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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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Abstract

Telemetry provides rich information on animal use of space, habitat preference and movement behaviour. Yet habitat models fit to these data often are blind to the underlying movement contexts. Conversely, movement models can be too slow for meaningful analysis of large telemetry data sets. Applying new fast-estimation tools, we show how mixed effects within a random walk movement model can rapidly infer among-individual variability in environment-movement relationships. We demonstrate our approach using southern elephant seal (*Mirounga leonina*) telemetry data. Seals consistently reduced speed and directionality (move persistence) with increasing sea ice coverage, had variable responses to chlorophyll *a* concentration, and consistently reduced move persistence in regions where circumpolar deep water shoaled. Our approach is scalable to large telemetry data sets and allows user-specified mixed effects to be evaluated via model selection, thereby illuminating the ecological context of animal movements that underlie habitat use.

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

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Introduction

Long-term environmental change is influencing southern elephant seal (*Mirounga leonina*) populations, with their trajectories possibly linked to individuals' foraging strategies and their long-term performance (Hindell et al., 2017). These seals undergo foraging migrations over huge distances from their breeding colonies, encountering a range of environmental conditions (Hindell et al., 2016). Foraging strategies vary among seals and are often tied to particular Southern Ocean habitats with individuals showing fidelity to these over several years (Authier et al., 2012). Quantifying how individuals differently respond to and use these habitats may aid future projections of current climate change effects on southern elephant seals.

Understanding animals' use of geographical and environmental space, where animals are and why they are there, is one of the central aims of ecology (Rosenzweig, 1981). Movement is a key process that defines space-use at spatial and temporal scales relevant to individual animals and telemetry is the predominant approach to observe this process (Kays et al., 2015; Hussey et al., 2015). Inferences about the ecological context of movements associated with, e.g., foraging, resting or predator avoidance are often made by relating movement patterns to physical habitat features (e.g., Breed et al., 2017).

Various spatial habitat modelling approaches are used to infer animal space-use and habitat preferences, by combining telemetry and remotely sensed environmental data (Aarts et al., 2008). Most habitat models infer animal habitat preference or selectivity from a combination of observed (presence) and simulated (pseudo-absence) tracking locations (Aarts et al., 2008) but are generally blind to the ecological context underlying those preferences (but see Avgar et al., 2016). State-space models, including hidden Markov models, can provide this context by inferring unobserved behavioural sequences from telemetry data and relating these to environmental features (Bestley et al., 2013; Michelot et al., 2017).

State-space models offer flexibility in modelling animal movement as a function of ex-

trinsic and/or intrinsic drivers (Bestley et al., 2013; Michelot et al., 2017). Although high individual variation is a commonly reported feature in telemetry analyses, models that account for among-individual variability in inferred movement - environment relationships are rare (e.g., McClintock et al., 2013). These random effects or hierarchical models can be computationally demanding, prohibiting realistic analysis of modern-sized telemetry data sets. There is a clear need for efficient movement modelling approaches, accessible to ecologists, where responses to environmental, physiological and/or social predictors can be inferred using flexible combinations of fixed and random terms (mixed effects) to account for variability among moderate to large numbers (10's - 100's) of individuals.

We present a modelling approach that takes advantage of fast estimation tools provided by the R package Template Model Builder (TMB, Kristensen et al., 2016). We build a mixed effect model for animal tracking data that uses TMB (Auger-Méthé et al., 2017) to estimate time-varying movement persistence. Rather than provide a complete framework to converge models of animal movement and habitat preference, we focus here on showing how the approach can be used to infer relationships between animal movement patterns and the environmental features they encounter. These models can be fit rapidly and flexibly with single or multiple random effects, enabling inference across multiple individuals and assessment of the extent to which relationships may differ among them. We demonstrate by inferring how southern elephant seals engaging different foraging strategies, ice-bound versus open ocean (pelagic) trips, may respond differently to their environment.

Methods

We build our modelling approach in three steps. First, we define a basic model that can be used to estimate changes in movement persistence along an animal's observed trajectory. Second, we expand the model to infer how these changes may be related to other variables. We focus on relationships with environmental variables but any combination of extrinsic or intrinsic variables could be modelled, provided they are measured at locations and/or times consistent with the telemetry data. Third, we add random effects to

the model to enable inference about how these movement - environment relationships may differ among individual animals.

Time-varying move persistence

Our modelling approach focuses on estimation of the persistence (sensu Patlak, 1953) of consecutive pairs of animal relocations (move steps) along an entire movement trajectory. Move persistence, which captures autocorrelation in both speed and direction, has been modelled as an average across entire movement trajectories (Jonsen, 2016), indicating whether that trajectory is, on average, uncorrelated (i.e., a simple random walk), correlated (i.e., a correlated random walk), or somewhere in between. Allowing move persistence to vary along a trajectory means it can be used as an index of behaviour (Breed et al., 2012), identifying segments of relatively low or high persistence:

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

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 animal's location $\boldsymbol{x}$ at times t and $t-1$. The random variable $\boldsymbol{\eta}_t = \mathrm{N}(\mathbf{0}, \boldsymbol{\Sigma})$, with variance-covariance matrix $\boldsymbol{\Sigma}$ specifying the magnitude of variability in the 2-dimensional movements. γ_t is the time-varying move persistence between displacements $\boldsymbol{d}_t$ and $\boldsymbol{d}_{t-1}$. γ_t is continuous-valued between 0 (low move persistence, Appendix S1: Figure S1a,c) and 1 (high move persistence, Appendix S1: Figure S1b,c). To avoid potential parameter identifiability issues between γ_t and $\boldsymbol{\Sigma}$, we set the covariance term in $\boldsymbol{\Sigma}$ to 0 but this constraint could be relaxed to better account for correlation in movements in the E-W and N-S directions. We assume γ_t follows a simple random walk in logit space:

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

where the random variable $\epsilon_t = \mathrm{N}(0, \sigma_\gamma)$ represents variability in move persistence along an animal's track.

This process model (Eqn's 1 and 2) can be fit: 1) to location data with minimal error; 2) to state-space filtered location data; or 3) coupled with an observation model for error-prone data. We focus on the second case with locations occurring at regular time intervals, but this could be relaxed (e.g., Auger-Méthé et al., 2017).

The time-varying move persistence model can be used to objectively identify changes in movement pattern. Here γ_t forms the behavioural index but unlike switching models (e.g., Jonsen, 2016; Michelot et al., 2017), these changes occur along a continuum (0 - 1) rather than as switches between discrete states.

Move persistence in relation to environment

To make inferences about the factors associated with move persistence, we can model γ_t as a linear function of environmental predictors measured at each location or time. With this approach, we replace the random walk on $\text{logit}(\gamma_t)$ (Eqn 2) with a linear regression of covariates on $\text{logit}(\gamma_t)$:

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

where β_0, $\beta_1, \ldots, \beta_n$ are the fixed intercept and regression coefficients, $m_{t,1}, \ldots, m_{t,n}$ are the predictor variables and $\epsilon_t = \text{N}(0, \sigma_\gamma)$ are the random errors. This model can be fit to a single animal track, or to multiple tracks pooled together. Typically, we wish to make inference across multiple individual tracks and assess the extent to which relationships may differ among individuals.

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:

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

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. However, estimation of multiple random effects can be computationally demanding, limiting the use of such models for animal telemetry data. 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, such as state-space models (Albertsen et al., 2015), 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`. This code draws on the `lme4` (Bates et al., 2015) and `glmmTMB` (Brooks et al., 2017) R packages to specify the mixed effects models in a flexible manner.

Data

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

tracks comprise a mixture of sea ice foraging trips on or near the Antarctic continental shelf (12 seals; Appendix S2: Figure S1a) and entirely pelagic foraging trips in sub-Antarctic waters (12 seals; Appendix S2: Figure S1b). Prior to fitting the move persistence models, we used a TMB implementation of a state-space model (Auger-Méthé et al., 2017) to filter the observed locations, accounting for error in the Argos telemetry, and to regularise the filtered locations to a 12-h time interval (see Appendix S2 for details).

Analysis

We fit the move persistence model (`mpm`; Eqn's 1 and 2) to the state-space filtered seal tracks. Fitting to filtered tracks accounts for some of the uncertainty inherent in telemetry data but potential effects of residual location uncertainty should be examined post-analysis. To ascertain whether γ_t adequately captures changes in the seals' movement patterns, we compare the γ_t-based behavioural index to discrete behavioural states estimated from a switching state-space model (Jonsen, 2016) fitted using the `bsam` R package. Details on how we fit the `bsam` model are in Appendix S3. We then fit the move persistence mixed effects model (`mpmm`; Eqn's 1 and 4) to the same state-space filtered seal tracks to infer how the seals' movement behaviour may be influenced by environmental features encountered during their months-long foraging trips. In both analyses, we fitted separate models to the ice and pelagic foraging trips. For the `mpmm`'s, we specified mixed effects models with random intercept and slopes to account for variability among individual seals. We fit all possible combinations of fixed and random effects and use AIC and likelihood ratios to find the best supported model for each set of tracks.

We examined 3 potential environmental correlates of elephant seal move persistence: sea ice cover (the proportion of time the ocean is covered by $\geq 85\%$ ice; ice), chlorophyll *a* concentration (near-surface summer climatology in mg m^{-3}; chl) and the salinity difference between 600 and 200 m depths (based on winter climatology averaged over 1955-2012 in psu; saldiff). These variables are known predictors of elephant seal habitat preference (Hindell et al., 2017) and foraging (McMahon et al. *unpublished data*). Data sources and

processing details are provided in Appendix S3. The environmental data values were extracted at each state-space filtered location. As saldiff is only calculated in areas where the bathymetry is deeper than 600 m this covariate is only relevant to the pelagic foragers (Appendix S4: Figure S1). Similarly, ice was excluded from the models fit to seals making pelagic foraging trips as they spent little time in regions with sea-ice cover (Appendix S3: Figure S1; Appendix S4: Figure S1). R code for the model selection exercise is in Appendix S5.

Results

Time-varying move persistence (`mpm`)

The ice-bound seals exhibited similar movement patterns (Fig. 1a), with high move persistence on their outbound migrations and lower move persistence near the Antarctic continent in areas of higher sea-ice coverage. Return migrations to Iles Kerguelen were more variable, with some individuals moving persistently and others meandering, possibly foraging en route. Pelagic foraging seals (Fig. 1b) migrated approximately 2000 km either east or west of Iles Kerguelen in relatively persistent fashion. Less persistent movements occurred at the distal ends of these migrations, although seals travelling to the west of Iles Kerguelen had markedly less persistent and slower movements, suggestive of more intense search and foraging, compared to those travelling to the east (Fig. 1b).

The γ_t-derived behavioural index is comparable but not identical to the discrete behavioural states estimated from the `bsam` SSSM (Appendix S3: Figure S1). The γ_t index captured the same changes in movement pattern but the magnitudes of those changes generally were smaller. Fitting the move persistence model, including the SSM filtering step, was almost 500 times faster than fitting the `bsam` SSSM (Appendix S3: Table S1).

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

Sea-ice strategy. The best supported model for elephant seals foraging in the sea-ice zone included fixed and random coefficients for both the proportion of ice cover and chlorophyll *a* concentration (Table 1). On average, seals had movements that became less persistent or

directed as sea-ice cover and chlorophyll a concentration increased (Fig. 2a,b). Among individuals, the relationship with ice was consistently negative but the degree to which move persistence declined differed markedly (Fig. 2a), whereas the relationship with chl was highly variable with 4 individuals having strong negative relationships and the rest weak to moderately positive relationships (Fig. 2b). Unsurprisingly, the chl fixed-effect was not significant (Z-value = -1.04, p = 0.3). Using the fixed effects from the best model, the prediction of γ_t over the spatial domain shows that the seals' move persistence changes, suggestive of foraging behaviour, south of 65° S (south of the black contour line, Fig. 2d).

Pelagic strategy. The best supported model for elephant seals foraging in the open ocean included fixed and random coefficients for the salinity difference between 600 and 200 m depths (saldiff, Table 1). On average, seals had movements that became strongly less persistent as the salinity difference decreased (Fig. 2c). Among individuals, this relationship was moderately variable with two individuals exhibiting relatively small changes in move persistence over the full range of saldiff (Fig. 2c). The spatial prediction of γ_t implies that animals generally adopt a movement pattern suggestive of search or forage once beyond the mid-latitudes near Kerguelen Island where saldiff is largest (i.e. south of the black contour line, in oceanic waters, or north in the vicinity of the Subantarctic Front; Fig. 2e).

Discussion

Our analyses revealed relatively consistent responses by individual animals to environmental variables we tested but substantial individual variability in foraging location was evident. Comparisons of model structures allowed these individual-level differences to be directly evaluated. Those animals whose forage migrations went towards the Antarctic continent showed low move persistence once in areas of higher sea ice coverage. Some individuals also showed positive responses to elevated chlorophyll a concentrations, targeting productive coastal polynya areas (Labrousse et al., 2018); however this was not a persistent response with many others foraging farther offshore in the marginal sea-ice zone where concentrations are lower (Appendix S4: Figure S1). This pattern might be suggestive of

density-dependent habitat selection, whereby seals distribute themselves so that foraging success is consistent across habitats of differing value (Morris, 2011). However, we expect that density-dependence would exert the strongest effect at or near the colony where seals are aggregated, rather than during long-range (multiple month) foraging trips. Such effects are likely to be smaller for capital breeders such as elephant seals and more important for income breeders (e.g. fur seals) that forage close to their colony during lactation. Even large tagging data sets, such as are available for southern elephant seals (Hindell et al., 2016), are unlikely to provide sufficient numbers for empirical evaluation of density-dependence during remote foraging at sea.

For the pelagic foraging animals, our results indicated seals moved persistently away from the region in which salty Circumpolar Deep Water was confined to depths (i.e., where the salinity difference was highly positive). The majority then adopted a lower move persistence in areas where the Circumpolar Deep Water shoaled (salinity difference closer to zero, southern areas) with four animals targeting the vicinity of the Subantarctic Front (salinity difference negative) where cold, fresh Antarctic Intermediate Water subducts saline Subantarctic surface waters (northwestern areas, Appendix S4: Figure S1).

Substantial variability among individuals is a persistent feature reported from animal telemetry data. Understanding this variability is essential for scaling up from individuals to inferences of population processes (Morales et al., 2010) and for predicting future responses to a changing environment. For example, climate change within the Southern Ocean is impacting the sea-ice extent and duration, the location of major oceanic frontal features, and the meridional overturning circulation (whereby water masses sink and rise as governed by density gradients) with large-scale consequences for marine ecosystem structure, function and productivity (Constable et al., 2014).

Although the ultimate source of observed individual differences in movement - environment relationships is often unclear, three non-exclusive explanations seem likely. First, we often use relatively few predictors and these may represent the proximate influences which

predators are actually responding to (i.e., prey density and/or distribution) indirectly or imperfectly. This may inflate apparent individual differences in predator movement behaviour. Modelling more direct indices of prey availability, and/or reducing error within covariates by accounting for location uncertainty as discussed above, may help to reduce apparent variation among individuals.

Second, individual variation is likely a real feature of foraging ecology (Magurran, 1993), where individual quality and personality may confer real differences in foraging behaviour with relatively little difference in fitness (Stamps, 2007). For example, consistent boldness in foraging can generate important ecological trade-offs, effecting increases in growth and/or mortality rates (Stamps, 2007).

Third, the inclusion of multiple random effects raises the possibility of over-fitting, especially when the number of individual tracks is low. Artificial variability, propagating from uncertainty in the locations and/or environmental covariates, could lead to spurious inference of strong individual differences in foraging behaviour. A study design with repeat tagging of the same individuals would help resolve the issue. Ultimately, researchers must take care in addressing potential sources of error in their data and, when possible, use prior knowledge of their study species', and rely on established ecological theory (e.g., McLoughlin et al., 2010) to guide model selection and interpretation.

Modelling approach and extensions

Our model is composed of a linear mixed effects regression embedded within a correlated random walk process model for animal movement behaviour. While the linear mixed effects approach allows flexible combinations of fixed and random effects, there is scope for further enhancement. In many cases parametric, linear fixed effects may not adequately capture the complexity of movement - environment relationships and a nonparametric approach using penalised splines may improve inference (Langrock et al., 2017). Given the serial dependence structure of telemetry data, the unstructured covariance matrix we used for the random effects could be replaced with a first-order autoregressive covariance struc-

ture (Brooks et al., 2017). Diagnosing lack of fit in latent variable models can be problematic as there is no observed response variable. One-step-ahead prediction residuals provide a useful validation tool and can be estimated when fitting the model (Thygesen et al., 2017). Finally, there is a need to incorporate location uncertainty when sampling environmental covariates from spatially gridded remote-sensing data. This can be done using multiple imputation methods as implemented in momentuHMM R package (McClintock and Michelot, 2018), i.e., random draws of the environmental variables from the uncertainty of the state-space filtered location estimates.

Recent advances in habitat modelling methods (Avgar et al., 2016; Michelot et al., In Press) hold promise for capturing the currently missing behavioural context in species' habitat preferences and space-use. Here we model animal movement as a mixed effects function of environmental variables to gain deeper insight into how individuals and populations may actually use habitat. Our approach does not account for availability/accessibility of habitat in any way but this clearly must be considered when inferring habitat preferences. A reasonable approach for this might be to simulate animal tracks from our movement process model, examining implications of including/excluding environmental covariates. Pseudo-absence tracks can be combined into a habitat accessibility surface to condition spatial prediction of animal behaviour from our process model (e.g., Raymond et al., 2015).

Our results show that TMB allows fast estimation of multiple random effects by using the Laplace approximation to calculate the marginal likelihood of a movement behaviour process model. The model selection we conducted on 24 southern elephant seals took a total of 8 minutes to complete. This includes the time required both to state-space filter the original Argos tracks and to fit the 18 `mpmm`'s and is approximately 1500 times faster than a more limited hierarchical Bayesian model selection exercise, using Markov chain Monte Carlo simulation (Bestley et al., 2013). These dramatically faster computation times mean that analysis of movement - environment relationships can be scaled up to

very large telemetry data sets, e.g., 100's of animals. This computation speed also opens up possibilities for far more realistic models of animal movement, incorporating the third dimension for diving or flying animals and/or high-volume accelerometry data.

The process model used here differs markedly from the state-space model used by Bestley et al. (2013). Bestley et al. (2013) used discrete behavioural state Markov-switching embedded in a correlated random walk process model (Jonsen, 2016). Here, we used time-varying move persistence γ_t as a behavioural index that varied continuously between 0 and 1. This continuous index provides another tool for characterising animal movement patterns and for making inferences about the possible environmental drivers of animal movement and associated behaviour. In some cases, a continuous index may offer more nuanced insight into variable behavioural sequences (Breed et al., 2012), whereas a discrete state approach may offer more flexibility in capturing the known structure of animal movement patterns (Michelot et al., 2017).

Telemetry data obtained at the level of individuals poses a challenge to scale up to population ecology. Our approach enables multiple fixed (population) and random (individual) effects in movement-environment relationships to be fit simply and efficiently. This provides a feasible solution to analysing increasingly large and detailed data sets, and for harnessing individual-to-population level information on animal movement 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, following the `lme4` convention (Bates et al., 2015).

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

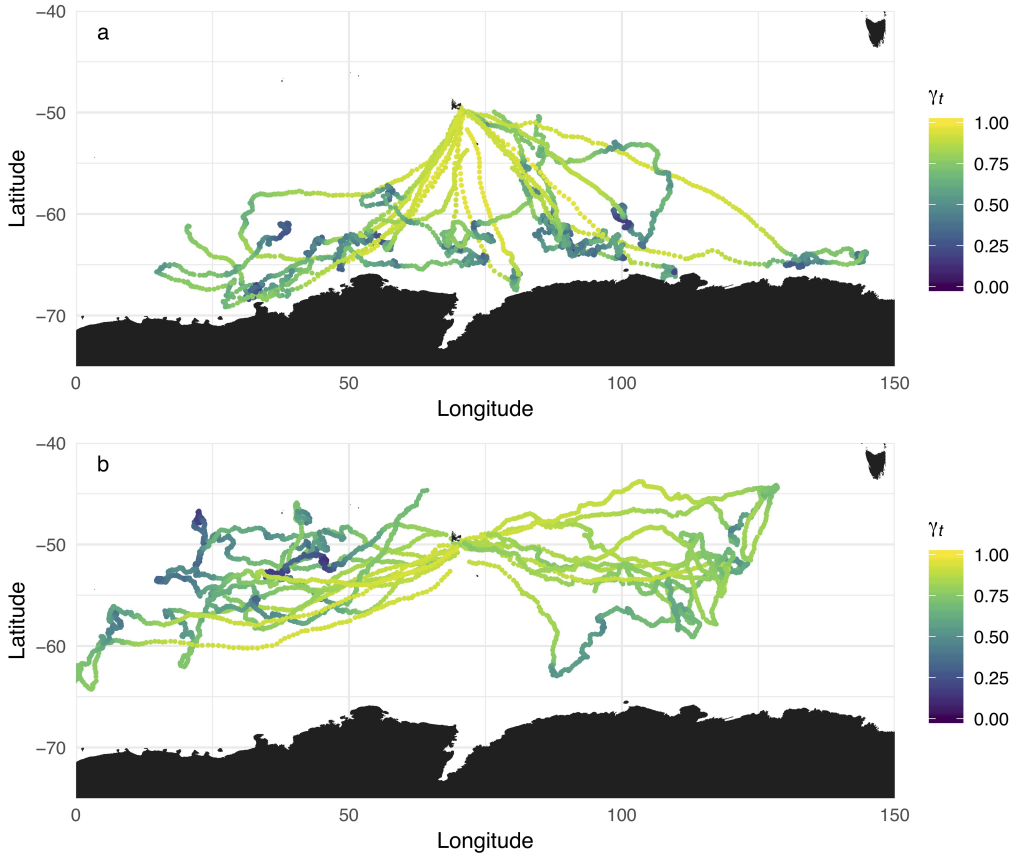

Figure 1: Maps of SSM-filtered southern elephant seal tracks originating from Iles Kerguelen. Ice-bound foraging trips (a) were predominantly directed to locations south of 60°S, whereas pelagic foraging trips (b) are predominantly north of 60°S. Each location is coloured according to its associated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

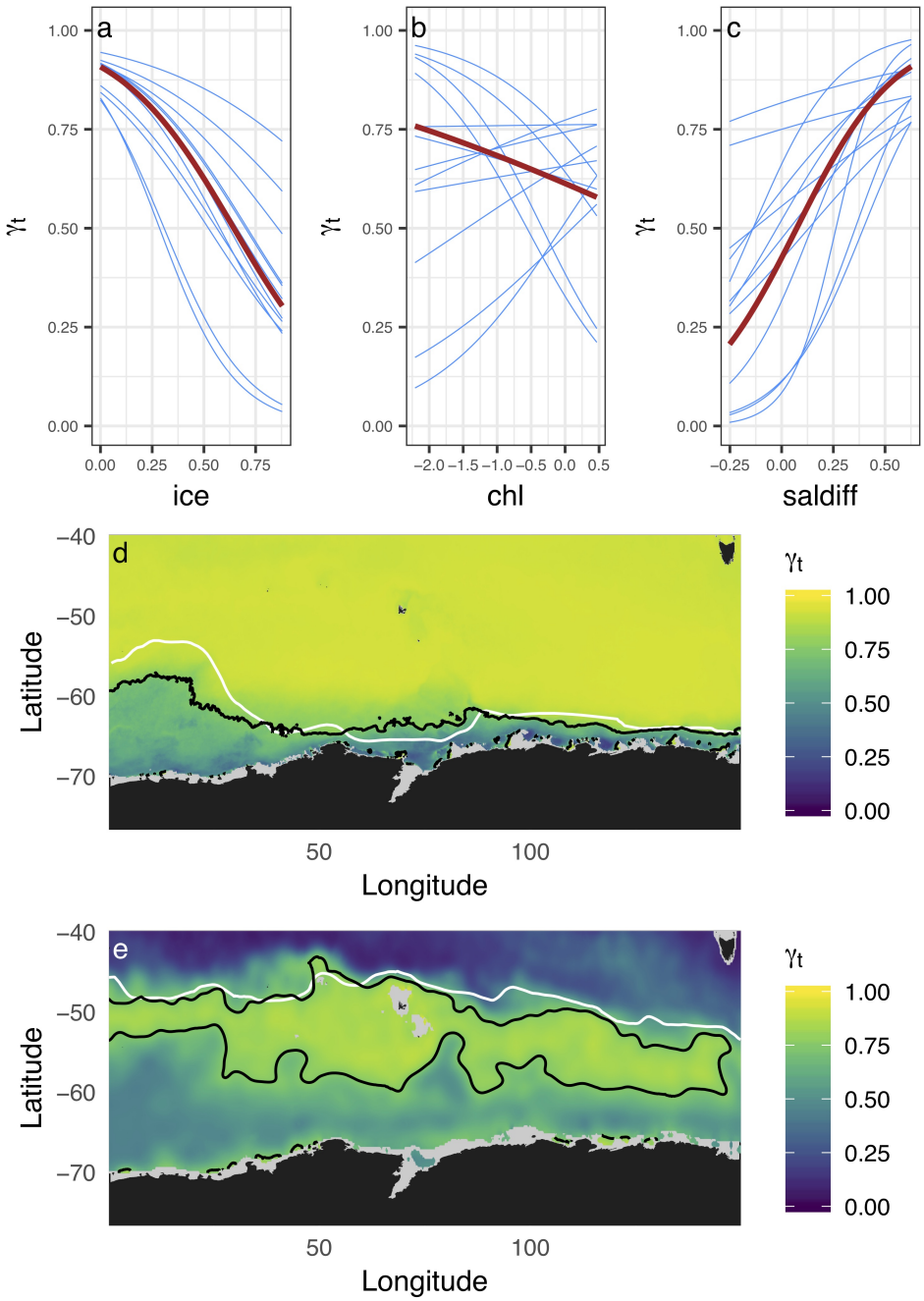

Figure 2: Fixed (red) and random (blue) effects relationships between move persistence γ_t and the proportion of ice cover (a) and chlorophyll *a* concentration (b) for ice foraging seals, and between γ_t and the salinity difference between 600 and 200m (c) for pelagic foraging seals. All three panels 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).