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Multi-scale assessment of distribution and density of procellariiform seabirds within the northern Antarctic Peninsula marine ecosystem

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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 procellariiformes 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,

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 ($n(3\text{km segments}) = 8,019$), 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 (*Phoebastria 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 glacialis*, 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 Presence-absence models

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 Density models

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 km². Areas in the southern Drake Passage where SST exceeded 2.5 °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)

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 °C and 2.5 °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 °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 $\sim 0.5^{\circ} - 1^{\circ} \text{C}$ (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 $> 2^{\circ} \text{C}$ with wind speeds of 20-30 knots, and white-chinned petrels preferred deeper waters with SST
375 $\sim 2^{\circ} \text{C}$ (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 $\sim 1^{\circ} \text{C}$ 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,

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.

646

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650

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946 **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.

949

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

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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.

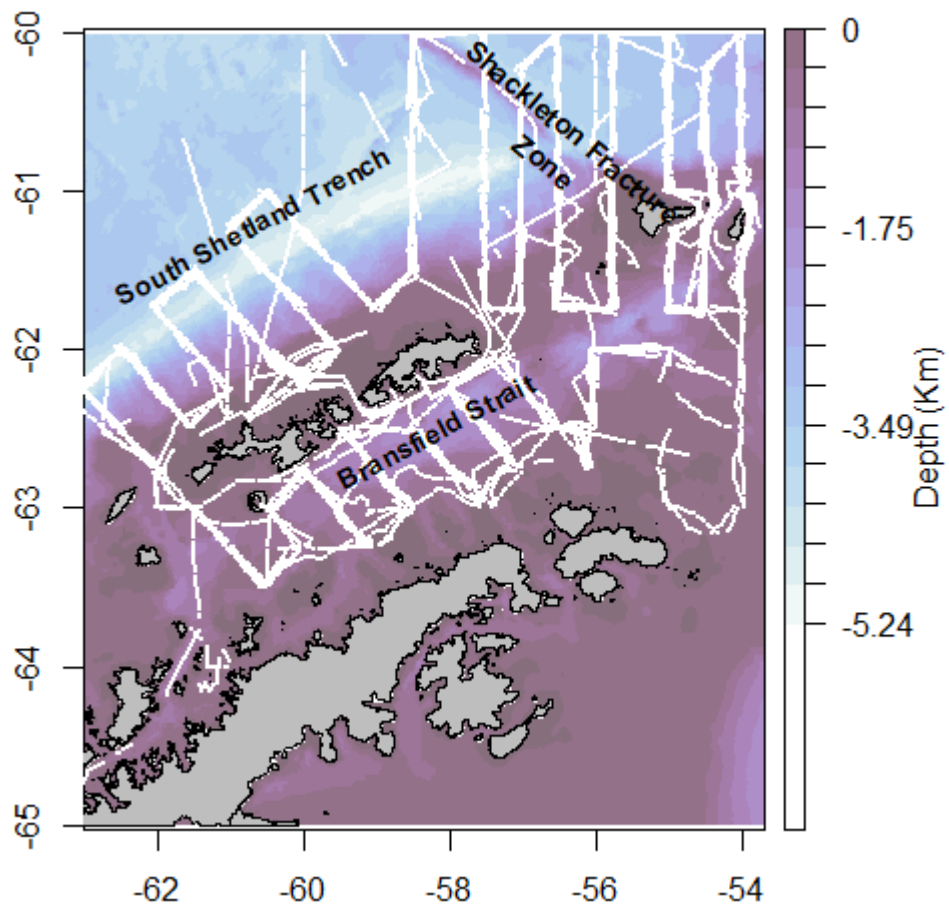
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963 Figure 4. The combined predicted distributions of eleven species of procellariiform around the
964 northern Antarctic Peninsula and South Shetland Islands. Predicted relative densities for each species
965 were normalised prior to summing all species.

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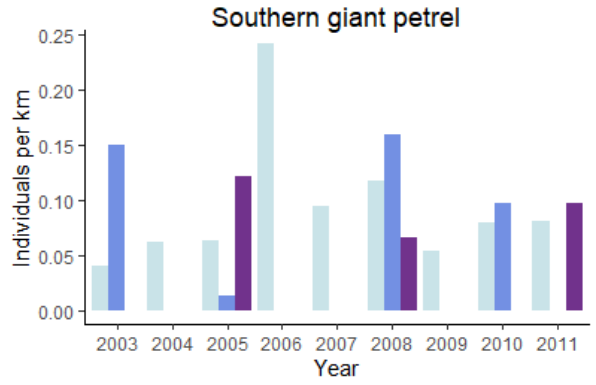
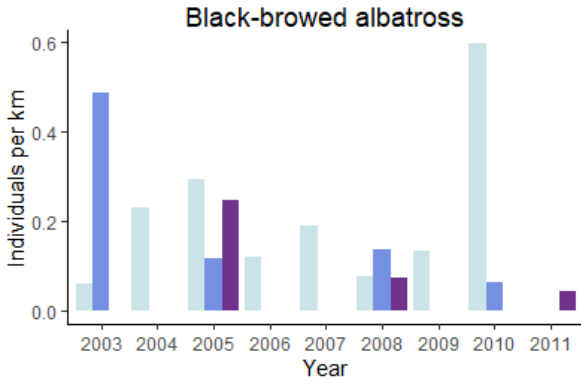
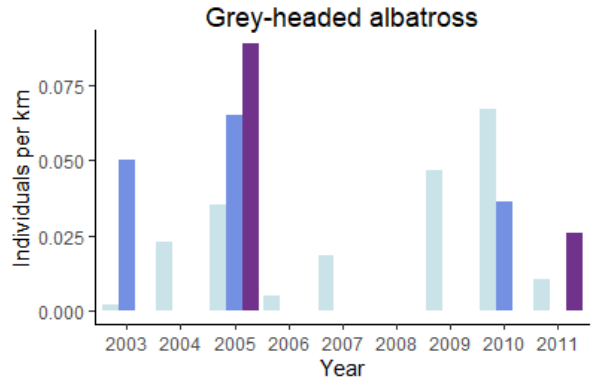
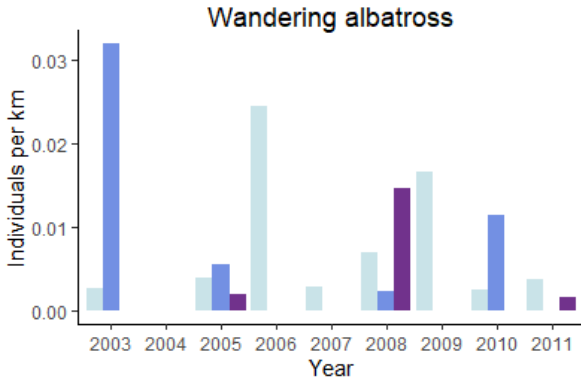
967 **Figures**

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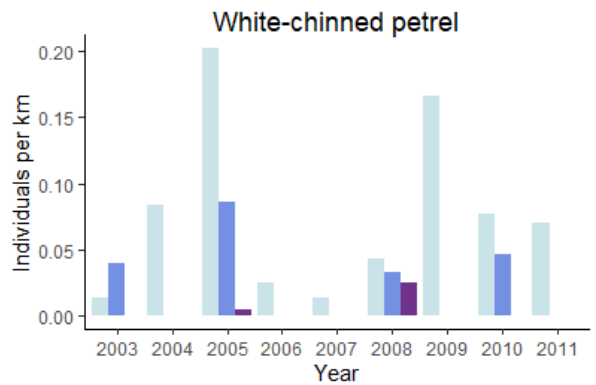
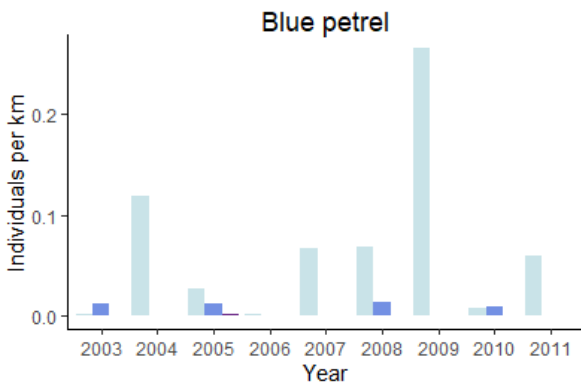
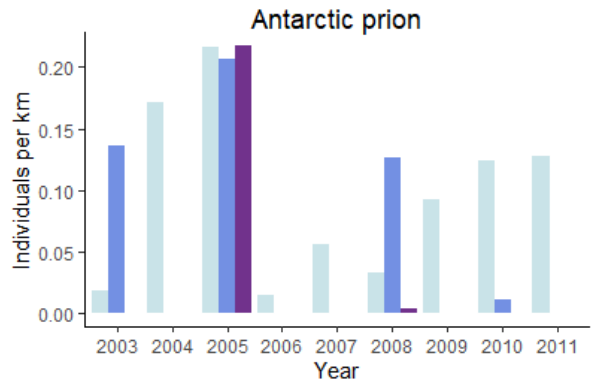
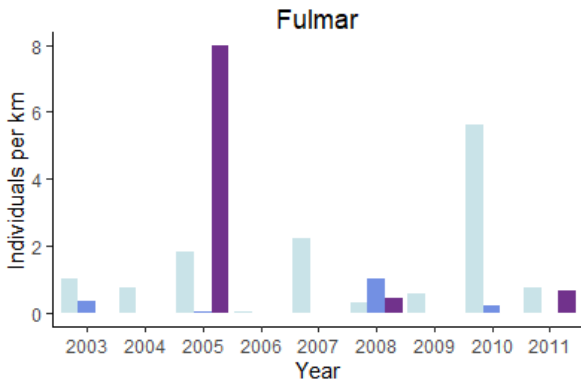


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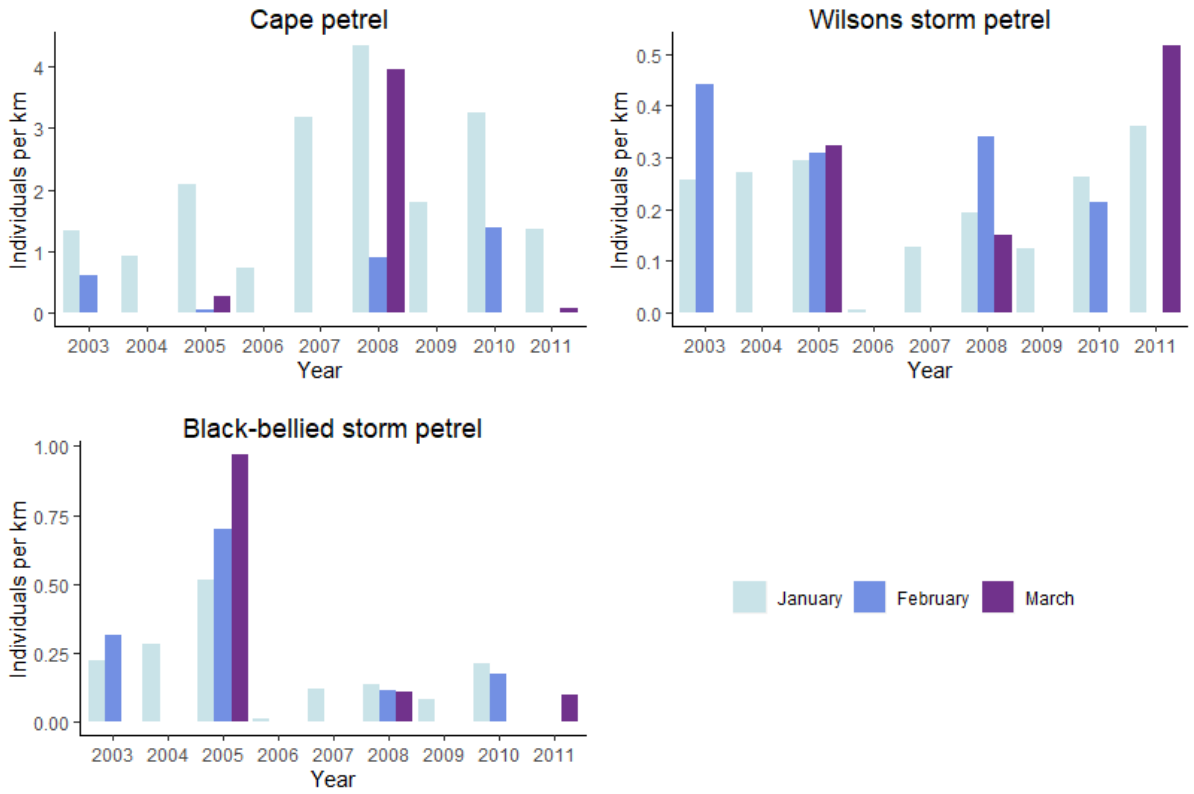
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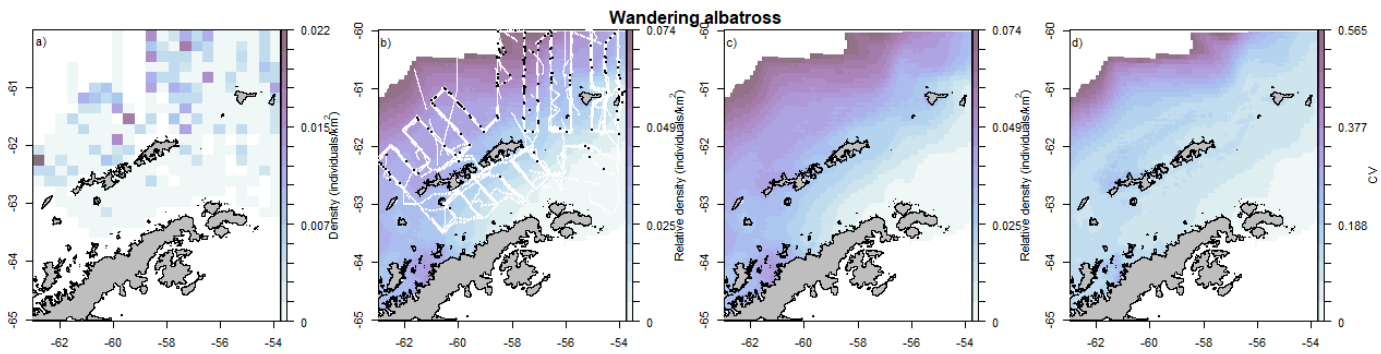
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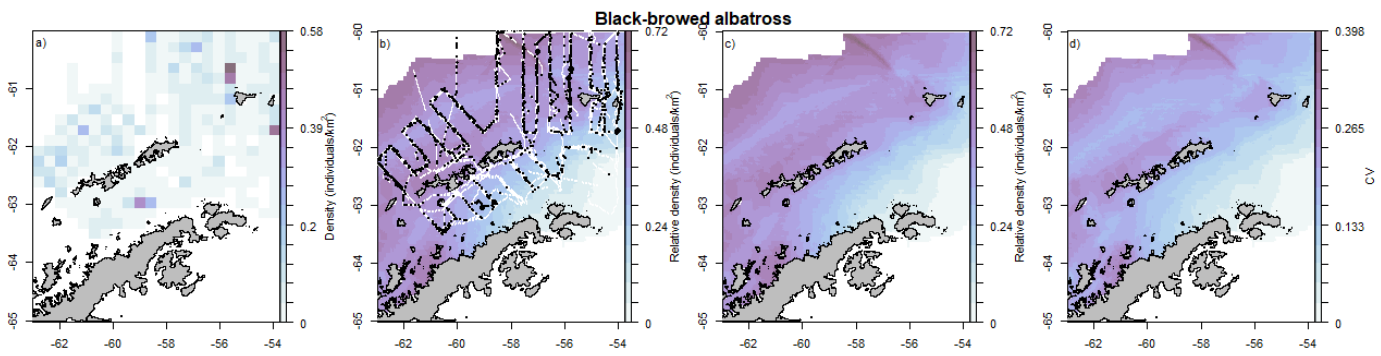
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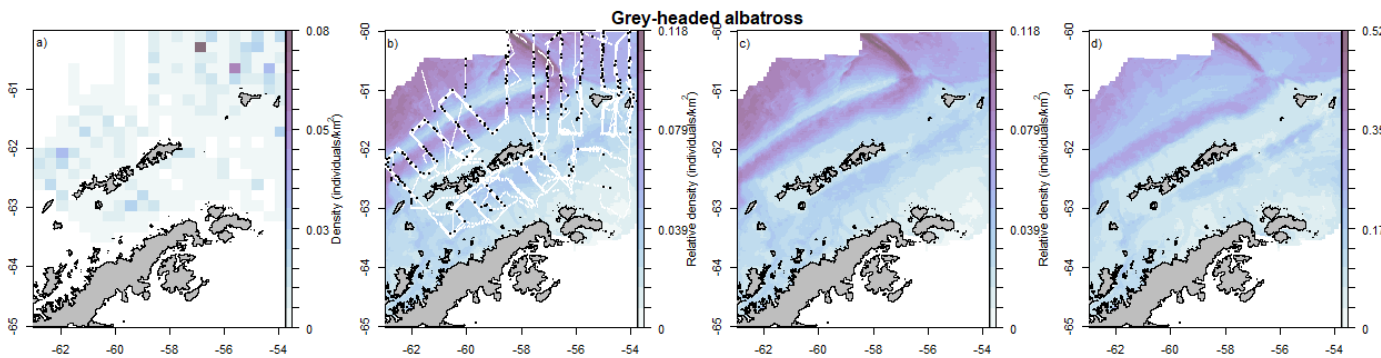
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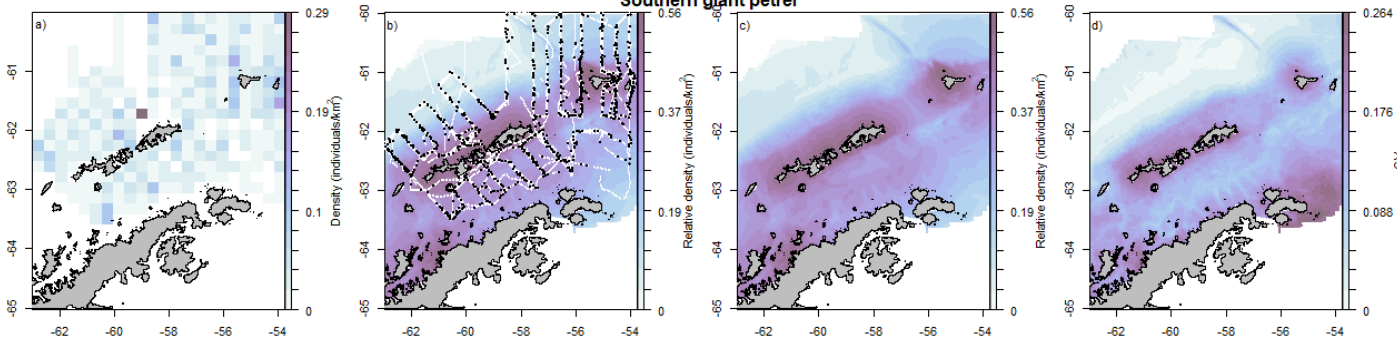
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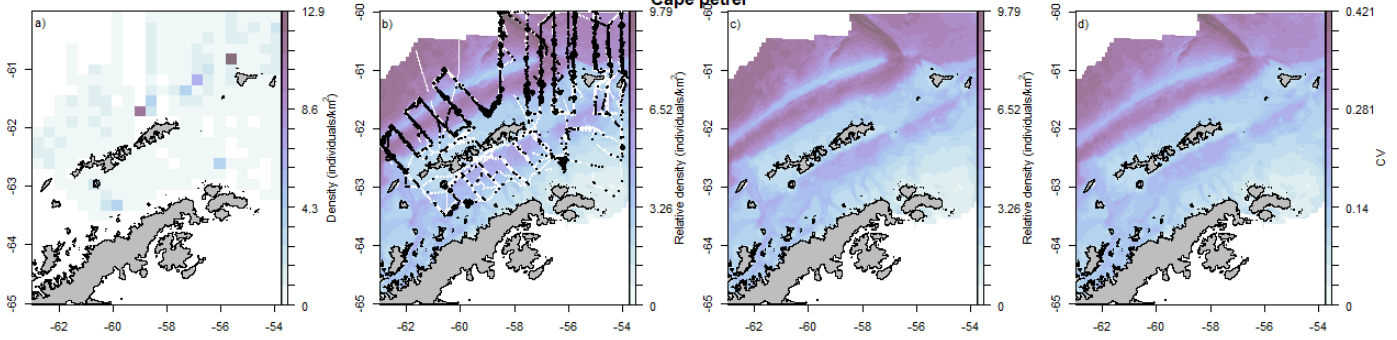


Southern giant petrel



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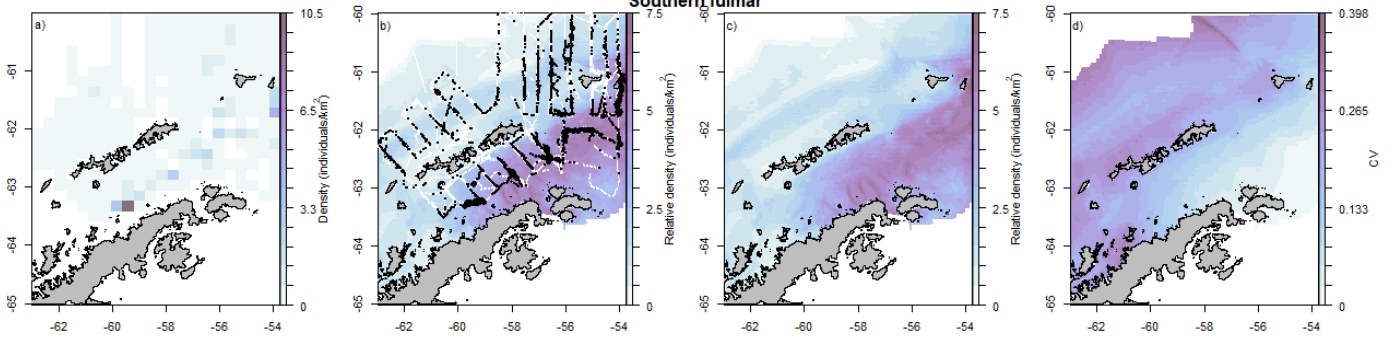
Cape petrel



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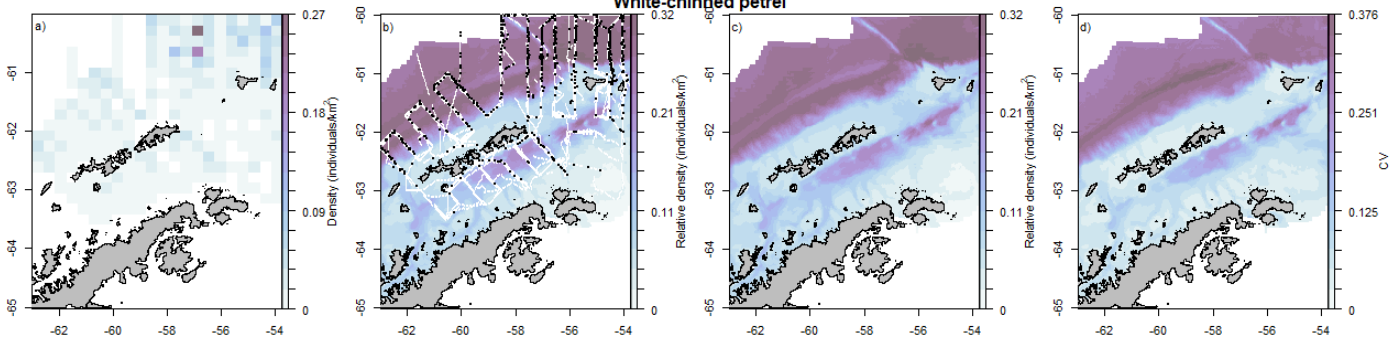
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Southern fulmar



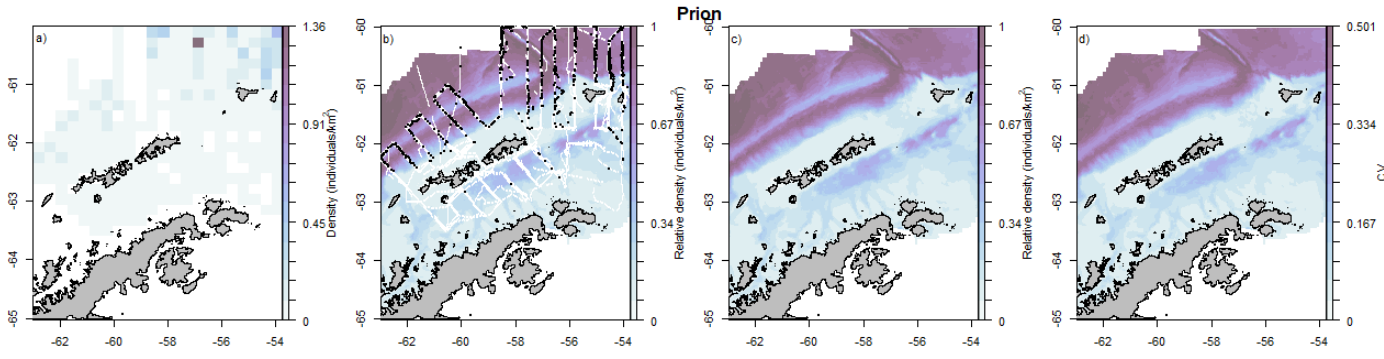
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White-chinned petrel

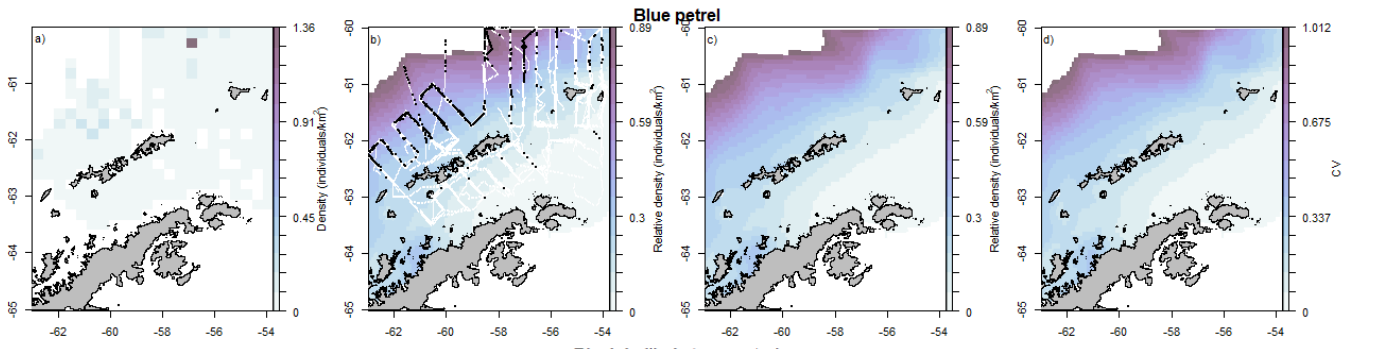


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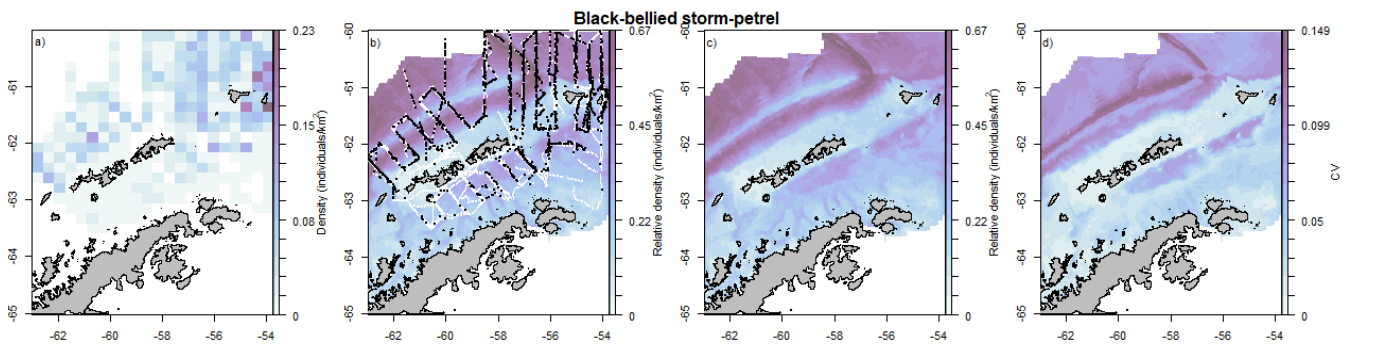
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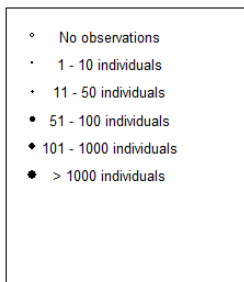
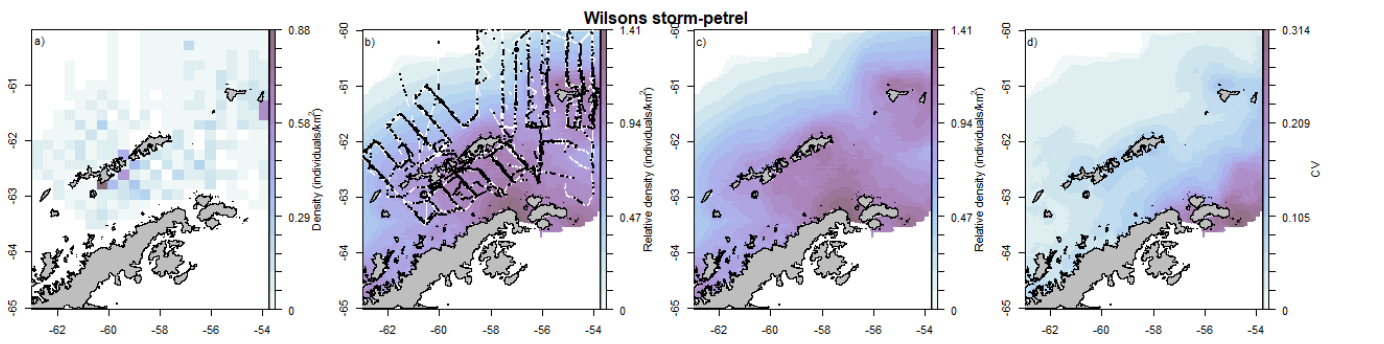
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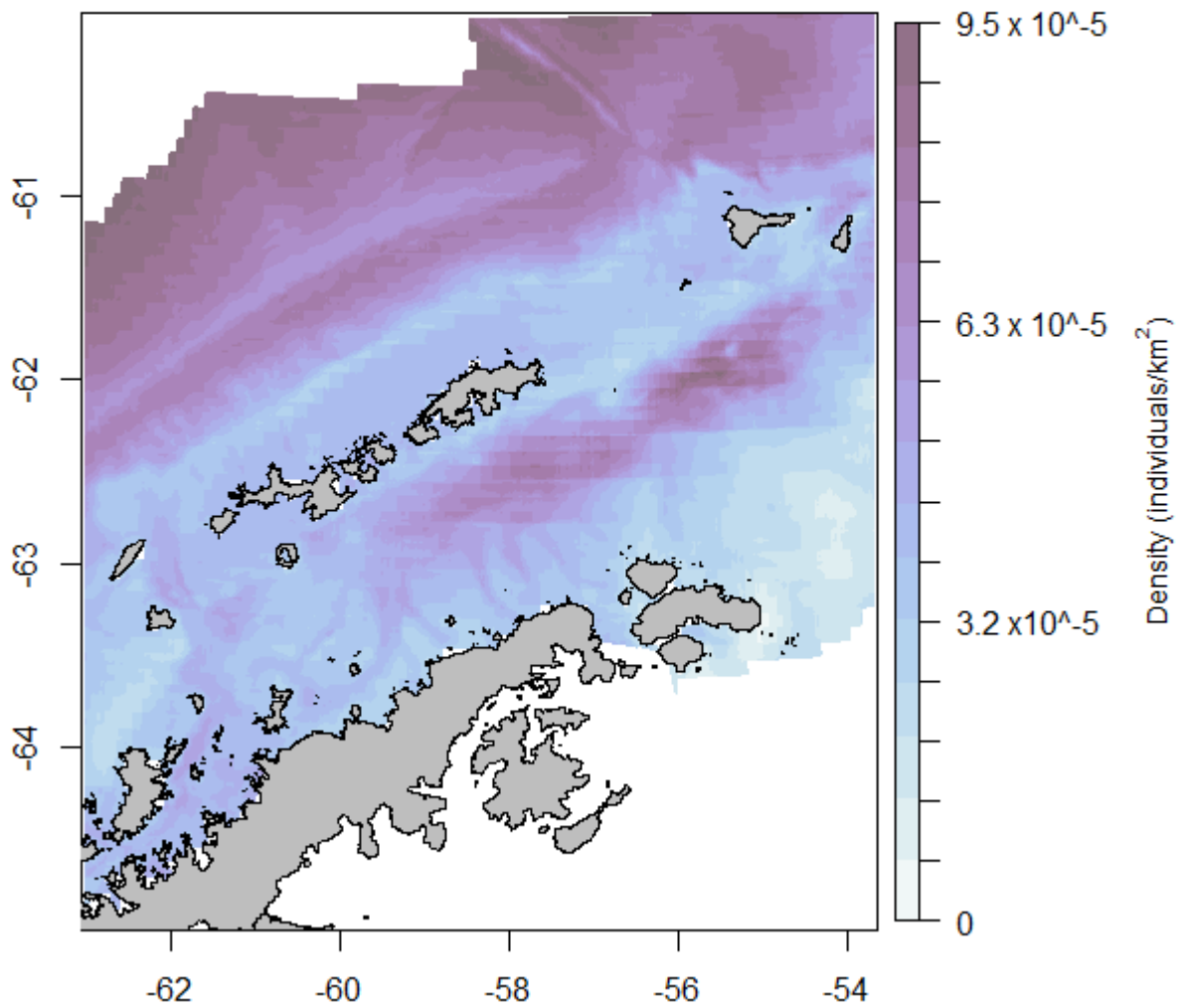


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995 Figure 3. Observed and predicted distributions of flying seabirds around the western Antarctic
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997 surveys, aggregated across all years of the survey (models were fitted to data for each year
998 independently) b) number of individuals observed in each grid cell obtained from ship surveys and
999 overlaid on predicted distributions of the relative density of species from model predictions. White
1000 dots indicate cells surveyed, black dots indicate observed individuals, increasing in size with the
1001 number of individuals observed c) predicted distributions of the relative density of species from
1002 models, d) Uncertainty in model predictions, calculated using a non-parametric bootstrapping
1003 approach.
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1007 Figure 4. The combined predicted distributions of eleven species of procellariiform
1008 northern Antarctic Peninsula and South Shetland Islands. Predicted relative densities for each species
1009 were normalised prior to summing all species.

1010 **Tables**

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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 <i>Raster</i>
	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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1020 **Table 3.** A summary of the explanatory variables used in the final models to describe the distribution
 1021 of seabirds in the west Antarctic Peninsula, and South Shetland Island region. Quantitative evaluation
 1022 of presence-absence and density predictions using area under the curve (AUC) and normalised root
 1023 mean squared error (NRMSE). NRMSE values for intercept only (null) models only are provided.

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Species	Presence-absence model	AUC	NRMSE 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 + Chl ² + 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

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1034 **Supplementary Information**

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1036 Table S1. Estimates for autocorrelation in model residuals using global *Morans I* tests

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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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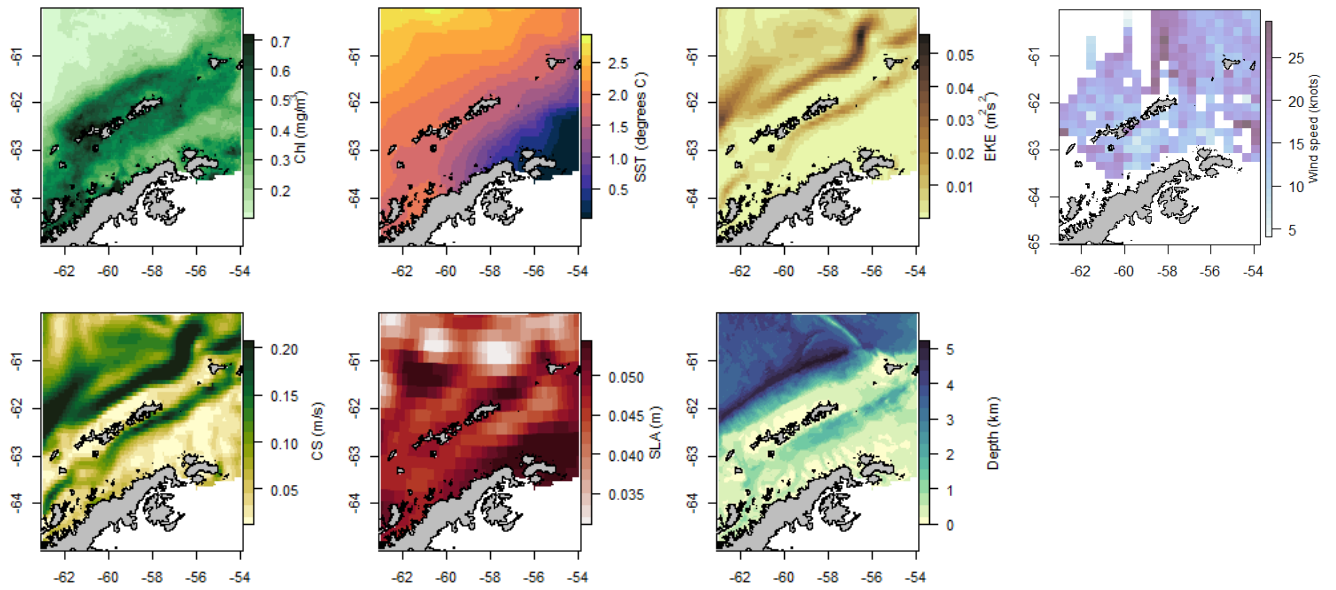
1040 **Table S2.** Pearson’s correlation coefficients between the environmental explanatory variables used
 1041 in model selection. Covariates for which correlation was > 0.7 were not included in the same models.
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var 1	var 2	correlation
EKE	Wind speed	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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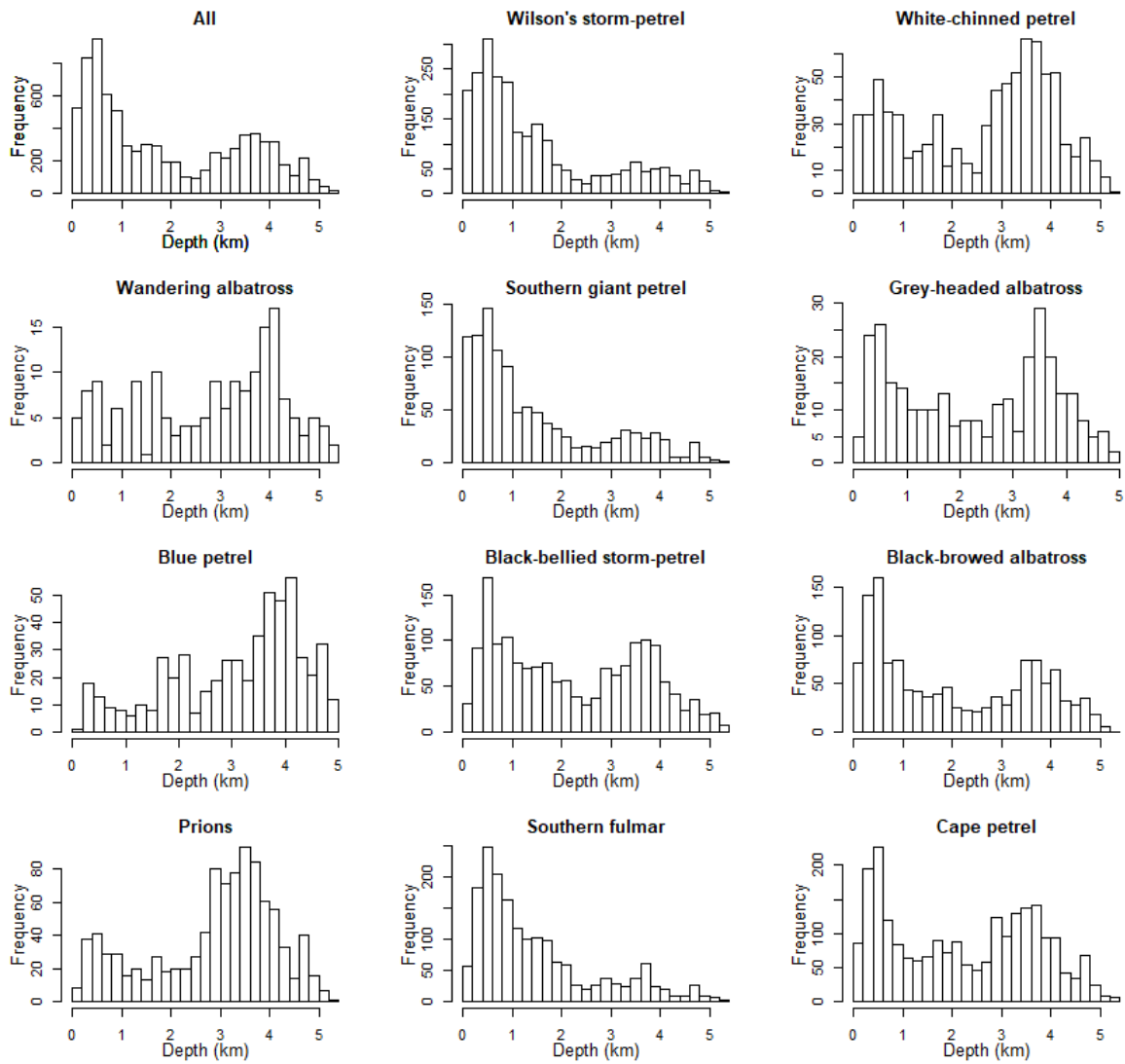


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1046 Figure S1. Climatological values for the environmental variables used in hurdle models to describe
 1047 the at-sea distribution of seabirds: a) Chlorophyll-a concentration, b) Sea surface temperature, c)
 1048 Eddy kinetic energy, d) Current speed, e) Sea level anomaly, f) Depth.

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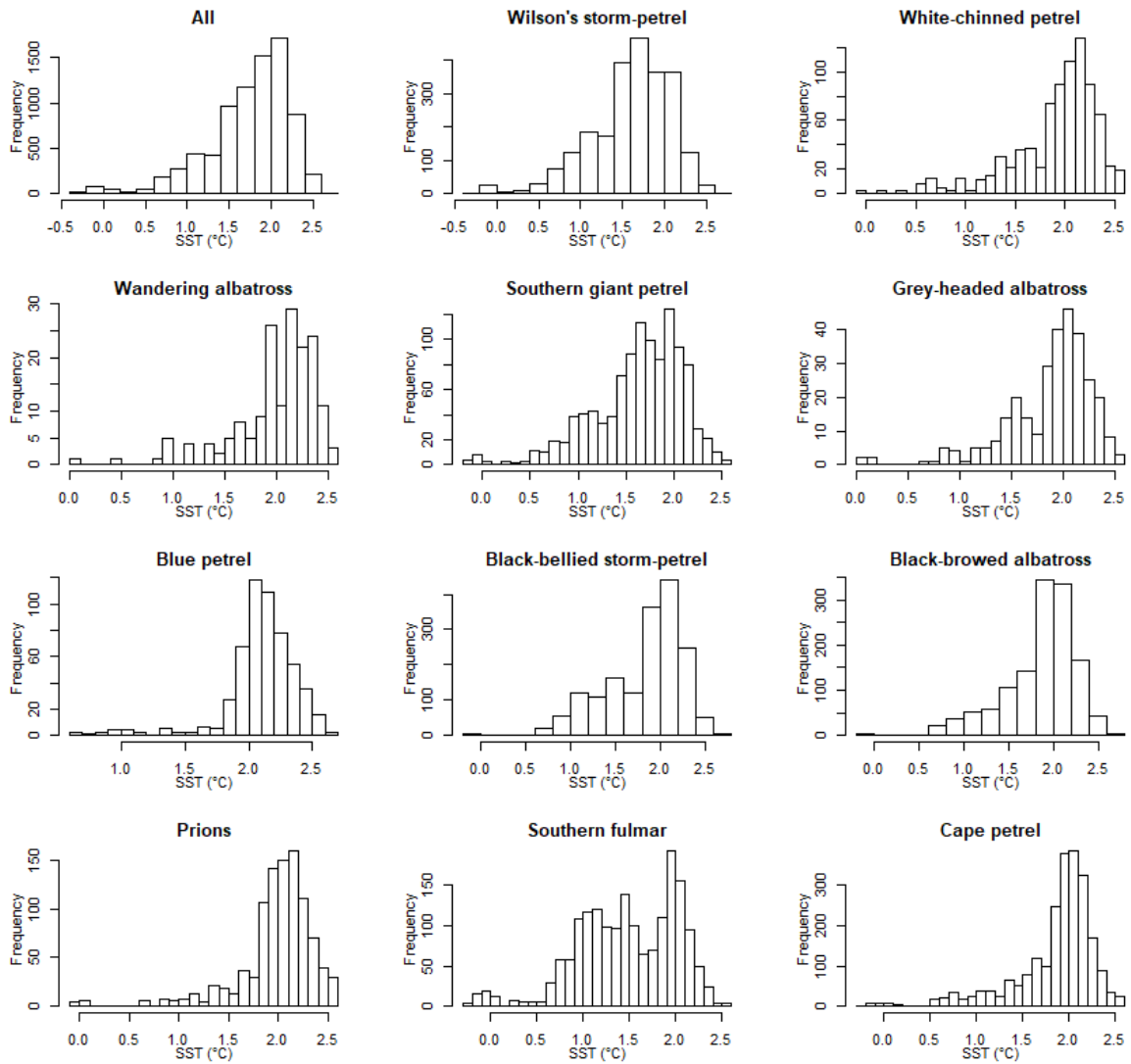
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1052 Figure S2. The frequency of sampling points a the frequency of individuals of each species sighted at
1053 different depths.

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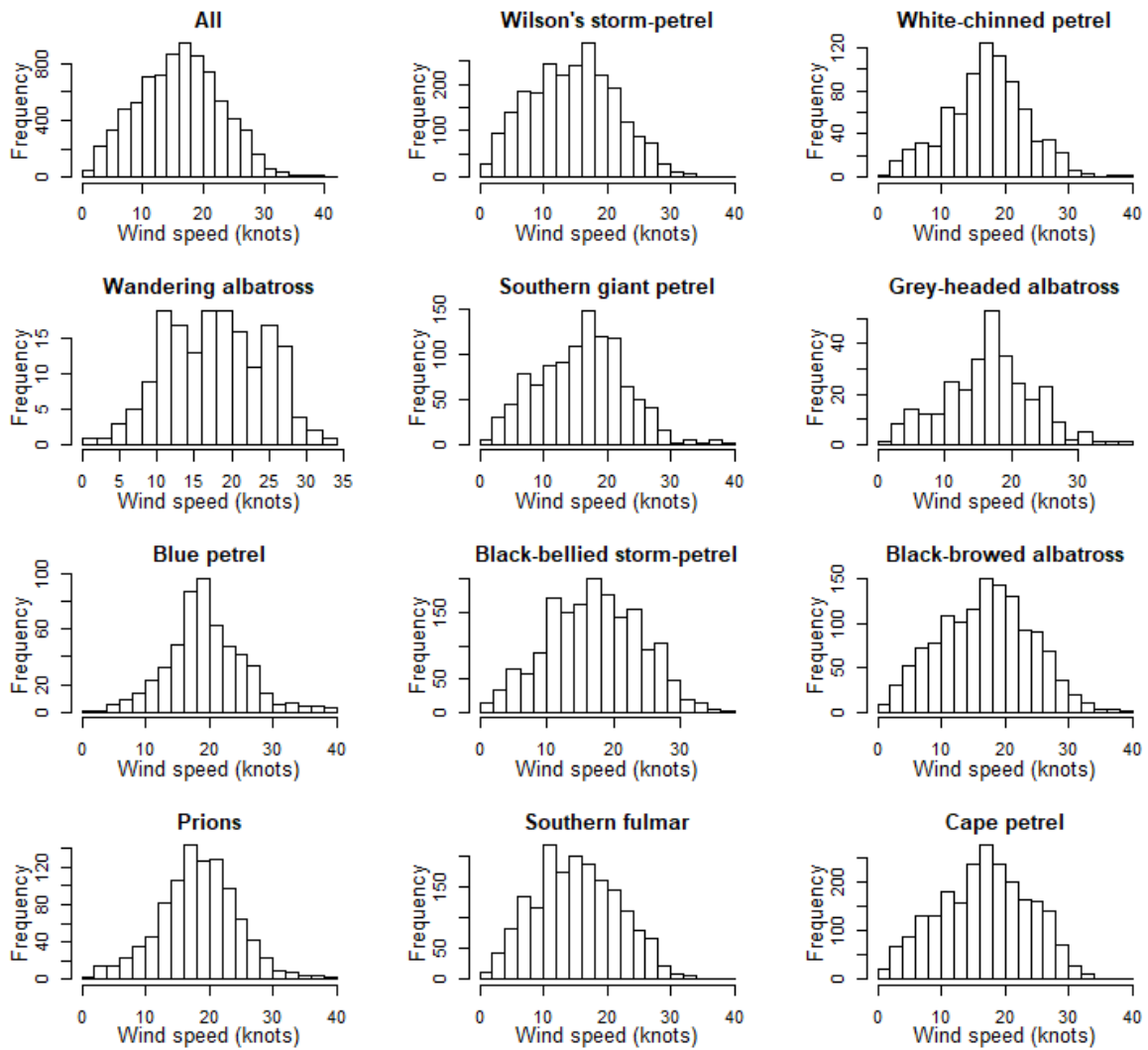
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1059 Figure S3. The frequency of sampling points and frequency of individuals of each species sighted

1060 across the temperature range.

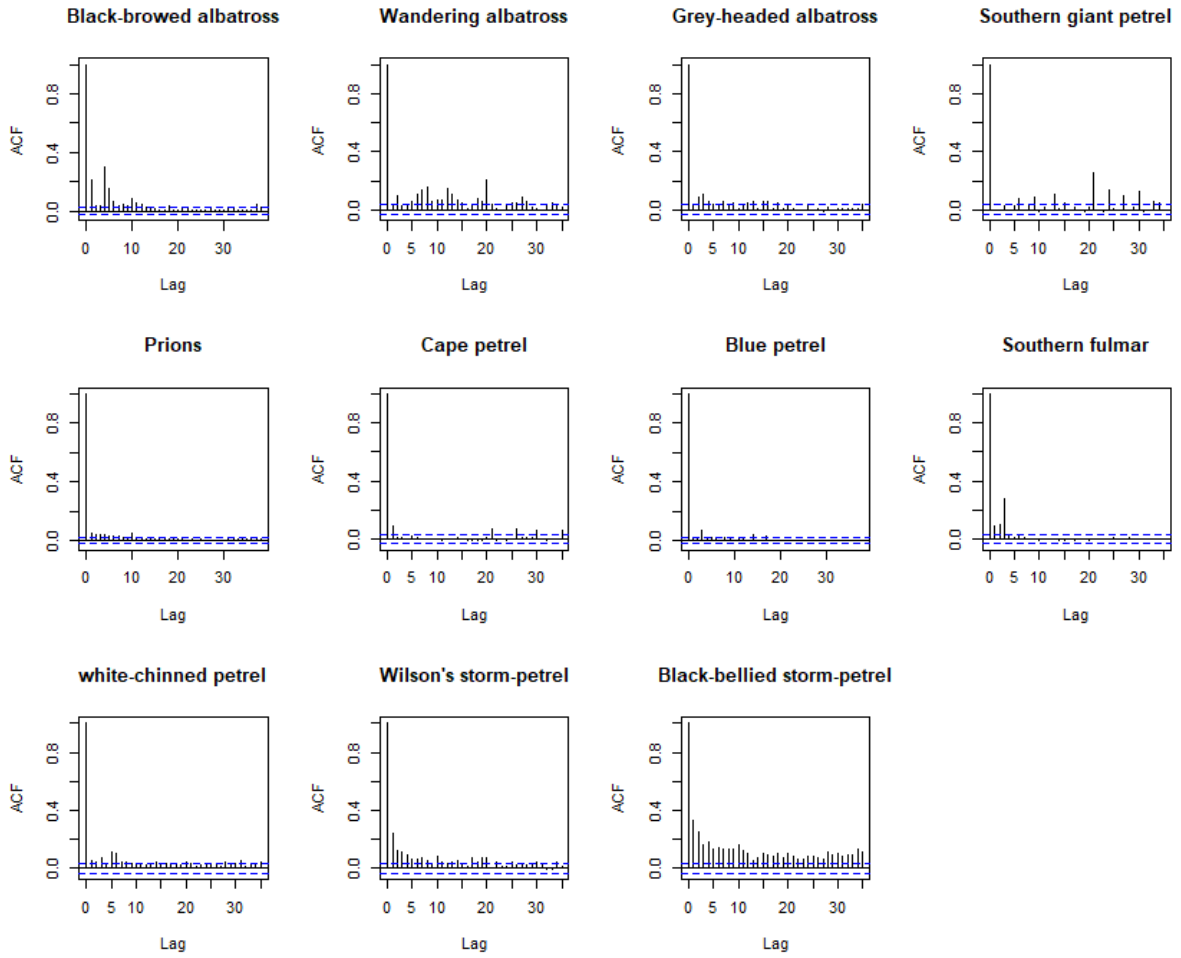
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1063 Figure S4. The frequency of sampling points and frequency of individuals of each species sighted

1064 across the wind speed range.



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1066 Figure S5. Autocorrelation plots for model residuals

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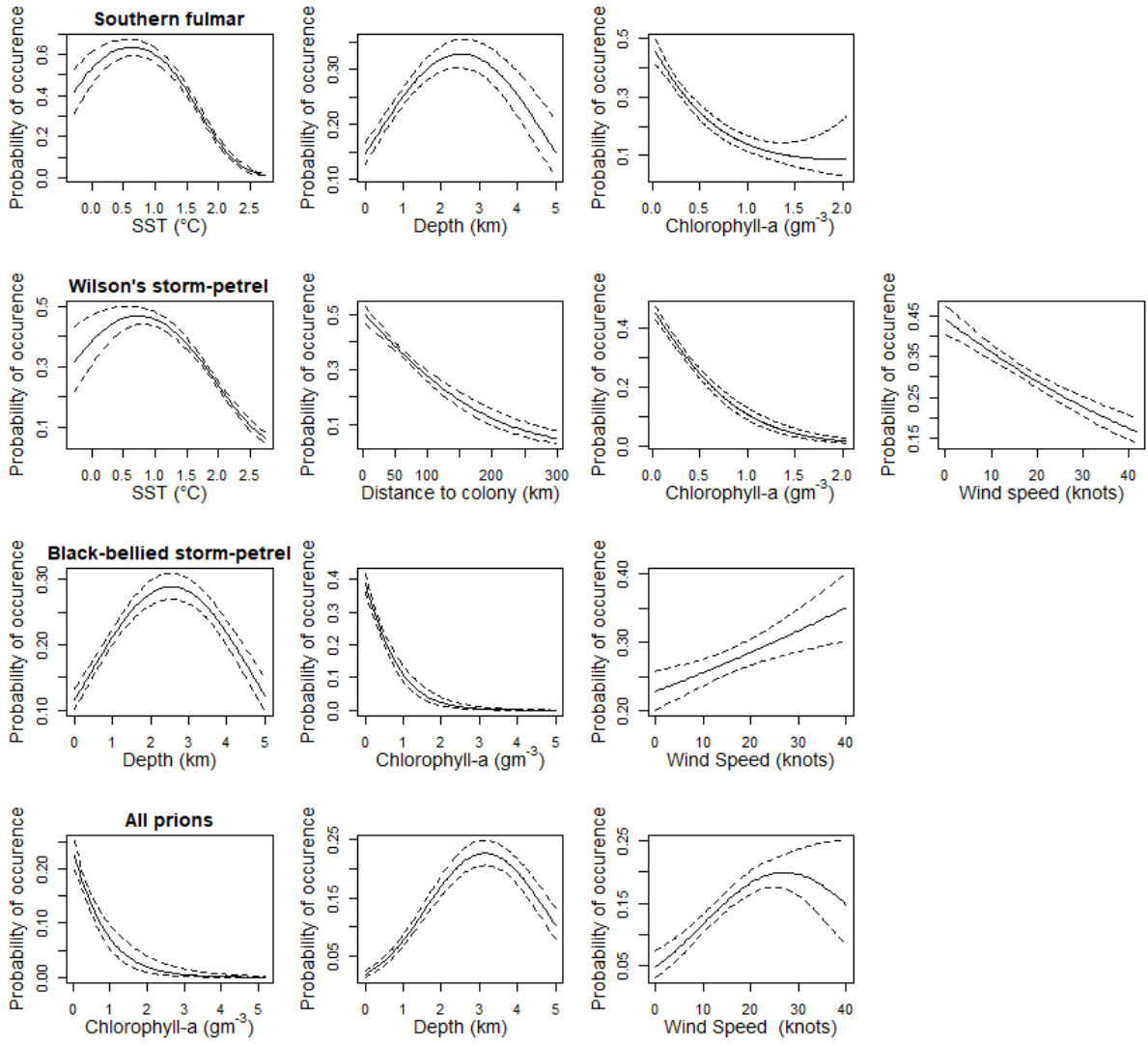
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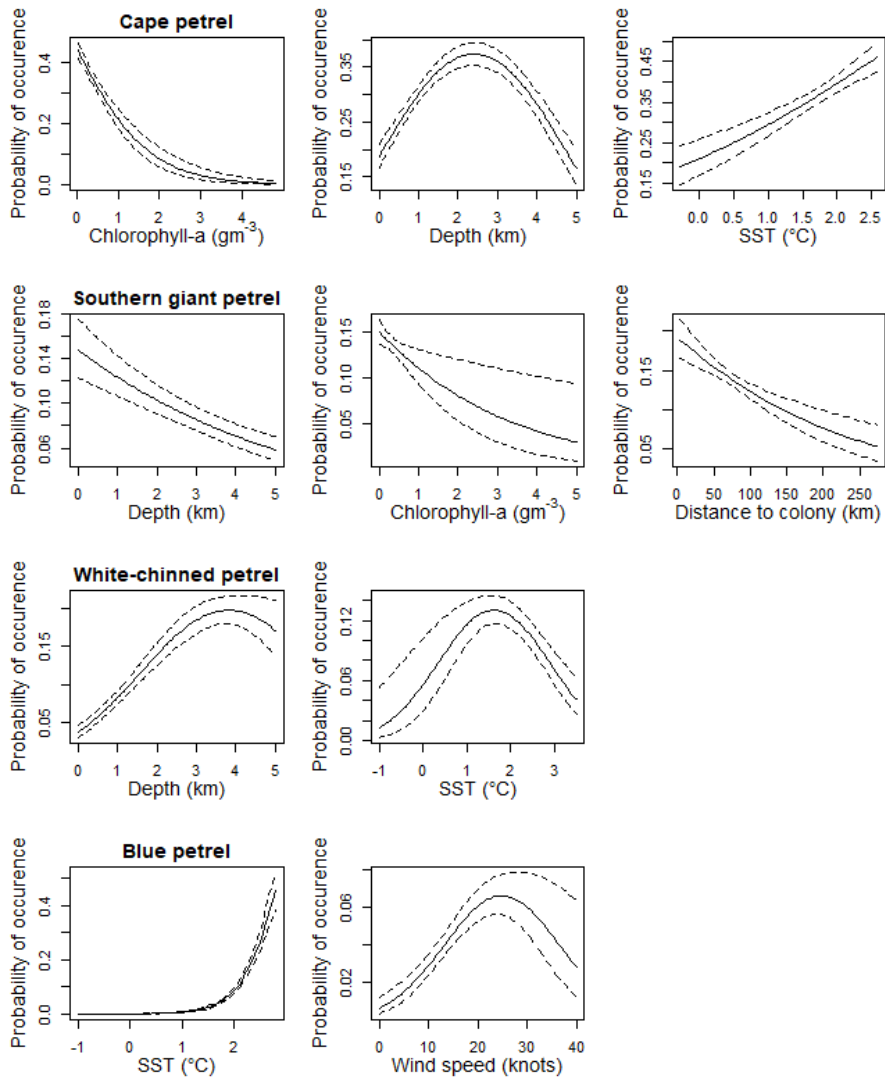
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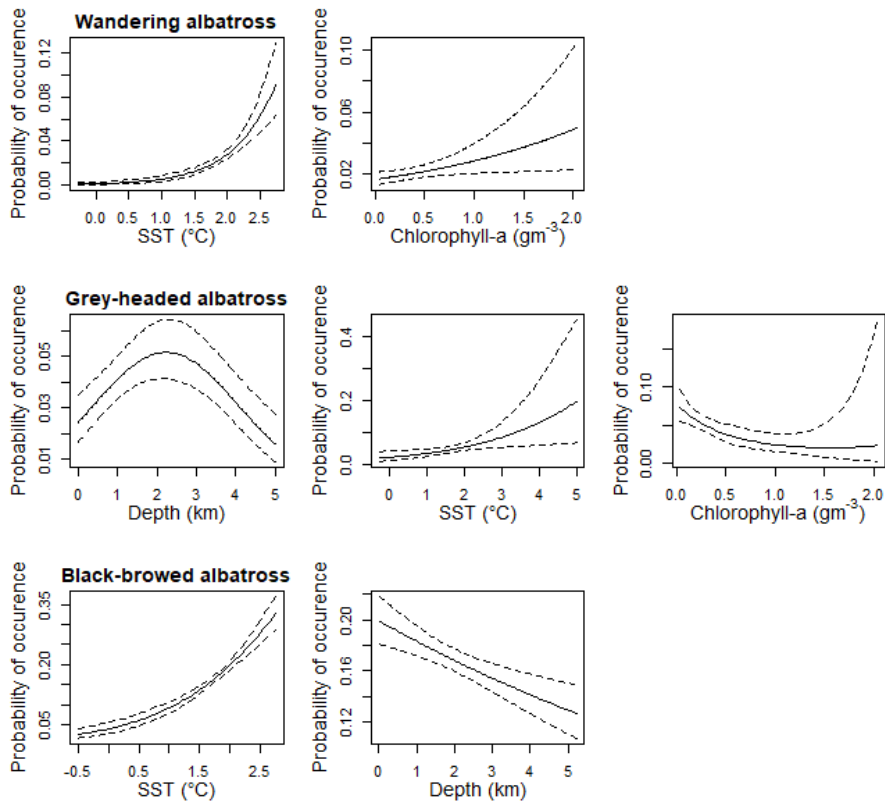
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1080 Figure S6. Response curves describing relationships between environmental variables and the at-sea
 1081 distribution of seabirds around the Antarctic Peninsula, and South Shetland Islands, created using
 1082 hurdle models. Confidence intervals were calculated using the standard errors provided with the
 1083 model output.

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