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Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model

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1 Abstract

2 Like many species, movement patterns of southern elephant seals (*Mirounga leonina*) are
3 being influenced by long-term environmental change. These seals migrate up to 4000 km
4 from their breeding colonies, foraging for months in a variety of Southern Ocean habi-
5 tats. Understanding how movement patterns vary with environmental features and how
6 these relationships differ among individuals employing different foraging strategies can pro-
7 vide insight into foraging performance at a population level. We apply new fast-estimation
8 tools to fit mixed effects within a random walk movement model, rapidly inferring among-
9 individual variability in southern elephant seal environment-movement relationships. We
10 found that seals making foraging trips to the sea-ice on or near the Antarctic continen-
11 tal shelf consistently reduced speed and directionality (move persistence) with increasing
12 sea ice coverage and had variable responses to chlorophyll *a* concentration, whereas seals
13 that foraged pelagically reduced move persistence in regions where circumpolar deep water
14 shoaled. Given future climate scenarios, pelagic foragers may encounter more productive
15 habitat but sea-ice foragers may see reduced habitat availability. Our approach is scalable
16 to large telemetry data sets and allows flexible combinations of mixed effects to be evalu-
17 ated via model selection, thereby illuminating the ecological context of animal movements
18 that underlie habitat use.

19 **Key Words:** correlated random walk; habitat; latent variable; telemetry; Template Model
20 Builder; random effects; southern elephant seals; spatial ecology

21 Introduction

22 Long-term environmental change is influencing southern elephant seal (*Mirounga leonina*)
23 populations, with their trajectories linked to the success of individuals' foraging migra-
24 tions (Hindell et al., 2017). These seals migrate long distances from breeding colonies to
25 forage, encountering a range of environmental conditions during many months at sea (Hin-
26 dell et al., 2017). Foraging strategies vary among seals and are often associated with open
27 ocean or Antarctic continental shelf habitats, with individuals showing fidelity to these

28 over several years (Authier et al., 2012). Quantifying how individuals differently respond

29 to their environment is a challenge due to a paucity of accessible analytical tools that can

30 account for among-individual differences in movement patterns.

31   Spatial habitat modelling approaches often are used to infer habitat usage and prefer-

32 ence from animal movement data (Aarts et al., 2008). Most of these approaches infer pref-

33 erence or selectivity from a combination of observed (presence) and simulated (pseudo-

34 absence) locations (Aarts et al., 2008) but are blind to the ecological mechanisms, such

35 as density dependence (McLoughlin et al., 2010) and individual behaviour (Bestley et al.,

36 2013; Auger-Méthé et al., 2017), underlying those preferences.

37   Although high individual variation is common in studies of animal movement, models

38 that account for among-individual variability in inferred movement - environment relation-

39 ships are rare (e.g., McClintock et al., 2013). These random effects or hierarchical models

40 can be computationally demanding, inhibiting realistic analysis of ever-growing animal

41 movement data sets. There is a need for efficient movement modelling approaches, accessi-

42 ble to ecologists, where responses to environmental, physiological and/or social predictors

43 can be inferred using flexible combinations of fixed and random terms (mixed effects) to

44 account for variability among moderate to large numbers (10's - 100's) of individuals.

45   We present a mixed-effects modelling approach for animal movement data that takes

46 advantage of new fast-estimation tools. Our model estimates time-varying movement per-

47 sistence (autocorrelation in speed and directionality) along animal movement trajectories.

48 We focus here on showing how the approach can be used to infer relationships between an-

49 imal movement patterns and the environmental features they encounter. The model can

50 be fit rapidly and flexibly with single or multiple random effects, enabling inference across

51 individuals and assessment of the extent to which relationships may differ among them.

52 We apply our approach to infer how southern elephant seals engaging different foraging

53 strategies, ice-bound versus open ocean (pelagic) trips, may respond differently to their en-

54 vironment. This represents a step towards bridging models of animal movement and habi-

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55 tat preference, which in future may converge in a more complete framework.

Methods

57 We build our modelling approach in three steps. First, we define a basic model that can

58 be used to estimate changes in move persistence along an animal's observed trajectory.

59 Second, we expand the model to infer how these changes may be related to environmen-

60 tal variables. Any combination of other extrinsic or intrinsic variables could be modelled,

61 provided they are measured at locations and/or times consistent with the telemetry data.

62 Third, we add random effects to the model to enable inference about how these movement

63 - environment relationships may differ among individual animals.

Time-varying move persistence

65 We focus on estimating the persistence (sensu Patlak, 1953) of consecutive pairs of animal

66 relocations (steps) along an entire movement trajectory. Move persistence, which captures

67 autocorrelation in both speed and direction, has been modelled as an average across entire

68 movement trajectories (Jonsen, 2016), indicating whether that trajectory is, on average,

69 uncorrelated (i.e., a simple random walk), correlated (i.e., a correlated random walk), or

70 somewhere in between. Allowing move persistence to vary along a trajectory means it can

71 be used as an index of behaviour (Breed et al., 2012), identifying segments of relatively

72 low or high persistence:

$$\boldsymbol{d}_t = \gamma_t \boldsymbol{d}_{t-1} + \boldsymbol{\eta}_t \tag{1}$$

73 where displacements $\boldsymbol{d}_t = \boldsymbol{x}_t - \boldsymbol{x}_{t-1}$ and $\boldsymbol{d}_{t-1} = \boldsymbol{x}_{t-1} - \boldsymbol{x}_{t-2}$ are the changes in an ani-

74 mal's location $\boldsymbol{x}$ at times t and $t-1$. The random variable $\boldsymbol{\eta}_t = \mathrm{N}(\boldsymbol{0}, \boldsymbol{\Sigma})$, with variance-

75 covariance matrix $\boldsymbol{\Sigma}$ specifying the magnitude of variability in the 2-dimensional move-

76 ments. γ_t is the time-varying move persistence between displacements $\boldsymbol{d}_t$ and $\boldsymbol{d}_{t-1}$. γ_t is

77 continuous-valued between 0 (low move persistence, Appendix S1: Figure S1a,c) and 1

78 (high move persistence, Appendix S1: Figure S1b,c). To avoid potential parameter identi-

79 fiability issues between γ_t and $\boldsymbol{\Sigma}$, we set the covariance term in $\boldsymbol{\Sigma}$ to 0 but this constraint

80 could be relaxed to better account for correlation in movements in the E-W and N-S direc-

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81 tions. We assume γ_t follows a simple random walk in logit space:

$$\text{logit}(\gamma_t) = \text{logit}(\gamma_{t-1}) + \epsilon_t \tag{2}$$

82 where the random variable $\epsilon_t = \text{N}(0, \sigma_\gamma)$ represents variability in move persistence along an

83 animal's track.

84   This process model (Eqn's 1 and 2) can be fit: 1) to location data with minimal error;

85 2) to state-space filtered location data; or 3) coupled with an observation model for error-

86 prone data. We focus on the second case with locations occurring at regular time intervals,

87 but this could be relaxed (e.g., Auger-Méthé et al., 2017).

88   The time-varying move persistence model can be used to objectively identify changes

89 in movement pattern. Here γ_t forms the behavioural index but unlike switching models

90 (e.g., Michelot et al., 2017), these changes occur along a continuum (0 - 1) rather than as

91 switches between discrete states.

92 **Move persistence in relation to environment**

93 To make inferences about the factors associated with move persistence, we can model γ_t

94 as a linear function of environmental predictors measured at each location or time. With

95 this approach, we replace the random walk on $\text{logit}(\gamma_t)$ (Eqn 2) with a linear regression of

96 covariates on $\text{logit}(\gamma_t)$:

$$\text{logit}(\gamma_t) = \beta_0 + \beta_1 m_{t,1} + \cdots + \beta_n m_{t,n} + \epsilon_t \tag{3}$$

97 where β_0, $\beta_1, \ldots, \beta_n$ are the fixed intercept and regression coefficients, $m_{t,1}, \ldots, m_{t,n}$ are

98 the predictor variables and $\epsilon_t = \text{N}(0, \sigma_\gamma)$ are the random errors. This model can be fit to a

99 single animal track, or to multiple tracks pooled together. Typically, we wish to make in-

100 ference across multiple individual tracks and assess the extent to which relationships may

101 differ among individuals.

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Incorporating individual variability

To account for variation among individual responses to environment, we can expand Eqn 3 to a mixed-effects regression of covariates on $\text{logit}(\gamma_t)$, within the behavioural model:

$$\text{logit}(\gamma_{t,k}) = (\beta_0 - b_{0,k}) + (\beta_1 - b_{1,k})m_{t,1,k} + \cdots + (\beta_n - b_{n,k})m_{t,n,k} + \epsilon_t \qquad (4)$$

where k indexes individual animals, the β's are the fixed intercept and slope terms as in Eqn 3, $b_{0,k}$ is a random deviation for the intercept of the k-th individual, $b_{1,k}, \ldots, b_{n,k}$ are random deviations for the slopes of the k-th individual and $m_{t,1,k}, \ldots, m_{t,n,k}$ are the covariates measured along the k-th individual's track. As in Eqn 3, the random variable ϵ_t are the fixed effects errors. We use an unstructured covariance matrix for the random effects.

Estimation

In principle, any combination of fixed and random effects can be specified within the movement model described in equations 1 and 4. Here we use TMB to fit the move persistence models (Auger-Méthé et al., 2017). The TMB package allows complex latent variable mixed effects models to be specified in C++ and fit efficiently via maximum likelihood using reverse-mode auto-differentiation and the Laplace approximation (Kristensen et al., 2016). The Laplace approximation avoids the need for high-dimensional integration, which massively speeds calculation of the marginal likelihood. Comparing Bayesian and TMB versions of a location-filtering model, Auger-Méthé et al. (2017) found a 30-fold decrease in computation time for the TMB fit with no loss of accuracy. All code for fitting these models in R is available at `https://github.com/ianjonsen`.

Data & analysis

We use Argos telemetry data collected from 24 adult female southern elephant seals. The seals were captured at Iles Kerguelen (49.35° S, 70.22° E) between late January and mid-March in 2009 and 2013-2015, at the end of their annual moult. Animal handling and instrument attachment details can be found elsewhere (McMahon et al., 2008). These data were sourced from the Australian Integrated Marine Observing System (IMOS) deploy-

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127 ments at Iles Kerguelen and are publicly available (`http://imos.aodn.org.au`). The

128 tracks comprise a mixture of sea ice foraging trips on or near the Antarctic continental

129 shelf (12 seals; Appendix S2: Figure S1a) and entirely pelagic foraging trips in sub-Antarctic

130 waters (12 seals; Appendix S2: Figure S1b). Prior to fitting the move persistence models,

131 we used a TMB implementation of a state-space model (Auger-Méthé et al., 2017) to filter

132 the observed locations, accounting for error in the Argos telemetry, and to regularise the

133 filtered locations to a 12-h time interval (see Appendix S2 for details).

134   We fit the move persistence model (`mpm`; Eqn's 1 and 2) to the state-space filtered seal

135 tracks. Fitting to filtered tracks accounts for some of the uncertainty inherent in teleme-

136 try data but potential effects of residual location uncertainty should be examined post-

137 analysis. To ascertain whether γ_t adequately captures changes in the seals' movement pat-

138 terns, we compare the γ_t-based behavioural index to discrete behavioural states estimated

139 from a switching state-space model (Jonsen, 2016) fitted using the `bsam` R package. De-

140 tails on how we fit the `bsam` model are in Appendix S3. We then fit the move persistence

141 mixed effects model (`mpmm`; Eqn's 1 and 4) to the same state-space filtered seal tracks to

142 infer how the seals' movement behaviour may be influenced by environmental features en-

143 countered during their months-long foraging trips. In both analyses, we fitted separate

144 models to the ice and pelagic foraging trips. For the `mpmm`'s, we specified mixed effects

145 models with random intercept and slopes to account for variability among individual seals.

146 We fit all possible combinations of fixed and random effects and use AIC and likelihood

147 ratios to find the best supported model for each set of tracks.

148   We examined 3 potential environmental correlates of elephant seal move persistence: sea

149 ice cover (the proportion of time the ocean is covered by $\geq 85\%$ ice; ice), chlorophyll a

150 concentration (near-surface summer climatology in mg m^{-3}; chl) and the salinity differ-

151 ence between 600 and 200 m depths (based on winter climatology averaged over 1955-2012

152 in psu; saldiff). These variables are known predictors of elephant seal habitat preference

153 (Hindell et al., 2017) and foraging (McMahon et al. *unpublished data*). Data sources and

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154 processing details are provided in Appendix S3. The environmental data values were ex-

155 tracted at each state-space filtered location. As saldiff is only calculated in areas where

156 the bathymetry is deeper than 600 m this covariate is only relevant to the pelagic foragers

157 (Appendix S4: Figure S1). Similarly, ice was excluded from the models fit to seals making

158 pelagic foraging trips as they spent little time in regions with sea-ice cover (Appendix S3:

159 Figure S1; Appendix S4: Figure S1). R code for the model selection is in Appendix S5.

Results

Time-varying move persistence (`mpm`)

162 The ice-bound seals exhibited similar movement patterns (Fig. 1a), with high move per-

163 sistence on their outbound migrations and lower move persistence near the Antarctic con-

164 tinent in areas of higher sea-ice coverage. Return migrations to Iles Kerguelen were more

165 variable, with some individuals moving persistently and others meandering, possibly for-

166 aging en route. Pelagic foraging seals (Fig. 1b) migrated approximately 2000 km either

167 east or west of Iles Kerguelen in relatively persistent fashion. Less persistent movements

168 occurred at the distal ends of these migrations, although seals travelling to the west of Iles

169 Kerguelen had markedly less persistent and slower movements, suggestive of more intense

170 search and foraging, compared to those travelling to the east (Fig. 1b).

171   The γ_t-derived behavioural index is comparable but not identical to the discrete be-

172 havioural states estimated from the `bsam` SSSM (Appendix S3: Figure S1). The γ_t index

173 captured the same changes in movement pattern but the magnitudes of those changes gen-

174 erally were smaller. Fitting the move persistence model, including the SSM filtering step,

175 was almost 500 times faster than fitting the `bsam` SSSM (Appendix S3: Table S1).

Individual variability in move persistence - environment relationships (`mpmm`)

177 *Sea-ice strategy.* The best supported model for elephant seals foraging in the sea-ice zone

178 included fixed and random coefficients for both the proportion of ice cover and chlorophyll

179 *a* concentration (Table 1). On average, seals had movements that became less persistent

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180 or directed as sea-ice cover and chlorophyll *a* concentration increased (Fig. 2a,b). Among

181 individuals, the relationship with ice was consistently negative but the degree to which

182 move persistence declined differed markedly (Fig. 2a), whereas the relationship with chl

183 was highly variable with 4 individuals having strong negative relationships and the rest

184 weak to moderately positive relationships (Fig. 2b; Z-value = -1.04, p = 0.3). Using the

185 fixed effects from the best model, the prediction of γ_t over the spatial domain implies that

186 seal move persistence changes, suggestive of search and foraging behaviours, south of 65° S

187 (south of the black contour line, Fig. 2d).

188   *Pelagic strategy.* The best supported model for elephant seals foraging in the open ocean

189 included fixed and random coefficients for the salinity difference between 600 and 200 m

190 depths (saldiff, Table 1). On average, seals had movements that became strongly less per-

191 sistent as the salinity difference decreased (Fig. 2c). Among individuals, this relationship

192 was moderately variable with two individuals exhibiting relatively small changes in move

193 persistence over the full range of saldiff (Fig. 2c). The spatial prediction of γ_t implies that

194 animals generally adopt a movement pattern suggestive of search or forage once beyond

195 the mid-latitudes near Kerguelen Island where saldiff is largest (i.e. south of the black con-

196 tour line, in oceanic waters, or north in the vicinity of the Subantarctic Front; Fig. 2e).

Discussion

198 Southern elephant seals employing specific foraging strategies respond to different environ-

199 mental factors. Our modelling approach clearly identifies these responses, including strong

200 decreases in move persistence associated with increasing ice coverage (sea-ice foragers) and

201 decreasing salinity difference (pelagic foragers). Move persistence responses were relatively

202 consistent among seals adopting either a sea-ice or a pelagic foraging strategy, but sub-

203 stantial individual variability in foraging location was evident.

204   Those animals whose forage migrations went towards the Antarctic continent showed low

205 move persistence once in areas of higher sea ice coverage. Some individuals also showed

206 positive responses to elevated chlorophyll *a* concentrations, targeting productive coastal

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207 polynya areas (Labrousse et al., 2018); however this was not a consistent response with

208 many others foraging farther offshore in the marginal sea-ice zone where chlorophyll *a*

209 concentrations are lower (Appendix S4: Figure S1). This pattern might be suggestive of

210 density-dependent habitat selection, whereby seals distribute themselves so that foraging

211 success is consistent across habitats of differing value (Morris, 2011).

212 For the pelagic foraging animals, our results indicated seals moved persistently away

213 from the region in which salty Circumpolar Deep Water was confined to depths (i.e., where

214 the salinity difference was highly positive). The majority then adopted a lower move per-

215 sistence in areas where the Circumpolar Deep Water shoaled (salinity difference closer to

216 zero, southern areas) with four animals targeting the vicinity of the Subantarctic Front

217 (salinity difference negative) where cold, fresh Antarctic Intermediate Water subducts

218 saline Subantarctic surface waters (northwestern areas, Appendix S4: Figure S1).

219 Future climate scenarios project stronger westerly winds, leading to intensified ocean

220 overturning circulation (Gao et al., 2018, and references therein). With increased upwelling

221 of nutrient-rich Circumpolar Deep Water, we might expect enhanced near-surface ocean

222 productivity to benefit pelagically foraging southern elephant seals in future. Expectations

223 for sea-ice foraging seals are highly uncertain due to complex physical processes occurring

224 over the Antarctic continental shelf. However, projections of reduced sea-ice extent and

225 duration may lead to reduced availability of foraging and/or resting habitat.

226 While the ultimate source of observed individual differences in movement - environment

227 relationships is often unclear, three non-exclusive explanations seem likely. First, we often

228 use relatively few predictors and these may indirectly or imperfectly represent the proxi-

229 mate influences to which predators are actually responding (i.e., prey density and/or dis-

230 tribution). This may inflate apparent individual differences in predator movement. Mod-

231 elling more direct indices of prey, and/or reducing error within covariates by accounting

232 for location uncertainty, may help to reduce apparent variation among individuals.

233 Second, individual variation is likely a real feature of foraging ecology (Magurran, 1993),

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234 where individual quality and personality may confer real differences in foraging behaviour

235 with relatively little difference in fitness (Stamps, 2007). For example, consistent bold-

236 ness in foraging can generate important ecological trade-offs, effecting increases in growth

237 and/or mortality rates (Stamps, 2007).

238 Third, the inclusion of multiple random effects raises the possibility of over-fitting, espe-

239 cially when the number of individual tracks is low. Artificial variability, propagating from

240 uncertainty in the locations and/or environmental covariates, could lead to spurious in-

241 ference of strong individual differences in foraging behaviour. A study design with repeat

242 tagging of the same individuals would help resolve the issue. Ultimately, researchers must

243 take care to address potential sources of error in their data and to use prior knowledge of

244 their study species to guide model selection and interpretation.

245 Interpreting among-individual variability in movement - environment responses can be

246 aided by considering established ecological theory. For example, density-dependent habi-

247 tat selection and functional responses to prey availability likely underpin inferred relation-

248 ships (Mason and Fortin, 2017). Accounting for such effects when fitting and interpreting

249 resource selection functions and habitat preference models can clarify understanding and

250 thereby assist forecasting of species' distributions (McLoughlin et al., 2010).

Modelling approach and extensions

252 Our model is composed of a linear mixed effects regression embedded within a correlated

253 random walk process model for animal movement behaviour. While the linear mixed ef-

254 fects approach allows flexible combinations of fixed and random effects, there is scope for

255 further enhancement. In many cases parametric, linear fixed effects may not adequately

256 capture the complexity of movement - environment relationships and a nonparametric ap-

257 proach using penalised splines may improve inference (Langrock et al., 2017). Given the

258 serial dependence structure of telemetry data, the unstructured covariance matrix we used

259 for the random effects could be replaced with a first-order autoregressive covariance struc-

260 ture (Brooks et al., 2017). Diagnosing lack of fit in latent variable models can be problem-

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261 atic as there is no observed response variable. One-step-ahead prediction residuals pro-

262 vide a useful validation tool and can be estimated when fitting the model (Thygesen et al.,

263 2017). Finally, there is a need to incorporate location uncertainty when sampling environ-

264 mental covariates from spatially gridded remote-sensing data. This can be done using mul-

265 tiple imputation methods as implemented in momentuHMM R package (McClintock and

266 Michelot, 2018), i.e., random draws of the environmental variables from the uncertainty of

267 the state-space filtered location estimates.

268 Recent advances in habitat modelling methods (e.g., Avgar et al., 2016) hold promise

269 for capturing the currently missing behavioural context in species' habitat preferences

270 and space-use. Here we model animal movement as a mixed effects function of environ-

271 mental variables to gain deeper insight into how individuals and populations may actually

272 use habitat. Our approach does not account for availability/accessibility of habitat in any

273 way but this clearly must be considered when inferring habitat preferences. A reasonable

274 approach for this might be to simulate animal tracks from our movement process model,

275 examining implications of including/excluding environmental covariates. Pseudo-absence

276 tracks can be combined into a habitat accessibility surface to condition spatial prediction

277 of animal behaviour from our process model (e.g., Raymond et al., 2015).

278 Our results show that TMB allows fast estimation of multiple fixed and random effects

279 in an animal movement process model. Dramatically faster computation times allow anal-

280 yses of movement - environment relationships in large telemetry data sets (100's of ani-

281 mals). This computation speed also opens up possibilities for more realistic models of ani-

282 mal movement, where warranted, perhaps by incorporating the third dimension for diving

283 or flying animals and/or high-volume accelerometry data.

284 The process model used here differs markedly from the state-space model used by Best-

285 ley et al. (2013). Bestley et al. (2013) used discrete behavioural state Markov-switching

286 embedded in a correlated random walk process model (Jonsen, 2016). Here, we used time-

287 varying move persistence γ_t as a behavioural index that varied continuously between 0 and

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288 1. This continuous index provides another tool for characterising animal movement pat-

289 terns and for making inferences about their environmental drivers. In some cases, a con-

290 tinuous index may offer more nuanced insight into variable but unknown behavioural se-

291 quences (Breed et al., 2012), whereas discrete states may offer more flexibility in capturing

292 the known structure of animal movement patterns (Michelot et al., 2017).

293 Telemetry data obtained at the level of individuals poses a challenge to scale up to pop-

294 ulations (Morales et al., 2010). Our approach enables multiple fixed (population) and

295 random (individual) effects in movement - environment relationships to be fit simply and

296 quickly. This provides a feasible solution to analysing increasingly large and detailed data

297 sets, and for harnessing individual-to-population level information on animal movement

298 responses to environment.

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Table 1: Model rankings by ΔAIC and likelihood ratios (LR) for the `mpmm`'s fit to the 24 foraging seals, split by foraging strategy (sea-ice or pelagic). Absolute AIC and deviance values for the best ranked model are displayed on the first row, under the ΔAIC and LR headings. All other ΔAIC and LR values are relative to the best ranked model. Computation time to convergence is also reported. Random effects are included in parentheses in the model formulas.

Foraging strategy	Model formula	df	ΔAIC	LR	Time (s)
sea-ice	$\sim$ ice + chl + (ice + chl | id)	12	-9954.21	-9978.21	4.76
	$\sim$ ice + chl + (chl | id)	9	0.78	6.78	3.61
	$\sim$ ice + chl + (1 | id)	7	21.06	31.06	4.17
	$\sim$ ice + (1 | id)	6	21.08	33.08	2.63
	$\sim$ ice + chl + (ice | id)	9	23.59	29.59	5.76
	$\sim$ ice + (ice | id)	8	24.14	32.14	4.55
	$\sim$ chl + (chl | id)	8	219.74	227.74	4.09
	$\sim$ chl + (1 | id)	6	245.16	257.16	3.48
	$\sim$ 1 + (1 | id)	5	339.28	353.28	2.79
pelagic	$\sim$ saldiff + (saldiff | id)	8	-13897.26	-13913.26	3.87
	$\sim$ saldiff + chl + (saldiff | id)	9	1.68	-0.32	4.96
	$\sim$ saldiff + chl + (chl | id)	9	3.25	1.25	3.97
	$\sim$ saldiff + chl + (1 | id)	7	29.81	31.81	4.04
	$\sim$ saldiff + (1 | id)	6	36.35	40.35	3.21
	$\sim$ chl + (chl | id)	8	51.37	51.37	4.54
	$\sim$ chl + (1 | id)	6	107.41	111.41	4.19
	$\sim$ 1 + (1 | id)	5	129.93	135.93	2.34
	$\sim$ saldiff + chl + (saldiff + chl | id)	12	NA*	NA*	6.02

*model failed to converge

Figure Captions

Figure 1. Maps of SSM-filtered southern elephant seal tracks originating from Iles Kerguelen. Ice-bound foraging trips (a) were predominantly directed to locations south of 60°S, whereas pelagic foraging trips (b) are predominantly north of 60°S. Each location is coloured according to its associated move persistence (see γ_t scale bar) estimated from the move persistence model.

Figure 2. Fixed (red) and random (blue) effects relationships between move persistence γ_t and the proportion of ice cover (a) and chlorophyll a concentration (b) for ice foraging seals, and between γ_t and the salinity difference between 600 and 200m (c) for pelagic foraging seals. All three panels display both random intercept and slopes, as per the best ranked models in Table 1. Spatial predictions of γ_t based on the fixed effect coefficients for the best fitting models for ice foraging seals (d) and pelagic foraging seals (e). The $\gamma_t = 0.75$ contour (black line) is displayed to aid delineation of predicted high move persistence ($\gamma_t > 0.75$; green - yellow) and low move persistence regions ($\gamma_t \leq 0.75$; green - blue). The southern boundaries of the Antarctic Circumpolar Current (d) and the Subantarctic Front (e) are displayed for reference (white lines).

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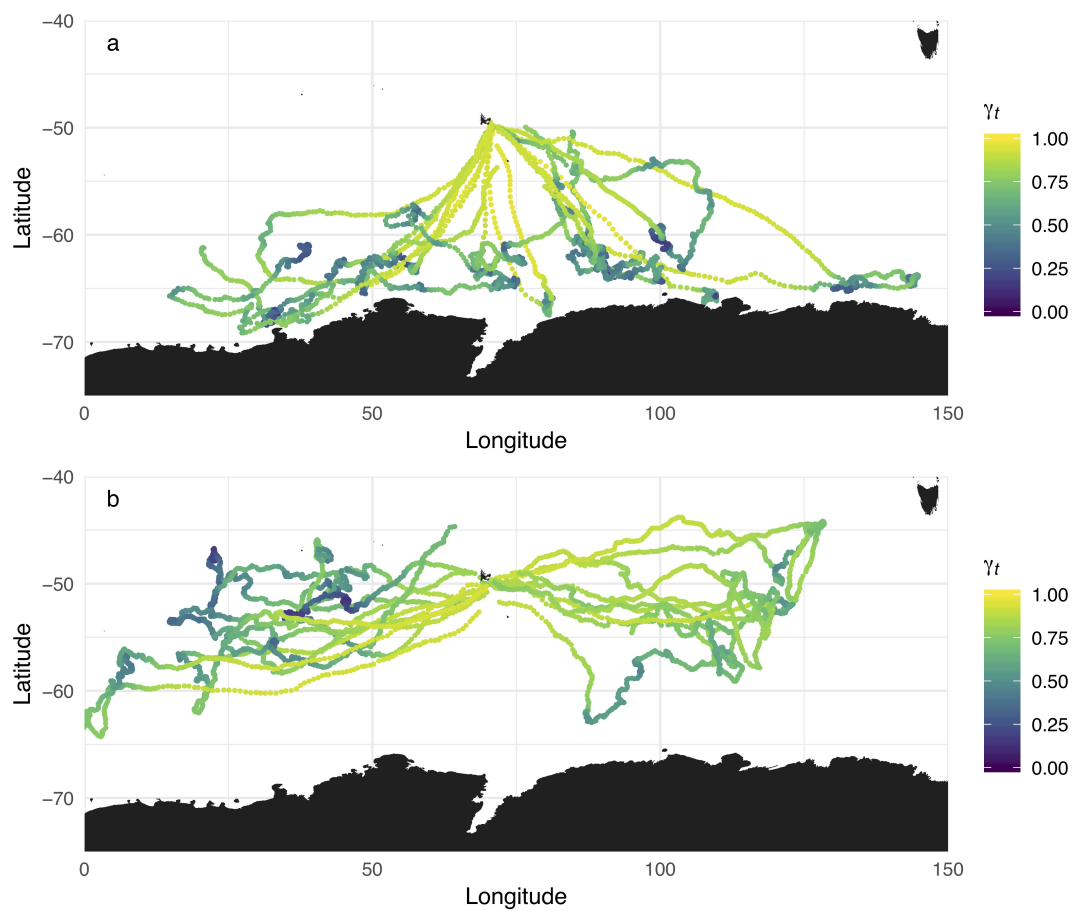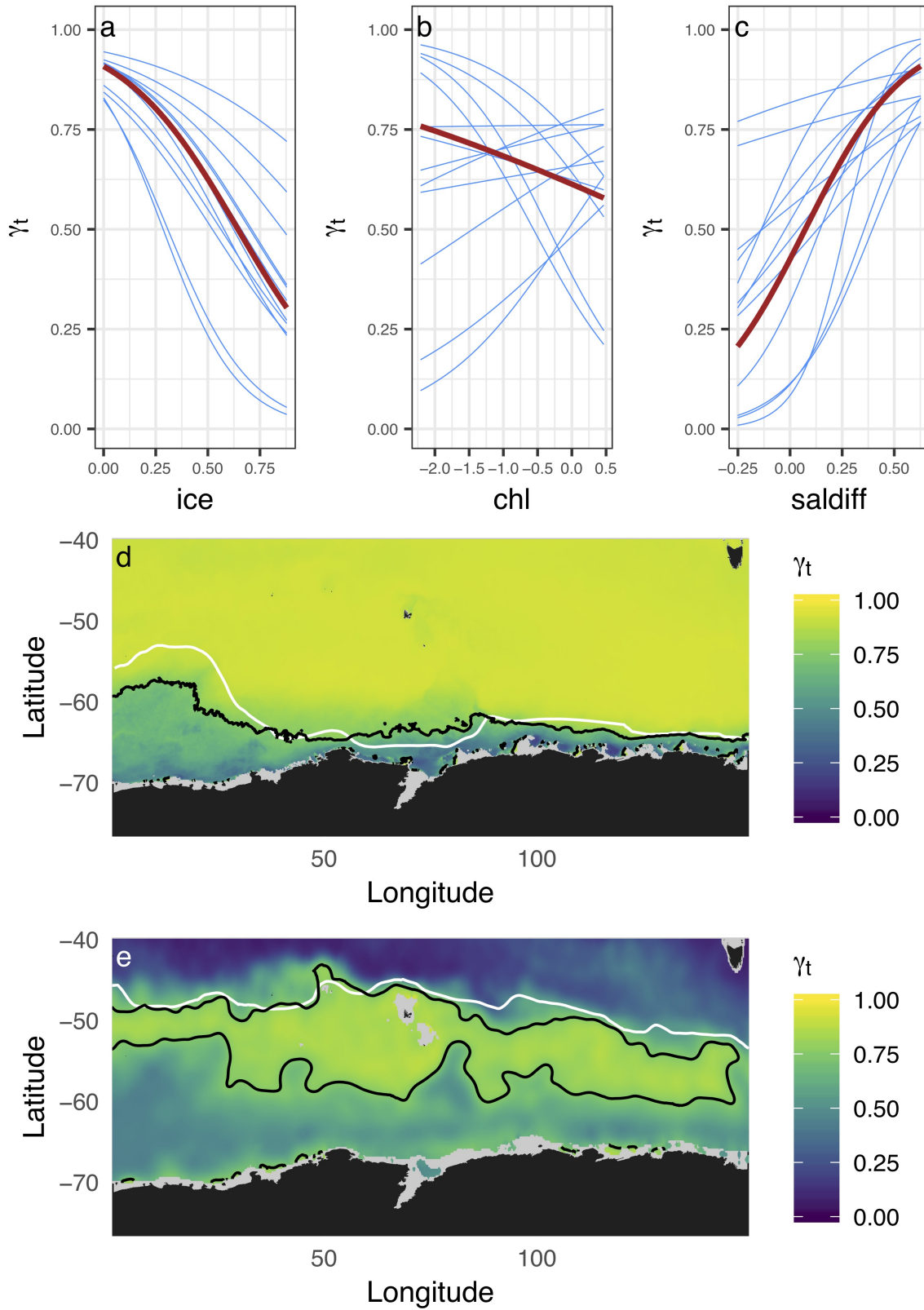Figure 1:

Figure 2: