

# Hierarchical Error in Covariates Title

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**Summary:** The population of northern fur seals (*Callorhinus ursinus*) in the Pribilof Islands, Alaska has declined dramatically during the past 35 years. Arresting the decline of the species requires an understanding of their foraging behaviour at sea and is particularly important for those adult females whose foraging success is also linked to pup survival. We capture behaviour patterns of a set of tagged female northern fur seals by relating an autoregressive movement model to the numerical properties of the state space. The at-sea behaviour states were then matched, spatially and temporally, to a set of environmental variables, some of which were averages that represented the oceanic conditions over a large spatial area. The mismatch of scale between fur seal behaviour and the environmental variables was accounted for by modeling the errors associated with these covariates in a Bayesian hierarchical regression framework. Using this approach, we were able to link together northern fur seals that went to disparate regions of the eastern Bering Sea, with widely variable information about their underlying environmental fields into a single model. This application of a hierarchical model relates changes in identifiable behavioural states of the northern fur seal to changes in the Alaska commercial groundfish industry over a 24-hour foraging cycle.

**Keywords:** Northern fur seal; Multinomial; Bayesian hierarchical model, Error-in-covariates; Diel pattern; Walleye Pollock

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## 1. INTRODUCTION

The population of northern fur seals in the Pribilof Islands, Alaska has declined dramatically during the past 35 years, and continues to decline without any obvious reason yet identified (Towell et al. 2006). Arresting the decline of the species requires an understanding of the foraging strategies of the northern fur seal (Antonelis et al. 1997), particularly for those adult females whose foraging success is also linked to pup survival. The relationship between lactating northern fur seal movement and habitat is shaped by foraging success and the physiological constraints of feeding a stationary pup left on a beach at its natal rookery. Understanding the relationship between movement, behavior and environment is a critical part of understanding population processes (Bowler and Benton 2005), and has been identified as one of the highest-level priorities by the northern fur seal conservation plan (NMFS 2007).

Analysis methods have been hampered until recently by difficulties in reconstructing the three-dimensional foraging tracks through the oceanic environment (Harcourt and Davis 1997). Movement is a complex 3-dimensional process that does not always simplify into lower dimensions, yet there is mounting evidence to demonstrate the potential perils of inferring animal behaviour based on horizontal trajectories alone (e.g. McClintock et al. 2013 and references therein). Methods that calculate horizontal straightness indices (e.g. area restricted search: ARS) have found this poorly correlates to feeding behaviours (Austin et al. 2006, Weimerskirch et al. 2007). Another metric measuring passage time through a horizontal region of fixed radius (e.g. first passage time: FPT) has been linked to covariates but suffers from the confounding of slow speeds due to rest behaviours, and fast speeds with tortuous paths taking similar times to traverse a similar radius. Other methods based on depth (e.g. Gentry et al. 1986, Goebel 2002) are dependent on arbitrary depth descriptions. The methods used here take advantage of recent advances in 3-D bio-logging technology and use movement models based on processes that describe dive types in a mechanistic way.

This approach to classifying behaviour links the vertical dimension to the horizontal spatial field that describes the environment in which the behaviour is observed. The framework is a flexible, analytical method for extracting more out of the increasing wealth of information from recent advances in bio-logging technology. We show how to incorporate this information into understanding the environmental factors influencing at-sea behaviour.

The environment undoubtably influences northern fur seal behaviour, but identification of the extent of these influences is limited, and remains poorly understood (Ream et al. 2005). Linking behaviour to changes in the environment at the landscape level is important in understanding the processes that limit at-sea success in the Bering Sea. The main barrier to developing models addressing these landscape level questions is the vast difference in scale between the at-sea behaviour of the individual seal and the oceanic environment through which that fur seal passes. The environment is typically only observed incompletely and with large and unknown amounts of measurement error and data uncertainty. As well, the environment can only be approximated by combining various data sources, often at very different scales. These issues can represent a significant amount of modelling uncertainty, and this is true of any analysis that aims to link animal movement to the spatial environment. The amount of uncertainty in the data can depend on a number of factors. For example, spatial data can be collected from ships running transects across time and space, or can be derived from remotely sensed satellite data. Each data collection agency usually has its own way of pre-processing the data to account for limitations of the sampling method.

The general approach to hierarchical modelling can be considered as a large set of stochastic formulations that include many popular models such as random effects models and generalized linear mixed models, and are flexible enough to solve a variety of inference problems (e.g. Gelman et al. 2004, Chapters 5, 15, and references cited therein). We introduce in this paper a hierarchical Bayesian model as a means to account for multiple sources of uncertainty in the measurement and quantification of the fur seal's at-sea environment. We

develop a Bayesian hierarchical model for processing 3-D movement models and the effects of covariates for multiple individuals motivated by the problem of (i) processing a dataset collected from satellite-linked, archival tagged female northern fur seals with pups, and (ii) understanding their at-sea behaviour in response to changes in the environment. We will formally acknowledge the randomness in both seal behaviour and the environment process by building a hierarchy of conditional models to describe the complexity of our data and the process that generates animal behaviour (Cressie et al. 2009). We do not set out to identify which sections of the Bering Sea might be of conservation priority with respect to foraging hotspots, and therefore have not approached this as a spatial problem. Our goal is to understand if there was something in the variable field through which the fur seal swam, that influenced the observed fur seal's behaviour. Our specific goals are:

1. To use archival tag technologies recording movement at scales of seconds, in conjunction with coarse location data from Argos satellite transmitting tags, to understand how lactating fur seals partition their time between different identifiable behaviours such as active feeding, exploratory diving, and non-feeding behaviours such as sleeping, resting, grooming or surface transiting.
2. To understand how these identified behaviours can be linked to their at-sea habitat and used to understand how physical and biological factors influence their behaviour.

While the primary focus of this paper is on the behaviour of northern fur seals at a rookery site on the Pribilof Islands, it is important to emphasize that the methodology is adaptable. As data quality improves, as well as our understanding of the underlying environmental processes, these methods are flexible enough to allow for better, more mechanistic, and less error-prone models of behaviour. As well, this framework will allow for the characterization of the relationship of the behaviours we classified, but also of other behaviours and other descriptors of pelagic habitat and foraging success, and presumably, of other marine predators.

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## **2. METHODS**

### **2.1. Instruments**

During the 2005 and 2006 breeding seasons, 18 lactating northern fur seals were captured at Reef Rookery on St. Paul Island (57.18° N, 170.27° W; 5 in 2005, 13 in 2006).

Three different tag technologies were employed in which all instruments were attached mid-dorsally using methods described in Boyd and Coxall (1992). The first of these tags was a dead-reckoner tag (Driesen & Kern GmbH, Bad Bramstedt, Germany). The dead-reckoner tags were programmed to collect data at 2-second or 5-second intervals for the full length of the foraging trip. Two of the 2005 tags were set to sample at 5-second intervals, and the remaining 2005 and all 2006 tags were programmed to sample at 2-second intervals. The dead-reckoner was a 10-channel logger with a 32 MB flash memory that recorded time, depth, speed (using a swim paddle system), temperature, light, pitch, roll, compass heading (in three-dimensions), and body orientation (belly up or belly down).

The second tag attached was an ARGOS (Platform Transmitter Terminal or PTT) satellite transmitter (Spot5, Wildlife Computers, Redmond, Washington, USA), recording latitude and longitude to recalibrate dead-reckoner route calculations from cumulative errors associated with ocean drift.

The third tag attached was a VHF radio transmitter (A2920 Glue On, Advanced Telemetry Systems, Isanti, Minn., USA), to allow the animals to be relocated when they returned to the rookery. All females were recaptured to remove the tracking devices and retrieve the data series logged from their at-sea foraging trips.

## 2.2. Track Reconstruction

The 2- and 5-second resolution data recorded on the dead-reckoner tags and the Argos transmitters were integrated to link swimming position to the satellite location data (Mitani et al. 2003). The 3-dimensional fur seal track was calculated using the dead reckoner channels that recorded compass bearing, depth, and speed-through-the-water to calculate the direction and horizontal speed over the water surface for each female. We pre-processed the tag's speed channel to correct for cumulative errors due to bias in the speed paddle's position. We identified zero-speed periods (sleeping) using short (13 minute) time windows with near-zero variance, and used a linear interpolation to re-zero speed (Figure 1). Each foraging track was then corrected for errors associated with ocean drift by matching times of the two tags, and forcing the dead-reckoner track to lie between the (assumed to be correct) Argos locations. This was done by translating the dead-reckoner track into polar coordinates, rotating the angle of movement, and rescaling the radial coordinate to match the direction and great circle distance between consecutive Argos locations (Figure 2). This resulted in a 2- or 5-second resolution track reconstruction that infills between the Argos satellite locations. These high-resolution track reconstructions allowed a space and time linkage between the environmental conditions encountered and the behavioural response of each northern fur seal. We trimmed each female's data record to include only those data in which she was at sea. The trimmed tracks ranged from 90,000 to 480,000 3-dimensional data records per animal (Figure 3).

[Figure 1 about here.]

[Figure 2 about here.]

[Figure 3 about here.]

### 2.3. Behaviour Data

Once the fine-scale locations were resolved for all fur seal tracks, we identified fur seal behaviour along segments of track using an augmented state space modelling approach, with the aim of linking the solution space to a set of biological and physical variables that describe the changing at-sea environment.

We identify the behavioural response variable by following the augmented state space methods described in Dowd and Joy (2011) on the archival dead-reckoner tag. Our analysis proceeds by differencing the tag's depth channel to create a measure of "vertical velocity". The 2- or 5-second resolution data series of vertical velocity is then sectioned into 26 minute windows over which we use a discretized 2<sup>nd</sup>-order ordinary differential equation (AR-2 difference equation) as the process model in the augmented state space. The process model's continuous parameter solutions describe fur seal vertical movement and can be translated to classifications of behaviour by studying the qualitative form of the general solution to the AR-2 difference equation. We applied a locally optimized kernel smoother to the continuous parameter solutions to compensate for errors from unresolved tag measurement error and the random stochasticity in state space solutions (Herrmann 2003, R library "*lokern*"). For each time window, we use the numerical properties of the parameter solutions to define the conditions for uncorrelated pseudo-periodicity, asymptotic stationarity and white noise (Priestly 2004, Shumway and Stoffer 2006), and relate these to three unordered discrete behaviour classes: "Active Diving", "Exploratory Diving", and "Non-Diving" (Dowd and Joy 2011).

For example, the solution space for the state space parameters describing movement identifies two distinct regions that characterize unique numerical properties (Figure 4). We interpret solutions that fall in the yellow region as repetitive diving reminiscent of an oscillating pendulum, and call this behaviour mode "*Active Diving*". Parameter solutions that fall in the red area represent more intermittent diving characterized by a correlated

random walk. We call the behaviour mode, “*Exploratory Diving*”.



[Figure 4 about here.]

Vertical velocity is small for both sleeping or resting animals and for horizontal surface movement such as transiting, and hence we could not distinguish between these two modes. For purposes of the behavioural analyses, transiting, resting, and sleeping were considered the same non-diving behavioural state, as these behaviours are characterized by a lack of engagement in the immediate environment. We used the off-line estimate of system variance for each window for vertical speed (described in Appendix ?? of Dowd and Joy 2011) to identify non-diving states (eg. Figure ??). We called this behaviour mode, “*Non-Diving*”.

For illustration, Figure (6) demonstrates the movement parameters and corresponding behaviour for Track 3 for a single day (August 18<sup>th</sup>, 2006). Figure (7) shows how the fine-scale 3-D movement for the entire track is translated into the three behaviour modes.

[Figure 5 about here.]

[Figure 6 about here.]

[Figure 7 about here.]

We concatenated similar 26-minute windows of the behavioural types together into coherent “segments” of similar behaviour. This better relates the observed seal behaviour to the scale of the spatial covariate information and defines the response variable as the observed behaviour of a fur seal over a variable-length segment of time and space. Each behaviour mode of each female fur seal is then associated in space and time to a position in the Bering Sea that changes as the fur seal moves.

## 2.4. At-Sea Environmental Conditions: Covariate Data

### 2.4.1. Commercial Groundfish Catch and Walleye Pollock

A major goal of the study was to ascertain the extent (if any) to which fur seal behaviour was associated with fish abundance, and in particular, walleye pollock density. As a proxy for fish abundance we used the US Department of Commerce domestic observer data of the Alaska groundfish fishery for 2004-2008 (NMFS 2012). We spatially linked the fur seal tracks to each groundfish haul to the nearest 1/60th of a degree longitude and latitude ( $\sim 1.85$  km). We selected 2 variables of interest; the first was total catch weight for each groundfish haul (including both retained and discarded species), and the second was haul weight of walleye pollock.

We limited the fish catch data to July 9th, the beginning date of the breeding season (Trites 1992), and November 11th in 2005, and November 18th in 2006, the median dispersal dates for pups on St. Paul Island (Lea et al. 2009). Initially, we matched fishing effort by year to our track data but found the catch data for 2005 and 2006 were too sparse to be reliable. Therefore we included all data for the years 2004 through 2008, with the acknowledgment that although small scale commercial fishing hotspots change over years, by including multiple years we had smoothed over temporal variability, but captured persistent spatial hotspots. Where multiple hauls were linked per track segment, we took the median catch weight and median pollock weight to represent that segment of track.

for each of the behavior states along the length of each foraging track. Where multiple hauls were linked for a single segment of track, we took the median haul measurement for that behaviour segment as representative.

### 2.4.2. Sea surface temperature

Sea surface temperature data was retrieved from the dead-reckoner tag. We filtered all data that were observed outside of the top two metres of the ocean surface.

#### *2.4.3. Primary Productivity*

We assigned primary productivity over the foraging track by constructing a composite field of weighted averages along the fur seals track by linearly interpolating time between the 8-day NOAA CoastWatch net primary productivity product (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserAK.jsp>) to match the time and location of the fur seal track. This derived measure of net primary productivity is based on satellite-collected chlorophyll-a concentration and photosynthetically available radiation (PAR) measurements, corrected for the amount of organic carbon used by planktonic organisms in respiration (Behrenfeld and Falkowski, 1997), and gridded at 1/6th of a degree (~18.5 km). This was done so that each female's track was overlayed with a slightly different productivity field that was linked to the particular time range and location of each foraging trip.

#### *2.4.4. Wind Speed*

Also for each 24 hour period, we extracted NCDC blended satellite wind speeds at 17:00 local time (<http://www.ncdc.noaa.gov/oa/rsad/air-sea/seawinds.html>). This wind speed product blends satellite wind speeds from multiple platforms such as scatterometers, and passive microwave radiometers (Zhang et al. 2006). The best nominal resolution is 1/4 degree (28km) but as winds are spatially coherent on scales of hundreds of kilometres, we estimated wind speed once per day of each track, at the midpoint of the entire track and used linear interpolation across time to estimate windspeed for each behavioural segment.

#### *2.4.5. Ocean Depth*

As the bathymetry of this region of the Bering Sea is dominated by on-shelf shallow waters < 200 metres deep and off-shelf waters with ocean depths of 3000 metres or more, we simplified bathymetry into an on-shelf/off-shelf categorical variable. Note the maximum dive

depth of a northern fur seal is  $\sim 200$  metres (Gentry et al. 1986). For ocean depth data, we matched longitude and latitude of the track to the nearest depth measurement from the ETOPO1 bathymetry model

([http://www.ngdc.noaa.gov/mgg/gdas/gd\\_designdgrid.html](http://www.ngdc.noaa.gov/mgg/gdas/gd_designdgrid.html), Amante and Eakins 2009), which gives bathymetry output in arc minutes,  $1/60^{\text{th}}$  of a degree, ( $\sim 1.85$  kilometers). We then calculated the median depth for each of the behavior states along the at-sea track. For example if the seal was in an active diving mode between midnight and 4am, we took the median depth of the ocean during that period of the track, and classified it as on-shelf or off-shelf. We also followed methods and depth definitions of Call et al. (2008) and described depth as a three level categorical variable: inner/middle shelf (0-100 m), outer shelf (100-200 m), and off-shelf ( $>200$  m).

#### 2.4.6. Time of Day

Time for each behavioural state was taken once from the dead-reckoner tag at the start of each behavioural period. As northern fur seals have strong circadian patterns in behavior (Ream et al. 2005), we transformed the time of day into a circular variable to capture this periodic rhythm, and to ensure that the interpretation of time at 24:00 is equal to that at 00:00. We modelled the dependence on time of day as a sine wave with a 24 hour period. Using a standard trigonometric identity, we rewrite *time of day*,  $t$ , as a sine wave with a 24-hour period as follows

$$\begin{aligned} A \sin\left(\frac{2\pi t}{24} + \phi\right) &= A \sin(\phi) \cos\left(\frac{2\pi t}{24}\right) + A \cos(\phi) \sin\left(\frac{2\pi t}{24}\right) \\ &= \alpha_1 \cos\left(\frac{2\pi t}{24}\right) + \alpha_2 \sin\left(\frac{2\pi t}{24}\right) , \end{aligned} \quad (1)$$

where  $A$  is the amplitude of the wave,  $\phi$  is the phase shift,  $\alpha_1 = A \sin(\phi)$  and  $\alpha_2 = A \cos(\phi)$ . This provides a regression-type equation with the sine and cosine functions serving as the

covariate data and  $\alpha_1$  and  $\alpha_2$  can be solved as regression parameters.



### 3. ENVIRONMENTAL MODEL



Our goal was to see if the coupled environmental variables at each location could be used to provide insight into northern fur seal behavior. For this, we build the following hierarchical Bayesian model to examine the relationship between behaviour mode and at-sea habitat by matching the set of environmental variables in time and space to the observed behaviour model at the horizontal position of the fur seal's track.

#### 3.1. Observation Model

Our Bayesian hierarchical model begins with an observational process that describes fur seal behaviour and is accounted for via a likelihood or observation model. The multinomial probability density is one such observation model that relates the set of observed outcomes  $\mathbf{y}$  to their outcome probabilities  $\mathbf{p}$ . Let  $\mathbf{y}_{ij}$  be a random vector of length equal to the number of discrete behaviour outcomes or modes, where  $\mathbf{y}_{ij}$  describes the behavioural response for the  $i^{th}$  fur seal over the  $j^{th}$  segment of track. The elements of  $\mathbf{y}_{ij}$  are all zero except for the class of behaviour the fur seal is observed in, such that  $\sum_{k=1}^K y_{ij}^{(k)} = 1$ .

#### 3.2. Local Process Model

The underlying (latent) probability vector describing the relative probabilities of each behaviour category  $\{p_{ij}^{(1)}, p_{ij}^{(2)}, \dots, p_{ij}^{(K)}\}$  can be linked to the set of covariates described in Section (2.4), and a set of linear regression coefficients ( $\boldsymbol{\beta}_i$ ), via a multinomial regression model for each fur seal (McCullagh and Nelder 1989). We model the logarithm of the ratio of the probability of each category relative to that of a baseline category, written logit  $p_{ij}^{(k)}$ , selecting the most commonly observed category, “Non-Diving”, as the denominator or

baseline category,  $p_{ij}^{(1)}$ , in the logit ratio (i.e. when  $k = 1$ , baseline parameters  $\beta_i^{(1)} = 0$ ), following the advice of Agresti (1990).

The joint likelihood for the three categorical outcomes from the observation model and the multinomial process regression for all track segments for the  $i^{th}$  fur seal can be rearranged and written



$$P(\mathbf{p}_i | \mathbf{X}_i, \boldsymbol{\beta}_i) = \exp \left\{ \sum_{k=2}^K \left( \boldsymbol{\beta}_i^{(k)} \left[ \sum_{j=1}^{J_i} y_{ij}^{(k)} \mathbf{X}_{ij} \right] \right) - \sum_{j=1}^{J_i} \log \left( 1 + \sum_{k=2}^K e^{\mathbf{X}_{ij} \boldsymbol{\beta}_i^{(k)}} \right) \right\}. \quad (2)$$

### 3.2.1. Including Error in Covariates



An important aspect of process error problems is the difficulty in accurately estimating regression parameters when there is error contained within the covariate data (Stephens and Dellaportas 1992). Standard regression models assume that all covariates have been measured exactly, i.e. without error. In the case when some covariates are associated with error, estimation based on the standard assumption of no error in the covariates leads to biased and inaccurate inference about the true underlying covariate associations between regression covariates and response variable (Gustafson 2004).

In Equation (2), all measured covariates for the  $i^{th}$  fur seal were represented by  $\mathbf{X}_i$ . Henceforth, we distinguish between covariates measured with error, written as  $\mathbf{W}_i$ , and those without error, written as  $\mathbf{Z}_i$ . As well, we redefine  $\mathbf{X}_i$  to be a covariate that we don't directly measure, but instead infer from observing the related variable  $\mathbf{W}_i$ . We are now assuming an implicit random effect model that is informed about the true data  $\mathbf{X}_i$  through an error prone measure  $\mathbf{W}_i$ .

The goal is to obtain unbiased estimates of regression parameters,  $\boldsymbol{\beta}_i$  but the parameters of the regression of *logit*  $\mathbf{p}_i^{(k)}$  on  $(\mathbf{Z}_i, \mathbf{W}_i)$  are different from those of *logit*  $\mathbf{p}_i^{(k)}$  on  $(\mathbf{Z}_i, \mathbf{X}_i)$ , and substituting  $\mathbf{W}_i$  for  $\mathbf{X}_i$ , without adjusting the model for this substitution, leads to inaccurate

and biased estimates (Gustafson 2004, Carroll et al. 2006).

In our models, the major source of “error” is due to the environmental field being divided up into behavioural segments, for which there is one measure per segment, and a single measure is likely an inadequate measure of the range of values experienced for that segment. If the observed covariate measure,  $\mathbf{W}_{ij}$ , is an index of a range of values over the  $j^{th}$  segment of track for the  $i^{th}$  fur seal, then we write an error model to reflect that the (latent) true measure,  $\mathbf{X}_{ij}$ , is more variable than its observed value,  $\mathbf{W}_{ij}$  (Richardson and Gilks 1993, Carroll et al. 2006), and form an error model as simple as

$$\mathbf{X}_{ij} = \mathbf{W}_{ij} + \mathbf{U}_{ij}. \quad (3)$$

We assume the observed covariate  $\mathbf{W}_{ij}$  is unbiased for the true covariate  $\mathbf{X}_{ij}$ , and treat  $\mathbf{W}_{ij}$  as fixed data in our Bayesian model thus allowing us to condition on it. We assume  $\mathbf{U}_{ij}$  is a normal, independent and identically distributed random variable according to  $\sim \mathcal{N}(\mathbf{0}, \sigma_{iU}^2 \mathbf{I})$  where  $\sigma_{iU}^2$  describes the measurement error variance for the  $i^{th}$  fur seal. Measurement errors of the type found in Equation (3) are called Berkson errors (Berkson 1950), and are typically chosen when all observations (along a segment of track) within an individual are given the same error-prone covariate.

We treat the covariate model (Equation 3) as the prior for  $\mathbf{X}_i$ , selecting the multivariate normal distribution ( $\mathcal{MVN}$ ) as the form of that prior, and select independent conjugate inverse gamma distributions ( $\mathcal{IG}$ ) for  $\sigma_{iU}^2$ , i.e.,

$$\mathbf{X}_i \sim \mathcal{MVN}(\mathbf{W}_i, \sigma_{iU}^2 \mathbf{I}_{J_i}) \text{ where } \mathbf{I}_{J_i} \text{ denotes an identity matrix of dimension } J_i \quad (4)$$

$$\sigma_{iU}^2 \sim \mathcal{IG}(a_U, b_U). \quad (5)$$

(cf. Appendix ?? for justification of this and all following prior distributions). We used a Metropolis-Hastings step for sampling from the posterior distribution of  $\mathbf{X}_i$ , and used a

Gibbs sampling step for sampling from the posterior of  $\sigma_{iU}^2$ . We selected  $\mathcal{IG}(a_U = 3, b_U = 1)$  as the prior distribution for  $\sigma_{iU}^2$ , but limited the sampling range for the prior to be within a factor of 5 standard deviations of the prior distribution mean.

The following environmental covariates were modelled with error (1) total catch weight of groundfish haul, (2) haul weight of walleye pollock, (3) primary productivity, (4) sea surface temperature, and (5) wind. (Total catch weight and haul weight of walleye pollock were positively correlated ( $r = 0.85$ ), and therefore were not entered into the same model to protect analyses from matrix singularities.) We also considered (6) bathymetry (or on-shelf/off-shelf) and (7) time of day which were covariates that we assumed to be measured without error. We discuss the Bayesian priors for the lower level regression parameters,  $\beta_i$ , in the following section.

### 3.3. Population Parameter Model

The population model links the lower-level models for each fur seal. This is done by selecting a joint prior for the lower-level regression parameters,  $\beta$ , as the population model. It is natural to give the parameters of all 11 fur seals a common distribution, and develop this level of hierarchy that has the advantage of providing a single unified probability framework. We selected the multivariate normal distribution as a joint prior of the lower-level regression parameters:

$$\beta \sim \mathcal{MVN}(\mathbf{1}\mathbf{B}, \Sigma_\beta). \quad (6)$$

This shared prior distribution for  $\beta$  that links all the lower-level models and forms a higher-level multivariate normal likelihood as the population model. The following inverse Wishart ( $\mathcal{IW}$ ) and multivariate normal distributions were selected as hyper-prior distribution for the

variance and mean of the prior for  $\beta$ , i.e.,

$$\Sigma_\beta \sim \mathcal{IW}(\nu_0, \mathbf{V}_0) \quad (7)$$

$$\mathbf{B} | \Sigma_\beta \sim \mathcal{MVN}(\mathbf{B}_0, \frac{1}{a_0} \Sigma_\beta). \quad (8)$$

We chose a diffuse inverse Wishart prior distribution that had parameters  $\nu_0 = m + 3$  degrees of freedom (such that  $\nu_0 > m$ ), and scale matrix  $\mathbf{V}_0 = \nu_0 \times \mathcal{I}_m$  where  $\mathcal{I}_m$  denotes an identity matrix of dimension  $m$ ; i.e.  $\Sigma_\beta$  and  $\mathcal{I}$  are  $m$  by  $m$  matrices. We selected the multivariate normal distribution with mean  $\mathbf{B}_0 = \mathbf{0}$ , a vector of zeros of length  $m$ , and variance  $\frac{1}{a_0} \Sigma_\beta$ , where  $a_0 = 0.01$  to make the scale matrix diffuse. As the priors for both  $\mathbf{B}$  and  $\Sigma_\beta$  were conjugate to the higher-level  $\mathcal{MVN}$  likelihood, we sampled from these posteriors using a Gibbs sampling step.

By linking regression models via a shared prior, we acknowledge a different source of randomness, the variability in the population (Cressie et al. 2009) and can “borrow strength” between animals (Ntzoufras 2009). We can now think of the set of regression parameters specific to a single animal (e.g.  $\beta_i$ ) as a sample from a distribution of possible values (i.e. random coefficients), and the posterior of each unit-level  is then a weighted mean of the corresponding animal’s regression and the overall population effect.

### 3.4. MCMC Model Set-up

We have described the set up of a hierarchical multinomial Bayesian error-in-covariate model to describe the relationship between a fur seal’s behaviour and her environment, as described by matched covariates along a set of at-sea foraging tracks. By considering segments of track in which behaviour was consistent, and by matching each segment of track to one observation for each covariate,  we have averaged over both temporal and spatial autocorrelation, and the analysis is somewhat simplified. We use a hierarchical framework that includes a lower-level parameter model for each tagged northern fur seal and describes the uncertainty in the

relationship between each fur seal's behaviour and her at-sea environment, and then build a higher-level population model that describes the variability in the underlying process by assuming the set of tagged northern fur seals are a random sample from a population of similar animals nursing pups at Reef Rookery on St Paul Island in the Pribilof Islands. (Cressie et al. 2009). We implement an MCMC Metropolis-within-Gibbs sampling algorithm to sample from the joint state space of the model unknowns.

We ran the MCMC simulation for 1,000,000 iterations. We used the partial correlation coefficient to fix the decimation rate for the MCMC chain. We fit autoregressive models of successively higher-orders until the lag suggested non-significant partial correlations between chain components. Chains were thinned to every 50<sup>th</sup> iteration. We initialised the chains from three different starting points using different random seeds, but found posterior summary statistics were insensitive to initial conditions.

We visually assessed convergence by inspection of MCMC trace plots, as well, we calculated the Gelman-Rubin ( $\hat{R}$ ) as modified by Brooks and Gelman (1998; using R library “*coda*”) as a quantitative measure of convergence.

### 3.5. Model Comparison and Model adequacy

#### 3.5.1. Information-Theoretic Model Selection



Model comparison and selection is central to the scientific process by allowing different hypotheses to be evaluated about potential associations between variables (Pitt and Myung 2002). The best model from an *a priori* set of models and can be described as the one that explains the maximum level of detail in the simplest possible way (Burnham and Anderson 2002). *AIC* (Akaike 1973) estimates the relative information content of the models by trading off between the fit of the data to the model and the corresponding complexity of the model, and can be used in comparisons between non-nested models (Burnham and Anderson 2002). In hierarchical modelling, we cannot uniquely define a ‘likelihood’ or ‘model

complexity' without specifying the level of the hierarchy that is the focus of the modelling exercise (Gelfand and Trevisani 2002), i.e. inference at the population or at the individual level. Since we were interested in understanding fur seal behaviour in general and not simply the behaviour (or prediction of the behaviour) of the sampled fur seals, inference around population parameters is the focus and marginal-likelihood methods such as *AIC* are appropriate.

We report the posterior mean deviance  $\overline{D(\Theta)}$  as a Bayesian measure of fit or "adequacy" (Dempster 1974, Spiegelhalter et al. 2002),  $m_{DIC}$  as a diagnostic of leverage (Spiegelhalter et al. 2002), as well as *AIC*. These provide useful comparisons between candidate models, but do not provide insight into model adequacy.

### 3.5.2. Model Adequacy: Goodness of Fit and Posterior Predictive Checks

We examined model adequacy through a series of distributional summaries. We compared posterior predictive distributions of replicated data under the model with the observed data (Rubin 1984; Gelman et al. 2004 p.175). If the model accurately represents the process that generated the data, then replicated data generated under the model should look similar to the observed data (Brooks and Gelman 1998). An evaluation of closeness can be carried out using some summary function of discrepancy,  $d(\mathbf{y}, \Theta)$ , with assessment of the overall goodness of fit using posterior predictive *p*-values (Meng 1994, Carlin and Louis 2000). The proportion of times the summary function of discrepancy,  $d(\mathbf{y}_{rep}, \Theta)$ , is less or equal to  $d(\mathbf{y}, \Theta)$  is then recorded across iterations of the MCMC sampler, and used as a test of the model's capacity to reproduce the observed data.

Due to uncertain large sample properties of posterior predictive *p*-values (for example, see discussion in Bayarri and Berger 2000), we assume that a *p*-value around 0.5 indicates that the distributions of the replicated and actual data are close, while a value close to zero or one indicates strong differences between them (Gelman et al. 2004).

### 3.6. Simulation to investigate implications of sample size

We constructed a simulation study using the Kullback-Leibler (*KL*) divergence statistic to examine the effect of sample size on model inference. The *KL* divergence has been widely studied in statistical literature as a central index measuring qualitative similarity, or relative entropy, between two probability distributions, and is popular because it uses a likelihood ratio approach (Lee and Park 2006). We took 200 samples from the posterior distribution of the population-level models to use in generating 200 replicate datasets from each sample's posterior prediction. We then refit each of the 200 datasets using the MCMC model from which the data were generated. Posteriors of these replicate simulated datasets were gathered after burn-in, from a 10,000 long chain thinned to every 5<sup>th</sup> iteration. The *KL* divergence for each of the original model's 12 population parameter posteriors  $\mathbf{B}$  and the 200 simulated datasets and each of these model's parameter's posteriors were then calculated using R library “*FlexMix*” (Leisch 2004).

## 4. RESULTS

Ten of the eighteen lactating females captured at Reef Rookery yielded complete data sets from which the foraging paths and behaviour information could be retrieved. One of these animals provided data from two complete foraging trips giving us 11 complete foraging tracks. The remaining eight animals had only partial data records with lost data due to a number of tag failures including water entering the housing, the speed paddle breaking off, fish vertebrae lodged between the speed paddle and housing, and battery failure. We present the results of the behaviour analysis of the 11 complete northern fur seal foraging tracks from Reef Rookery on St. Paul Island during the pupping seasons of 2005 and 2006. Foraging trips ranged in length from 5.5 days to 11.2 days, with a median of 7 days spent at sea. There were an average of 40 AMGOS fixes, and 404,400 archival data records per trip.

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[Table 1 about here.]

Figure (3) depicts the foraging track reconstructions highlighting the locations of these 11 foraging tracks in the Bering Sea. The fur seals traveled an average maximum linear distance from St. Paul Island of 279 km, with a maximum distance away of 391 km. Five animals stayed on the continental shelf, one animal moved along the shelf break foraging in the canyons, and 5 animals went across the shelf break into the deep water of the central Bering Sea. The one animal for which we had 2 successive trips (Tracks 5.1, 5.2) went to a similarly located feeding area off-shelf in both foraging trips. In general, these fur seals covered a wide area of both on-shelf and deep, off-shelf waters in the Bering Sea and showed no preference for foraging in any single area.

Fur seals spent 35% of the time at sea engaged in either active (14%) or exploratory dives (21%). Fur seals spent 65% of time at the surface engaged in non-diving behaviours. The 11 foraging trips had a median of 41 segments in different behaviour modes, with those animals with longer foraging trips exhibiting more behaviour changes. Figure (8) plots the distribution of segment lengths of track. This figure shows that for all 421 behaviour segments observed across all animals, the most commonly observed segment length was < 1 hour, but this was by far the most frequent time length for active diving segments (44%), whereas exploratory diving and non-diving segments were comparatively less likely to be < 1 hour (26.5% and 15.1% respectively).

A three-dimensional reconstruction of one at-sea foraging route (Track 3) is presented in Figure (7) in which behaviours are identified by changes in colour.

[Figure 8 about here.]

[Figure 9 about here.]

#### 4.1. Model selection

We fit all main effect models with covariates described in Section (2.4). The strongest univariate predictor of behaviour was time of day (*Time*; Table 2), but behaviour was also found to be related to total (logged) haul size of all catch (*Total Catch*) and (logged) haul weight of walleye pollock (*Pollock*). We found behaviour unrelated to bathymetry, primary productivity, sea surface temperature or wind.

We then fit a series of models that all included time of day (*Time*) and one by one (additive) inclusion of the remaining covariates. Models fit with *Pollock* and *Total Catch* and bathymetry (*On/Off Shelf*) were the best subset by the model selection criteria presented earlier. *Total Catch* was related to behaviour (significant Bayesian *p*-value), but bathymetry was unrelated (Table 2). We found that the three depth categories described by Call et al. (2008) were not an improvement over the simplified depth categories (on *vs.* off-shelf) and are not discussed further.

We next fit a set of models with *Time*, another main effect, and a *Time*  $\times$  *main effect* interaction. The two models with time interacting with a measure of groundfish catch had the best fit diagnostics (*Pollock*, *Total Catch*; Table 2).

The model that included time of day and primary productivity failed the posterior predictive test, suggesting the model didn't fit the data well, despite having adequate higher-order parameter convergence in their respective MCMC's (i.e.  $\hat{R} \approx 1$ ). We failed to get satisfactory convergence ( $\hat{R} \gg 1$ ) with covariates sea surface temperature and wind, and these results are omitted from Table (2).

One additional step of model complexity was considered. We fit a three covariate model based on the best time-interaction model, and bathymetry (*Time*  $\times$  *Pollock* + *On/Off Shelf*). This model was penalized aggressively, suggesting the additional complexity was not warranted despite a fair goodness of fit to the data. Table (2) reports a subset of the results from the model fitting.

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[Table 2 about here.]

We considered a small subset of models for comparison of model fit with and without including measurement error in the covariates. In Table (3) and Figure (10), we see that the effect of including the measurement error in the model is to shrink the regression parameters towards zero, and to increase the uncertainty around the estimates of those parameters. Table (3) compares the model fit diagnostics, information criteria and posterior predictive checks both with and without error-in-covariates. By including the uncertainty in the measurement of haul size of pollock, the model fits significantly better.

[Table 3 about here.]

Our final selected model (*Time*  $\times$  *Pollock* with error in covariates) suggests that female at-sea behavior was influenced by time of day, and (logged) haul size of walleye pollock. *Time*  $\times$  *Total Catch* was a similarly good model with only marginally poorer criteria based on *AIC*, with similar model adequacy measures ( $\overline{D(\beta)}$ ), but a larger number of parameters estimated as implied by comparison of  $m_{DIC}$ . Coefficient magnitudes, and signs were similar for both models. Figure (10) and Table (4) depict the 95% credible intervals for each of the population parameters, and shows significance for the main effect of time of day, and for the interaction of time of day and haul size of pollock.

[Figure 10 about here.]

[Table 4 about here.]

[Figure 11 about here.]

#### 4.1.1. *Time* $\times$ *Pollock*

Figure (11) shows one daily cycle of behaviour in response to changes in time of day and commercial haul size of walleye pollock. This figure highlights the increase in relative

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probability of engaging in active dive behaviours in response to increasing weights of pollock catch. This is accompanied by a near-zero probability of non-dive behaviours during those times of active diving in high catch areas. One caution in the interpretation of this figure is that our model does not predict the length of time that the northern fur seals engage in particular behaviours, but rather predicts the probability of a behaviour beginning at various times of the day.

The interpretation of the regression coefficients that correspond to time of day are from Equation (1). This translation of time is a 1<sup>st</sup>-order Fourier expansion, which limits the functional form to a sinusoidal curve with a period of 24 hours. Within this restriction, the model suggests the peak in the start of exploratory dive behaviours is around noon. It suggests fur seals are most likely to begin active diving behaviours at just past 8:00 in the evening, and most likely to end diving and begin non-diving behaviours around 5:00 in the morning. Comparing results for a haul size of 10  $t$  vs. 0.5  $t$  suggests there is a higher probability of starting active dive behaviours sooner in the evening, and hence a lower (near-zero) probability of non-dive behaviours at that time.

## 4.2. Convergence and Sensitivity

The length of chain (1,000,000 samples) and the rate of decimation (every 50<sup>th</sup> sample was selected to ensure full sampling of the posterior. However, for a subset of covariate models we were unable to obtain satisfactory convergence (e.g. models containing covariates the following covariates: sea surface temperature and wind; these results were omitted from Table 2).

For the model with the best fit diagnostics (Time x Pollock), some of the fur seals did not have enough information in the covariates to identify both the latent unobserved covariate  $\mathbf{X}_i$  and the estimate of measurement error,  $\sigma_{iU}^2$ . We experimented widely with different parameter values for the prior for  $\sigma_{iU}^2$ , and found that this prior not only affected

convergence but also informed the location of posteriors for higher level parameters. The more restrictive the prior we put on the variance of the covariate error, the greater the coefficient effect and the poorer the model fit ( $AIC$  was larger). For example, a variance of zero implies a model without measurement error in the covariates, and the effect of including the error in the covariate measure is that this pulls the magnitude of the associated parameter estimate towards zero, as well as increasing the uncertainty around that estimate. In our implementation, to allow for identification in those tracks with weakly identifiable for  $\sigma_{iU}$  and  $\mathbf{X}_i$ , we opted to reject any posterior samples of  $\sigma_{iU}$  that were greater than 5 standard deviations from the expected value of the prior distribution. Since the selected prior distribution was diffuse, this was not a restrictive condition except for two fur seal tracks, Tracks 1 and 10.2. As the priors for each  $\sigma_{iU}^2$  are independent priors, this restriction on the magnitude of the measurement error will not directly affect the measurement error estimates of the other fur seal's data. In other applications, careful examination of the prior specification may impose enough constraint to allow for identification, without restricting variance components.

#### 4.3. Kullback-Leibler (KL) divergence and sample size

Central to the Bayesian paradigm is the notion that as the data quantity and quality increase, the posterior is less sensitive to prior assumptions (Cressie et al. 2009). The results in Figure (12) summarizing the  $KL$  divergence simulation described in Section (3.6) show there is an important gain in model performance as the number of tagged fur seals approaches 30, after which the  $KL$  divergence becomes a relatively flat function. These results therefore suggest that having data collected from  $\sim 30$  tagged northern fur seals would provide dependable posterior predictive inference, and that our sample size is too small for the data to assume such a dominant role in the assessment of how these spatial at-sea covariates affect northern fur seal behaviour (as one might suspect with only eleven tracks).

[Figure 12 about here.]

## 5. DISCUSSION



The hierarchical Bayesian framework used in this analysis has permitted us to significantly relate dive behaviours to the temporal and spatial fields through which lactating northern fur seals must forage in the eastern Bering Sea. We have established relationships between three distinct dive behaviours observed in lactating northern fur seals to the time of day and measures of walleye pollock abundance around St. Paul Island, Alaska. Our analysis has shown that the interaction of time and prey abundance provides interesting insights into the organization of dive behaviours around a 24 hour, diel pattern.

### *5.0.1. Northern Fur Seals exhibit a broad foraging range*

Our data were collected during the summer pupping seasons when female northern fur seals are nourishing pups and tied to a central place. This limits their effective foraging range in both time spent away, and distance traveled from the natal rookery of their dependent pup. Female northern fur seals in this study embarked on relatively long pelagic journeys averaging 279 km in linear distance from the rookery, and lasting from 5.5 to 11.2 days. This number is consistent but slightly longer than the linear distances reported in Nordstrom et al. 2013 (228 km) and Goebel et al. 1991 (200 km), and the length of time of the foraging trip is consistent with reported lengths from other studies (e.g. Gentry and Holt 1986, Nordstrom et al. 2013; from 1 to 14 days). Predictable food is thought to drive seasonal movements because pup survival depends on the amount of food available to parents for building body reserves prior to provisioning their offspring. Therefore within a broad range of a central place, foraging habitat is selected in which they must get energy to feed themselves and their pup while still returning to the rookery in time to feed a waiting pup.

All of the fur seals showed directional movement, but the foraging tracks of our tagged females were unconstrained and at the broadest scale did not appear collectively to prefer any one region around St. Paul Island. Individuals may, however, have such preferences. The one female for which we had two consecutive tracks went to a similarly located feeding area off-shelf in both foraging trips. Call et al. (2008) similarly showed that 27 of 36 female fur seals with repeated recorded trips tended to travel to the same type of site following the same general direction they used in each of their previous trips. This implies that fur seals know where they are going, and suggests they may adopt a strategy of returning to the same places as used previously to forage for as long as this strategy is successful. However, none of our tracks, or those recorded by other researchers, showed consensus among the fur seals about where to feed, as none of the tracks showed fur seals traveling to a single location before swimming directly back to nurse their pups. Rather the 3-dimensional dive profiles (e.g. Figure 7) and horizontal behaviour maps (e.g. Figure 9) showed consistent changes in diving behaviours throughout the at-sea foraging trips with active and exploratory dive behaviours distributed over much of the paths they swam. In other words, there was no single grocery store or hot spot where the fur seals spent concentrated time. In other studies, northern fur seals from Reef Rookery have been found to use all hydrographic domains around St. Paul Island (eg. Robson et al. 2004), including both on-shelf and off-shelf habitats (Loughlin et al. 1987, Goebel et al. 1991, Sterling and Ream 2004, Call et al. 2008), and scat samples from the same rookery contained both on-shelf (e.g. walleye pollock, Pacific herring) and off-shelf species (e.g. myctophids; Zeppelin and Orr 2010). The lactating fur seals in this study also appear to be constantly on the move, actively feeding and exploring the ocean as they traveled through broad regions of the Bering Sea.

### 5.0.2. Persistence



We do not know what the animals we tracked were seeking or what they caught during their foraging trips. However, juvenile walleye pollock of year-classes 0 to 5 are the most common prey in both stomach and scat diet studies (Perez and Bigg 1986, Sinclair et al. 1994, Sinclair et al. 1996, Gudmundson et al. 2006, Zeppelin and Ream 2006), and walleye pollock comprised 89.3% of fur seal diet measured in scats collected within a month of our 2006 tagged females foraging trips from Reef Rookery (Zeppelin and Orr 2010). We found that in at-sea locations with more abundant walleye pollock, northern fur seals were more likely to be actively diving, particularly if those locations overlapped with the nighttime. It is unlikely that our source for the horizontal distribution and abundance of walleye pollock, which was the US Department of Commerce domestic observer data of the Alaska groundfish industry aggregated over both time and space, is directly measuring the real-time abundance of prey that the fur seals actually encountered along their foraging route at any single location. It is more likely that our measure of walleye pollock abundance represents a persistent horizontal feature that is attractive to foraging northern fur seals, but not a very accurate measure of prey availability. Likewise, Nordstrom et al. (2013) linked foraging of northern fur seals to oceanic surface fronts (eddies and filaments) and Kuhn (2011) to thermocline depth; features that may also be proxies for the horizontal and vertical distribution of prey species. Hence, available evidence indicates that fur seals forage more heavily in areas where either commercial catch data (this study) or oceanographic conditions (Kuhn 2011, Nordstrom et al. 2013) point to increased prey abundance. As well, individuals tend to return to the same general area on successive foraging trips, from where they have no trouble finding the way back to the rookery. Hence, they certainly navigate successfully over hundreds of kilometres in the Bering Sea. Yet little is known to date about the extent to which they can identify potentially persistent foraging “hot-spots” in advance.

### 5.0.3. Competition with Fisheries

In this study we did not include any direct measure of the bycatch of juvenile pollock in the commercial fishery, nor did we have any small scale evidence that commercial boats were fishing at the same time and location as our tagged females, thus we cannot draw conclusions about the potential for competition occurring between the commercial fishery and northern fur seals. However, we can say that being in the same area where fishing occurred would not necessarily imply competitive interactions unless it was known that the fur seals were feeding on the same fish targeted by the fishery, and whether the abundance of that target prey was limited. Evidence suggests that juvenile pollock of year-class 0 to 5 are preferred by foraging fur seals (Gudmundson et al. 2006, Zeppelin and Ream 2006), which are typically smaller than the > 40 cm adults taken by the commercial fishery (Ianelli et al. 2007). However, inter-year variability of pollock can be as high as two orders of magnitude (1.7 t/km<sup>2</sup> in 2004, 328 t/km<sup>2</sup> in 2007 for the same region; Sigler et al. 2012). In anomalous years with poor juvenile survival combined with poor persistence of the available prey, it could be difficult for foraging females to find prey.

### 5.0.4. Dive types

Our analysis is built upon the numerical properties of an AR-2 movement model to describe dives in terms of foraging behaviour rather than focusing on the depth at which the dives were, or the tortuosity of the at-sea path. The AR-2 process provides a mechanistic way of categorizing dive types, that is based around interpretable movement signatures, and therefore is exempt from arbitrary classification such as those distinguishing dive types based on depth (e.g. Gentry et al. 1986, Goebel 2002). Furthermore, the mechanistic approach protects us from limitations of other studies where deeper dives associated with foraging at or near the bottom were observed when fur seals were moving in straight lines and not

identified as the typical tortuous paths of foraging regions (eg. Nordstrom et al. 2013, Benoit-Bird 2013a, Benoit-Bird 2013b).

Each of the three behavioural modes described by dive types has an intuitive movement interpretation. Shallow, repeated dives with short surface-time intervals, as well as deeper, repeated *U*-shaped dives with comparatively longer surface recovery times are well described by the solutions of a periodic AR-2 process. *U*-shaped dives have been attributed to foraging behaviours in an array of top marine predators such as gray seals (Austin et al. 2006), southern elephant seals (Gallon et al. 2013), Australian fur seals (Arnould and Hindell 2001), harbour seals (Baechler et al. 2002), Gentoo Penguins (Wilson et al. 1996), and others. When the surface time between dives is longer but the vertical profile of the dive is more *V*-shaped, the solutions reflect a correlated random walk without a periodic component. It is less clear what the underlying motivation for intermittent *V*-shaped dives is, but others have attributed them to foraging on larger pelagic fish or squid in northern gannets (Garthe et al. 2000), or non-foraging activities, including predator avoidance, and explorations (Bengston and Stewart 1992). Non-diving and non-foraging behaviours such as resting, sleeping, grooming and surface transiting are described in the solution space as uncorrelated white noise.

### 5.0.5. Diel pattern

Modeling results depicted in Figure (11) highlight the strength of the diel pattern in foraging northern fur seals, and that the dive pattern the female engages in is that which best fits her prey environment. For example, we found that females showed strong preferences for active diving at night, while preferring non-dive behaviours such as resting or transiting in the mornings. Afternoons were typically associated with exploratory *V*-shaped dive behaviours. The model suggests that nighttime is characterized by repetitive dives of active feeding (or an AR-2 periodic solution). Kuhn et al. (2010) proposed that shallow foraging bouts at night may be related to juvenile walleye pollock's nighttime migrations to the surface as they follow

vertically migrating zooplankton.

It should be energetically advantageous to the northern fur seal to be able to catch prey at shallower depths, resulting in a shorter chase, and possibly also allowing the fur seal to keep physical contact with the school of prey. Northern fur seals may therefore prefer epipelagic (shallow) diving, and only transition into deeper *U*-shaped foraging dives when epipelagic resources in an area are scarce. For example, deeper foraging behaviour has been associated with fur seals targeting concentrated groups of juvenile pollock at the thermocline (Kuhn 2011, Nordstrom et al. 2013). If northern fur seals are spatially aware of broad-scale suitable feeding areas based on prior experience or some other knowledge, then it is possible they could reduce search time and energetic costs of foraging by anticipating changes in broad scale prey density and positioning themselves strategically at optimal foraging locations come nightfall.

#### *5.0.6. Data requirements*

These eleven fur seal foraging trips generated some useful, basic insight into at-sea behavioural patterns across time and space. The Kullback-Leibler values of Figure (12) suggest that another 10 to 20 tracks would have generated useful further precision. We also anticipate that other oceanographic information on, for example, frontal eddies and filament locations, could provide valuable further insight into the association between fur seals and the Bering Sea environment. Within the hierarchical structure, it would be interesting to link the foraging behaviour characteristics of the maternal fur seal to her pup weight gains, as well as residency times and other life history characteristics that would contribute to our understanding of pup survival.

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## 6. CONCLUSIONS

Our analysis did not attempt to answer the question of where in the ocean did the fur seals chose to forage relative to not forage. With only 11 tracks over an area with a radius of  $> 200 \text{ km}$  (or area  $> 125,000 \text{ km}^2$ ), this would have been too ambitious. Instead we answer the conditional question, “Given that the fur seal swam through this location, can we predict its most likely behaviour based on a set of local environmental variables”. Using a hierarchical Bayesian approach, we were able to link together northern fur seals that went to disparate regions of the eastern Bering Sea, with widely variable information about their underlying environmental fields into a single model that informed us about the expected behaviour of a population of maternal, female northern fur seals at Reef Rookery on St. Paul Island. Our analysis has focussed on three typical fur seal behaviours, and how these behaviours are associated with time of day, and a set of environmental data. The approach and analysis presented here is to use hierarchical Bayesian modelling to bring together coarse estimates of the at-sea environment, and the dynamics of fur seal behaviour through identification of variable-length segments of coherent behaviours. In this, we have successfully shown that northern fur seal behaviour actively forage more at night, and in areas where their preferred prey species, juvenile walleye pollock, appears to be more abundant.

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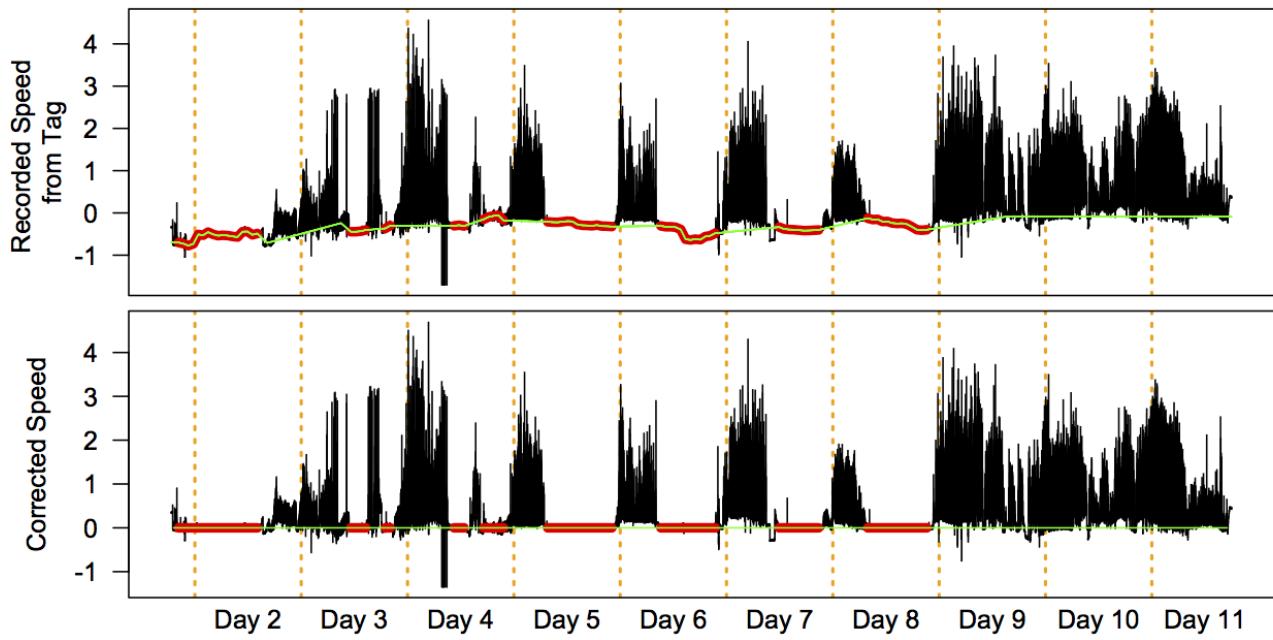
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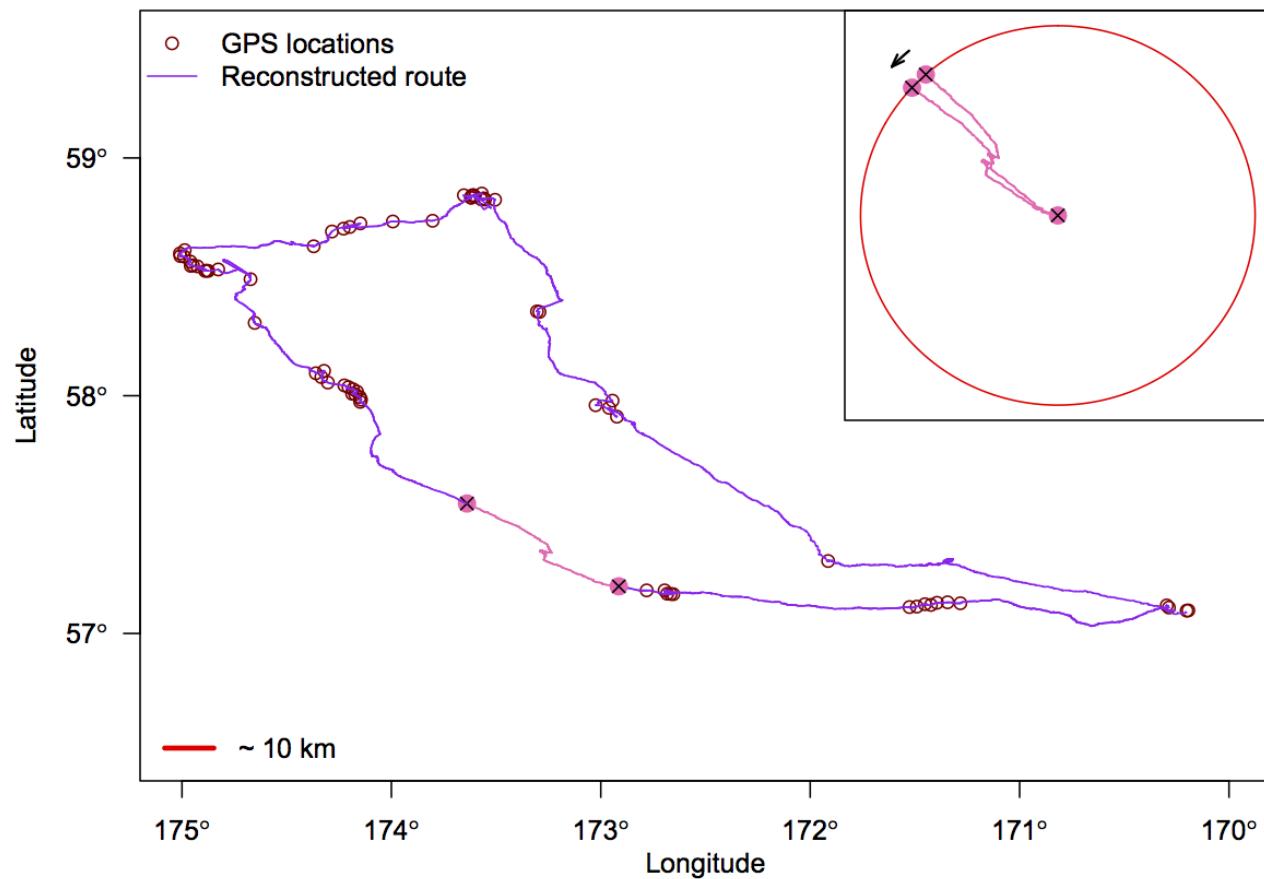
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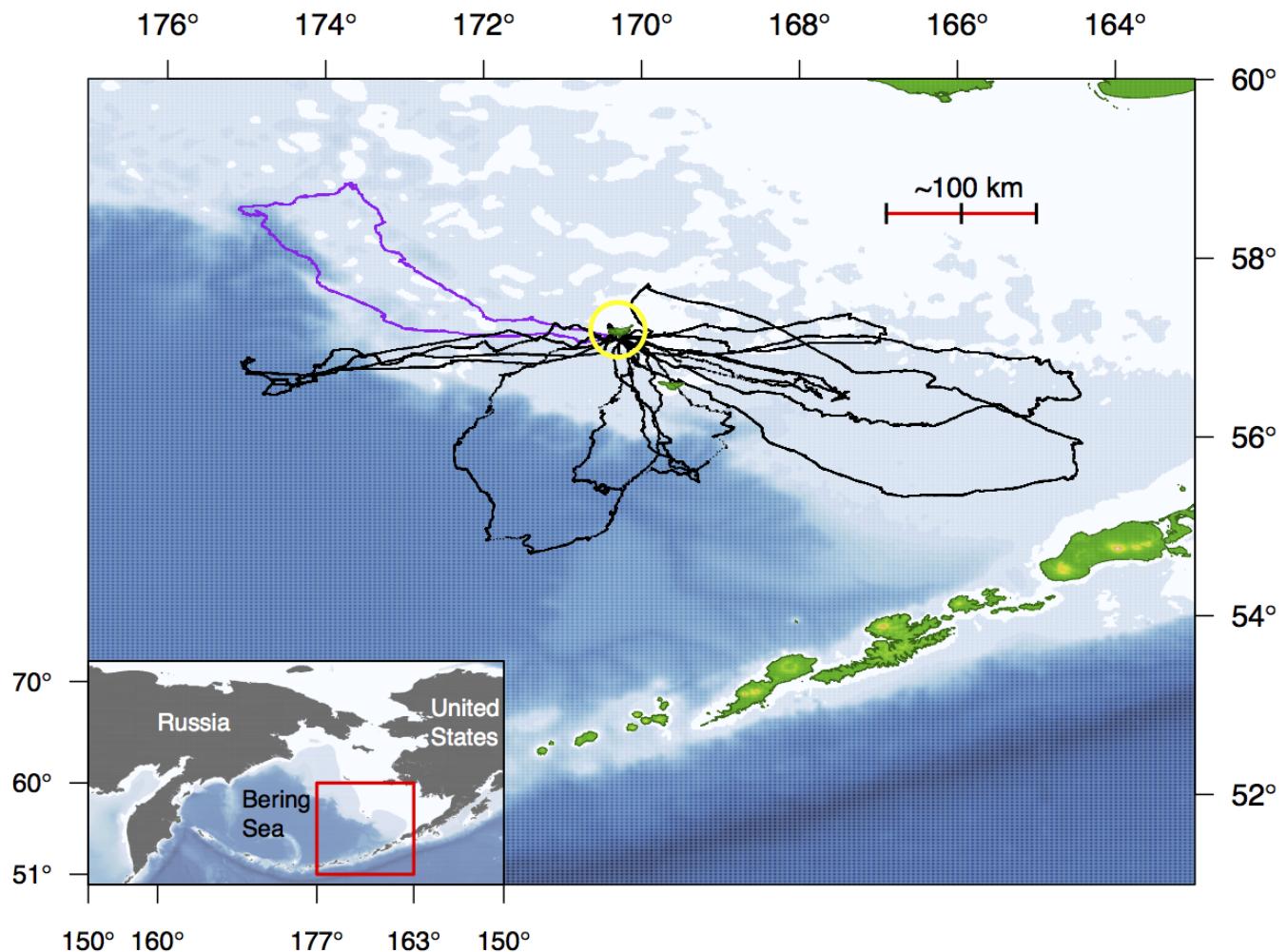
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**Figure 1.** The entire raw data record for 1 female northern fur seal from the dead-reckoner's *speed-through-the-water* channel, before and after the data series is corrected for drift from zero speed. Speed is measured as speed through the water, and not over the ocean bottom, and is a tentative, approximate measure until an updated, satellite-based location can be obtained along the track. Changes in day (at midnight) are represented in this figure by the dashed vertical lines. Length of data series depicted here is 482,400 elements, and we refer to this track in the text as "Track 3".



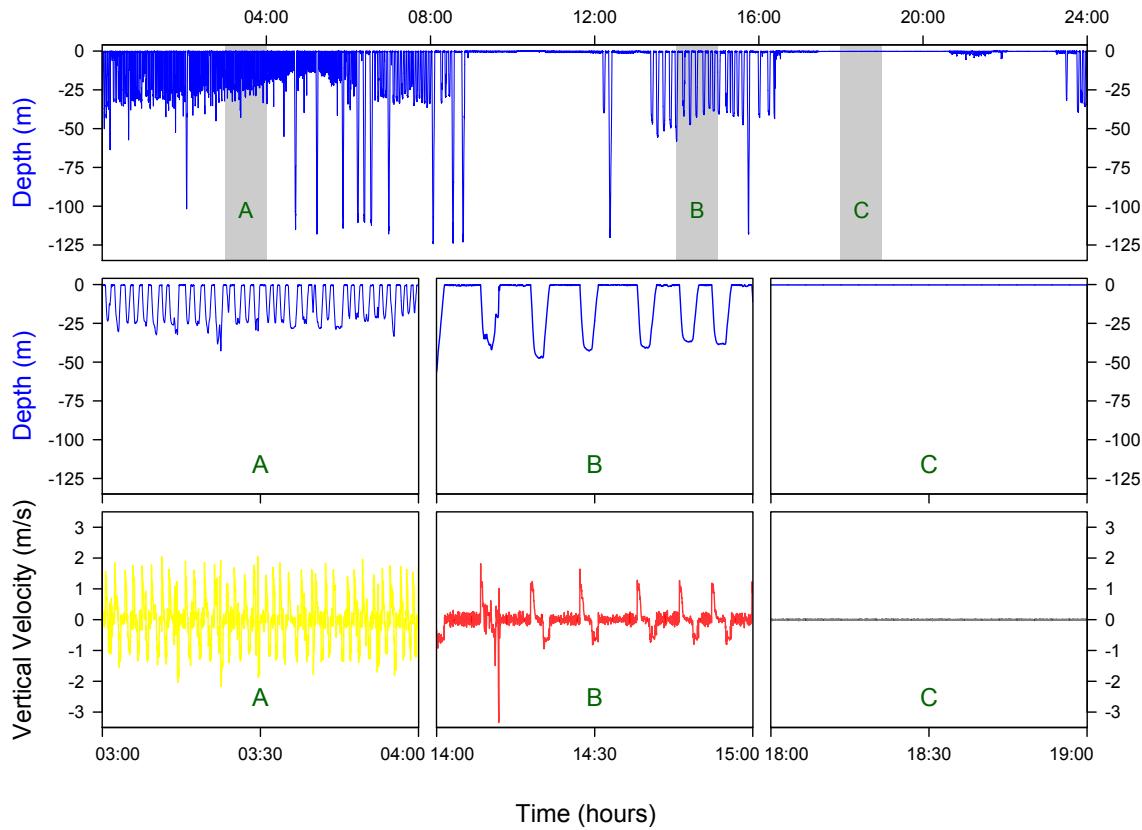
**Figure 2.** A two-dimensional reconstruction of the at-sea track called “Track 3”. Constructing the best estimate of the actually track (shown as a purple line) requires connecting the high resolution archival location with the sparsely located Argos satellite locations (shown as open circles). Inset figure represents an example of the rotation step required in processing the raw dead-reckoner location data between 2 ARGOS GPS satellite locations, thus correcting for oceanic drift from currents, and other accumulated error in the dead-reckoning between GPS fixes. The section of track in the inset figure is shown in the larger figure as a *pink* portion along the out-going track. Reef Rookery on St. Paul Island is the right-hand-most location in the figure.



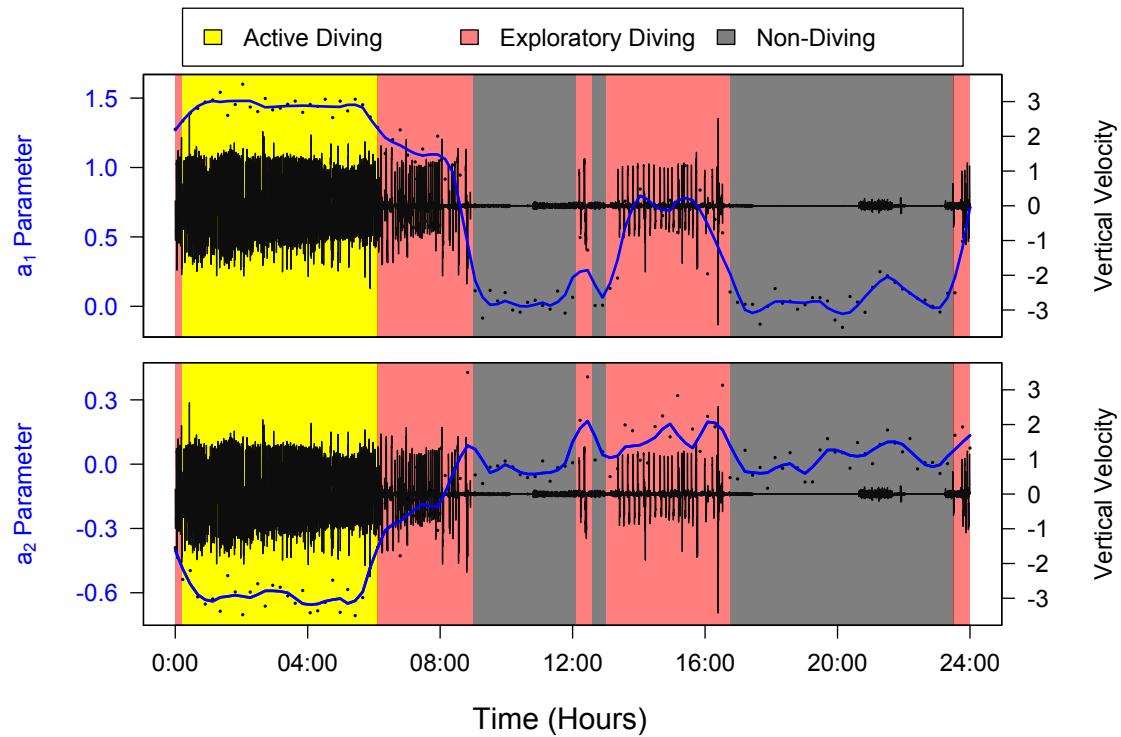
**Figure 3.** Eleven at-sea foraging tracks of lactating female northern fur seals tagged at Reef Rookery on St. Paul Island, in the Pribilof Islands in the Bering Sea, Alaska, USA. St. Paul Island is circled in yellow. The seal represented in Figure 2 is coloured in purple for reference. Darker shades of blue indicate deeper ocean bathymetry, in particular the transition from light blue to dark found west of St. Paul Island indicates the location of the continental shelf break (also refer to Figure ?? in the introduction).



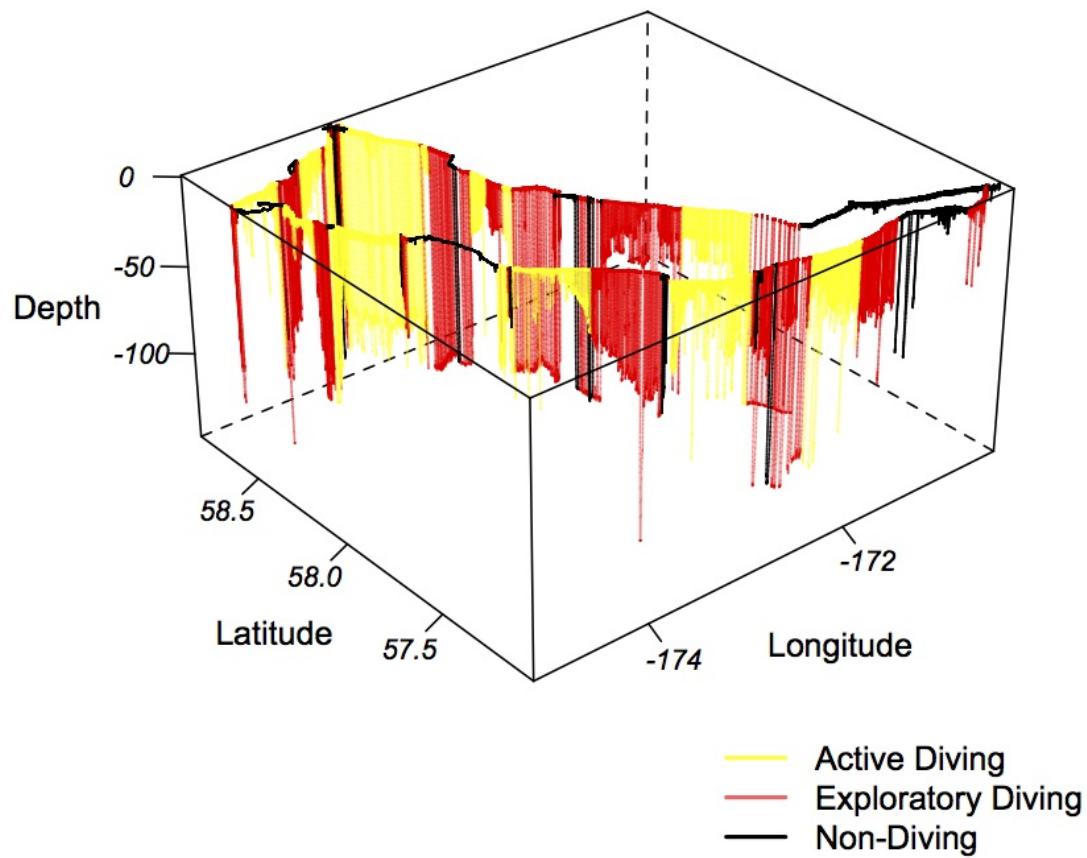
**Figure 4.** Parameter plane for the solution space of a set of movement parameters  $a_1$  and  $a_2$  that solve a set of stationary AR(2) difference equations.



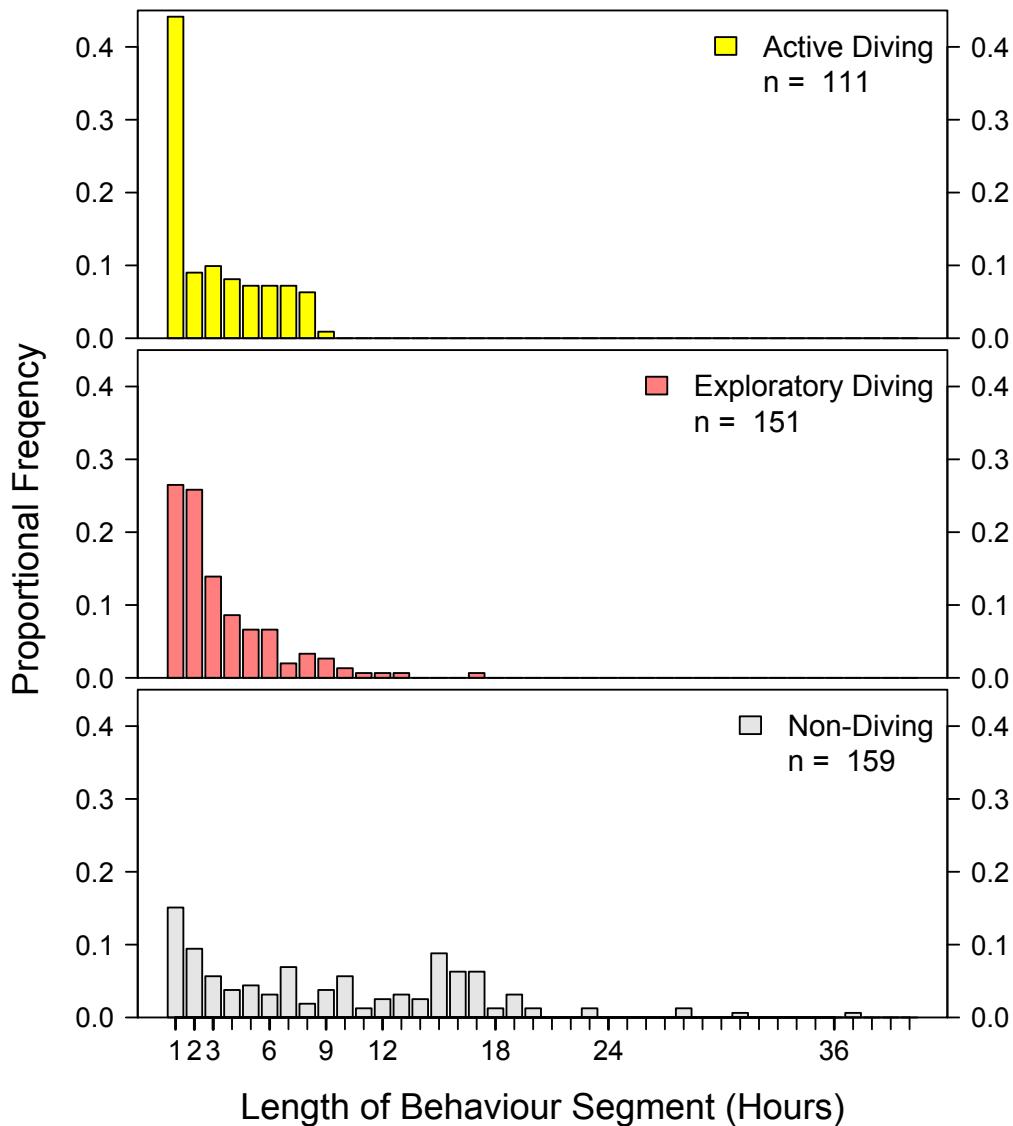
**Figure 5.** Observed time series taken from an archival tag for “Track 3” showing depth and derived vertical velocity of dives over a 24 hour period on August 18<sup>th</sup>, 2006. Upper and middle panels show depth (in blue). The three lower figures shown in yellow, red and black, represent the vertical speed variable derived from the depth channel. These lower panels highlights three 1-hour periods stretched out accordion-style to better see the features of this high density data series and show the three northern fur seal behaviours identified in our models. Region A corresponds to a section of “active diving”; Region B corresponds to a section of “exploratory diving”; Region C corresponds to an area of “non-diving”. This data section is linked to Figures (??), (??), (??) and (??) in Chapter (??).



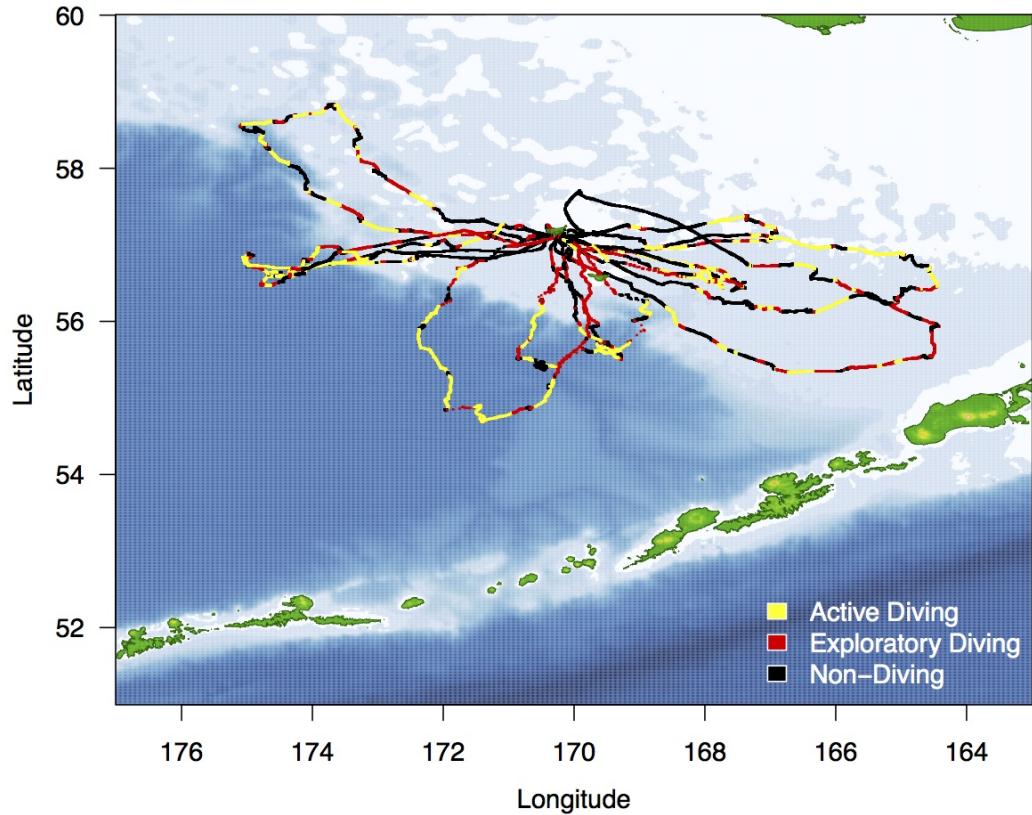
**Figure 6.** Time series for Track 3 of the smoothed movement parameters (blue line) overlaid with the original data series of vertical velocity (black lines) for a single day. These coloured blocks correspond to regions in the parameter plane for the solution space of a set of AR-2 difference equations, and regions of minimal system noise variance. The block coloured *yellow* corresponds to a region of “*active diving*”, the block coloured *pink* corresponds to an area of “*exploratory diving*”, the block coloured *grey* corresponds to an area of “*non-diving*”. Recall Figure (4) depicting the phase plane. See also Figure ?? for the associated plots of the series’ system noise and observation error variances, and Figure (5) for the original data series for this same day, August 18<sup>th</sup>, 2006.



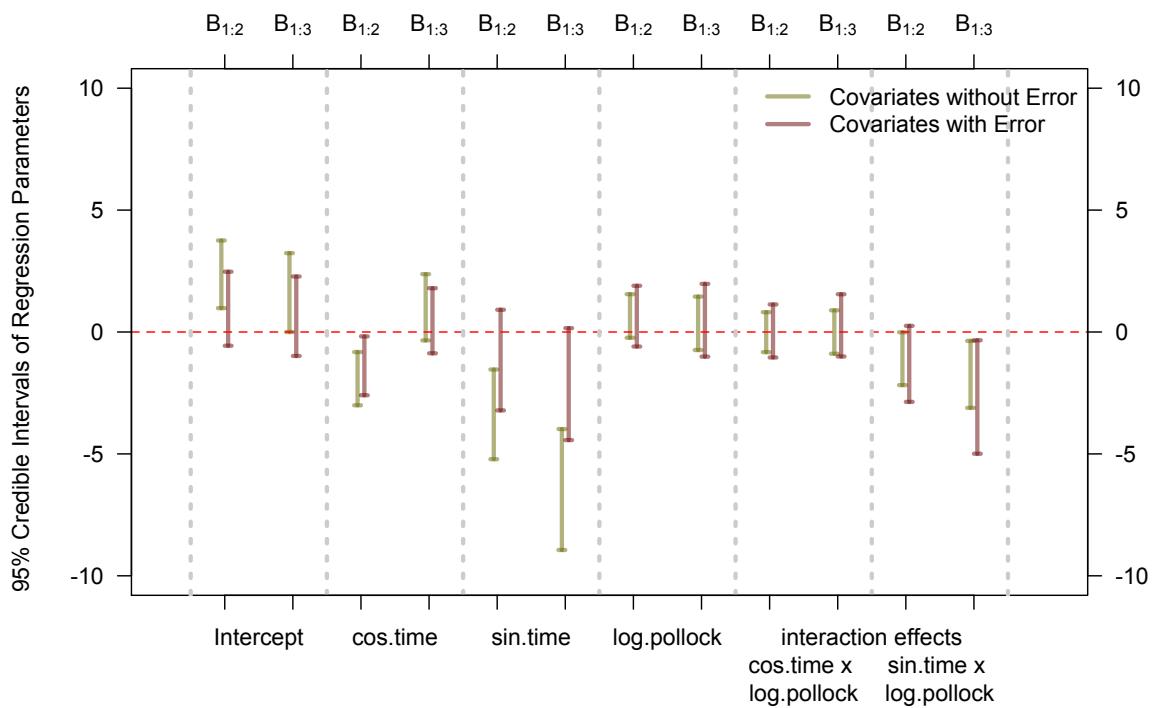
**Figure 7.** Three-dimensional reconstruction of a single northern fur seal's 11.2 day at-sea foraging track with assigned behaviour overlaid in space and time. This track corresponds to the same track (Track 3) pictured in Figures 1 – 6. Reef Rookery (start/end point) is located at the far right of this figure, the fur seal swims closer to the viewer on the way out, and returns to the rookery farther from the viewer, by way of a long transiting section.



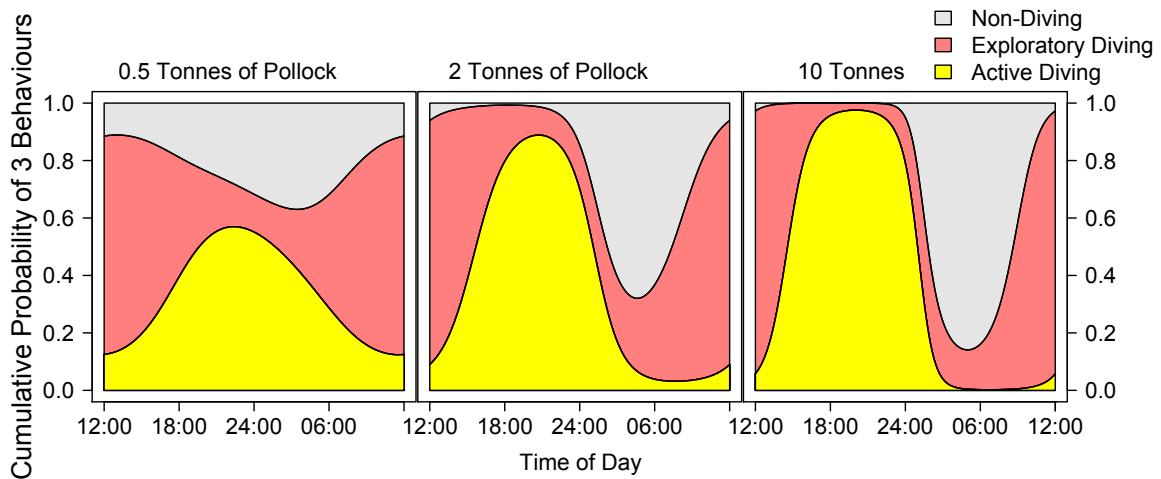
**Figure 8.** Length distribution of 421 behavioural segments measured from 11 at-sea foraging tracks of female northern fur seals. Each panel shows the distribution of one of the three behaviour states: *active diving*, *exploratory diving* and *non-diving*, where each bar represents the relative frequency of observed segments of lengths up to that hourly measure. For example, the first bar labeled “1” represents the frequency distribution of segments between 0 and 1 hour long, the second bar labeled “2” represents the frequency distribution of segments between 1 and 2 hours long, etc.



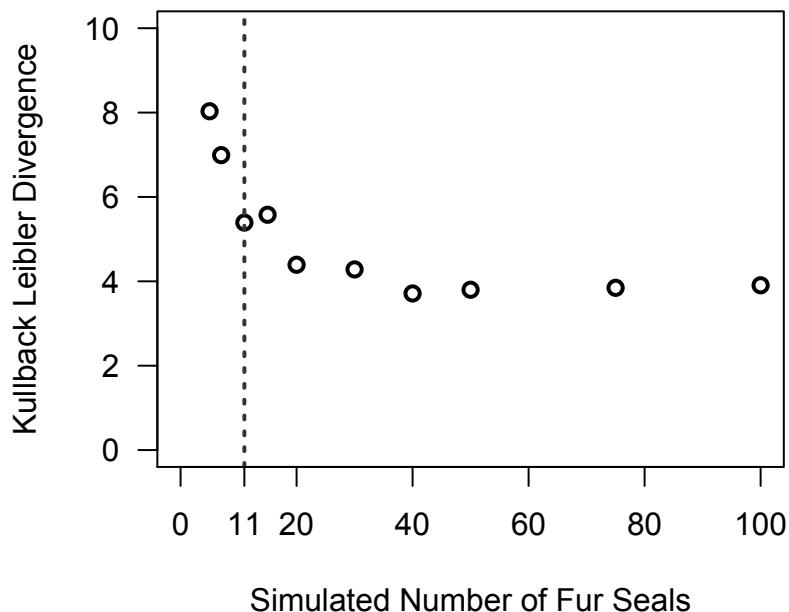
**Figure 9.** Identified behaviours of northern fur seal overlaid on eleven at-sea foraging tracks of lactating female northern fur seals from St. Paul Island, Alaska.



**Figure 10.** 95% credible intervals for twelve regression parameters  $\mathbf{B}$  from the population level model that includes *time of day* and (logged) haul size of *pollock* (*Time*  $\times$  *Pollock*) measured without error and with error. Each pair of  $\mathbf{B}$  coefficients show the credible intervals of the population-level parameters linking northern fur seal behaviour to at-sea habitat.  $B_{1:2}$  denotes the regression parameters corresponding to the logit response  $\log(p_{ij}^{(2)}/p_{ij}^{(1)})$ , or the log odds of exploratory diving vs. baseline non-diving.  $B_{1:3}$  denotes the regression parameters corresponding to the logit response  $\log(p_{ij}^{(3)}/p_{ij}^{(1)})$ , or log odds of active diving vs. baseline non-diving).



**Figure 11.** Stacked probabilities of behaviour modes *Active Diving*, *Exploratory Diving*, and *Non-Diving* in response to time of day and increasing commercial catch size of walleye pollock. The left panel of graph shows the predicted relative probabilities of behaviours in areas of small-sized walleye pollock hauls (0.5 tonnes), the middle panel shows predicted relative probabilities of behaviours in areas of medium-sized hauls (2 tonnes), and the right panel shows predicted relative probabilities of behaviour in areas of larger-sized hauls of pollock (10 tonnes). Note that the  $x$ -axis depicts time of day where the axis starts and finishes at noon to highlight the maximum amplitude of active foraging (in yellow) that happens at night.



**Figure 12.** Effect of increasing sample size on Kullback-Leibler ( $KL$ ) divergence for one selected population-level parameter  $B_{12}$ . A  $KL$  divergence is 0 if and only if the posterior distribution for a simulated dataset is identical to the model from which it was generated. The dashed vertical line at 11 corresponds to the sample size for this study.

**Table 1.** Summary of archival (data-logger) and Argos GPS tag data collected during 11 northern fur seal at-sea foraging tracks through the Bering Sea. Fur seals were tagged at Reef Rookery on St. Paul Island during the pupping seasons of 2005, 2006. The female corresponding to Track 3 who's track (or portions thereof) is visualised in Figures 1, 2, 3, 6, and 7 appears in **bold** font in this table. Tracks 5.1 and 5.2 correspond to the same female that took 2 trips and the tag was not recovered after her first at-sea track. Tracks 10.1, 10.2 correspond to the same tag that was deployed twice, on two separate and independent female northern fur seals.

Variable	Female fur seal track ID										
	1	2	3	4	5.1	5.2	6	7	8	10.1	10.2
Departure date	Jul 13 2005	Jul 15 2005	<b>Aug 16 2006</b>	Aug 14 2006	Aug 13 2006	Aug 23 2006	Aug 13 2006	Aug 29 2006	Jul 16 2005	Aug 17 2006	Aug 26 2006
Departure time	23:31	02:15	<b>23:28</b>	18:39	14:16	15:21	14:41	07:23	01:14	15:04	11:46
Return time	12:52	19:49	<b>03:52</b>	04:55	01:49	17:09	21:34	04:11	13:12	15:29	20:42
Trip length (days)	5.6	6.7	<b>11.2</b>	10.4	8.5	9.1	10.3	5.9	5.5	7.0	6.4
# of Argos fixes	60	15	<b>74</b>	53	27	28	54	23	31	47	40
# of Argos GPS fixes per day	10.7	2.2	<b>6.6</b>	5.1	3.2	3.1	5.2	3.9	5.6	6.7	6.3
# of archival tag data records	98800	291200	<b>482400</b>	451600	404400	430400	445200	240000	94560	303200	406400
Sampling rate per minute	20	30	<b>30</b>	30	30	30	30	30	20	30	30

**Table 2.** Model information criteria, and model fit diagnostics.  $AIC$  is a relative measures of model fit (smaller implies better fit),  $\overline{D(\beta)}$  is a measure of model adequacy (smaller implies better fit),  $m$  represents the number of population parameters in the upper level model, and  $m_{DIC}$  is an estimate of effective number of model parameters. Posterior predictive  $p$ -values ( $p_{pp}$ )  $> 0.05$  implies there is no evidence model is predicting poorly.

Model Name	$AIC$	$\overline{D(\beta)}$	$m$	$m_{DIC}$	$p_{pp}$
Time Only	346.5	351.3	6	31.9	0.80
Time and Main Effect Models	$AIC$	$\overline{D(\beta)}$	$m$	$m_{DIC}$	$p_{pp}$
Time + Total Catch	290.1	349.9	8	38.9	0.55
Time + Pollock	290.0	344.0	8	37.8	0.72
Time + On/Off Shelf	298.7	344.5	8	40.8	0.84
Time + $1^\circ$ Productivity	382.0	344.0	8	40.2	0.04
Time Interaction Models	$AIC$	$\overline{D(\beta)}$	$m$	$m_{DIC}$	$p_{pp}$
Time $\times$ Total Catch	285.6	322.8	12	48.5	0.32
<b>Time <math>\times</math> Pollock</b>	<b>284.3</b>	<b>323.2</b>	12	<b>44.3</b>	<b>0.72</b>
Time $\times$ On/Off Shelf	303.6	330.8	12	51.8	0.62
Time $\times$ $1^\circ$ Productivity	292.0	334.7	12	60.0	0.00
Three Covariate Model	$AIC$	$\overline{D(\beta)}$	$m$	$m_{DIC}$	$p_{pp}$
Time $\times$ Pollock + On/Off Shelf	332.3	314.1	14	66.2	0.51

**Table 3.** Comparing a selected model with and without consideration of the error in model covariates. This table presents model fit diagnostics for which the descriptions and definitions are comparable to those in Table (2).

Time × Pollock Models	<i>AIC</i>	$\overline{D(\beta)}$	<i>m</i>	$m_{DIC}$	$p_{pp}$
Time × Pollock without $\sigma_U^2$	297.0	329.4	12	58.8	0.461
<b>Time × Pollock with <math>\sigma_U^2</math></b>	<b>284.3</b>	<b>323.2</b>	<b>12</b>	<b>44.3</b>	<b>0.72</b>

**Table 4.** Posterior summaries for higher level model coefficients  $\boldsymbol{B}$ .  $B_{1:2}$  denotes the regression parameters corresponding to the logit response  $\log(p_{ij}^{(2)}/p_{ij}^{(1)})$ , or the log odds of exploratory diving vs. baseline non-diving.  $B_{1:3}$  denotes the regression parameters corresponding to the logit response  $\log(p_{ij}^{(3)}/p_{ij}^{(1)})$ , or log odds of active diving vs. baseline non-diving). The column labeled  $\hat{R}$  is the Gelman-Rubin Bayesian measure of convergence. Parameters with significant Bayesian  $p$ -values are noted in **bold**.

	$\boldsymbol{B}_{1:2}$	Mean	St. Dev.	Median	Credible Interval			$\hat{R}$
				$q_{.5}$	$q_{.025}$	$q_{.975}$		
Intercept	$\boldsymbol{B}_{1:2}$	0.932	0.772	0.928	-0.564	2.473	1.01	
	$\boldsymbol{B}_{1:3}$	0.645	0.828	0.649	-0.983	2.277	1.00	
cos(time)	$\boldsymbol{B}_{1:2}$	<b>-1.352</b>	<b>0.613</b>	<b>-1.336</b>	<b>-2.594</b>	<b>-0.179</b>	<b>1.02</b>	
	$\boldsymbol{B}_{1:3}$	0.422	0.680	0.413	-0.874	1.797	1.00	
sin(time)	$\boldsymbol{B}_{1:2}$	-1.144	1.055	-1.146	-3.216	0.913	1.00	
	$\boldsymbol{B}_{1:3}$	-2.111	1.175	-2.098	-4.434	0.159	1.04	
log(pollock)	$\boldsymbol{B}_{1:2}$	0.622	0.633	0.610	-0.597	1.897	1.03	
	$\boldsymbol{B}_{1:3}$	0.477	0.762	0.478	-1.011	1.974	1.03	
cos(time) $\times$ log(pollock)	$\boldsymbol{B}_{1:2}$	0.064	0.549	0.068	-1.045	1.131	1.01	
	$\boldsymbol{B}_{1:3}$	0.264	0.645	0.257	-1.005	1.549	1.01	
sin(time) $\times$ log(pollock)	$\boldsymbol{B}_{1:2}$	-1.258	0.789	-1.239	-2.866	0.252	1.00	
	$\boldsymbol{B}_{1:3}$	<b>-2.479</b>	<b>1.177</b>	<b>-2.419</b>	<b>-4.993</b>	<b>-0.339</b>	<b>1.05</b>	