4,728	1,968	1.7 (5.5)	1 (0)	120
Grey-headed albatross	729	556	1.2 (1.4)	1 (0)	30
Southern giant petrel	2,955	1,448	1.7 (2.8)	1 (0)	60
Southern fulmar	34,633	2,582	5.7 (32)	1 (2)	1300
Prions	6,871	3,073	2.2 (9.8)	1 (1)	500
Blue petrel	1,894	629	2.0 (16)	1 (0)	500
White-chinned petrel	2,059	1,183	1.4 (3.1)	1 (0)	100
Cape petrel	51,685	2,992	7.6 (63)	2 (2)	2500
Wilson's storm-petrel	7,802	3,215	1.5 (2.5	1 (0)	100
Black-bellied storm-petrel	6,114	2,718	1.4 (1.1)	1 (0)	30

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Table 3. A summary of the explanatory variables used in the final models to describe the distribution

of seabirds in the west Antarctic Peninsula, and South Shetland Island region. Quantitative evaluation

of presence-absence and density predictions using area under the curve (AUC) and normalised root

mean squared error (NRMSE). NMRSE values for intercept only (null) models only are provided.

Species	Presence-absence model	AUC	NMRSE null model
Wandering albatross	$T + Chl$	0.7	0.26
Black browed albatross	$T + Depth$	0.6	0.09
Grey-headed albatross	$Depth + Depth^2 + Chl + Chl2 + T$	0.64	0.21
Southern giant petrel	$Depth + Chl + Chl^2 + Distance\ to\ colony$	0.63	0.12
Southern fulmar	$Depth + Depth^2 + T + T^2 + Chl + Chl^2$	0.74	0.07
Prions	$Depth + Depth^2 + W + W^2 + Chl$	0.75	0.15
Blue petrel	$T + W + W^2$	0.80	0.18
White-chinned petrel	$Depth + T + T^2$	0.67	0.1
Cape petrel	$Depth + Depth^2 + Chl + T$	0.64	0.06
Wilson's storm petrel	$T + T^2 + Chl + Chl^2 + Distance\ to\ colony + W$	0.7	0.06
Black-bellied storm petrel	$Depth + Depth^2 + Chl + W$	0.63	0.11

Supplementary Information

Table S1. Estimates for autocorrelation in model residuals using global *Morans I* tests

Species	Moran I estimate	P-value
White-chinned petrel	0.02	0.08
Wandering albatross	0.017	0.12
Prions	0.17	<0.001
Grey-headed albatross	0.006	0.32
Southern giant petrel	0.16	0.11
Southern fulmar	0.08	<0.001
Black-browed albatross	0.006	0.67

Cape petrel	0.01	0.15
Blue petrel	4.1×10^{-4}	0.36
Black-bellied storm-petrel	0.11	<0.001
Wilson's storm-petrel	0.09	<0.001

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1040 **Table S2.** Pearson's correlation coefficients between the environmental explanatory variables used

1041 in model selection. Covariates for which correlation was > 0.7 were not included in the same models.

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var 1	var 2	correlation
EKE	Wind speed	0.1
MSLA	Wind speed	0.09
Current	Wind speed	0.13
SST	Wind speed	0.14
Chl	Wind speed	0.15
Distance to fulmar colony	Wind speed	0.12
Distance to Wilson's storm-petrel colony	Wind speed	0.21
Distance to southern giant petrel colony	Wind speed	0.20
Distance to cape petrel colony	Wind speed	0.19
Distance to black-bellied storm-petrel colony	Wind speed	0.08
Depth	Wind speed	0.17
EKE	Depth	0.28
MSLA	Depth	0.33
Current	Depth	0.56
SST	Depth	0.62
Chl	Depth	0.68
Distance to fulmar colony	Depth	0.60
Distance to Wilson's storm-petrel colony	Depth	0.57
Distance to southern giant petrel colony	Depth	0.58
Distance to cape petrel colony	Depth	0.58
Distance to black-bellied storm-petrel colony	Depth	0.35
MSLA	EKE	0.18
Current	EKE	0.90
SST	EKE	0.41
Chl	EKE	0.31
Distance to fulmar colony	EKE	0.31
Distance to Wilson's storm-petrel colony	EKE	0.10
Distance to southern giant petrel colony	EKE	0.09
Distance to cape petrel colony	EKE	0.11
Distance to black-bellied storm-petrel colony	EKE	0.04
Current	MSLA	0.21
SST	MSLA	0.34
Chl	MSLA	0.09

|		
Distance to fulmar colony	MSLA	0.10
Distance to Wilson's storm-petrel colony	MSLA	0.11
Distance to southern giant petrel colony	MSLA	0.01
Distance to cape petrel colony	MSLA	0.11
Distance to black-bellied storm-petrel colony	MSLA	0.24
SST	Current	0.52
Distance to fulmar colony	Current	0.35
Distance to Wilson's storm-petrel colony	Current	0.11
Distance to southern giant petrel colony	Current	0.1
Distance to cape petrel colony	Current	0.12
Distance to black-bellied storm-petrel colony	Current	0.08
Chl	Current	0.30
Chl	SST	0.29
Distance to fulmar colony	SST	0.45
Distance to Wilson's storm-petrel colony	SST	0.16
Distance to southern giant petrel colony	SST	0.01
Distance to cape petrel colony	SST	0.14
Distance to black-bellied storm-petrel colony	SST	0.03
Distance to fulmar colony	Chl	0.42
Distance to Wilson's storm-petrel colony	Chl	0.64
Distance to southern giant petrel colony	Chl	0.63
Distance to cape petrel colony	Chl	0.65
Distance to black-bellied storm-petrel colony	Chl	0.47

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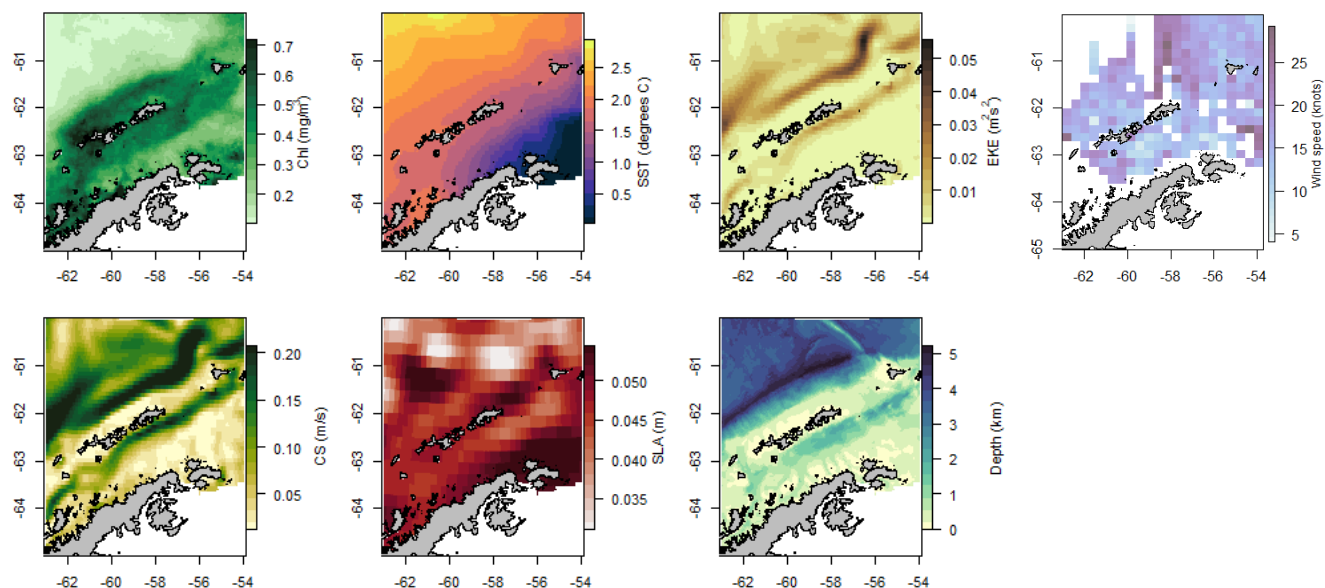
1046   Figure S1. Climatological values for the environmental variables used in hurdle models to describe

1047   the at-sea distribution of seabirds: a) Chlorophyll-a concentration, b) Sea surface temperature, c)

1048   Eddy kinetic energy, d) Current speed, e) Sea level anomaly, f) Depth.

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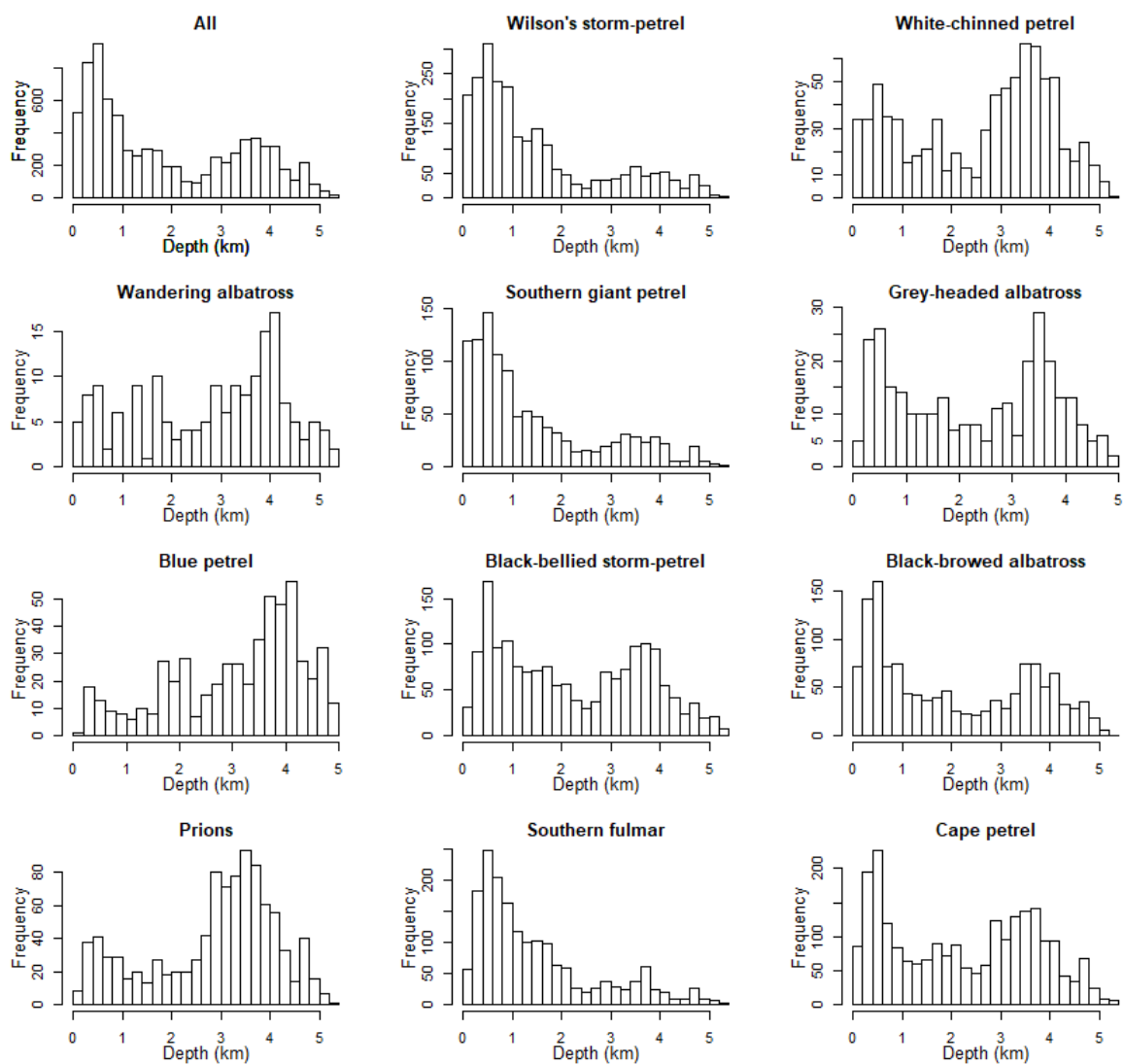
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1052   Figure S2. The frequency of sampling points a the frequency of individuals of each species sighted at
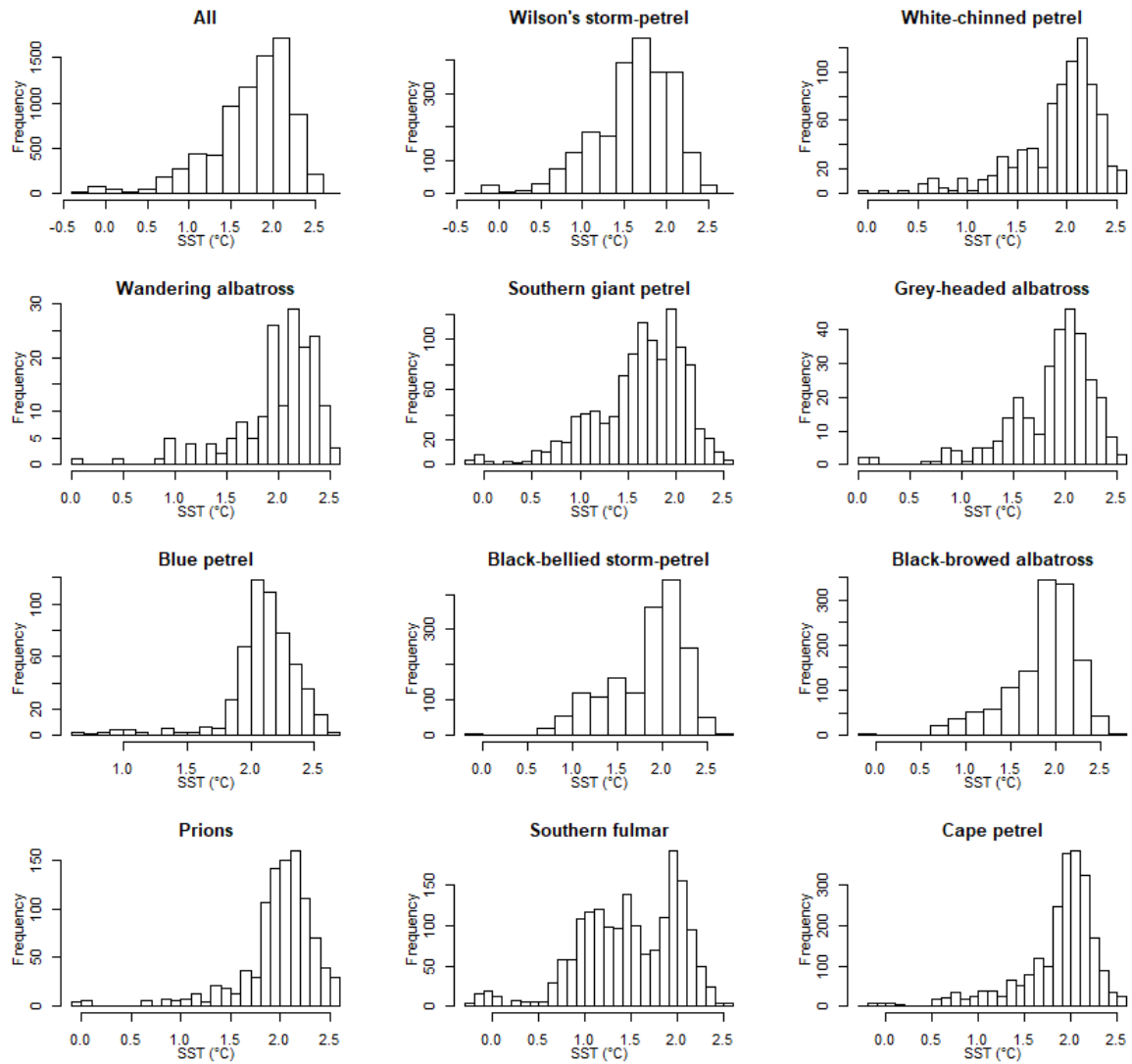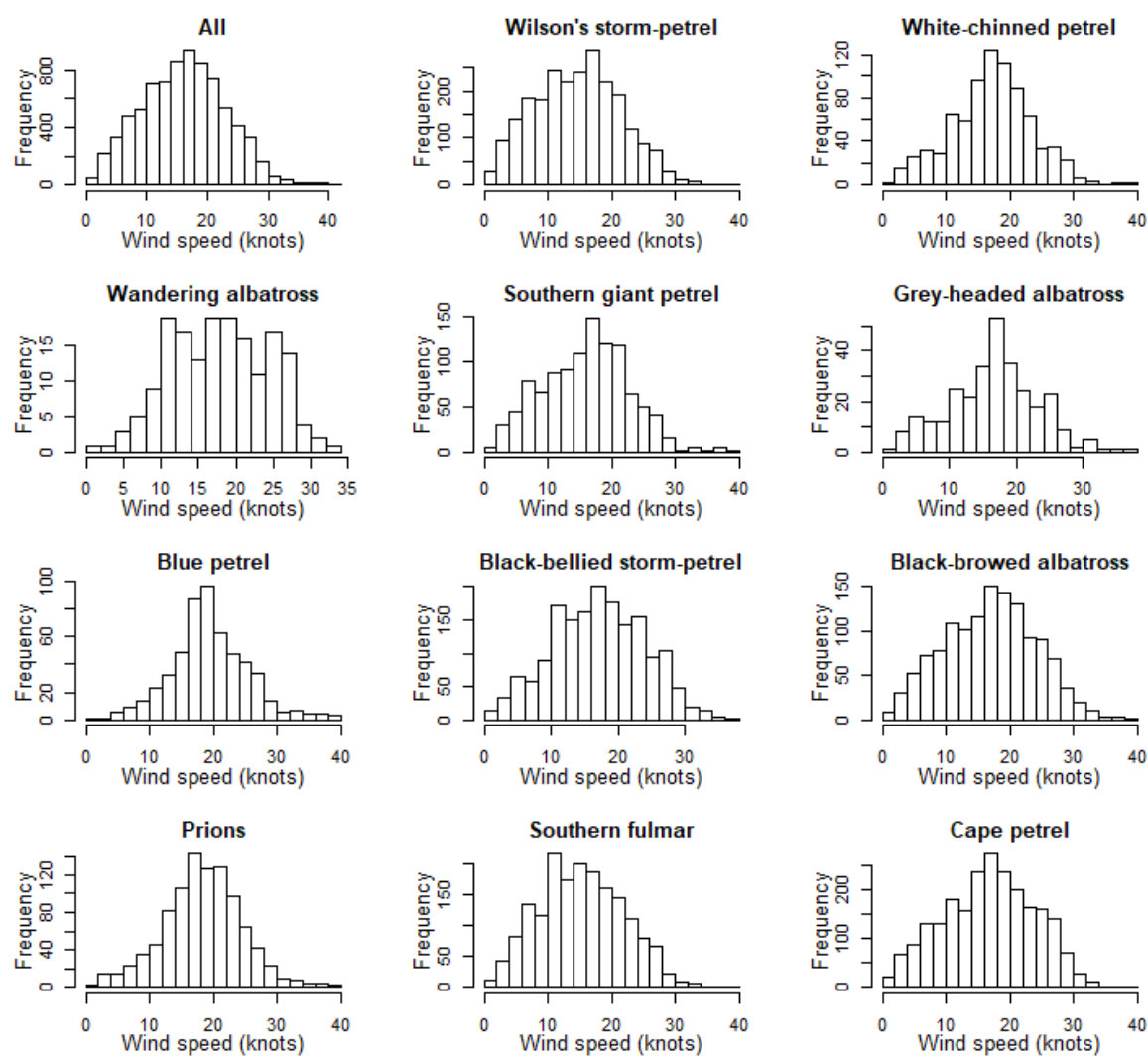
1053   different depths.

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1059   Figure S3. The frequency of sampling points and frequency of individuals of each species sighted

1060   across the temperature range.

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1063   Figure S4. The frequency of sampling points and frequency of individuals of each species sighted
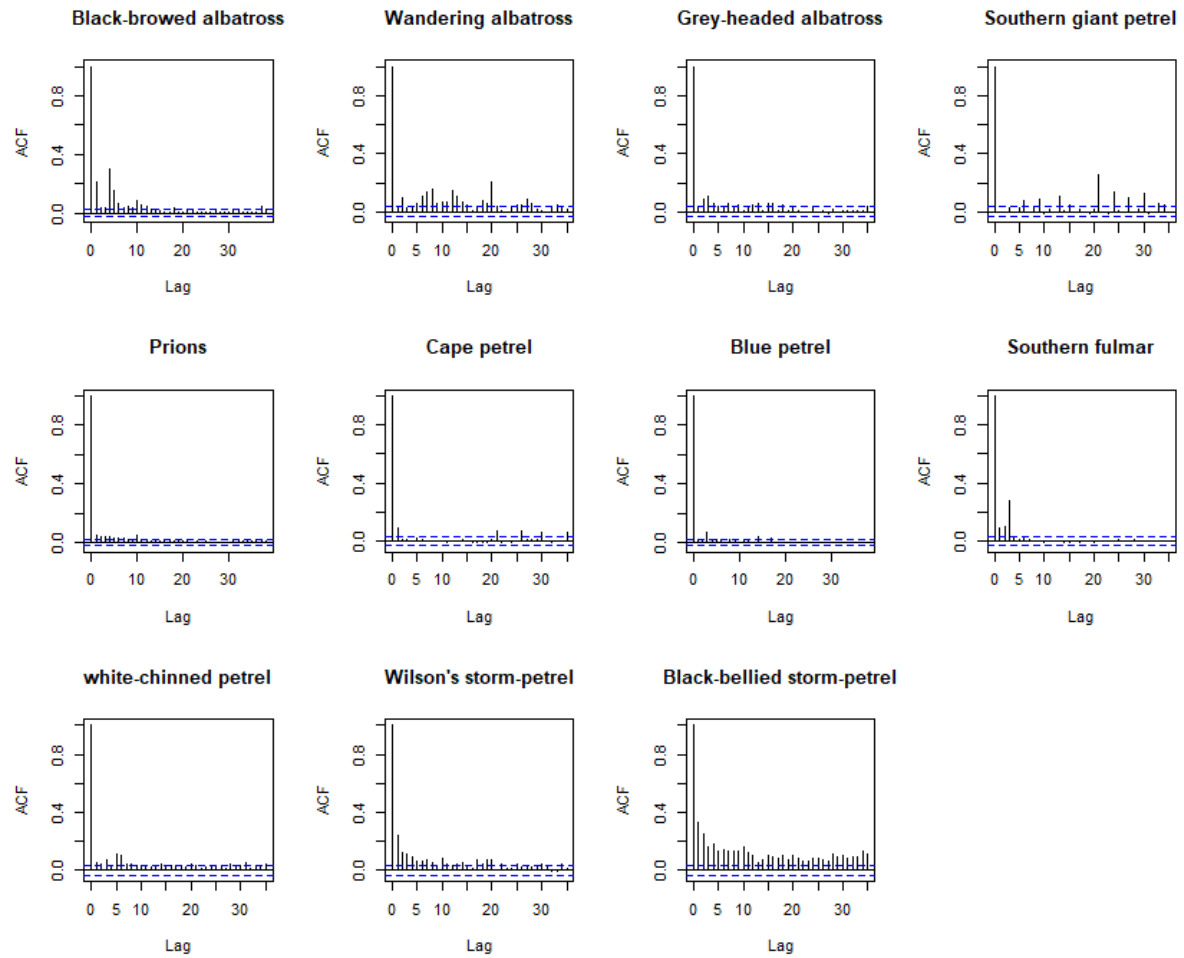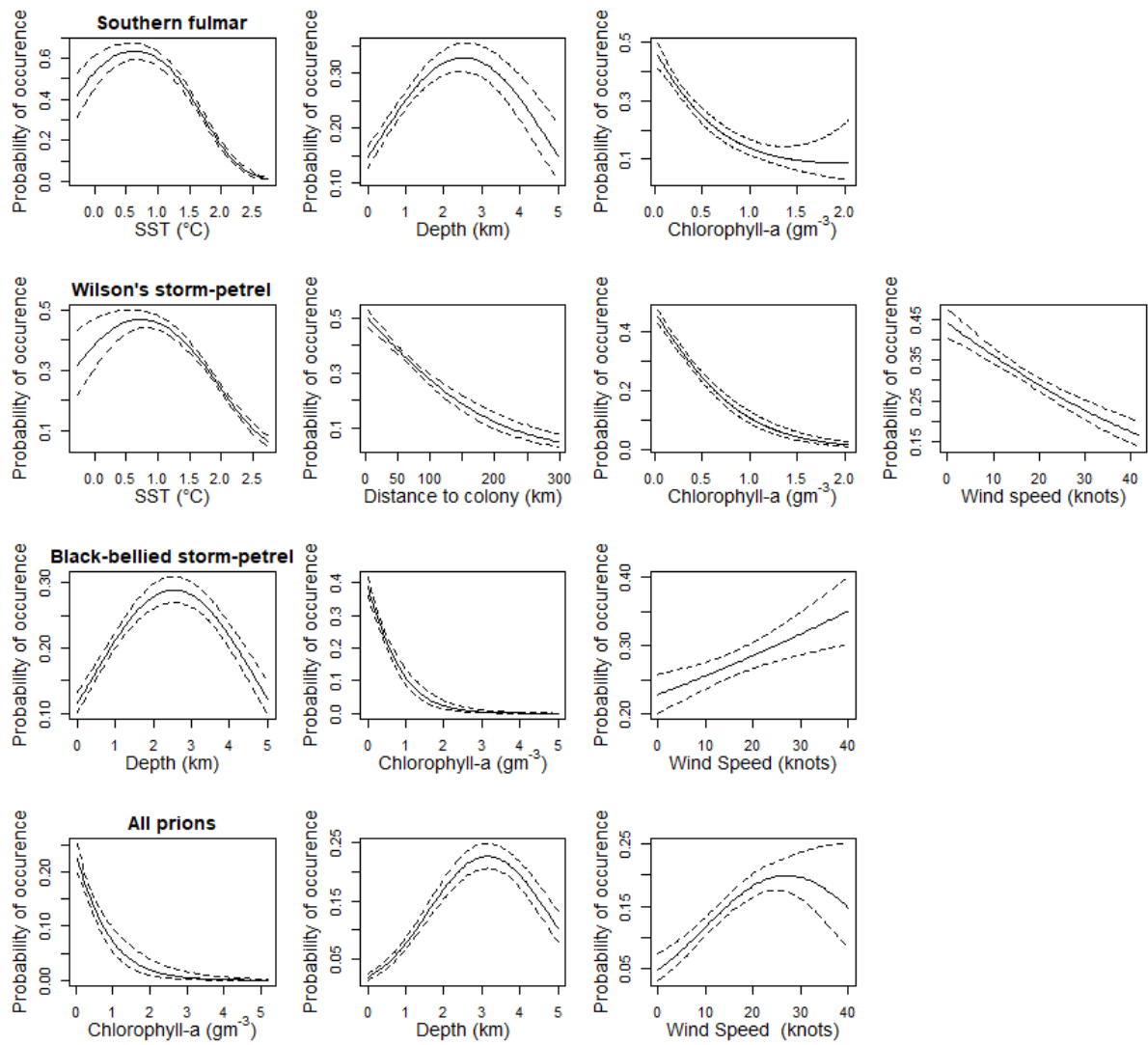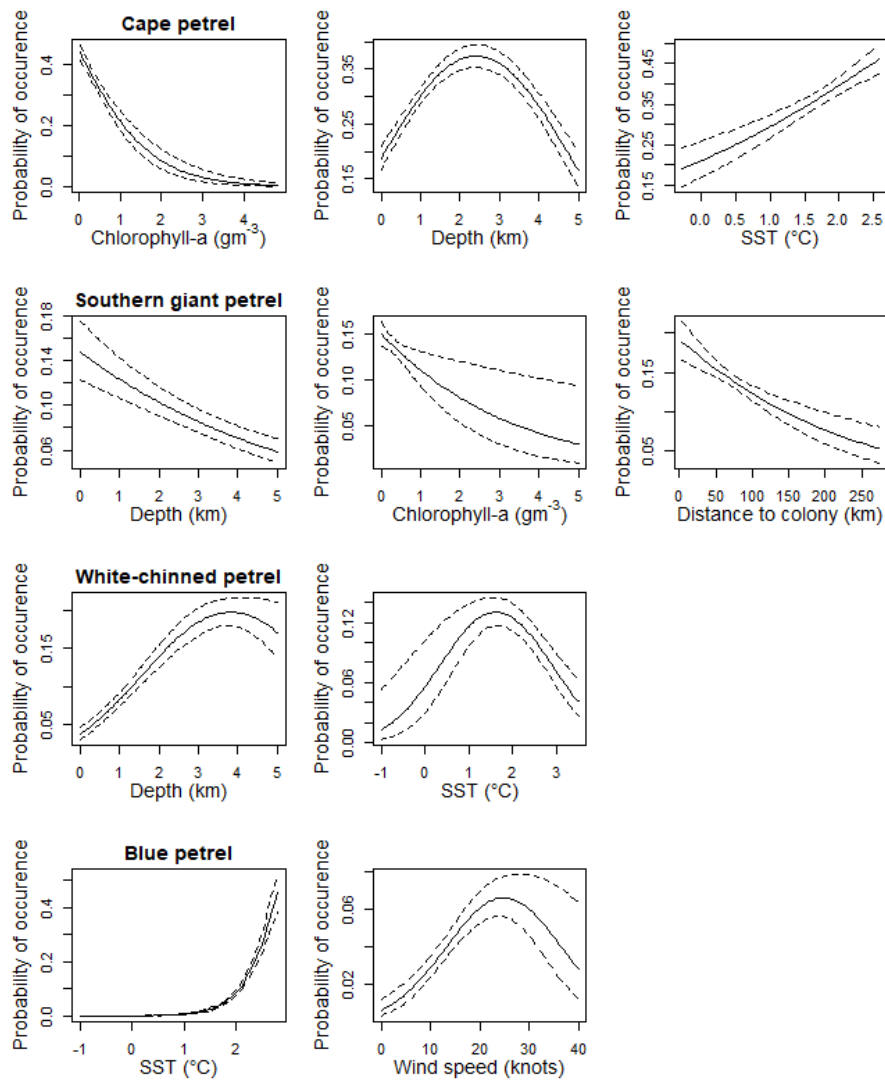
1064   across the wind speed range.

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1066   Figure S5. Autocorrelation plots for model residuals

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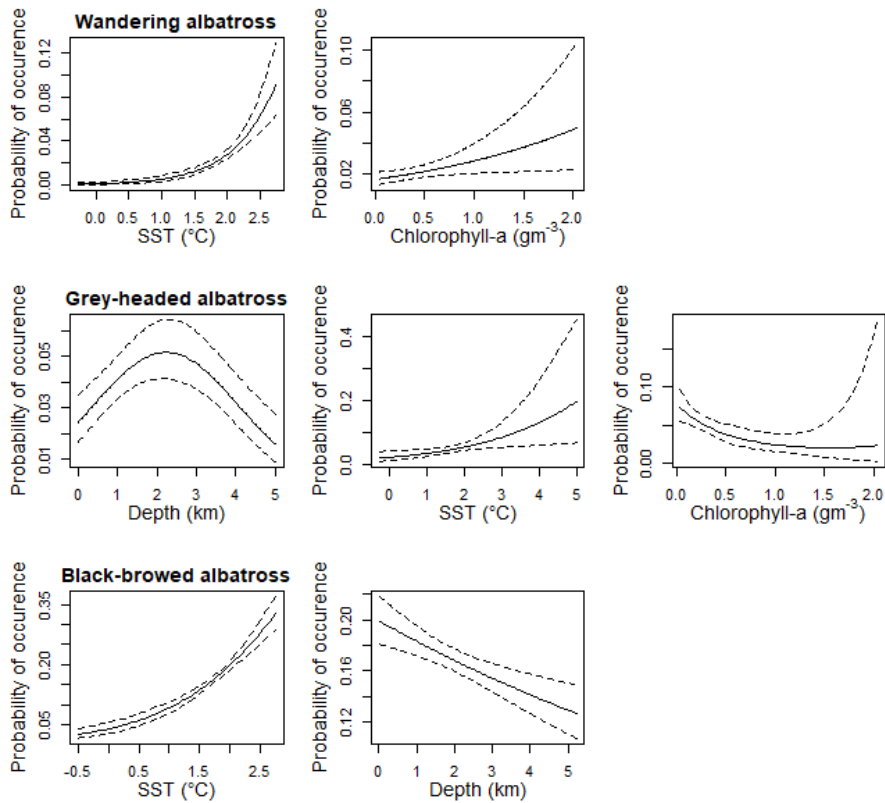1074

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1080 Figure S6. Response curves describing relationships between environmental variables and the at-sea

1081 distribution of seabirds around the Antarctic Peninsula, and South Shetland Islands, created using

1082 hurdle models. Confidence intervals were calculated using the standard errors provided with the

1083 model output.

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