

1 THE DEVIL IS IN THE DETAIL: SMALL-SCALE SEXUAL SEGREGATION DESPITE
2 LARGE-SCALE SPATIAL OVERLAP IN THE WANDERING ALBATROSS

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12 **ABSTRACT**

13

14 Sexual segregation in foraging habitat occurs in many marine predators and is usually
15 attributed to competitive exclusion, different parental roles of each sex or niche specialisation
16 associated with sexual size dimorphism. However, relatively few studies have attempted to
17 understand the patterns and underlying drivers of local-scale sexual segregation in marine
18 predators. We studied habitat use, diet and feeding ecology of female and male wandering
19 albatrosses *Diomedea exulans*, fitted with GPS and stomach-temperature loggers during the
20 chick-rearing period (austral winter) at South Georgia in 2009. During this period, when
21 oceanographic conditions were anomalous and prey availability was low in waters near the
22 breeding colony, the tracked wandering albatrosses showed high consistency in their foraging
23 areas at a large spatial scale, and both males and females targeted sub-Antarctic and
24 subtropical waters. Despite consistency in large-scale habitat use, males and females showed
25 different foraging behaviours in response to oceanographic conditions at a smaller scale.
26 Males appeared to be more opportunistic, scavenging for offal or non-target fish discarded by
27 fishing vessels in less productive, oceanic waters. They exhibited sinuous movements, feeding
28 mostly on large prey and consuming similar amounts of food during the outbound and return
29 parts of the foraging trip. In contrast, females targeted natural productivity hotspots, and fed
30 on a wide variety of fish and cephalopods. They commuted directly to these areas; most prey
31 were ingested on the outbound part of the trip, and they often started their return after
32 ingesting large prey at the farthest point from the colony. Together, these results indicate that
33 sexual segregation in core foraging areas of wandering albatrosses is driven by sex-specific
34 habitat selection due the low availability of prey in local Antarctic waters. This segregation
35 results in different feeding behaviour at local scales which may be explained by differing
36 breeding roles and degree of parental investment by each sex, with females investing more

37 than males in reproduction. Further investigations are necessary to confirm the existence of
38 this pattern through time under contrasting environmental conditions and to identify the
39 drivers responsible for local-scale sexual segregation in wandering albatrosses.

40

41 **KEYWORDS:** Habitat selection, Foraging strategy, Parental investment, Diet, Feeding
42 behaviour.

43 INTRODUCTION

44

45 Sexual segregation in at-sea distribution is widely reported in seabirds and usually
46 thought to reflect niche specialisation or competitive exclusion by the dominant sex (typically
47 of females by larger males), or be a consequence of different reproductive roles (Phillips et al.
48 2011; Mancini et al. 2013). These differences have been reported for a wide number of
49 colonial seabirds, especially during the breeding period, when foraging ranges are restricted
50 by the need to return to the breeding colony to provision the offspring and in which sexual
51 dimorphism in size appears to be related to habitat selection (Cleasby et al. 2015). However,
52 while the consequences of sex differences in habitat use are well described in the literature,
53 the underlying mechanisms driving sexual segregation and the influence of changes in
54 environmental conditions on those mechanisms are poorly understood.

55 Sexual segregation in habitat use occurs at several spatio-temporal scales, often
56 leading to dietary differences (Phillips et al. 2011) and can be influenced by oceanographic
57 conditions that affect the availability of particular prey (Paiva et al. 2017). Foraging ecology,
58 at-sea distribution and behaviour of seabirds are strongly influenced by spatial and temporal
59 fluctuations in prey availability or abundance (Paiva et al. 2013; Ramos et al. 2015). Annual
60 variation in large-scale environmental conditions, such as the El-Niño Southern Oscillation
61 (ENSO), can drive temporal or spatial variation in primary productivity and consequently
62 influence seabird diet and distribution through changes in prey (Meredith et al. 2008; Hill et
63 al. 2009; Fielding et al. 2012). In years of anomalous oceanographic conditions, productivity
64 can be reduced considerably, influencing all trophic levels of the marine food web (Paiva et
65 al. 2013). In this situation, studies of at-sea distribution and diet composition of seabirds can
66 provide insights into the extent to which sexual segregation and sex-specific feeding
67 behaviour is driven by the environment, particularly in monomorphic seabird species (Pinet et

68 al. 2012). If environmental conditions are unfavourable, seabirds may adopt different foraging
69 strategies, which can lead to habitat divergence and greater partitioning of marine resources
70 (Xavier et al. 2003b; Xavier et al. 2013; Jenouvrier et al. 2015).

71 In the Southern Ocean, seasonal and annual variation in the feeding ecology of
72 seabirds has been well studied for those species that breed during the austral summer;
73 however, considerably less is known about at-sea distribution and foraging behaviour of
74 species that raise chicks during the austral winter, particularly their responses to local poor
75 environmental conditions. In our study, we aimed to quantify sex differences in foraging
76 distribution, diet and feeding behaviour of wandering albatrosses *Diomedea exulans* from
77 South Georgia during the chick-rearing period in an unusual austral winter. In 2009, when our
78 study took place, satellite remote-sensing indicated exceptionally high sea surface and air
79 temperatures around South Georgia; mean monthly sea surface temperature (SST) peaked in
80 March 2009 at 4.4° C, in comparison with the long-term average of 3.9°C recorded since 1982
81 (Hill et al. 2009; Fielding et al. 2014), and SST continued to be higher than average until the
82 end of the austral winter (Xavier et al. 2017). Warm waters are usually characterized by low
83 primary productivity and thus reduced prey availability and abundance (Paiva et al. 2010a).
84 Indeed, the annual acoustic survey of the Antarctic krill *Euphausia superba* (hereafter krill) in
85 a fixed survey area to the west of South Georgia in the austral summer of 2009, recorded a
86 mean density of only 17.6 gm², the lowest mean since the surveys began in 1997 (Hill et al.
87 2009); in addition, only 28% of krill were in moderate to large swarms (Fielding et al. 2014).
88 As krill abundance and availability influence the Antarctic food web around South Georgia
89 (Murphy et al. 2007), predators may adjust their feeding and foraging strategies accordingly.

90 Wandering albatrosses travel long distances and exhibit pronounced sexual
91 differences in at-sea distribution (particularly in latitude), feeding behavior and diet, including
92 in the South Georgia population (Xavier and Croxall 2005; Phillips et al. 2011; Åkesson and

93 Weimerskirch 2014; Froy et al. 2015). At South Georgia, in a study that encompassed years
94 of apparently “average” (1999) and “anomalous” (2000) oceanographic conditions, female
95 wandering albatrosses consistently foraged further north than males during the chick-rearing
96 period, performing significantly longer trips and spending more time in oceanic waters in the
97 sub-Antarctic, reaching the Patagonian shelf-break and feeding mostly on cephalopods,
98 whereas males concentrated their foraging closer to the breeding colony, predominately in
99 shallow Antarctic waters, mostly scavenging for fish discards from longline vessels (Xavier et
100 al. 2004; Xavier and Croxall 2005). If local environmental conditions are unfavourable, sex-
101 specific differences in habitat use are expected to be greater; hence, we might expect male and
102 female wandering albatrosses to show more extreme sexual segregation or greater sex
103 differences in their foraging behavior at large scales, as birds adapt to the local foraging
104 environment. In addition, if availability of natural prey is low in waters close to the colony for
105 other predators (such as penguins; (Xavier et al. 2017)), we might anticipate that fisheries
106 discards would be increasingly important to wandering albatrosses as a key alternative food
107 supply (Xavier et al. 2004; Granadeiro et al. 2011; Grémillet et al. 2012). Moreover, we
108 expect that both sexes might show greater difference in feeding behaviour within the core
109 foraging areas, given low availability of prey in nearby Antarctic waters.

110 Devices that provide location (satellite-transmitters or GPS loggers) can be combined
111 with loggers that record saltwater immersion (wet-dry transitions) or prey ingestion to reveal
112 detailed information on foraging ecology, activity patterns and other aspects of seabird
113 behaviour (Catry et al. 2004; Zwolinski et al. 2010). Stomach temperature loggers measure
114 the reduction in temperature associated with the ingestion of cold, marine prey, providing data
115 on timing of ingestion and mass of solid prey, watery prey such as salps, or seawater
116 (Weimerskirch and Wilson 1992; Wilson et al. 1992; Wilson et al. 1995; Catry et al. 2004).
117 By combining these approaches with analyses of diet composition (from stomach contents), it

118 is possible to determine not only where and when the prey was captured, but also the species
119 and size, providing further insights into prey biogeography (Pereira et al. 2017).

120 Here we aimed to evaluate sex differences at local and large scales in foraging
121 strategies, at-sea distribution, diet composition and behavior of wandering albatrosses from
122 South Georgia during chick-rearing in an austral winter when conditions were particularly
123 unfavourable (high SST, low productivity and low krill availability near the colony) (Xavier
124 et al. 2017). We integrated data from GPS, immersion and stomach temperature loggers, diet
125 and oceanographic data to: (1) characterize sexual segregation in at-sea distribution; (2)
126 determine relative reliance on fisheries offal and discards as an alternative food supply; and
127 (3) assess sex differences in feeding behaviour within the core foraging areas.

128

129 **MATERIAL AND METHODS**

130

131 **Device deployments**

132

133 Devices were deployed on thirty-six wandering albatrosses (18 males and 18 females)
134 at Bird Island, South Georgia (54°00'S, 38°03'W) during the chick-rearing period in May –
135 October, 2009. Each albatross was fitted with three devices: (1) Global Positioning System
136 (GPS) logger, (2) saltwater immersion (activity) recorder and (3) stomach temperature probe.
137 The GPS loggers (48 x 15 x 30 mm, 25g; Jensen Software Systems, Kiel, Germany) were
138 programmed to record location at 20 minute intervals; 33 (92%) of the 36 devices deployed
139 were recovered and downloaded, but three tracks were incomplete and excluded from the
140 analysis. All immersion loggers (MK7, 18 x 18 x 6.5 mm, 3.6 g; British Antarctic Survey,
141 Cambridge) were recovered and successfully downloaded (18 males and 18 females); these
142 test for immersion every 3 secs. and record the time of every change of state from wet to dry,

143 and *vice versa*, that lasts ≥ 6 secs. Twenty-six stomach temperature probes (13 males and 13
144 females; 19 mm diameter x 150 mm long, 51.5 g; Jensen Software Systems, Kiel, Germany);
145 22 (85% of those deployed) were retrieved and downloaded. Given loss or failure of the
146 different types of loggers, concurrent data from all three devices for complete trips were
147 available for seventeen wandering albatrosses (9 males and 8 females).

148

149 **Area Restricted Search (ARS) zones**

150

151 The GPS data were used to determine zones of Area Restricted search (ARS) by
152 applying First Passage Time (FPT) analysis according to Fauchald and Tveraa (2003),
153 implemented through the package *adehabitatLT* (Calenge 2006) in the software R v. 3.3.2 (R
154 Development Core Team 2016). FPT by definition corresponds to the time that the animal
155 takes to pass through a circle with a given radius (Paiva et al. 2015). ARS zones for top
156 predators represent specific underlying behaviour patterns, reflecting foraging in patchy
157 environments; in these areas, flight paths of seabirds increase in sinuosity because of more
158 frequent turns as individuals respond to foraging cues (Fauchald and Tveraa 2003; Paiva et al.
159 2010b). ARS zones and time spent in those areas appear as peaks of variance in variograms of
160 FPT, plotted as a function of time since the start of the trip (Pinaud and Weimerskirch 2005;
161 Paiva et al. 2010a; Louzao et al. 2011). Locations of ARS zones were also compared with
162 high density areas from kernel analyses, and the outputs of the habitat suitability models (see
163 below).

164

165 **Oceanographic data**

166

167 To characterize the oceanographic conditions that are associated with ARS behaviour
168 in wandering albatrosses, we extracted: (1) bathymetry (BAT, blended ETOPO1 product,
169 0.01° spatial resolution, m), (2) net primary productivity – Ocean productivity proxy (NPP,
170 Aqua MODIS, 0.08°, C m⁻² day⁻¹), (3) sea surface temperature (SST, Aqua MODIS, 0.04°,
171 °C), and gradients in these 3 variables (4) BATG, (5) NPPG, (6) SSTG, respectively, (7) wind
172 intensity – modulus of wind (WM, QuickSCAT, 0.125°, m s⁻¹) and (8) maximum distance to
173 colony as a measure of accessibility. Bathymetry was downloaded from NOAA Global Relief
174 Model (<https://www.ngdc.noaa.gov/mgg/global/global.html>), NPP from the Ocean
175 Productivity website (<http://www.science.oregonstate.edu/ocean.productivity/standard.product.php>), SST from
176 NASA OceanColor browser (<http://oceancolor.gsfc.nasa.gov/cms/>) and WM from SeaWinds
177 database (<http://winds.jpl.nasa.gov>). Monthly composites (averages) were used for the
178 dynamic predictors (variables 2, 3, 5, 6 and 7). Gradients were determined by estimating rates
179 of change using a moving window function (3 x 3 grid cells; function = [(max. value – min.
180 value) × 100] / (max. value). As oceanic fronts appear as steep NPP and SST gradients at
181 zones of high chlorophyll *a* concentration, NPP and SST gradients allowed frontal regimes to
182 be identified. All environmental predictors were obtained for each cell in a 0.125° grid.

184 To characterize the inter-annual variability in oceanographic conditions around South
185 Georgia, we extracted the monthly sea surface temperature anomalies (SSTa) between
186 January 1990 – October 2009 within the foraging range of wandering albatrosses during short
187 trips (see below) (from the area bounded by 47–60°S and 25–50°W). Data were extracted
188 from
189 http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/.ssta/.

191

192 **Sinuosity analysis**

193

194 A sinuosity index was calculated for each foraging trip (both inbound and outbound
195 portions) using the ArcGIS Sinuosity toolbox, which measures the deviation of a line from the
196 shortest path, calculated by dividing the total length by the shortest possible path. This index
197 ranges between 0 and 1, with low values indicating higher sinuosity and a value of 1
198 indicating a completely straight line.

199

200 **Habitat suitability models (HSMs)**

201 **Data processing: autocorrelation and multicollinearity assessment**

202

203 Prior to modelling the occurrence of ARS behaviour (First Passage Time – FPT –
204 duration) in male and female wandering albatrosses we examined the correlations between all
205 environmental variables in order to detect possible problems with multicollinearity (Graham
206 2003; Naimi et al. 2011; Dormann et al. 2013; Halvorsen et al. 2016). We assumed that
207 strongly correlated variables ($|\geq 0.7|$) were problematic and thus were excluded from the
208 modelling process. Statistical parameters were then calculated for certain combinations of
209 predictors (e.g. between the standard products and their gradients). Generalized Linear Mixed
210 Models (GLMs) were constructed and the Akaike information criteria (AIC) values from each
211 model were examined in order to exclude the model with the highest AIC (from pairs of
212 highly correlated variables) from the modelling process (Warren and Seifert 2011; Paiva et al.
213 2017).

214

215 **Calibration and model assessment**

216

217 The environmental predictors that best explained the foraging distribution of
218 wandering albatrosses were identified using Maximum Entropy (MaxEnt) models for both
219 sexes, which are presence-only (version 3.3.3;
220 <http://www.cs.princeton.edu/~schapire/maxent/>). MaxEnt modelling creates predictions based
221 on the probability distribution of maximum entropy, supported by correlations between the
222 presence of the organism (occurrence) and a set of predictors or explanatory variables
223 (Phillips et al. 2006; Elith et al. 2011). Although absence data are not included, MaxEnt
224 creates a set of random background points to use as “pseudo-absences” for calibration
225 purposes, selected from cells with opposite environmental conditions to those identified as
226 suitable for the species occurrence (Barbet-Massin et al. 2012). In order to obtain models with
227 higher predictive performance, different strategies were implemented, namely (1) logistic
228 output format (resulting in a probabilistic scale ranging between 0 and 1 for each grid cell,
229 where higher scores indicate more similar environmental conditions), (2) duplicated presences
230 were removed (MaxEnt only considers one point per cell), and (3) 70% of the ARS locations
231 (each grid cell within ARS radius) were randomly assigned for the training area calibration,
232 and the remaining 30% of the ARS locations used for validation (Elith et al. 2006). Analyses
233 involved 50 random iterations (bootstrap) for each model and the results were summarized as
234 the average of these outputs. A Jackknife test was used to assess the contribution and
235 explanatory power of each oceanographic predictor in the final model.

236 In order to avoid threshold interference in the evaluation of model performance,
237 outputs were assessed using the Area Under the Curve of the Receiver Operating
238 Characteristics (AUC of ROC), a threshold-independent statistical measure (Pearson et al.
239 2006). This measure is considered appropriate for evaluating the performance of these
240 models, since it assesses the ability to discriminate suitable from unsuitable conditions (Lobo
241 et al. 2008). The AUC metric estimates the likelihood that a randomly selected presence point

242 is located in a raster cell with a higher probability score for species occurrence than a
243 randomly generated point (Araújo et al. 2005; Phillips et al. 2006; Elith et al. 2006). AUC
244 values range between 0.50 and 1, where 1 indicates perfect discrimination ability and 0.50
245 indicates a low discriminatory capacity. Output models are usually considered to have
246 excellent discriminatory ability when $AUC \geq 0.90$, good for $0.80 < AUC < 0.90$, acceptable
247 for $0.70 < AUC < 0.80$, bad for $0.60 < AUC < 0.70$ and invalid for $0.50 < AUC < 0.60$
248 (Engler et al. 2004; Araújo et al. 2005).

249

250 **Overlap analyses**

251

252 Utilization distributions (UDs) were generated for the areas in which the tracked
253 wandering albatrosses engaged in ARS behaviour using the *adehabitatHR* R package (kernel
254 UD) (Calenge 2006; Tancell et al. 2013). The most appropriate smoothing parameter (h) was
255 set at 1.5 km for the complete dataset, and then applied in a 0.125° grid (to match the
256 oceanographic predictors) in an equidistant cylindrical projection. We considered 95% and
257 50% kernel UD boundaries to represent home ranges and core areas, respectively. We then
258 used the *kerneloverlap* function of the *adehabitatHR* library to calculate the overlap of these
259 areas between sexes as an indication of sexual segregation.

260 We also quantified the spatial consistency in ecological niches by measuring the
261 similarity in predictions between all pairs of HSMs produced for both sexes, using ENMtools
262 version 1.4.4; this provides two similarity metrics: Schoener's *D* and *I* statistics (Warren et al.
263 2008; Warren et al. 2010). We used *I* statistics to measure the niche overlap by comparing the
264 estimates of habitat suitability calculated for each grid cell according to Hellingers' distance
265 (do Amaral et al. 2015). The statistical tests were conducted for two pairs of HSMs (males vs
266 females) and the outputs range from 0 to 1, with 0 indicating no niche overlap between the

267 models, and 1 indicating a perfect overlap between the predicted distributions of all pairs of
268 HSMs generated. The niche equivalency test, which tests whether the ecological niches from
269 two models are equivalent (in this study, comparing the sexes), were conducted with 100
270 iterations for each comparison to ensure that the null hypothesis can be rejected with higher
271 confidence (Warren et al. 2008; Broennimann et al. 2012).

272

273 **Prey capture**

274

275 Periods spent in flight and all landings on the water (presumably prey capture attempts
276 or for resting) were identified from the immersion data. Detailed analyses of feeding
277 behaviour were based on the 17 individual wandering albatrosses from which we obtained
278 data from all three devices (GPS, immersion and stomach temperature loggers). All ingestion
279 events (N=191) were identified by analysing the stomach temperature data using MT-Dive
280 software (Jensen Software Systems, Kiel, Germany), module MT-Temp (temperature
281 channel). Short (< 6 days and < 1200 km; hereafter local scale) and long (\geq 6 days and \geq 1200
282 km) foraging trips were distinguished based on the plots of frequency of occurrence of: (1)
283 trip duration (days), and (2) maximum distance from colony reached in each foraging trip (see
284 Fig. S1). Day/night times were based on timing of civil twilight (sun > 6° below the horizon)
285 at the colony (Bird Island) determined using <http://www.sunrisesunset.com/calendar.asp>.

286 Stomach contents were obtained using water off-loading for each tracked adult after it
287 returned to the colony, following methods in Xavier et al. (2004). Stomach contents were
288 sorted at the lab, and fish, cephalopod and crustacean components identified from otoliths,
289 beaks and whole organisms (or parts thereof, e.g. carapaces), respectively, with the help of
290 identification guides (Xavier et al. 2004; Xavier and Cherel 2009). Only fresh prey items were
291 quantified, to restrict results to the most recent foraging trip, following Xavier et al. (2006).

292 Note that a previous study on wandering albatrosses concluded that the digestion time of prey
293 items and foraging trip duration had little effect on predictions about the distribution of
294 individual prey (Xavier et al. 2006).

295 Reconstructed mass (M) and length (L) of prey were estimated using allometric
296 equations and matched to the mass of ingested prey items estimated from the stomach
297 temperature data using MT-Dive software. This information was used to determine the
298 probable location and timing of ingestion of individual items. After an ingestion event (of
299 food or water), there is a precipitous drop in temperature followed by an approximately
300 exponential rise (PDER) (Wilson et al. 1992; Wilson et al. 1995; Zwolinski et al. 2010). The
301 mass of prey associated with each PDER event was determined following Wilson et al.
302 (1995). We applied the *I*-Index used by Catry et al. (2004) to distinguish feeding on solid
303 prey; in this way, the ingestion of water or gelatinous prey were excluded from further
304 analysis (this accounted for 18% of PDER events). Larger prey ($M \geq 510\text{g}$) were
305 discriminated from smaller prey ($M < 510\text{g}$) according to a discontinuity (threshold) in the
306 frequency distribution of the mass of all ingested items.

307

308 **Statistical procedures**

309

310 Generalized linear models (GLMs), fitted to a quasi-poisson error distribution (log link
311 function) were used to test the effect of sex on (1) trip duration, (2) ARS scale, (3) FPT time,
312 (4) percentage of fish, (5) percentage of cephalopods and (6) percentage of other prey items,
313 and (7) bathymetry, (8) net primary productivity, (9) sea surface temperature, (10) wind
314 intensity and (11) maximum distance to colony within the 95% UD (home range). We also
315 tested the effect of sex on (1) sinuosity index, (2) number of landings, (3) number of landings
316 in daylight, (4) number of landings in darkness, (5) mean mass of prey ingested, (6)

317 bathymetry, (7) net primary productivity, (8) sea surface temperature, (9) wind intensity and
318 (10) maximum distance to colony within the 50% UD (core area). Student's T-tests were used
319 to evaluate how mean SSTa values within the foraging area of wandering albatrosses during
320 their short trips (47–60°S, 25–50°W) varied historically, by comparing (1) our study period
321 (May – October 2009) vs. monthly climatologies of May – October (1990-2008) and (2) six-
322 months prior to our tracking period (November 2008 – April 2009) vs. monthly climatologies
323 of November – April (1990-2008). Prior to analysis, data were tested for normality (Q-Q
324 plots) and homogeneity (Cleveland dotplots) (Zuur et al. 2009). All statistical analyses were
325 conducted within R environment v. 3.3.2 (R Development Core Team 2016). All data are
326 presented as mean \pm SD (standard deviation), unless otherwise stated. Differences were
327 considered to be statistically significant at $p \leq 0.05$.

328

329

330 **RESULTS**

331

332 **Oceanographic conditions around South Georgia**

333

334 During the tracking period (May – October 2009; corresponding to the austral winter),
335 the mean SSTa in the area used by wandering albatrosses during their short trips (47–60°S,
336 25–50°W) was not significantly higher than the mean for the winter months between 1990 and
337 2008 (mean SSTa of $0.02 \pm 0.17^\circ\text{C}$ in 2009 vs. $-0.13 \pm 0.12^\circ\text{C}$ in 1990-2008; one sample t-test
338 $t_{10} = 1.51$, $P = 0.18$). However, the mean SSTa in the 6-month period (October 2008 – April
339 2009; corresponding to the austral summer) prior to tracking was significantly higher than the
340 historical mean for the summer months between 1990/91 and 2007/08 (mean SSTa = $0.49 \pm$
341 0.16°C vs. $0.02^\circ \pm 0.07$; $t_{10} = 2.81$, $P = 0.02$) (Fig. 1). SSTa within the complete range of the

342 tracked birds (see Fig. 1) was highly variable by month and annually since 1999, with a
343 particularly long period of positive SSTa values between January 1999 and July 2000 (Fig.
344 S2).

345

346 **Consistency in foraging habitats**

347

348 The tracked wandering albatrosses from South Georgia foraged from cold Antarctic
349 waters (approx. 60° S) to warmer waters (approx. to 30° S), and from around 30° W to 60° W
350 (Fig. S3). There were no significant differences between males and females in large-scale
351 foraging parameters (ARS scale and FPT time), trip characteristics and habitat characteristics
352 within the home range (95% UD) for all trips (Table 1). Despite high consistency in habitat
353 use, wandering albatrosses exhibited sexual segregation in core foraging areas (50% UDs;
354 Fig. 2). Males and females also showed a similar pattern in terms of probability of occurrence
355 in the habitat suitability models (Fig. 3-A, 3-B). This was reflected in the Schoener's *I*
356 statistics (ca. 0.92) which indicated high niche overlap for every 100 pairwise comparison of
357 HSMs. Both habitat suitability models generated for males and females had excellent
358 discriminatory performance (AUC > 0.90). Despite this high niche overlap, the response
359 curves generated by the habitat suitability models suggested that males and females showed
360 different responses to the oceanographic conditions associated with ARS behaviour. WM,
361 BATG and, to a lesser extent, SSTG and DISTCOL were retained in models that explained
362 variation in FPT in the different habitats exploited by both males and females (Table 2).
363 Despite no differences in the large-scale foraging areas between males and females, males
364 tended to forage in warmer and deeper sub-Antarctic waters, further from the breeding colony
365 (Fig. 4-A), whereas females foraged in more productive waters at the Antarctic Polar Front

366 (APF) and in the strong upwelling systems at the Patagonian shelf slope and that surrounding
367 South Georgia (Fig. 4-B).

368

369 **Spatial segregation in core foraging areas and diet**

370

371 Although the habitat suitability models showed that different oceanographic
372 conditions were associated with ARS behaviour, there were no differences between male and
373 female wandering albatrosses in home ranges, indicating no clear sexual segregation at this
374 large spatial scale. However, there was evidence of sexual segregation within the core
375 foraging areas as well as sex differences in feeding behaviour and diet (Table 1). The mean
376 number of landings per day was significantly higher for males (mean \pm SD = 15.4 ± 11.7)
377 than for females (mean \pm SD = 4.3 ± 2.6) (Table 3). The number of landings during daylight
378 was also significantly higher for males (13.1 ± 10.3) than females (3.9 ± 2.2) (Table 3). The
379 range of meal masses estimated from stomach temperature probes varied from 978 grams to
380 34,629 grams (Fig. 4-A, 4-B.). Males ingested significantly more food than females (15,973.7
381 g and 3869.8 g, respectively) (Table 3). Diet samples from the tracked birds comprised fish,
382 cephalopods and other items (51.7%, 44.1% and 4.2% by mass, respectively); other items
383 were crustaceans and carrion. Males fed significantly more on fish (Table 1) obtained in
384 unproductive, oceanic waters further from the breeding colony (Table 3). The species
385 consumed most frequently by males were Patagonian toothfish *Dissostichus eleginoides*
386 (61.1% by number) and *Antimora rostrata* (22.2% by number). Males showed sinuous
387 movements and searching behaviour, feeding on similar amounts of food during both the
388 outbound and return portions of trips, randomly in oceanic waters and mostly on large prey (\geq
389 510 g, based on the histogram for all prey ingested; see Methods) (Fig. 4-A). By contrast,
390 females fed significantly more on cephalopods (Table 1), in colder, shallow Antarctic waters

391 (but with steeper gradients) at the edge of the South Georgia shelf (Table 3). The fish species
392 caught most frequently by females were also *D. eleginoides* and *A. rostrata* (both 33.3% by
393 number). Fish species of the Macrouridae family were recorded only in the diet of females.
394 The most frequent squid species were *Histioteuthis atlantica* (21.6% by number), *Kondakovia*
395 *longimana*, *Moroteuthis knipovitchi* and *Taonius* sp. B (Voss) (all 13.5% by number).

396 Trips by females were more likely to take the form of commute-feed-return, as most
397 prey were ingested in the outbound portion of the trip (Fig. 4-B). According to the analyses of
398 meal mass, females typically caught a large prey item at the furthest distance from the colony,
399 reduced ARS behaviour and returned directly to the chick (Table 3). Males, on the other hand,
400 fed at a consistent rate throughout their foraging trips.

401

402 **DISCUSSION**

403

404 There was high overlap both in utilisation distributions and large-scale habitat use
405 (based on the HSMs) between male and female wandering albatrosses in our study, despite
406 the anomalous environmental conditions in local waters (Xavier et al. 2017). This accords
407 with previous studies in the region which found similar foraging strategies in males and
408 females during the chick-rearing period and under the same anomalous oceanographic
409 conditions (Xavier et al. 2004; Xavier and Croxall 2005). However, it contrasts with other
410 studies in both the southwest Atlantic and Indian Oceans during the breeding and nonbreeding
411 period under more typical oceanographic conditions, which showed clear sexual segregation
412 in large-scale habitat use and foraging distributions of wandering albatrosses (Xavier et al.
413 2004; Xavier and Croxall 2005; Weimerskirch et al. 2012; Åkesson and Weimerskirch 2014;
414 Froy et al. 2015). However, by integrating GPS, immersion, STP and diet data from the
415 tracked birds with remotely-sensed information on the environment, we show that within core

416 foraging areas, male and female wandering albatrosses differed in the conditions associated
417 with ARS behaviour, location of feeding events, and prey species, thus providing evidence for
418 sex-specific habitat segregation at local scale. Despite the recent progress in bio-logging
419 technologies, there are still important gaps in our knowledge of how marine predators interact
420 with the environment and their use of resources (Catry et al. 2004; Pereira et al. 2017). By
421 combining data from multiple devices and conventional analysis of stomach contents, we
422 were able to critically assess the foraging strategies of wandering albatrosses with a
423 particularly high level of detail (Wilson et al. 1995; Weimerskirch et al. 1997b; Catry et al.
424 2004; Weimerskirch et al. 2007).

425

426 **Consistency in habitat use**

427

428 There was no evidence in our study for sexual segregation in habitat use of wandering
429 albatrosses at a large spatial scale (i.e. 95% UD) in this anomalous austral winter. Our results
430 are in line with Xavier et al. (2004), which showed that foraging strategies of males and
431 females were broadly similar in a previous winter when local waters were also unusually
432 warm. Both sexes responded to these warm, relatively unproductive oceanographic regimes
433 (high SST and low NPP within home ranges), in oceanic waters at long distances from the
434 breeding colony (Table 1). Under more typical oceanographic conditions, latitudinal
435 segregation by sex in the wandering albatross is evident in both southwest Indian and
436 southwest Atlantic oceans during the chick-rearing period (Weimerskirch et al. 1993;
437 Weimerskirch et al. 1997a; Xavier and Croxall 2005; Froy et al. 2015). The absence of large-
438 scale sexual segregation in wandering albatrosses may be related to the different investment in
439 reproduction by each sex. According to Weimerskirch et al. (1997a), wandering albatrosses in
440 the Indian Ocean perform one of two types of foraging trip. Long foraging trips in warmer

441 sub-Antarctic waters are usually attributed to self-maintenance, allowing wandering
442 albatrosses to restore their own body condition, whereas short foraging trips are thought to
443 benefit the offspring by reducing the feeding interval (Weimerskirch et al. 1997a;
444 Weimerskirch et al. 2000). Since in our study both sexes do not differ in large-scale habitat
445 use, the absence of sexual segregation in long foraging trips may be related to a similar
446 investment by both sexes in self-maintenance.

447 Nevertheless, we detected sex differences in foraging strategies and habitat use at a
448 local scale (50% UD). Contrary to our initial expectations, and the at-sea distribution patterns
449 apparent in austral winters 1999 and 2000 (Xavier et al. 2004) our study showed that female
450 wandering albatrosses within their core foraging areas captured prey mostly in cold and
451 shallow Antarctic waters near the South Georgia shelf-slope, whereas males fed
452 predominantly in warm, deep sub-Antarctic waters. Females therefore seemed to exploit prey
453 hotspots in more productive areas near the breeding colony when compared with males.

454

455 **Oceanographic cues and sex differences in foraging behaviour**

456

457 Although we show that male and female wandering albatrosses overlapped at large
458 spatial scales (95% UD), there were subtler differences between sexes in feeding strategies
459 and local-scale habitat use in core areas (50% UD). In our HSMs, depth, frontal regimes,
460 maximum distance to colony and wind intensity were the main predictors of variation in FPT,
461 and depth and wind intensity were the main triggers of ARS behaviour in both sexes. In
462 contrast, bathymetric gradient was a poor predictor of the foraging distribution of wandering
463 albatrosses from Crozet and Kerguelen islands in the south Indian Ocean during the
464 incubation and brooding periods in 1998-2008 (Louzao et al. 2011). Low prey availability
465 around South Georgia during the unusually warm austral winter in which our data were

466 collected, might have forced both sexes to expend greater foraging effort and to search for
467 food in oceanic waters (with steep bathymetric gradients), taking advantage of high winds to
468 reduce the energetic costs of the long-distance commutes (Sachs et al. 2012).

469 In the Indian Ocean, distributions of male and female wandering albatrosses from
470 Crozet overlap extensively from 40° to 50° S (Weimerskirch et al. 2012). However, the
471 suggestion is that to alleviate partitioning for patchy resources when environmental conditions
472 are typical of the long-term mean, males prefer colder waters near to the colony or further
473 south (to 60°S), whereas females forage to a greater extent in warmer, more northerly waters
474 (to 30° S), attracted by longline fisheries for tuna (Weimerskirch et al. 1993; Weimerskirch et
475 al. 2012; Åkesson and Weimerskirch 2014). According to our habitat suitability models,
476 males from South Georgia are most likely to forage where there are steeper bathymetric
477 gradients and respond to proxies of pelagic frontal regimes. Indeed, while exploiting pelagic
478 areas in the central south Atlantic, males seemed to take advantage of high wind velocities. In
479 the Indian Ocean, male wandering albatrosses exploit particular wind regimes to travel at
480 higher speeds more efficiently, allowing them to utilise Antarctic waters closer to the
481 breeding colony which are used much less by females; the latter typically forage in
482 subtropical and tropical waters north of Crozet Archipelago (Shaffer et al. 2001). Despite
483 exploiting the same broad home-range as males, foraging activity of female wandering
484 albatrosses in our study was mostly triggered by high productivity and associated with
485 shallower waters. Sex-specific differences in foraging behaviour of albatrosses are usually
486 attributed to the influence of sexual size dimorphism on foraging efficiency, or competition
487 (Shaffer et al. 2001; Phillips et al. 2004; Phillips et al. 2011). Indeed, competition may play a
488 major role in segregation of birds from different colonies (Wakefield et al. 2013). In
489 wandering albatrosses, larger males may exclude females from waters near the breeding
490 colony via indirect competition and relegate them to warmer, oceanic sub-Antarctic waters

491 (Xavier and Croxall 2005) Therefore, it is unlikely that competitive exclusion would explain
492 why males respond to steeper bathymetric gradients and pelagic frontal regimes in oceanic
493 waters, nor why females were not restricted to warmer sub-Antarctic waters farther from the
494 colony. Moreover, when the unusually high SST and air temperature, and locally low
495 availability of prey in Antarctic waters occurred (Hill et al. 2009; Xavier et al. 2017), females
496 seemed to exploit productive and shallower waters, suggesting that smaller females are not
497 excluded from this area.

498

499 **Sex differences in feeding behaviour and diet**

500

501 As we expected, male and female wandering albatrosses differed in feeding behaviour
502 at a local scale (50% UD); however, contrary to our initial predictions, they also differed in
503 prey choice. It therefore appears that when if food availability is low, the two sexes adopt
504 distinct foraging strategies. Similarly, previous studies of wandering and other albatrosses
505 breeding in the Indian and Atlantic oceans reported that the rate of landings during daylight is
506 usually higher than in darkness (Weimerskirch et al. 1994; Weimerskirch et al. 1997b; Catry
507 et al. 2004; Phalan et al. 2007). In terms of the mass ingested, our study showed that males
508 ingested near three times more mass per trip when compared with females and the food
509 ingested rates per individual were similar to those reported in Weimerskirch et al. (1994).
510 Assuming that food ingested at sea is correlated with the amount of food delivered to the
511 offspring, given the slow digestion rates (Xavier et al. 2006) our results are in line with those
512 of Weimerskirch et al. (2000) and Weimerskirch and Lys (2000) which reported that male
513 parents deliver larger meals and more food to their chicks (mainly after short foraging trips)
514 than females, which suggest a greater investment in chick provisioning by males. Moreover,
515 our data indicate that males are most likely to catch larger prey (fish) on both their outbound

516 and return trips, whereas females generally exhibit a consistent commute-forage-commute
517 type of feeding behaviour, mostly catching prey on the outbound portion of the trip.

518 Overall, the bulk of the diet of wandering albatrosses at South Georgia comprises
519 demersal fish caught in neritic waters, and cephalopods (Xavier et al. 2004; Xavier and
520 Croxall 2005; Phillips et al. 2011). Previous studies conducted at South Georgia in typical
521 winters (cf. 2009) reported sex differences in diet composition; male had a less varied diet
522 consisting primarily of fish, whereas females consumed a wider variety of fish and squid
523 (Xavier and Croxall 2005). For example, in 1999, males consumed more fish (74% by mass),
524 whereas females ate more cephalopods (67% by mass) and foraged further to the north
525 (Xavier et al. 2004). By contrast, in the following winter (2000), when conditions were
526 warmer, both males and females fed much more on fish (91% and 78% by mass, respectively)
527 than on cephalopods (Xavier et al. 2004). This contrasts with results from a decade later, in
528 2009; males fed mostly on fish (62.1% by mass) and females on squid (51.2% by mass) (this
529 study). This could possibly indicate that male and female wandering albatrosses try to avoid
530 competition for the same prey (due to the lack of prey available locally), and thus diverge in
531 habitat preference near the breeding colony where intra-specific competition is intense.

532 As some of the most numerous squid species in their diet - *Histioteuthis atlantica* and
533 *Taonius* sp. B (Voss) - are known to be distributed in sub-Antarctic and subtropical waters
534 (Xavier et al. 2016), our results suggest that in years of extreme oceanographic conditions,
535 female wandering albatrosses spend more time in more northerly waters, increasing their
536 overlap with longline fisheries for tuna and other billfishes, and hence the risk of bycatch
537 (Jiménez et al. 2016). Similarly foraging areas of female giant petrels *Macronectes giganteus*
538 overlapped more with zones of intense squid fishing activities in northern waters on the
539 Patagonian shelf and around the Falklands Islands, while males concentrated their foraging

540 areas in southern waters where effort in these types of fisheries is much lower (Krüger et al.
541 2016).

542 Sex-differences in feeding ecology during the austral winter of 2009 were also
543 apparent for other marine predators from South Georgia. Male and female gentoo penguins
544 *Pygoscelis papua* differed in their main prey; males fed mainly on fish (54% by mass)
545 followed by crustaceans (38% by mass) whereas females fed mainly on crustaceans (89% by
546 mass) followed by fish (4% by mass) (Xavier et al. 2017).

547 In terms of the fish component, our study showed that wandering albatrosses fed most
548 on Patagonian toothfish (61.1% by number) and *Antimora rostrata* (22.2% by number), in
549 agreement with previous studies (Xavier et al. 2003b; Xavier et al. 2004). These were also the
550 two fish species consumed more frequently by males. Moreover, males do not seem to exhibit
551 the consistent commute-forage-commute feeding tactic used by females, but instead
552 consumed broadly the same mass of food on both the outbound and return portions of trips,
553 and exhibited sinuous flight paths; this suggests greater use of visual cues during searching
554 (Nevitt et al. 2008). According to Weimerskirch et al. (1997a), during long foraging trips,
555 both males and females follow a looping course generally north of Crozet, indicating that at
556 large scales, wandering albatrosses from the southwest Indian Ocean, similarly to birds from
557 the southwest Atlantic, forage in patchy environments searching for unpredictable and patchy
558 prey. In addition, in their short foraging trips, females commute rapidly to specific sectors
559 where they spend several hours to several days, and return straight to the colony to feed the
560 chick (Weimerskirch et al. 2007). Results from previous studies (Weimerskirch et al. 1997a;
561 Weimerskirch et al. 2000; Shaffer et al. 2003) reported that chick-provisioning effort of
562 wandering albatrosses is adjusted by parents in relation to prey availability. Therefore, this
563 foraging behaviour could also suggest that when facing low prey availability in Antarctic
564 waters, females may perform a different provisioning strategy and greater investment in

565 reproduction, as shown in other seabirds such as the black-legged kittiwake *Rissa tridactyla*
566 (Jodice et al. 2002; Jodice et al. 2006). In our study, females performed shorter trips (in
567 distance and duration) than males, possibly reflecting preferences for different feeding
568 habitats (see above). The sex-specific differences in feeding behavior may indicate that in
569 years when prey availability is low in local Antarctic waters, males may have greater
570 difficulties than females in provisioning their chick, and so females increase their investment
571 in reproduction.

572 The low availability of prey in the study year may also have required males to adopt
573 more opportunistic behaviour, and might also explain their preference for fish, particularly
574 large demersal species (Patagonian toothfish and *Antimora rostrata*) discarded by commercial
575 fisheries in sub-Antarctic waters (Xavier et al. 2004; Jiménez et al. 2016). How wandering
576 albatrosses are able to capture demersal fish remains unclear. Although many are obtained by
577 scavenging behind fishing vessels (Nel et al. 2002; Xavier et al. 2004), some species appear to
578 also be caught naturally, as they were already present in the diet before the increase in
579 fisheries in the Southern Ocean (Cherel et al. 2017). Wandering albatrosses are scavengers
580 and the most likely explanation for the abundance of deep-sea fish in their diet could be that
581 moribund animals rise to the surface during their vertical migrations, or are caught as
582 juveniles (Cherel et al. 2017).

583 Female wandering albatrosses in this study fed on a wider variety of fish (47.4% by
584 mass) and squid (51.2% by mass). Some, including Patagonian toothfish (33.3% by number)
585 and *Antimora rostrata* (33.3% by number), were likely obtained as discards from local
586 fisheries, along with macrourids in other years, which together represent the bulk of the fish
587 found in the diet of wandering albatrosses (Xavier et al. 2004). Females also consumed
588 *Muraenolepis microps* (8.3% by number) and several species of macrourids (25% by
589 number), which were probably also obtained as fishery discards around the South Georgia

590 shelf and shelf-slope (Xavier et al. 2004; Jiménez et al. 2016). Although females fed on a
591 wider variety of squid than males, there was considerable overlap. Both sexes fed more on
592 *Histioteuthis atlantica*, *Kondakovia longimana* and *Taonius* sp. B (Voss). *Kondakovia*
593 *longimana* are too big to have been ingested intact by a wandering albatross, as it is assumed
594 that cephalopods heavier than 500 g are unlikely to be captured alive (i.e. naturally), so
595 probably became available at the surface, post-mortem (Croxall and Prince 1994; Xavier et al.
596 2003a; Xavier and Croxall 2007). Males also fed on *Moroteuthis knipovitchi*, a species from
597 Antarctic waters, likely caught in the shelf slope around South Georgia (Xavier et al. 1999;
598 Seco et al. 2016). *Histioteuthis atlantica*, *Taonius* sp. B (Voss) and *Galiteuthis glacialis*,
599 present in the diet of both sexes, were likely captured during long foraging excursions to sub-
600 Antarctic and subtropical waters (Xavier et al. 1999; Xavier et al. 2016; Pereira et al. 2017).

601

602 **Conclusions**

603

604 Overall, our results highlight the importance of oceanographic conditions in shaping
605 the extreme life-history strategies of pelagic seabirds, and the spatial ecology of male and
606 female wandering albatrosses in particular, suggesting that sexual segregation in this species
607 is mediated by habitat selection and prey availability. During an anomalous austral winter,
608 male and female wandering albatrosses from South Georgia showed high overlap in foraging
609 areas at a large spatial scale, despite low prey availability in local waters (i.e. around South
610 Georgia), suggesting that both sexes invested equally in self-maintenance during the long
611 foraging trips. Their foraging behaviour at smaller spatial scales seemed to be triggered by
612 different environmental conditions, with males more likely to forage around oceanic fronts in
613 sub-Antarctic waters, taking advantage of higher winds, whereas females foraged over
614 hotspots of ocean productivity in shallow Antarctic waters. In addition, sex-specific feeding

615 behaviour appeared to be an adaptation to local habitat conditions, and prey availability. Our
616 results also emphasise the importance of scavenging on fisheries discards, which provide an
617 alternative food supply particularly in years when the availability of natural food is low.
618 These observations highlight that marine predators (such as wandering albatrosses) can show
619 considerable flexibility in response to variation in the marine environment. However, only
620 multiple years of tracking has shed light into the underlying drivers of large-scale foraging
621 patterns in this population.

622 Our results suggest that differences in parental investment may play an important role
623 in segregating birds from the same colony, especially when prey availability is locally scarce.
624 Facing low prey availability, both male and female wandering albatrosses differed in their
625 feeding and provisioning strategies, and showed divergent habitat selection and prey
626 preference during short trips near to the breeding colony. Females performed shorter trips,
627 commuting directly into known productive areas around the breeding colony, increasing their
628 investment in provisioning the offspring and feeding mostly on a wide range of cephalopod
629 species, whereas male targeted oceanic waters, mostly feeding on deep-sea fish species
630 usually obtained by association with fishing vessels.

631

632 **COMPLIANCE WITH ETHICAL STANDARDS**

633

634 All authors declare they have no conflict of interests. All applicable international,
635 national, and/or institutional guidelines for the care and use of animals were followed. The
636 animal procedures used in this this study were reviewed and approved by the Joint British
637 Antarctic Survey - Cambridge University Animal Welfare and Ethical Review Committee.
638 Permits to operate were issued by the Government of South Georgia and the South Sandwich
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640

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642

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893 **Table 1.** General Linear Models (GLM) testing the effect of sex on foraging trip
 894 characteristics, diet composition and habitat characteristics of the home range (95% UD) of
 895 wandering albatrosses *Diomedea exulans* tracked from Bird Island, South Georgia during
 896 chick-rearing in austral winter 2009. Values are mean \pm SD. ARS - Area Restricted Search
 897 and FPT – First Passage Time. Significant results in **bold**.

	Sex		Test	
	Males	Females	GLM: F _{1,28}	P
Foraging trip characteristics				
N track [N Birds]	15 [15]	15 [15]	—	—
Trip duration (days)	5.4 \pm 4.4	6.8 \pm 6.0	0.54	0.47
Spatial ecology parameters				
ARS scale (km)	16.7 \pm 16.2	18.3 \pm 22.8	0.05	0.83
FPT time (hours)	34.3 \pm 26.7	37.6 \pm 31.2	0.10	0.75
Diet composition (by mass)				
Fish (%)	62.1 \pm 43.3	47.4 \pm 43.6	8.52	0.02
Cephalopods (%)	34.8 \pm 41.74	51.2 \pm 44.7	9.92	0.02
Crustaceans (%)	0	0.1 \pm 0.5	—	—
Others * (%)	3.1 \pm 7.5	1.3 \pm 4.9	6.12	0.05
Habitat in the home-range (95 % kernel UD)				
Bathymetry (BAT; m)	2754.7 \pm 2020.8	2534.9 \pm 1817.6	0.06	0.81
Net Primary Productivity (NPP, C/m ² /day)	0.6 \pm 0.2	0.6 \pm 0.3	0.31	0.58
Sea Surface Temperature (SST; °C)	4.6 \pm 3.5	3.7 \pm 4.1	0.76	0.39
Wind Intensity (WM; m/s)	4.6 \pm 1.5	4.7 \pm 1.5	0.04	0.84
Maximum distance to Colony (DISTCOL; Km)	941.3 \pm 619.7	686.3 \pm 664.9	1.31	0.26

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899 * Carrion, jellyfish and longline fishing hooks.

900 **Table 2.** Estimates of model fit and relative contributions of the oceanographic predictors to
 901 the MaxEnt models generated for the foraging distribution of wandering albatrosses
 902 *Diomedea exulans* tracked from Bird Island, South Georgia during chick-rearing in austral
 903 winter 2009. AUC/ROC - Area Under Curve of the Receiver Operating Characteristics Curve.

	Males	Females
Test AUC (%)	91.7	92.2
Parameter contribution (%)		
Bathymetry (BAT)	—	—
Net Primary Productivity (NPP)	—	30.0
Sea Surface Temperature (SST)	—	—
Wind Intensity (WM)	44.9	31.0
Maximum distance to Colony (DISTCOL)	<0.1	<0.1
Gradient in BAT (BATG)	36.1	30.5
Gradient in NPP (NPPG)	6.5	—
Gradient in SST (SSTG)	12.5	8.5
Permutation contribution (%)		
Bathymetry (BAT)	—	—
Net Primary Productivity (NPP)	—	35.1
Sea Surface Temperature (SST)	—	—
Wind Intensity (WM)	51.0	40.8
Maximum distance to Colony (DISTCOL)	<1.0	<1.0
Gradient in BAT (BATG)	24.0	15.7
Gradient in NPP (NPPG)	7.4	—
Gradient in SST (SST)	17.6	8.3

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905 **Table 3.** Characteristics of complete trips (with data from all three devices; N = 17 individuals), landings, mass meals and the habitats visited by male and
 906 female wandering albatrosses tracked from Bird Island, South Georgia during chick-rearing in austral winter 2009. Values are mean \pm SD, unless otherwise
 907 stated. Results are from General Linear Models (GLM) testing the effect of sex. Significant results ($p < 0.05$) in **bold**.
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	Sex		Test	
	Males	Females	GLM: $F_{1,12}$	P
Trip characteristics				
Sinuosity (0 – 1)	0.2 \pm 0.1	0.4 \pm 0.3	5.44	0.04
Mean landings per trip (landings)	15.4 \pm 11.7	4.3 \pm 2.6	9.33	0.01
Mean landings daylight per trip (landings)	13.1 \pm 10.3	3.9 \pm 2.2	8.98	0.01
Mean landings darkness per trip (landings)	2.3 \pm 1.8	0.4 \pm 0.8	7.19	0.02
Mean mass ingested per trip (grams; g)	15973.7 \pm 12883.1	5645.3 \pm 3869.8	17.92	< 0.001
Core area overlap among sexes (%)	51 \pm 46		—	
Foraging habitat (within core areas; 50% UD)				
Bathymetry (BAT; m)	2003.7 \pm 1966.0	1283.3 \pm 1162.6	3.52	0.05
Net Primary Productivity (NPP, C m ⁻² day ⁻¹)	1.0 \pm 0.6	1.3 \pm 0.8	1.98	0.20
Sea Surface Temperature (SST; °C)	2.5 \pm 2.9	1.3 \pm 1.0	3.31	0.03
Wind Intensity (WM; m s ⁻¹)	3.3 \pm 1.6	4.9 \pm 2.2	1.01	0.23
Maximum distance to Colony (DISTCOL; Km)	474.1 \pm 399.7	352.0 \pm 266.9	5.65	0.05

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912 **List of Figures**

913

914 **Figure 1.** Monthly Sea Surface Temperature anomalies (SSTa) between January 2009 and
915 October 2009, within the foraging range of wandering albatrosses during short trips (47–60°S,
916 25–50°W). Data extracted from [http://ingrid.ldeo.columbia.edu/SOURCES/](http://ingrid.ldeo.columbia.edu/SOURCES/NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOlv2/.weekly/.ssta/)
917 [NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOlv2/.weekly/.ssta/](http://ingrid.ldeo.columbia.edu/SOURCES/NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOlv2/.weekly/.ssta/).

918 **Figure 2.** Foraging distribution of male (blue) and female (red) wandering albatrosses
919 *Diomedea exulans* tracked from Bird Island, South Georgia (yellow stars), during the chick-
920 rearing period in austral winter 2009. Dotted contours correspond to home range (95% UD)
921 and filled contours correspond to core foraging areas (50% UD) overlaid on bathymetry
922 (BAT), net primary productivity (NPP), sea surface temperature (SST) and wind intensity –
923 modulus of wind (WM). Dynamic predictors are showed as averaged composites in May-
924 October. Set of oceanographic predictors shown in background were selected based on the
925 importance of those variables in habitat suitability models (MaxEnt).

926 **Figure 3.** Habitat suitability maps for (A) male and (B) female wandering albatrosses tracked
927 from Bird Island, South Georgia (yellow star) during the chick-rearing in austral winter 2009.
928 Predictions derived by maximum entropy (MaxEnt) modelling technique. For calibration of
929 HSMs, we included 172 occurrences for males and 185 occurrences for females. Dotted
930 contours correspond to home range (95% UD) and filled contours correspond to core foraging
931 areas (50% UD). Predicted habitat suitability ranges from low (0) to high (1) scores on a
932 constant colour ramp between plots.

933 **Figure 4.** Short foraging trips (< 6 days; see methods) of (A) male (blue) and (B) female (red)
934 wandering albatrosses tracked using three devices (GPS, immersion and stomach temperature
935 loggers) from Bird Island, South Georgia (yellow star) during chick-rearing in austral winter

936 2009. Points indicate prey capture events (PDER) and different colours with different density
937 radius were used for meals of different mass (in grams).

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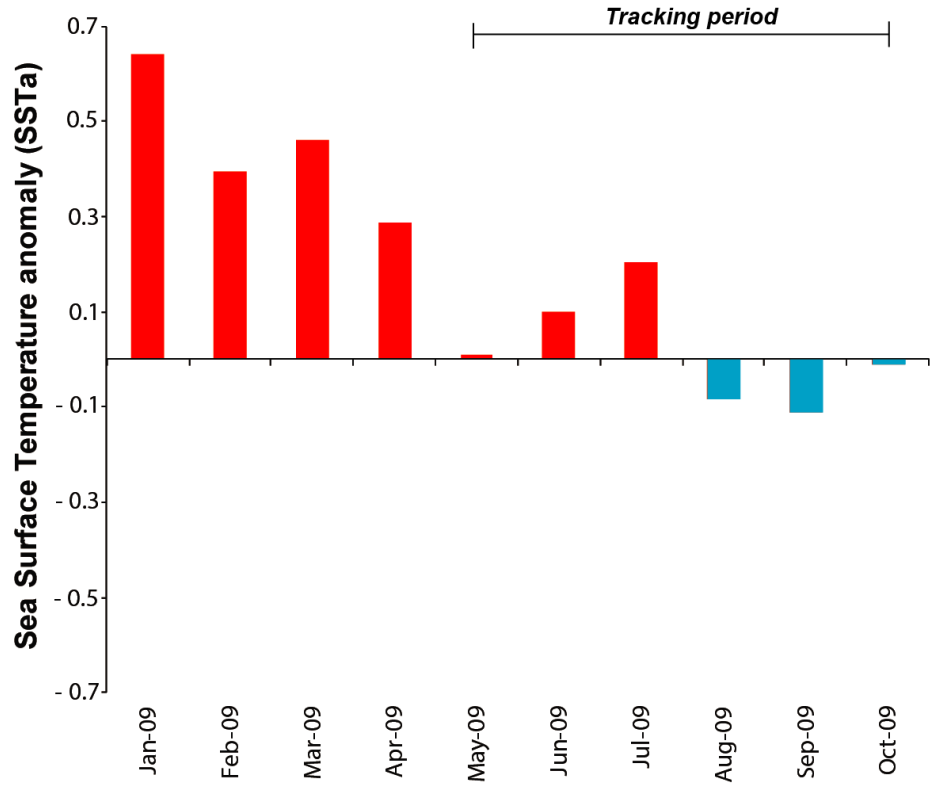
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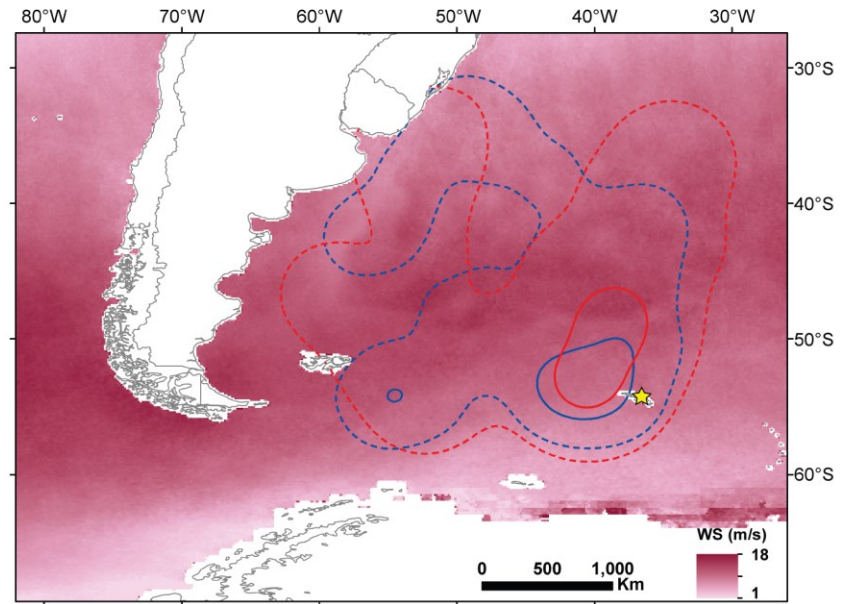
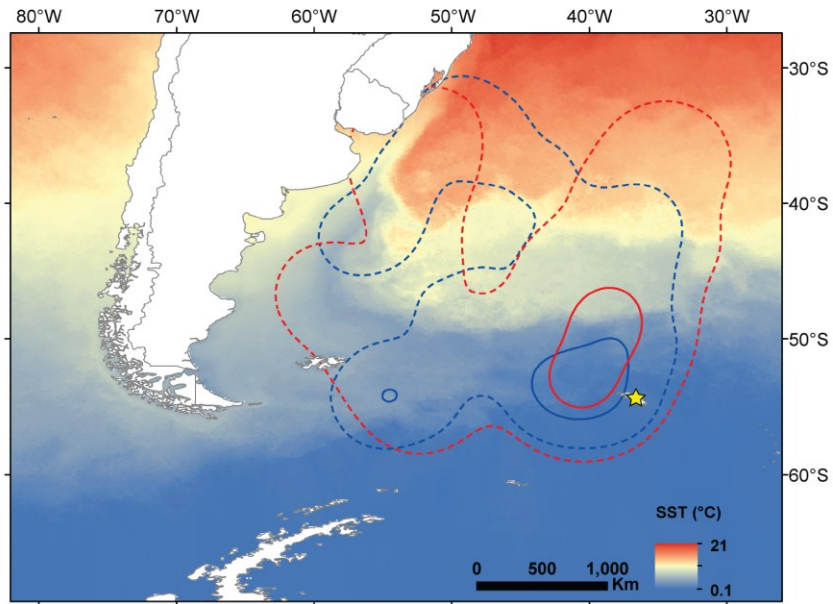
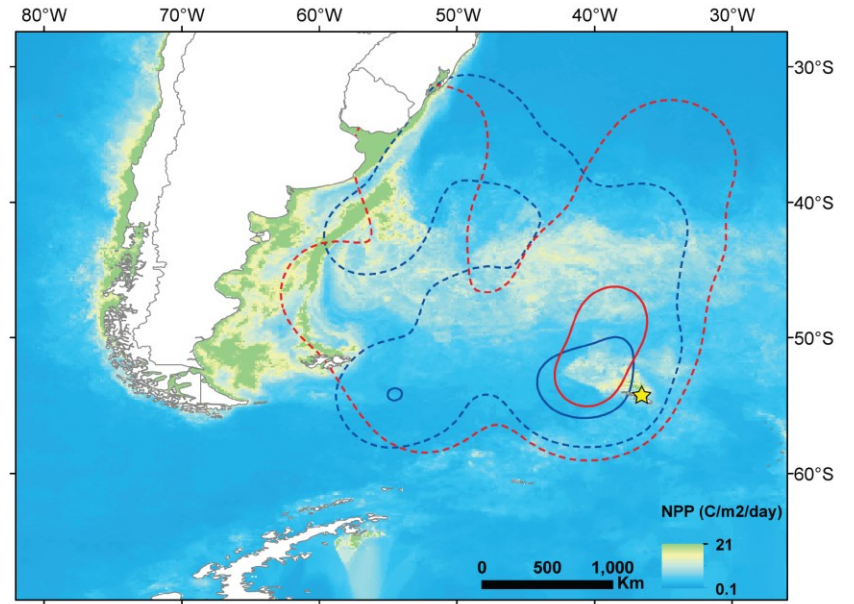
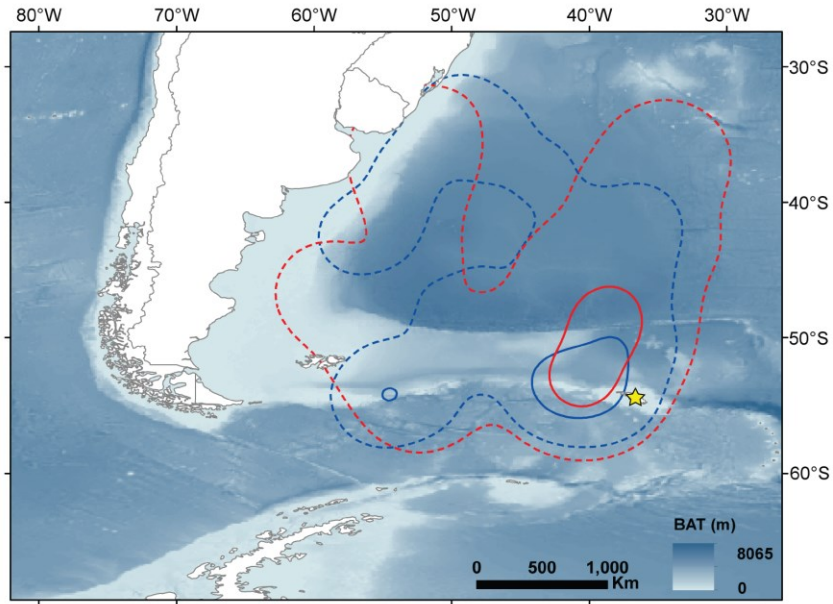
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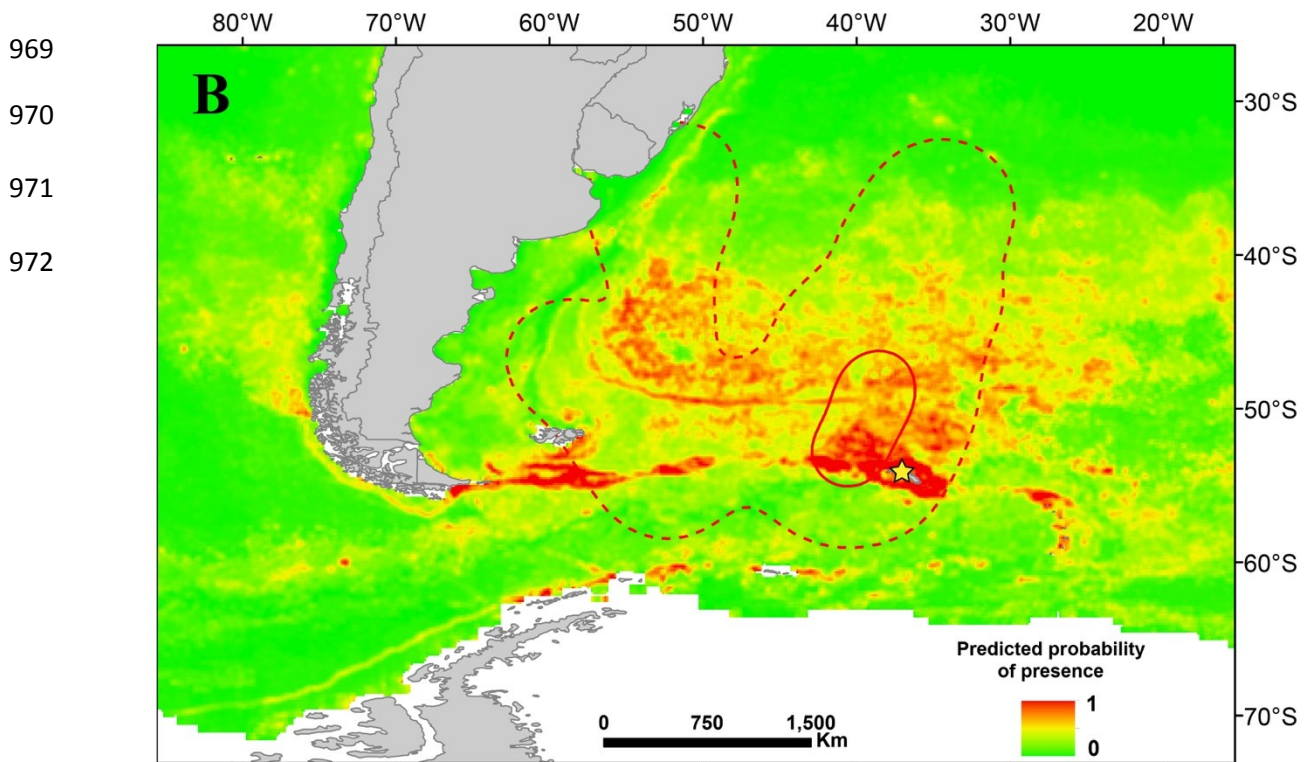
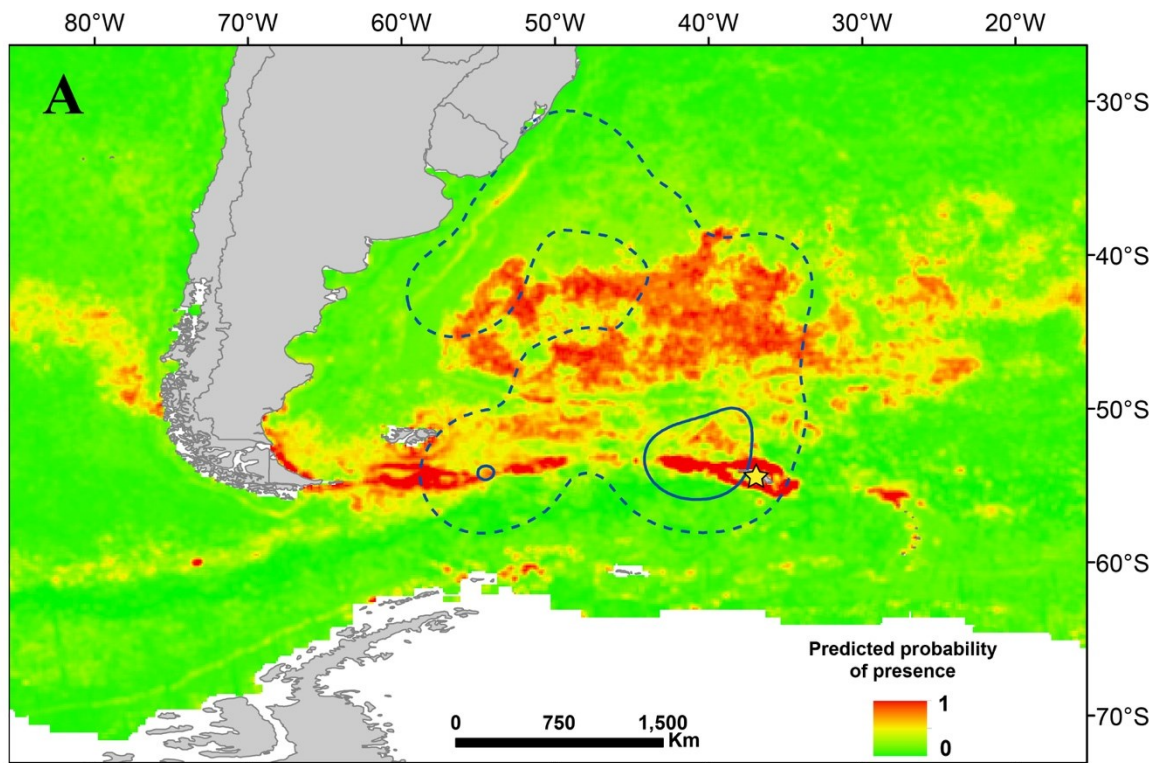
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