

1 **Title page**

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3 **Title:** Environmental drivers of humpback whale foraging behavior in the remote Southern

4 Ocean

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22 **ABSTRACT**

23 Satellite telemetry and animal movement models advance our ability to remotely monitor the
24 behavior of wide-ranging species. Understanding how different behaviors (e.g. foraging) are
25 shaped by dynamic environmental features is fundamental to understanding ecological
26 interactions and the impact of variability. In this study we deployed satellite-linked tags on
27 humpback whales (*Megaptera novaeangliae*) and used state-space models to estimate locations
28 and to infer underlying behavioral states. We then modelled the association between whale
29 behavior (e.g. foraging or transiting) and environmental variables using linear mixed-effect
30 models. We identified the importance of two recently discovered Southern Ocean feeding areas
31 for Oceania humpback whales as well as the key environmental drivers affecting whale behavior.
32 We detected behavioral differences between whales utilizing the two adjacent feeding regions
33 (~2,000 km apart), which were likely caused by animals trying to efficiently locate prey in relation
34 to the dynamic environmental characteristics of each habitat. We observed a seasonal pattern
35 in foraging behavior, with the peak occurring in the middle of summer. Whales also foraged
36 more intensively with increasing proximity to areas from which the ice edge had recently
37 retreated, suggesting heightened productivity in these areas. The relationship between the
38 animals and the physical features of the seascape, as well as the behavioral plasticity observed,
39 could have implications for the future recovery of these whales in a changing Southern Ocean.

40

41 **Key words:**

42 Foraging behavior; Habitat use; Migration; Telemetry; Whales

43 INTRODUCTION

44

45 Many animal behaviors, such as movement and habitat use, are driven by responses to internal
46 cues as well as the external conditions experienced by the animal (Nathan et al. 2008).
47 Understanding how the physical environment shapes the behavior and distribution of animals
48 as they try to satisfy their resource requirements is a fundamental topic in behavioral ecology
49 (e.g. Ballance et al. 2006; Aarts et al. 2008; Davies et al., 2012). A wide range of animals from
50 moths to caribou (*Rangifer tarandus*) migrate between critical habitats following pulses in
51 resource availability and abundance (Jiang et al. 2011; Le Corre et al. 2017). In many terrestrial
52 and aquatic taxa the decision to depart for a new habitat is often controlled by variables such as
53 photoperiod, temperature, snow fall and severe weather at the initial location, at which point
54 the animals cannot predict the habitat conditions at the end destination (Jonsson and Ruud-
55 Hansen 1985; Vøllestad et al. 1986; Cotton 2003; Balbontín et al. 2009; Jiang et al. 2011; Rivrud
56 et al. 2016). Memory of long-term average conditions may also play a role in directing migrants
57 to their destination (Bracis and Mueller 2017; Abrahms et al. 2019). Upon arrival at a new
58 location resources, such as prey, are often patchily distributed throughout space and time, at
59 which point animals initiate search strategies to locate and secure prey (Benhamou 1992; Boyd
60 1996; Sims et al. 2008; Humphries et al. 2010; Carroll et al. 2017). In marine systems specifically,
61 biological productivity can be highly variable due to the heterogeneity of the many physical
62 processes in the environment (Haury et al. 1978). This results in some habitats being more
63 productive than others, which in turn influences prey availability and predator behavior. To
64 forage efficiently predators must move through their dynamic environment in search of prey
65 while maximizing time spent foraging in the most productive areas (Stephens and Krebs 1986;
66 Fauchald and Tveraa 2006). In patchy environments individuals may even adjust aspects of their
67 foraging behavior depending on the external environmental conditions (Weimerskirch 2007;
68 Sebastiano et al., 2012; Kirchner et al. 2018).

69 Obtaining direct observations of movement and behavior in wide-ranging predators can be
70 challenging, and more indirect techniques, such as animal-borne transmitters and data loggers,
71 are often required to detect and identify behavior. Advancements in satellite telemetry and
72 tagging technology have improved the ability to remotely collect animal movement data at high
73 spatial and temporal resolutions (Hussey et al. 2015; Gurarie et al. 2016; Chimienti et al. 2017).
74 Different movement models can be applied to these remotely collected data to identify
75 underlying behavioral states such as foraging (Morales et al. 2004; Jonsen et al. 2005, 2006;
76 Michelot et al. 2017). Various statistical models can then be used to link animal locations and
77 behavior with ecological variables. Such models are useful tools for explaining spatial
78 distribution patterns of highly mobile animals, for identifying critical habitats, and they have
79 many applications including addressing management and conservation questions (Mandel et al.
80 2008; Gregor et al. 2013; Guisan et al. 2013).

81 In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) migrate thousands
82 of kilometers annually from the tropics to the Southern Ocean to feed on their main prey, the
83 Antarctic krill (*Euphausia superba*; Kawamura 1994; Murase et al. 2002). The endogenous and
84 exogenous cues used by the whales to navigate to the feeding grounds and to search for prey
85 remains unresolved (Horton et al. 2011, 2017; Torres, 2017). Directly observing the foraging
86 behavior and characterizing the foraging habitat of large marine predators, such as humpback
87 whales, in the Southern Ocean is notoriously difficult due to the logistical challenges associated
88 with accessing this remote and vast area (Griffiths 2010). Therefore, our knowledge of the fine-
89 scale behavior and patterns of habitat use by humpback whales in this region remains limited,
90 compared to for example the more accessible Antarctic Peninsula (e.g. Friedlaender et al. 2013,
91 2016).

92 During the commercial whaling era, Southern Hemisphere humpback whale stocks were highly
93 overexploited and hunted to near extinction (Ivashchenko and Clapham 2014; Clapham and
94 Baker 2017). Since being granted protection from whaling, humpback populations have shown
95 variable recovery. The Oceania humpback whales, comprising whales from multiple breeding

96 ground subpopulations from the Pacific Islands (spanning New Caledonia to French Polynesia)
97 are estimated to be <50% of pre-exploitation numbers and recovering more slowly than the
98 neighboring east Australian population (Childerhouse et al. 2008; Constantine et al. 2012;
99 International Whaling Commission 2015). To date there has been little information available on
100 the Oceania humpback whales within the Southern Ocean feeding grounds, and we only recently
101 revealed their migration paths and location of the feeding grounds (Riekkola et al. 2018). As a
102 consequence, we do not know whether the feeding behavior and patterns of habitat use by
103 these humpback whales could be linked to the different population recovery rates (International
104 Whaling Commission 2015).

105 Here we applied a movement model to satellite tagging data of humpback whales on their
106 Southern Ocean feeding grounds to infer underlying behavioral states: transiting and area
107 restricted search (ARS), a behavior indicative of foraging (Weinstein et al. 2017; Andrews-Goff
108 et al. 2018). We expected that aspects of whale foraging behavior would change throughout the
109 feeding season. For example, we hypothesized that there would be an increase in foraging effort
110 as prey becomes more abundant with the onset of spring and summer. We then used a statistical
111 model to investigate the relationship between the inferred behavioral states (specifically the
112 occurrence of ARS-foraging) and different environmental variables. We expected the whales'
113 behavior to be affected by different environmental factors, and that behavioral differences
114 would exist between animals utilizing different regions of the Southern Ocean. By linking whale
115 movement data and behavioral changes to the conditions of their foraging habitat, this study
116 ultimately contributes to a better understanding of the behavior of wide-ranging predators.

117

118 **MATERIALS AND METHODS**

119 **Satellite tag deployment**

120 Wildlife Computers (Redmond, WA, USA) SPOT 5 Platform Transmitting Terminals (PTTs) were
121 attached to 25 adult humpback whales during the peak of their southern migration past the

122 Kermadec Islands, New Zealand, between September and October 2015 (Figure 1). The tags
123 were deployed using a modified version of the Air Rocket Transmitter System (Heide-Jørgensen
124 et al. 2001) at a pressure of 10-12 bars. Observed locations were calculated by the Argos System
125 using the Doppler Effect on transmission frequency when multiple messages from a tag were
126 received by a satellite. An estimated error and a location class (in descending order of accuracy:
127 3, 2, 1, 0, A, B, Z) were assigned to each location (see Argos user's manual 2016). Location classes
128 A and B have no accuracy estimation and Z is an invalid location. The tags were duty cycled to
129 transmit for 21 hours each day to maximize the time with overhead Argos satellites. The
130 maximum number of transmissions per day was set to 600 at a repetition rate of 45s.
131 Reproductive status (mother with a calf, or adult) of the tagged whales was inferred in the field
132 based on the presence of a calf closely associated with the satellite tagged animal (Clapham et
133 al. 1999). Molecular sex identification was conducted using tissue samples collected at the time
134 of tagging (Riekkola et al. 2018).

135

136 **Data processing and hierarchical state-space model**

137 Raw Argos locations were speed filtered using the R package *argosfilter* (Freitas et al. 2008) at
138 a conservative maximum speed of 36km/h to remove only highly erroneous and unrealistic
139 locations. We used a hierarchical version of a Bayesian state-space model (SSM; Jonsen et al.
140 2005, 2006) to estimate locations (via an observational model) and behavioral states (via a
141 movement model). We used a 6-h time-step in the model to provide detailed whale movement
142 data. Obtaining whale data on an even finer scale was not necessary given the low resolution of
143 some of the environmental covariates (see section 'Explanatory variables for statistical model'
144 and Table 1). The SSM was fitted in R (version 3.5.1, R Core Team 2018) using the software JAGS
145 (Plummer 2013) and the R packages *rjags* (Plummer 2016) and *bsam* (Jonsen et al. 2015). Where
146 a gap of >1 day existed in the satellite data transmission, the individual track was split and ran
147 as segments to avoid interpolating over long periods of time with no data. Two Markov chain
148 Monte Carlo (MCMC) chains were run in parallel, each for a total of 200,000 simulations. The

149 first 100,000 samples were discarded as a 'burn-in', and the remaining samples were thinned,
150 retaining every 100th sample to reduce autocorrelation. The final 2,000 samples were used to
151 compute the posterior distribution of the model parameter estimates: the mean turning angles,
152 and movement persistence (i.e. the autocorrelation in speed and direction). The behavioral
153 mode estimate (b), ranging between 1 and 2, was inferred from the means of the MCMC
154 samples. A behavioral mode close to 1 ($b < 1.25$) indicates transiting behavior, which is persistent
155 and highly directional movement with low turning angles (near 0°). Animals are expected to be
156 in transiting mode during migration or when traveling between favorable locations (e.g. prey
157 patches). A behavioral mode close to 2 ($b > 1.75$) indicates area-restricted search (ARS) behavior,
158 a more variable movement with large turning angles (near 180°) and increased rate of turning.
159 ARS is generally considered to be indicative of foraging, resting or breeding behavior (e.g.
160 Weinstein et al. 2017; Andrews-Goff et al. 2018). Locations with a mean b estimate between
161 1.25 and 1.75 were treated as 'uncertain'.

162

163 **Explanatory variables for statistical model**

164 We used both static and dynamic variables estimated at each state-space modelled location
165 as explanatory variables to identify those that had most effect on the whales' behavioral mode
166 (specifically the occurrence of ARS-foraging). We selected environmental variables which, based
167 on prior knowledge, are likely to be biologically relevant (e.g. Friedlaender et al. 2011; Bombosch
168 et al. 2014; Trudelle et al. 2016; Andrews-Goff et al. 2018; Table 1), and that were available for
169 the entire spatial extent of location data.

170 Daily sea ice concentration data were obtained from the National Snow and Ice Data Center
171 (NSIDC, <https://nsidc.org/data>). Distance to the ice edge was calculated from the daily ice
172 concentration as the minimum distance between whale locations and the 15% sea ice
173 concentration contour (e.g. Gloersen et al. 1992; Stammerjohn and Smith 1997). One month
174 and two-month lags were calculated as the distance of each SSM-estimated whale location to
175 where the ice edge was one month and two months prior. It takes approximately one to two

176 months after ice melt for productivity to peak in the marginal ice zone (Lehodey et al. 1998;
177 Arrigo et al. 2008; Dalpadado et al. 2014). Altimeter derived daily sea surface heights (SSH) and
178 daily sea surface current velocity data were obtained using E.U. Copernicus Marine Service
179 Information (<http://marine.copernicus.eu>). SSH and sea surface current velocity gradients can
180 be used to trace the locations of the Antarctic Circumpolar Current fronts, and therefore by
181 using these variables we could account for possible interactions with the fronts (e.g. Sokolov
182 and Rintoul 2009). Sea surface current velocity was log transformed prior to analysis. Data on
183 sea ice, SSH, and sea surface current velocity were obtained through the Australian Antarctic
184 Data Centre and extracted using the R package *raadtools* (Sumner 2016).

185 Bathymetry was obtained from the International Bathymetric Chart of the Southern Ocean
186 (IBCSO) digital bathymetric model of the circum-Antarctic waters (Arndt et al. 2013). IBCSO is a
187 regional mapping project of the General Bathymetric Chart of the Oceans (GEBCO) and the
188 digital bathymetric model is publicly available (www.ibcso.org). Slope was derived from the
189 IBCSO digital bathymetric model using the '*slope*' tool in ArcGIS (version 10.5, Esri, Redlands, CA,
190 USA) and was log transformed prior to analysis.

191 Month for each point was obtained from the SSM estimated locations. We chose to include
192 month as a continuous variable in the model. Therefore, November, the first month for which
193 there were data within the feeding grounds, was labelled '0' (followed by December = 1 through
194 to June = 7) in order to set November as the baseline and to maintain chronological order.

195 Prior analysis of the satellite tags had revealed that the whales diverged to two broad feeding
196 regions (Riekkola et al. 2018). To make comparisons between these feeding areas, each location
197 was assigned a 'region' based on whether it occurred west (Ross Sea) or east (Amundsen and
198 Bellingshausen Seas) of the 130°W meridian (Figure 1). Studies have identified regional trends
199 in the Antarctic sea ice variability, with increasing sea ice extent occurring in the Ross Sea region,
200 and contrasting decrease in sea ice extent occurring in the Amundsen and Bellingshausen Seas
201 region (e.g. Zwally et al. 2002; Turner et al. 2009). Future ocean and sea-ice changes are also
202 projected to affect the growth rates of krill (the whales' main prey), with modelled high potential

203 growth rates in Ross Sea, and low or negative potential growth rates in the Amundsen and
204 Bellingshausen Seas (Murphy et al., 2017).

205

206 **Environmental drivers of behavior**

207 To assess the influence of the explanatory variables on the SSM estimated behavioral modes,
208 we fitted a series of linear mixed-effect models (LMMs) by maximum likelihood (ML) using the
209 R software package *nlme* (Pinheiro et al. 2018). Similar to previous studies, we adjusted the
210 behavioral mode (*b*) to range between 0 and 1 (by subtracting 1 from each value), after which
211 the variable (continuous) was logit transformed (O'Toole et al. 2015, Cerchio et al. 2016). We
212 dealt with sample proportions equal to exactly zero or one by adding the smallest non-zero
213 proportion (ϵ) to the numerator and denominator of the logit function (i.e. $\log(y+\epsilon / 1-y+\epsilon)$) as
214 per Warton and Hui (2011). Individual whales (i.e. unique tag numbers/PTTs) were fitted as a
215 random effect to account for individual variation, and a first order AR(1) autocorrelation
216 structure for each individual whale was assumed. We first built LMMs with the full data set using
217 region as a factorial variable, and then split the data to build region specific models.

218 The remotely sensed variables SSH and sea surface current speed included missing values
219 ($n=31$ and $n=35$ respectively, representing 0.9% of the data), most likely due to sea ice coverage.
220 To maintain the same number of observations between models, the rows including missing
221 values were removed from the data set prior to model fitting. The variables sea surface current
222 velocity and slope were log transformed prior to analysis. A quadratic term was included for
223 month and the different 'distance to ice edge' candidate variables following examination of the
224 relationships visually. All continuous variables were tested for pairwise correlation (Electronic
225 Supplementary Material, Figure ESM 1). SSH and log transformed sea surface current velocity
226 had a Spearman correlation of 0.66. All other variables showed a Spearman correlation of ≤ 0.5 .

227 As the different 'distance to ice edge' candidate variables represent the same environmental
228 process, we included each of these terms sequentially during the model building (Table 2).
229 Several model combinations of the different main effects and various interaction terms were

230 run (Table 2). For model selection we explored both backward selection following Zuur et al.
231 (2009; starting with a full model with all explanatory variables included, dropping individual
232 variables one by one until all remaining variables are significant) and automated model selection
233 (function *dredge* in R package *MuMIn*; Bartoń 2018) to check for all possible variable
234 combinations. We used the Akaike Information Criterion (AIC) to select the most parsimonious
235 (lowest AIC value) model as the criterion penalizes for the use of more variables (Burnham and
236 Anderson 2002; Burnham et al. 2011). The best model based on AIC was then run using
237 restricted maximum likelihood (REML) to obtain the final parameter estimates (as per Zuur et
238 al. 2009). The normality of residuals was checked graphically.

239

240 **RESULTS**

241 **Whale movement and behavior**

242 Out of 25 tags deployed, 18 transmitted sufficient data for the SSM analysis (Table 3). This
243 included 5 females without calves, 6 females with calves, 5 males and 2 individuals of unknown
244 sex (PTT102211 had no tissue sample; molecular sex identification for PTT112722 was
245 unsuccessful). Ten tags had data gaps of >1 day (range: 2-76 d), excluding those tags that did not
246 begin transmission straight after deployment. The average number of location fixes per day
247 received from a tag was 22 (range: 10-42).

248 The tags of 14 individual humpback whales transmitted data within the feeding grounds south
249 of 60°S, covering a temporal period from November 2015 to June 2016 and a spatial range from
250 175°E to 80°W. The number of active tags transmitting data varied between months (range: 1-
251 14; Table 4). The SSM distinguished well between the two behavioral states (Electronic
252 Supplementary Material, Table ESM 2) and classified 6.3% of locations as ARS-foraging, and
253 79.3% of locations as transiting behavior, with the remaining 14.4% classified as uncertain
254 (Figure 1). The average behavioral mode (i.e. likelihood of ARS-foraging behavior) increased as
255 the feeding season progressed, peaking in March (February-March for whales on the Ross Sea
256 side only; Figure 2a). Overall, the whales on the Ross Sea side were consistently farther away

257 from the continental shelf break (Figure 1) and from the ice edge than the whales in the
258 Amundsen and Bellingshausen Seas region (Figure 2b). In general, the whales' distance from the
259 ice edge increased between December and January (December-February for Ross Sea whales)
260 and decreased between January and April (February-May for Ross Sea whales; Figure 2b).

261

262 **Environmental drivers of behavior**

263 Out of the highly correlated variables SSH was identified as being a more important predictor
264 than log transformed sea surface current speed and was therefore kept in the model.
265 Examination of the different 'distance to ice edge' scenarios resulted in 2-month lag being
266 identified as the most relevant, and out of several trials with different interaction terms
267 interaction between month (representing time) and region was found to be most significant
268 (Table 2). The most parsimonious model identified month, 2-month lag in the distance to the ice
269 edge, SSH and the interaction between region and month as important predictors of the
270 behavioral state of humpback whales within their Southern Ocean feeding grounds (Table 2,
271 Table 5). Non-linear relationships indicated that the whales were more likely to exhibit ARS-
272 foraging behavior during the middle of the summer feeding season, and near where the marginal
273 ice-edge had been two months prior. Humpback whales were also more likely to exhibit ARS-
274 foraging behavior at lower SSH values, and there was a significant interaction between region
275 and month (Table 5, Figure 3). The model provided some indication of possible differences
276 between regions. The variable 'region' was marginally significant (F-test $p=0.06$), although the
277 coefficient estimate was not significantly different from zero (t-test $p=0.36$). Dredge automated
278 model selection identified region to be a significant variable in 70% of 1664 model variations.

279

280 **DISCUSSION**

281 Humpback whales foraging in the Southern Ocean changed their ranging behavior and habitat
282 use patterns throughout the summer feeding season suggesting that behavioral plasticity is
283 important for this large predator. The changes were related to the environmental features of

284 the different habitats, in particular to an important lag effect in the ice edge dynamics, and
285 consequently the whales ended up utilizing these areas very differently. Similar to other long-
286 distance migrants that move between critical habitats for different life functions (Both and
287 Visser 2001; Le Corre et al. 2017), these whales time their arrival at their feeding grounds to
288 exploit the habitat optimally without knowing the precise habitat conditions when beginning
289 their migration ~7,000km north. The large-scale sensitivity to environmental cues enabling
290 prediction of conditions in another geographic location is key to the success of migratory
291 animals, e.g. barn swallow (*Hirundo rustica L.*, Balbontín et al. 2009), caribou (Le Corre et al.
292 2017).

293

294 **Characterizing whale movement and behavior on the Southern Ocean feeding grounds**

295 The SSM results revealed two important resource sites for Oceania humpback whale foraging;
296 one within the Amundsen and Bellingshausen Seas and one north of the Ross Sea, ~2,000 km
297 west (Figure 1). The majority of ARS-foraging locations for the whales within the Amundsen and
298 Bellingshausen Seas occurred near the continental shelf break (within ~200km) where high
299 densities of krill are expected to be found due to life history related movement (e.g. Pauly et al.
300 2000; Nicol 2006; Davis et al. 2017), as well as near the ice edge (~210km on average) where ice
301 melt stimulates primary production which in turn supports elevated concentrations of higher
302 trophic level organisms (e.g. Brierley et al. 2002; Nicol 2006; Meyer et al. 2017). In contrast, the
303 main aggregation of ARS-foraging locations north of the Ross Sea did not occur near the shelf
304 break (>500km away; Figure 1) nor the ice edge (~370km on average; Figure 2b). However, the
305 ARS-foraging locations of the Ross Sea whales occurred in a reported hotspot, with increased
306 chlorophyll *a* as an indicator of primary production (Schine et al. 2015). The observed differences
307 between the foraging regions suggest that humpback whales utilize different environmental
308 cues, with some cues being of greater importance for whales in one area than the other.

309 Although we were not able to confirm ARS behavior identified by our SSM as foraging, both
310 previous studies and the general knowledge about humpback whale behavior south of 60°S

311 suggest that ARS behavior identified by the SSM is largely foraging (Chittleborough 1965;
312 Weinstein et al. 2017; Andrews-Goff et al. 2018). With this assumption in mind, the high overall
313 amount of transiting behavior south of 60°S might serve as an indicator of prey distribution,
314 whereby whales may have to move quite long distances between prey patches. For instance,
315 the Amundsen and Bellingshausen Seas reportedly have generally low chlorophyll *a*
316 concentration with only isolated pockets of high productivity (e.g. Constable et al. 2003;
317 Stambler 2003). This could result in smaller prey aggregations that are highly spread out,
318 increasing the whales' need to transit between foraging patches.

319 Humpback whales in the northern hemisphere have been shown to exhibit strong maternally
320 inherited feeding ground fidelity (Palsbøll et al. 1995; Stevick et al., 2006; Baker et al., 2013). In
321 contrast, humpback whales from discrete Oceania breeding grounds do not show such clear
322 patterns of feeding ground fidelity (Rosenbaum et al. 2017). Additionally, as satellite tagged
323 Oceania mothers with calves migrated to the Ross Sea and given that whales still also migrate
324 to the Amundsen and Bellingshausen Seas (Riekkola et al. 2018), these whales may not have
325 maternally inherited feeding grounds. Knowing the approximate location of profitable foraging
326 areas and consistently returning to them may increase foraging success and individual fitness,
327 which could be highly advantageous for the slowly recovering Oceania population. Memory of
328 long-term average conditions may be more important for cetaceans than previously thought
329 (Abrahms et al. 2019), and some marine species in the Southern Ocean have been found to
330 consistently return to foraging areas that may have arisen as a consequence of predictable
331 oceanographic conditions (Weimerskirch 2007; McIntyre et al. 2017; Sztukowski et al. 2018).
332 Data on the Oceania whales across multiple years could help identify persistent patterns in the
333 whales' behavior to determine the role of memory, and assess the stability of the two feeding
334 areas over time, especially given the predicted future changes in ice dynamics due to climate
335 change (de la Mare 1998; Turner et al. 2009). Changes in global oceanographic events are
336 becoming more common, for example they are likely to have disrupted the long-term feeding
337 ground fidelity in humpback whales in southern Alaska (Neilson & Gabriele 2019).

338

339 **Environmental effects on whale movement and behavior on the Southern Ocean**
340 **feeding grounds**

341 Because large baleen whales have very high energetic demands (Lockyer 1981), we expect that
342 humpback whale behavior on the feeding grounds is largely driven by the distribution and
343 availability of krill; especially given they effectively undertake all foraging during the ~five
344 months they spend in the Southern Ocean. Previous studies have linked the behavior and
345 distribution of humpback whales to krill abundance and distribution (e.g. Friedlaender et al.
346 2006, 2011, 2013; Curtice et al. 2015). However, as obtaining reliable data on krill abundance
347 and distribution for the large temporal and spatial extent covered by our satellite telemetry data
348 is all but impossible, we examined how the behavior of these whales was affected by more easily
349 recorded, remotely sensed environmental parameters. In the absence of easily obtained prey
350 field data understanding how marine top predators, such as whales, pinnipeds and seabirds,
351 respond to more easily recorded variables (which act as proxies for prey availability) is often the
352 only approach available (Raymond et al. 2015; Reisinger et al. 2018).

353 The best LMM indicated that the inferred behavioral states of humpback whales within the
354 Southern Ocean feeding grounds were most affected by timing within the feeding season
355 (month), where the marginal ice edge was two months prior, SSH, and to some extent the region
356 (Table 5, Figure 3). All these variables are thought to be linked to krill availability and distribution
357 associated with local and regional scale oceanographic features. By targeting and favoring areas
358 with environmental conditions that are associated with increased prey availability, large marine
359 predators, such as humpback whales, can improve their foraging opportunities (Heerah et al.
360 2016). In the absence of prior knowledge regarding potential prey locations, whales might use
361 environmental cues to place themselves in likely profitable foraging areas.

362 As the feeding season progressed the likelihood of adopting ARS-foraging behavior increased,
363 peaking in February-March (Figure 2a). This was expected as the whales would be finding

364 sufficient prey to feed on after several months of fasting, and as productivity should increase
365 following the spring/summer ice melt (Lehodey et al. 1998; Arrigo et al. 2008; Dalpadado et al.
366 2014). After the peak, the likelihood of ARS-foraging behavior decreased likely in response to
367 productivity declining in late summer-autumn months, however data for the last two months
368 came from only one whale (Table 4).

369 The results indicated that foraging behavior was more likely to occur near where the ice edge
370 was two months prior. As the sea ice melts, the ice-free waters promote phytoplankton blooms
371 which in turn trigger grazers such as krill to aggregate at the sea ice edge (Nicol 2006; Arrigo et
372 al. 2008). This link between humpback whales and the ice indicates that the whales do not
373 actively track the ice edge itself, but instead the productivity that occurs following ice melt (i.e.
374 after a time lag). Organisms do not always respond immediately to changes in the physical or
375 biotic environment. Animal population trends respond to fluctuations in the environment after
376 appropriate time lags (e.g. Baker et al. 2007; Walker et al. 2013), however distribution and
377 foraging behavior can also show lagged responses to environmental conditions (Pinaud and
378 Weimerskirch 2005). Our findings therefore support the importance of including time-lagged
379 variables when modelling the relationships between animals and their environment, which is
380 applicable to both aquatic and terrestrial species across a broad array of ecosystems.

381 The humpback whales were also more likely to exhibit ARS-foraging behavior at lower SSH
382 values. Lower (more negative) SSH values are linked to meso-scale eddies, which stimulate
383 productivity near the surface through vertical mixing of deep nutrient rich waters, and trap
384 aggregations of buoyant and weakly swimming plankton and fish (Olson and Backus 1985; Nel
385 et al. 2001; Hyrenbach et al. 2006). However, whether the whales can detect changes in SSH and
386 relate them to krill presence is unknown. As noted above, areas with lower SSH are generally
387 linked to productivity and prey, and SSH is therefore functioning as a proxy for prey in our model.

388 There was some evidence that the behavioral mode of the whales was affected by the feeding
389 region they were in, and the interaction between region and month suggests that the whales
390 behave differently in the different regions during different points of the season (Figure 2a).

391 Animals are expected to strive to maximize foraging success while minimizing the associated
392 effort and costs (MacArthur and Pianka 1966; Schoener 1971). Predators foraging in complex
393 and patchy environments should therefore adjust their movements and foraging behavior
394 according to prey availability (and density) to maximize foraging efficiency. They might for
395 instance employ distinct foraging strategies in different habitats (Arthur et al. 2016). We expect
396 that the observed regional foraging behaviors by the humpback whales are the result of region-
397 specific decisions made in response to the dynamic characteristics of the environment in each
398 habitat, suggesting that there is behavioral plasticity in this population. Many ecological studies
399 have treated conspecific individuals as ecological equivalents, but the existence of intraspecific
400 plasticity in foraging behavior (in the form of dietary differences, variation in habitat use or
401 foraging strategies for example) is widespread among taxonomic groups and can be ecologically
402 important (Bolnick et al. 2003; Ceia and Ramos 2015; McHuron et al. 2018). The predicted
403 climate change induced spatial variability in factors that influence krill populations, such as sea
404 ice characteristics and seasonal dynamics, are likely to result in region-specific responses in the
405 whales' main prey (e.g. Constable et al. 2014), which might necessitate region-specific foraging
406 strategies in the future.

407 In order to respond dynamically to sensory cues from the dynamic environment whales likely
408 use multimodal sensory systems (Carroll et al. 2017; Torres 2017). Additionally, species-habitat
409 relationships are often scale dependent, and different environmental parameters may have a
410 stronger influence on animals at different scales (Redfern et al. 2006; Ballance et al. 2006). For
411 example, during long distance migration to the feeding grounds (thousands of kilometers)
412 humpback whales, as well as other cetaceans, use large-scale oceanographic patterns and
413 features to navigate (Horton et al. 2017; Torres 2017). Once near or within the feeding grounds
414 the whales are expected to change their movement to a smaller-scale prey search pattern, and
415 will likely utilize different, finer-scale environmental cues (Ballance et al. 2006; Doniol-Valcroze
416 et al. 2007; Torres 2017; Kirchner et al. 2018). It is therefore important to use temporal and
417 spatial scales that are appropriate for the main objectives of the analysis and relevant for the

418 ecology of the target species (e.g. Ballance et al. 2006; Redfern et al. 2006; Fernandez et al.
419 2017). Unfortunately, the temporal and spatial scale used is often determined by the availability
420 of the environmental data. We were not immune to this problem, yet we aimed to use
421 resolutions closest to our modelled data to best capture the whales' behavior patterns. Using
422 different movement/behavioral modelling techniques (e.g. McClintock et al. 2015; McClintock
423 and Michelot 2018) it can be possible to further improve the accuracy of the animal locations.
424 In our case, due to the low resolution of many of the environmental covariates (raster data),
425 improving the whale location estimates would have likely resulted in us sampling from the same
426 environmental raster cell. In studies covering a smaller study area and having higher quality
427 environmental data increasing the accuracy of the animal locations would be more paramount.
428 Despite some caveats, using the available remotely sensed data and spatial modelling
429 techniques enabled us to uncover the behavioral patterns of these whales spread over 4,000km
430 across the Southern Ocean largely devoid of distinct land mass features, apart from the Antarctic
431 continent. The whales' ability to detect and use environmental cues to locate patchily
432 distributed prey in this vast ocean environment is remarkable and identifying the key variables
433 for these animals will help us better understand their behavior and how they might respond to
434 changes in their environment.

435 In many animal taxa (including insects, birds and mammals) the decision to begin migrating
436 from one critical habitat to another often occurs in response to environmental conditions, social
437 cues or sexual hierarchy, and is highly affected by individual variation (Chittleborough 1965;
438 Gunnarsson et al. 2006; Balbontín et al. 2009; Jiang et al. 2011; Rivrud et al. 2016; Berdahl et al.
439 2017). Climate change has a variety of effects on the critical habitats of different animals, for
440 example by altering the distribution and seasonal availability of food as well as the size of
441 suitable breeding areas (Fitter and Fitter 2002; Walther et al. 2002; Derville et al. 2019). If the
442 timing of migration relies on endogenous cues that are not affected by climate change
443 (compared to e.g. weather cues), the migration of such species will not advance even though
444 they need to arrive earlier on their breeding or feeding grounds (Both and Visser 2001). It is yet

445 unclear whether climate change will influence whale arrival at the Southern Ocean feeding
446 grounds earlier, and whether this would have a positive or a negative effect on their fitness.
447 Waiting for krill to become available could incur an energetic cost due to the wait time, yet the
448 whales might adapt and prey switch which has, to forage more on already available prey; this
449 has been documented in different humpback whale populations (e.g. Weinrich et al. 1992;
450 Fleming et al. 2015).

451

452 **CONCLUSIONS**

453 Here we used spatial modelling techniques to identify underlying behavioral states from
454 movement data for a wide-ranging marine predator inhabiting a remote area, and related those
455 behaviors with environmental conditions. We identified two important Southern Ocean feeding
456 areas for humpback whales and observed differences in behavior, likely related to decisions
457 made about the local environmental variation between the two adjacent habitats. Behavioral
458 plasticity is critical to survive in environments that are unpredictable and changing (Stien et al.
459 2010; Wong and Candolin 2015; Courbin et al. 2017). This could therefore be of advantage to
460 whales in a changing Southern Ocean, especially as the two feeding areas are experiencing
461 different responses to climate change; sea ice increase in the Ross Sea, sea ice retreat in the
462 Amundsen and Bellingshausen Seas (e.g. Zwally et al. 2002; Turner et al. 2009) and regional
463 differences in food web structure (e.g. Murphy et al. 2012; Constable et al. 2014). Environmental
464 changes may therefore elicit different behavioral and demographic responses for populations
465 inhabiting different, yet adjacent, regions of the Southern Ocean. Having whales of the same
466 population being subject to different environmental conditions provides an opportunity to study
467 changes in their distribution and behavior within and between circum-Antarctic regions, which
468 in turn can be used as indicators of change in the ecosystem (e.g. prey distribution) for all marine
469 predators (Raymond et al. 2015). The phenomena of range shifts and behavioral adaptations in
470 response to environmental change are better understood in the northern hemisphere where
471 such events are more apparent (Both and Visser 2001; Post et al. 2009).

472

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Tables and table legends

Table 1. The unit of measure, source and resolution of the environmental predictor variables used to construct the species distribution models

Variable	Definition and unit	Source	Resolution	
			Spatial	Temporal
Dynamic				
Ice concentration (ice conc)	Percentage of ocean area covered by sea ice	National Snow and Ice Data Center (NSIDC)	25 x 25km	Daily
Distance to ice edge (dist ice)	Distance of whale location to ice edge (15% ice concentration; km) on the same day	Derived from ice concentration	25 x 25km	Daily
Distance to ice edge – 1-month lag (dist ice lag 1)	Distance of whale location to where the ice edge was 1 month prior	Derived from ice concentration	25 x 25km	Daily
Distance to ice edge – 2-month lag (dist ice lag 2)	Distance of whale location to where the ice edge was 2 months prior	Derived from ice concentration	25 x 25km	Daily
Sea surface height (SSH)	Sea surface height (m)	E.U. Copernicus Marine Service Information (CMEMS)	0.25 x 0.25°	Daily
Sea surface current velocity (current)	Surface current velocity (m/s)	Derived from SSH	0.25 x 0.25°	Daily
Static				
Bathymetry (bathy)	Depth (m)	International Bathymetric Chart of the Southern Ocean (IBCSO)	500 x 500m	
Slope	Topographic gradient (degrees)	Derived from bathymetry	500 x 500m	
Other				
Month	Month	SSM estimated locations		
Region	Ross Sea or Amundsen and Bellingshausen Seas cut-off at 130°W	SSM estimated locations		

Table 2. Model selection results of the best linear mixed-effect models to explain the effects of different variables on humpback whale behavioral mode (b).

Variables	K	AIC	Δ AIC
<u>Comparison of different ice distance variables</u>			
Month + Month ² + Region + dist ice lag 2 + dist ice lag 2 ² + Ice conc + SSH + bathy + slope(log)	13	18471.5	
Month + Month ² + Region + dist ice lag 1+ dist ice lag 1 ² + Ice conc + SSH + bathy + slope(log)	13	18475.2	3.7
Month + Month ² + Region + dist ice + dist ice ² + Ice conc + SSH + bathy + slope(log)	13	18475.6	4.1
<u>Comparison of different interaction terms</u>			
All models have the same base: Month + Month ² + Region + dist ice lag 2 + dist ice lag 2 ² + Ice conc + SSH + bathy + slope(log)			
+ Region*Month + Region*Month ²	15	18449.9	
+ Region*SSH	14	18468.9	19.0
+ Region* dist ice lag 2 + Region* dist ice lag 2 ²	15	18471.2	21.3
<u>Reduced version of the best model</u>			
Month + Month ² + Region + dist ice lag 2 + dist ice lag 2 ² + SSH + Region*Month + Region*Month ²	12	18447.5	

All models include the individual whale (unique tag number, PTT) fitted as a random effect. For each candidate model we report the Akaike's Information Criterion (AIC) and the change in AIC (Δ AIC) compared to the best model of each scenario. K = number of parameters. The best overall model is bolded.

Table 3. Summary of satellite tag deployments and tracking data for 18 humpback whales used in the state-space model.

PTT	Transmitted south of 60°S	Sex (*=with calf)	Deployment date	First location	Last location	Transmitting days	Data gaps (d ₁ ,d ₂ ,d _n)	Total no. of locations	Mean no. locs/day (± SE; range)	% Argos location class							Mean time (h) between locs (± SE)
										3	2	1	0	A	B	Z	
88727	Yes	F*	08-Oct-2015	08-Oct-2015	14-Jan-2016	99		2,665	27 (±1.3; 1-64)	3.3	6.1	7.0	2.0	16.3	64.9	0.3	0.9 (±0.02)
102211	Yes	U	10-Oct-2015	11-Oct-2015	19-Dec-2015	57	14	594	10 (±0.9; 1-26)	0.2	0.2	0.0	0.2	4.7	94.1	0.7	2.8 (±0.57)
102218	Yes	M	10-Oct-2015	11-Oct-2015	20-Jun-2016	249	2,4	8,659	33 (±1.1; 1-85)	4.1	10.1	12.2	3.8	15.1	54.7	0.0	0.7 (±0.02)
111866	Yes	F	04-Oct-2015	06-Nov-2015	15-Mar-2016	130	2	3,820	29 (±1.1; 4-65)	2.1	4.3	5.7	2.2	13.5	72.1	0.1	0.8 (±0.02)
112722	Yes	U	10-Oct-2015	11-Oct-2015	03-Apr-2016	174	2,2	6,390	37 (±1.0; 3-71)	12.8	17.0	11.4	2.5	18.9	37.4	0.0	0.7 (±0.02)
131173	Yes	M	30-Sep-2015	30-Sep-2015	08-Apr-2016	184	8,2	5,925	32 (±1.1; 2-70)	2.9	7.9	11.1	3.9	16.7	57.5	0.1	0.8 (±0.04)
131175	Yes	M	04-Oct-2015	04-Oct-2015	18-Jan-2016	97	11	2,077	21 (±1.1; 4-47)	0.7	1.7	1.7	1.1	11.2	83.4	0.2	1.2 (±0.13)
131178	Yes	F*	08-Oct-2015	09-Oct-2015	17-Jan-2016	101		2,167	21 (±1.1; 2-58)	0.8	1.7	4.7	1.6	14.4	76.7	0.2	1.1 (±0.03)
131179	Yes	M	02-Oct-2015	07-Dec-2015	22-Mar-2016	84	23,2	1,785	21 (±0.9; 6-50)	0.3	0.6	1.6	0.3	6.2	90.9	0.2	1.4 (±0.30)
131182	Yes	F	01-Oct-2015	02-Oct-2015	02-Apr-2016	150	30,5,2	6,264	42 (±1.2; 11-90)	10.0	27.9	22.0	5.8	12.1	22.1	0.0	0.7 (±0.12)
131185	Yes	F	02-Oct-2015	27-Nov-2015	06-Jan-2016	41		886	22 (±1.4; 1-44)	0.1	0.3	1.0	0.2	6.2	91.6	0.5	1.1 (±0.06)
131187	Yes	F	30-Sep-2015	01-Oct-2015	02-Jan-2016	94		1,876	20 (±0.9; 6-51)	1.4	1.6	2.6	0.9	10.5	82.9	0.0	1.2 (±0.04)
131188	Yes	F*	29-Sep-2015	30-Sep-2015	11-Dec-2015	73		1,310	18 (±0.7; 8-37)	1.0	2.8	2.3	0.8	13.4	79.7	0.0	1.3 (±0.04)
131190	Yes	F*	08-Oct-2015	08-Oct-2015	20-Mar-2016	90	76	2,334	26 (±0.9; 1-45)	5.8	13.5	13.4	4.4	18.4	44.5	0.0	1.7 (±0.78)
111871	No	F	08-Oct-2015	09-Oct-2015	04-Nov-2015	26	2	308	12 (±1.1; 1-20)	1.9	4.5	4.2	1.0	14.0	74.4	0.0	2.1 (±0.20)
112718	No	M	05-Oct-2015	05-Oct-2015	13-Nov-2015	40		562	14 (±0.6; 2-21)	2.1	3.4	3.4	0.9	14.4	75.4	0.4	1.7 (±0.08)
112721	No	F*	09-Oct-2015	10-Nov-2015	28-Nov-2015	19		224	12 (±1.1; 5-24)	0.4	1.3	1.3	0.0	6.3	90.2	0.4	2.0 (±0.16)
112723	No	F*	06-Oct-2015	07-Oct-2015	18-Oct-2015	12		204	17 (±1.7; 2-24)	2.5	2.9	4.9	2.9	18.1	68.6	0.0	1.3 (±0.08)

All tags were deployed at Raoul Island (Kermadec Islands, New Zealand). PTT = unique tag number. Only whales whose tags transmitted data south of 60°S were used in the linear mixed-effect model.

F = female, M = male, U = unknown sex, and * denotes animals that had a calf. All dates are in UTC. Transmitting days = number of days when one or more locations were received.

Data gaps = any gaps in data transmission >1 day in length, data gap length is in days, multiple data gaps for the same animal are separated with a comma.

Percent of locations belonging to each of the seven Argos service provider assigned location classes. Location classes in a descending order of accuracy: 3, 2, 1, 0, A, B and Z. See Argos user's manual 2016

Table 4. Number of unique tags transmitting in any given month, and the number of state-space modelled data points (in brackets) within the feeding grounds (south of 60°S).

Year	Month	Ross Sea	A&B Seas	Total
2015				
	November	4*(119)	2*(48)	5 (167)
	December	11†(717)	6†(487)	14 (1204)
2016				
	January	5‡(373)	7‡(453)	11 (826)
	February	2 (187)	4 (365)	6 (552)
	March	3 (323)	4 (378)	7 (701)
	April	2 (45)	2 (127)	4 (172)
	May	1§(80)	1§ (39)	1 (119)
	June	1 (77)	0 (0)	1 (77)

In total, the tags of 14 individual whales transmitted data within the feeding grounds.

A&B seas = Amundsen and Bellingshausen Seas.

* PTT131182 travels through both regions during the month of November

† PTT102218, PTT131175 and PTT131187 travel through both regions during the month of December

‡ PTT131175 travels through both regions during the month of January

§ PTT102218 travels through both regions during the month of May

Table 5. Results of the best Linear Mixed Effect model, with logit transformed behavioral state (*b*) as a response variable and individual whales as a random effect. Higher b-values indicate an increasing likelihood of whales exhibiting ARS-foraging behavior.

Parameter	Estimate	SE	DF	t-value	p-value
Intercept	-9.49	1.10	3796	-8.61	<0.001
Region_Ross Sea	-0.55	0.58	3796	-0.96	0.34
Month	1.91	0.38	3796	4.99	<0.001
Month ²	-0.35	0.06	3796	-5.40	<0.001
dist ice lag 2	0.00	0.00	3796	0.26	0.80
dist ice lag 2 ²	-0.00	0.00	3796	-3.55	<0.001
SSH	-4.92	1.08	3796	-4.57	<0.001
Region_Ross Sea*Month	-0.93	0.48	3796	-1.95	0.05
Region_Ross Sea*Month ²	0.24	0.08	3796	3.16	<0.01

Estimates are in log-odds scale. During model selection all models were fitted using maximum likelihood for comparing models with different fixed effects. The best model was then fitted with restricted maximum likelihood to obtain final parameter estimates. Variables with a significant parameter estimate (<0.05) are in bold.

Figure legends

Figure 1: Migration pathways for 18 Oceania humpback whales satellite-tagged at the Kermadec Islands, New Zealand. Left column: State-space model estimated behavioral states: red dot = area restricted search (ARS; inferred foraging); black dot = inferred transit; grey dot = uncertain behavioral mode. Bottom left: Tracks of 14 whales whose tags transmitted on their Southern Ocean feeding grounds with circles denoting the approximate locations of the two key foraging grounds. The background color scale indicates the bathymetric depth (derived from the International Bathymetric Chart of the Southern Ocean (IBCSO) digital bathymetric model of the circum-Antarctic waters). Right column: Satellite tracks color coded by month.

Figure 2. a) Average behavioral mode (*b*) by month. Values closer to 1 indicate transiting behavior and values closer to 2 indicate ARS-foraging behavior, and b) distance to ice edge (km; all locations) by month. Black dashed = all whales, green = Ross Sea, blue = Amundsen & Bellingshausen Seas.

Figure 3. The relationship between significant explanatory variables a) month, b) distance to the ice edge (2-month lag) and c) SSH (sea surface height) and the logit transformed behavioral mode (*b*). Green = Ross Sea, Blue = Amundsen and Bellingshausen Seas. Higher predicted *b*(logit) values indicate an increasing likelihood of whales exhibiting ARS-foraging behavior. A negative value for 'distance to ice edge' indicates that the whale has moved past the point where the ice edge was two months prior. Simplified univariate regression lines from the mixed-effect model analysis (without random effects and autocorrelation structure) were added to b) and c) to highlight the overall trend in the data for the sample population.

Figures

Figure 1.

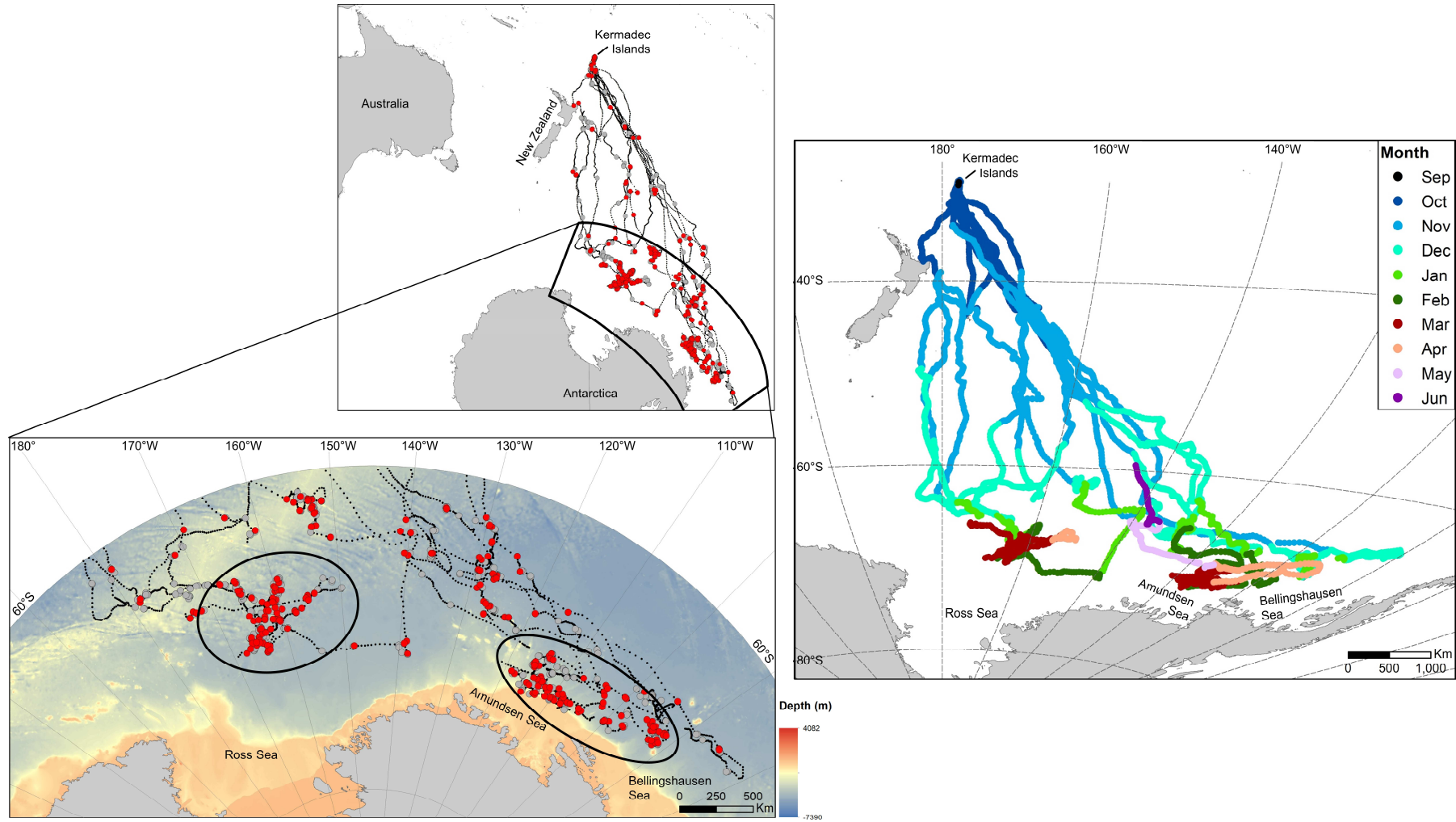
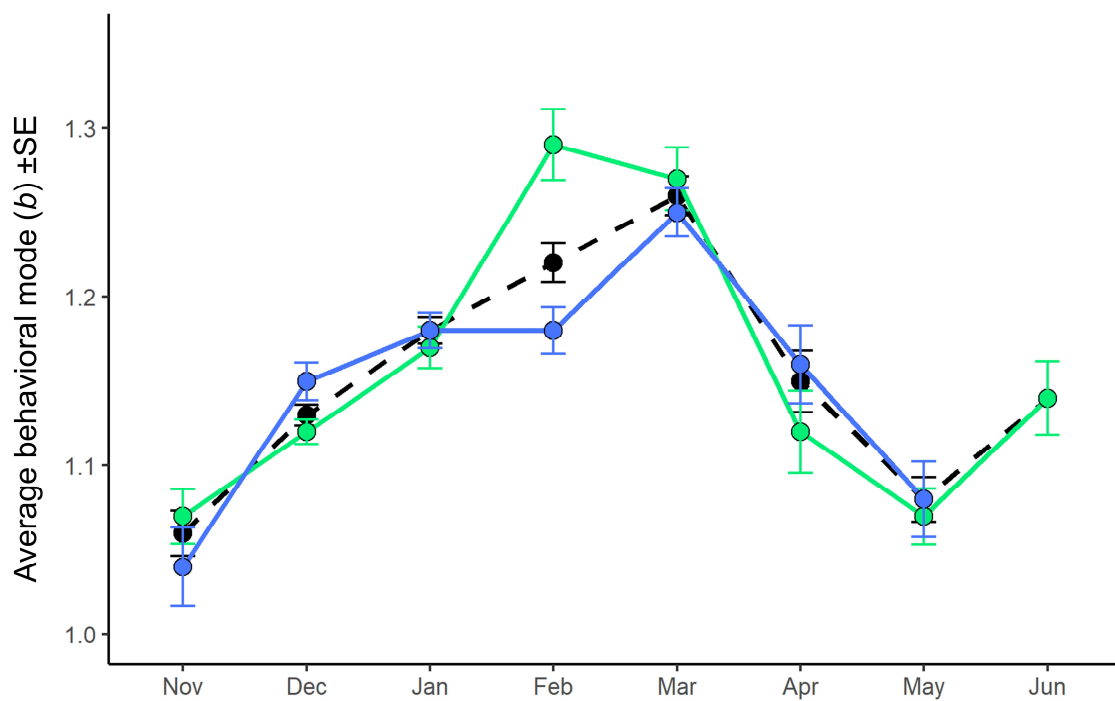


Figure 2.

(a)



(b)

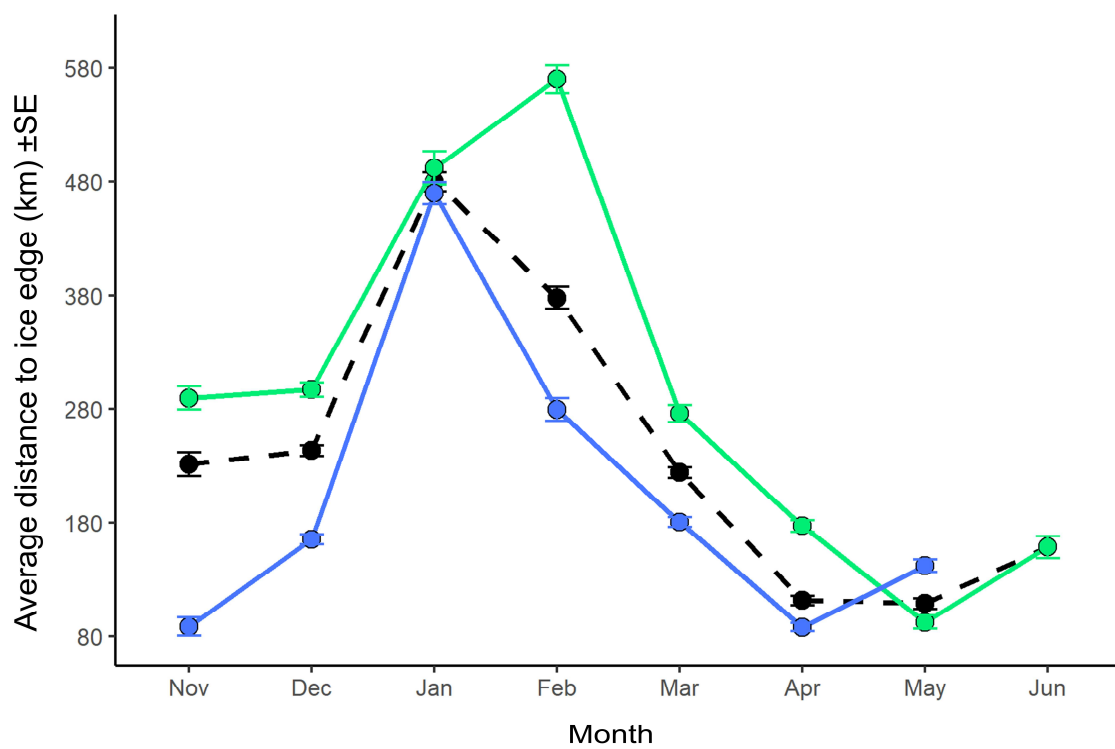
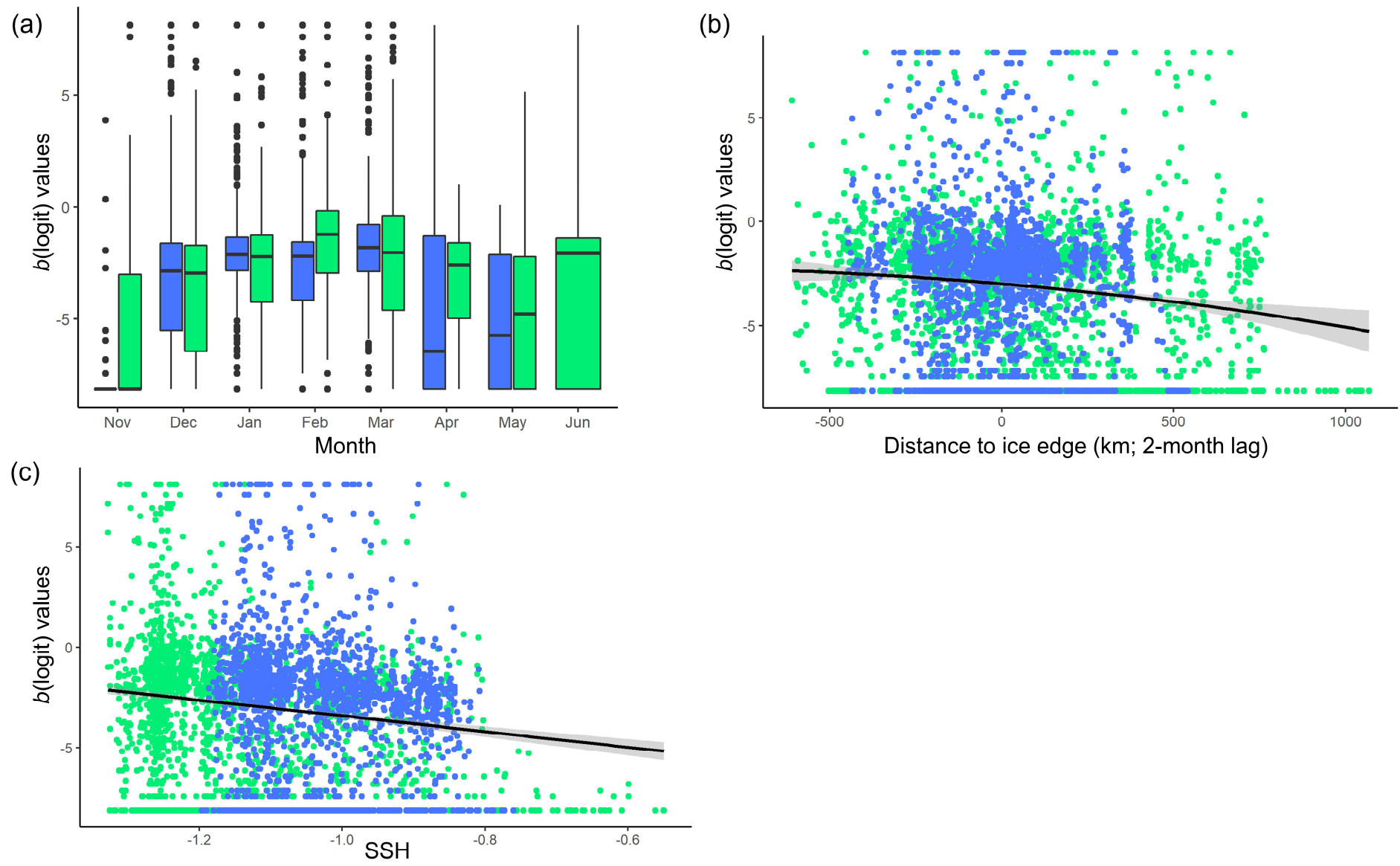
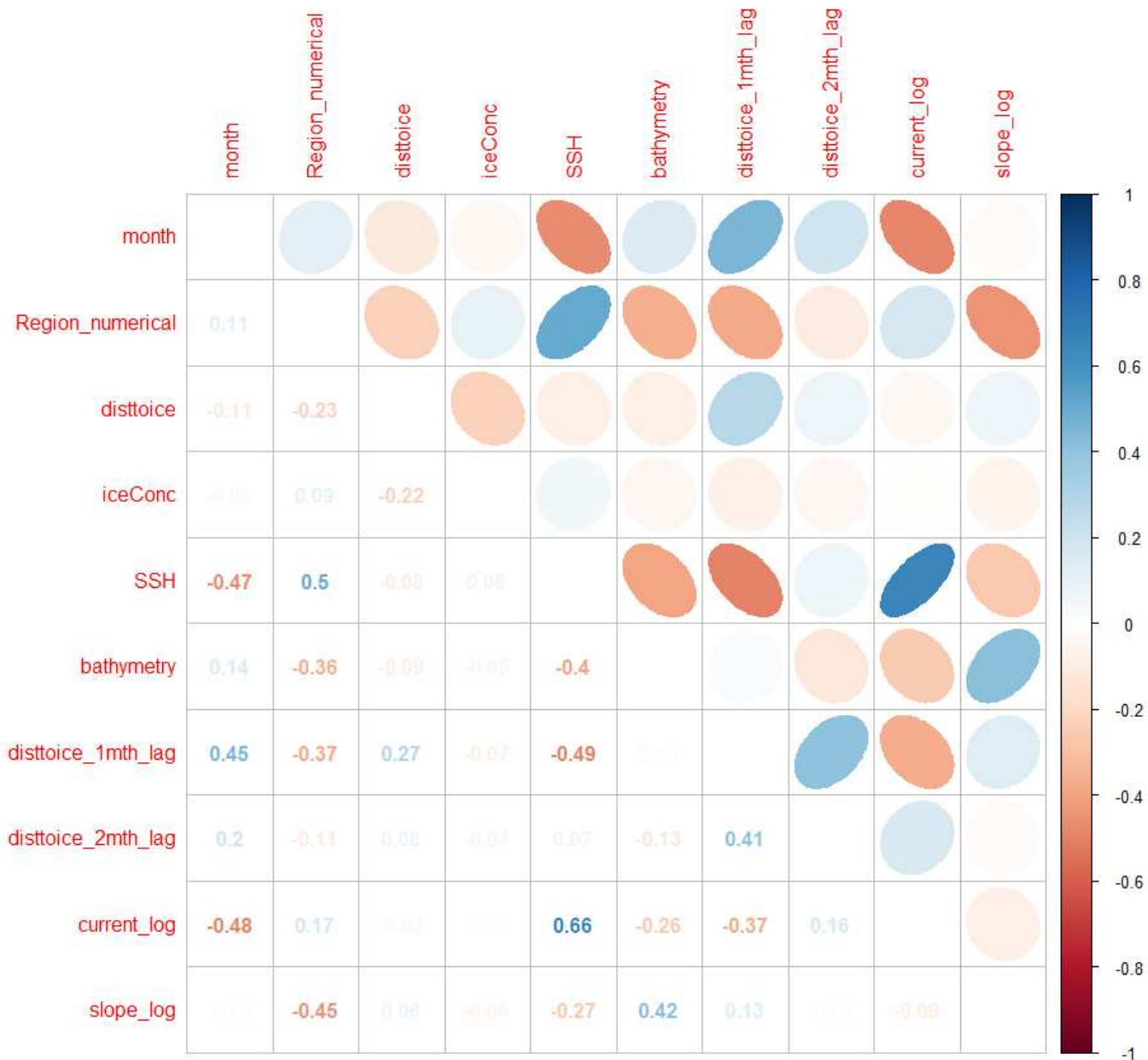


Figure 3.



Electronic Supplementary Material, Figure ESM 1. Spearman correlation matrix of the 10 covariates used in the statistical model.



Electronic Supplementary Material, Table ESM 2. Posterior sample means and 95% confidence intervals for movement parameters (transit, and area-restricted search; ARS) estimated using a hierarchical state-space model. γ = autocorrelation in speed and direction, θ = turning angles (radians).

	State	Lower 95%	Mean	Upper 95%
γ	ARS	0.0491	0.0497	0.0503
	Transit	0.9545	0.9546	0.9547
θ	ARS	2.9088	2.9156	2.9224
	Transit	0.0042	0.0043	0.0044