DIVING AND DEPTH USE IN SEALS : INFERENCES FROM TELEMETRY DATA USING REGRESSION AND RANDOM WALK MOVEMENT

Theoni Photopoulou

A Thesis Submitted for the Degree of PhD at the University of St Andrews

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Diving and depth use in seals: inferences from telemetry data using regression and random walk movement models

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Abstract

This thesis focuses on methods for using telemetry data to make inferences about the diving behaviour of seals, in terms of their use of depth over time. Three species are considered: grey seals (*Halichoerus grypus*) and elephant seals (*Mirounga leonina* and *Mirounga angustirostris*). Data come from Geographic Positioning System phone tags (GPS phone tags) for grey seals, and Conductivity Temperature Depth Satellite Relay Data Loggers (CTD-SRDLs) for southern elephant seals (*M. leonina*); both are instruments that transmit information in abstracted form. Data for northern elephant seals (*M. angustirostris*) come from an archival prototype SRDL-type instrument that stored tri-axial acceleration information at high resolution and required recovery to obtain the data. The usefulness of maximum dive depth as a measure of depth use in grey seals, known to forage on the seabed, is explored with a logistic regression analysis using a Generalized Additive Model. Often, maximum dive depth will not be a representative measure of the way seals apportion their time in the water column, so a framework for quantifying depth use is developed for abstracted dive data from southern elephant seals and validated with high resolution time-depth data from northern elephant seals. The implications of using a broken-stick model for abstracting dive data on-board CTD-SRDLs are investigated in terms of its performance and uncertainty. A method for obtaining limits on the time-depth area within which these abstracted dives occurred is developed and used as part of a Bayesian state-space random walk model framework to reconstruct dive trajectories and estimate depth use profiles for abstracted dive data.
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Declaration

I, Theoni Photopoulou, hereby certify that this thesis, which is approximately 37,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in May 2008 and as a candidate for the degree of Doctor of Philosophy in May 2009; the higher study for which this is a record was carried out in the University of St Andrews between 2008 and 2012.

Date: Signature of candidate:

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1

General Introduction
1.1 Animal movement in three dimensional space

Animals move in three spatial dimensions but, for most terrestrial animals, movement effectively occurs on the plane of latitude and longitude. For flying and swimming animals, the third dimension of movement is represented in height above the plane or depth below the plane. Without considering environmental context, there does not seem to be an 
a priori reason to expect movement in latitude and longitude, from a given point, to differ in terms of accessibility. It could be argued that, for flying animals and swimming, diving animals, movement is fundamentally different, from a physiological, locomotory and also a cognitive perspective. Direct observations of behaviour in a three dimensional context are often difficult or practically impossible. Instead, behavioural data tend to be collected remotely using animal-attached instruments. As a result, inferences on movement behaviour must often based on proxies and this should be formally acknowledged and dealt with appropriately in analyses of remotely collected data.

1.2 Seals and diving

In this thesis, diving is considered in the context of marine mammals, and a dive is defined as a movement trajectory in a volume of water starting and ending at the surface. According to this definition, all marine mammals, marine turtles and some seabirds are divers. Because of the constraint on these divers to return to the surface to breathe, dives can be thought of as analogous to foraging trips from a central place, irrespective of the function of individual dives.

For seals, which travel and forage below the water’s surface, diving is the currency with which they move through their environment, rest, avoid risk and acquire prey. Knowing where, when, and why seals dive to different depths is essential, because it is a measureable expression of their use of space in the vertical dimension, which has implications for other aspects of their biology, such as diet, as well as their vulnerability to human activity in the water column. The diving characteristics of a species (e.g., dive depth, dive duration, dive frequency, time-depth dive profile) are determined by the diving capability of individuals and the way they exploit their environment. Specifically, the depth
characteristics of dives contain information about the type of prey seals will encounter, within the wider context of the geographical and environmental space that is accessible to them, and where in the water column humans are likely to encounter seals. It seems reasonable to expect some of the measurable features of individual dives to be related to successful resource acquisition in space and time, even though successful foraging may be interspersed by, or associated with, a range of other activities such as travelling, searching, resting and unsuccessful foraging.

Phocid seals are long-lived, large-bodied and often sexually dimorphic marine mammals that can perform extended foraging trips at sea. Marine foraging is interrupted by periods of terrestrial fasting, during which they breed and moult, on ice or on land (King 1983). Adult females breed annually and produce up to one pup per year. Their life-history is both the cause and product of phylogeny, body size, and the spatial separation of resource acquisition at sea and breeding on land (Bartholomew 1970, Boyd 2000, Schulz and Bowen 2005, Ferguson 2006). Grey seals and elephant seals represent two contrasting scenarios of diving and foraging ecology.

1.2.1 Elephant seals

Southern elephant seals are the largest phocid seals. Males can weigh 1,500 to 3,000 kg and females 400 to 600 kg (Le Boeuf and Laws 1994). They occur throughout the Southern Ocean with breeding colonies on all the major subantarctic islands, as well as some mainland sites. South Georgia is the biggest colony with an estimated 54% of the total population (Boyd et al. 1996). The total population of southern elephant seals was estimated at 664,000 in 1990 (Le Boeuf and Laws 1994). Northern elephant seal males weigh slightly less than southern elephant seals, but females of the two species have not been found to differ in mass. Northern elephant seals breed on the California coast and offshore islands. In elephant seals, the period between moulting and breeding can be an uninterrupted trip to sea during which animals range widely diving continually, without hauling out on land.

Elephant seals typically dive to 400 m and dives last 20 min (e.g., mean dive depth 435.00 ± 236.30 standard deviations, mean dive duration 23.82 ± 10.62 standard deviation, for data
used in this study from 45 individuals instrumented at South Georgia between 2007 and 2009; Biuw et al. 2010, Costa et al. 2010) but the deepest dives exceed 2,000 m and can last more than 90 min (e.g., maximum dive depth 2,369 m, maximum dive duration 95.25 min, this study; Costa et al. 2010). Surface intervals between dives are characteristically short in elephant seals, lasting 2 - 3 min (e.g., mean surface duration 2.19 ± 0.84 standard deviation, maximum surface duration 9.48 min, this study). Dive depth and duration often vary diurnally and in response to environmental covariates (e.g., McConnell et al. 1992, Bailleul et al. 2007a, Bailleul et al. 2007b, Biuw et al. 2010, Dragon et al. 2010) as well as individual characteristics (e.g., McConnell et al. 1992, Le Boeuf et al. 2000, Bennett et al. 2001, Simmons et al. 2007).

1.2.2 Grey seals
Grey seals are the larger of two seal species that are resident in the UK. Grey seal males can weigh more than 300 kg and females 150 to 200 kg. They occur in the North Atlantic around two centres; Canada and the UK. Roughly half the population breed in the UK, 90% of which breed in Scotland (SCOS 2010). The population of grey seals for the whole of the UK was estimated to be between 82,000 and 138,700 at the beginning of the 2009 breeding season (SCOS 2010). Grey seals in the UK carry out shorter trips to sea and can be seen hauled out throughout the year but particularly during the annual moult, between January and March (McConnell et al. 1999).

Grey seals around the UK can dive down to the continental shelf (SCOS 2010), though on the east coast, the shallow depths typical of the North Sea limit dive depth. In this area dives reach approximately 50 - 100 m and last 4 min (e.g., mean dive depth 42.93 ± 21.33 standard deviation, maximum dive depth 162.20 m, mean dive duration 3.86 ± 1.62 standard deviation, maximum dive duration 16.30 min, for data used in this study from 7 individuals instrumented in 2008; McConnell et al. 1999). Surface intervals between dives are usually short, lasting 1 min (e.g., mean surface duration 0.93 ± 0.44 standard deviation, this study) but can also be extensive, lasting hours (maximum surface duration > 127.70 min, this study). As in elephant seals, grey seal dive depth and duration have been shown to vary with environmental, temporal, and intrinsic covariates (Thompson et al. 1991, McConnell et al. 1999, Beck et al. 2000, Beck et al. 2003).
1.3 Animal telemetry

1.3.1 The role of telemetry

The diving behaviour of seals cannot be directly observed over long periods or in remote at-sea locations. Animal-borne wildlife telemetry devices are routinely used to collect quantitative data on movement characteristics of seals and directly measure physical characteristics of the environment they experience. The use of animal-attached devices for logging and transmitting data was pioneered on marine mammals in the late 1940s (e.g., Scholander et al. 1942). This field of marine research has grown rapidly, aided by the increasing availability of sophisticated and affordable technology, and is generating large volumes of data. The consequences of the sampling design and the types of data generated by different instruments are critical in determining and developing the analytical techniques that can be used to interpret them (Matthiopoulos 2003, Matthiopoulos et al. 2004, Jonsen et al. 2005, Johnson et al. 2007, Patterson et al. 2008, Aarts et al. 2008). Dive data collected by telemetry are most commonly represented in two dimensions, as time-depth profiles. The shape of time-depth dive profiles can sometimes represent biological function. A number of different methods have been used to classify dive profiles into functional groups, such as cluster analysis (Lesage et al. 1999, Tinker et al. 2007), classification trees (Biuw et al. 2007), principal component analysis (Schreer and Testa 1995), discriminant function analysis (Schreer and Testa 1995, Lesage et al. 1999, Baechler et al. 2002), as well as empirical classification based on descriptive statistics of dive profiles (Naito et al. 1989; Hindell et al. 1991, Tremblay and Cherel 2000). The biological interpretation of data that have been collected remotely hinges on knowing how they have been collected.

1.3.2 Satellite Relay Data Loggers (SRDLs)

The instruments used in the present study log information, process it, and relay it via a satellite platform or mobile phone communication system (see Appendix I for technical information on software and hardware, and an overview of the data collection specifications). The SMRU (Sea Mammal Research Unit) SRDL has been developed as a data collection and processing device for the longitudinal study of at-sea behaviour of large marine vertebrates, and the environments they visit. The niche of SRDLs among animal telemetry instruments is to relay information that has been collected at fine resolution (1 to
4 sec) and summarized at medium resolution (minutes to hours) that enables the study of animal movement and behaviour over large spatial and temporal scales (over many months and thousands of kilometres). SRDLs have been deployed, and modified for deployment, on many marine species (e.g., Lydersen et al. 2002, Gaspar et al. 2006, Biuw et al. 2007). CTD-SRDLs (Conductivity Temperature Depth - SRDLs, that incorporate a range of oceanographic sensors, Boehme et al. 2009) are responsible for collecting over 80% of the publically available ocean data ever collected from high latitudes. Animal-borne sensors now comprise an important means of obtaining environmental data from inaccessible regions (e.g., Boehme et al. 2008a, Boehme et al. 2008b, Costa et al. 2008, Nicholls et al. 2008, Costa et al. 2010). These oceanographic profiles are a subset of the even larger volume of dive data - over twenty one million dive profiles - that have been collected since 1991 and continue to be collected worldwide using all types of SRDL (SMRU 2012, unpublished data).

There are two types of SRDLs with regard to the mode of information transmission and location determination. SRDLs and CTD-SRDLs use polar orbiting satellites operated by System Argos to determine location and relay information from a platform to a ground station (McConnell et al. 1992). Locations obtained from the Argos satellite system, fall into seven classes relating to the number of messages received by the satellite system and the estimate of the error, when available, associated with each location (Argos 1986, Argos 1989, Vincent et al. 2002, Myers et al. 2006, Royer and Lutcavage 2008, Lonergan et al. 2008, Costa et al. 2010). GPS phone tags have been developed in the last 10 years, and these use Fastloc GPS (Global Positioning System) to determine location and mobile phone networks to relay data to a ground station as a text message when in range, while incorporating the same sensors as a standard SRDL (McConnell et al. 2004). This makes it possible to store and transmit a much higher volume of data and has accommodated the use of GPS technology for marine animal locations. This type of instrument is particularly suitable for species with small-scale movement patterns that regularly come within range of the coast or other areas where there is mobile phone coverage for data transmission. Unlike location data delivered by Argos, GPS location data from phone tags do not have error classes associated with them. Locations are generally accurate and precise (within 0.2 km, Russell 2010, unpublished), but can also have errors of up to 1 km or in extreme case over
100 km. These extreme cases are identifiable by the size of the error estimate associated with a location, and also by eye in individual movement tracks.

1.4 The need for data abstraction

Collection and delivery of telemetry data are constrained in quantity and resolution by features of the hardware, software and the animal platform (Fedak et al. 2001, Fedak et al. 2002). The battery life of the telemetry device, the bandwidth of the communication system used, the behaviour of the animal, and the software specifications of the device interact to determine how often transmissions are possible and how much information can be sent in each transmission. This creates a situation in which there is a trade-off between the temporal resolution of the resulting data, the rate of data sampling and delivery, and the operational longevity of the telemetry device. This trade-off is less severe in the case of GPS phone tags, but historically, it has driven the development of efficient software and memory-saving processing routines for abstracting data on-board SRDLs due to the short length of messages that Argos is able to relay (see Appendix I).

On-board GPS phone tags deployed on grey seals, where bandwidth and animal behaviour are often less limiting, dives are abstracted using a fixed number of points at regular intervals throughout the dive. To increase the amount of information contained in each message, dive and oceanographic data are collected at high resolution and then abstracted on-board SRDLs and CTD-SRDLs using a broken-stick model (BSm). This is a piecewise linear approximation method that iteratively generates a profile made up of line segments between the most “important” depth points in the profile for characterizing a dive. These constraints lead to data-sparse dive profiles and make it challenging to characterize the position in the water column where animals dedicate most of their time within a dive.

In addition to abstracted time-depth profiles or other indices of whole dive trajectories (Fedak et al. 2001) used to describe a species’ diving behaviour, a statistic returned by most telemetry devices is the maximum depth visited during a dive. This is not an informative measure of how an animal apportions its effort in the water column throughout the dive, especially if swim speed and body angle (with respect to vertical) are not constant and the
maximum depth is an outlier in the distribution of depths visited during a dive. However, if maximum dive depth is representative of depth use during a dive, it can hold information about where in the water column diving species go to locate prey. For example, there is evidence that grey seals feed on benthic and demersal prey throughout the year (Prime and Hammond 1990, Hammond et al. 1994a, Hammond et al. 1994b, Bowen and Harrison 1994, Beck et al. 2007), so in this species, maximum dive depth should correspond to the geographic and environmental space in which grey seals obtain prey at least some, if not most, of the time.

1.5 Relating diving behaviour to features of the physical environment

Depth is a particularly relevant variable when studying air-breathing divers because, irrespective of diving ability, they are committed to returning to the sea-surface to breathe. The ocean is an environment that varies in four-dimensions: in latitude and longitude, in depth and through time, so depth can represent gradients of many different resources, such as light, oxygen and nutrients, which lead to stratification in marine communities. In the absence of direct information about the type and abundance of prey resources available to diving animals in the marine environment, physical characteristics such as depth can serve as proxies for these resources, both for researchers and, potentially, the divers themselves. Therefore, interpreting the behaviour of diving animals at depth requires information about the marine environment at relevant scales in time and three-dimensional space.

Remote sensing datasets provide large-scale environmental data and are still used extensively as an environmental context for animal behaviour. A potential drawback when considering diving animals is that remote sensing data provide primarily two-dimensional information on sea surface or sea floor characteristics, which may not be suitable for the interpretation of three-dimensional dive data. The use of environmental data collected by the animals themselves is often a more appropriate alternative. The development of satellite systems and telemetry devices have made possible the study of seal diving behaviour in relation to the environmental conditions they experience, as well as the collection of highly accurate oceanographic data from them as platforms of opportunity (Boehme et al. 2008b). The CTD-SRDL in particular, and other SRDLs incorporating various
sensors, have been developed for this purpose and have enabled the collection of high-resolution oceanographic data from habitats actually visited and experienced by instrumented animals (Boehlert et al. 2001; Charrassin et al. 2002; Fedak et al. 2006; Biuw et al. 2007; Boehme et al. 2008a, Boehme et al. 2008b).

1.6 Choosing an analytical approach

Making inferences about the conditions under which seals dive to different depths is complicated by a) the need for collection of data using telemetry instruments and data abstraction, b) the behaviour of the animals, and c) the analytical requirements of the resulting data.

Frequentist and Bayesian methods represent two different frameworks for making inferences from data. From a practical standpoint, the advantages and disadvantages of each are case specific, although philosophically the two differ fundamentally in their definitions of probability (Barnett 1973, Wasserman 2005). According to the frequentist approach, probability is viewed as the relative frequency of an event or outcome, such as a specific sample of data being obtained, after a large number of trials. Inference is then based on the probability of obtaining those data, given a belief about the long-run tendency of the quantity of interest. This approach does not incorporate any prior knowledge regarding this quantity. The long-run tendency is assumed to be fixed, and the data are considered stochastic, in that each sample will be different. According to the Bayesian approach, probability describes a state of knowledge about an event, rather than a long-run expectation. Under this approach, inference is based on the sample of data and any pre-existing information about the quantity of interest, expressed as probability statements. Here, the data are considered fixed, and are used to make inferences about the probability of a belief being true regarding the quantity of interest (Gelman et al. 2003).

Frequentist methods have been used widely in ecology and are often well-suited analytical approaches for ecological data. They make use of distributions that have known properties to describe parameters of interest. This makes the calculation of probabilities associated with these distributions (such as tail probabilities) straightforward, because they have
analytical formulae associated with them. As a result, a wide range of computational methods have been implemented and made available through most software packages. This makes them accessible and easy to use. A commonly used type of model that is fitted in a frequentist context is logistic regression. Regression models can be used to investigate relationships between variables without making assumptions about the way those relationships arise. To provide valid results, models need to be chosen to match the structure of the data and the kind of relationships that are apparent therein. For example, linear models are appropriate when linear relationships are apparent or expected between the response and covariates. In ecology, relationships can often be non-linear and using non-linear or additive models can accommodate this. Appropriate treatment of the structure of the data is equally important in ensuring valid results. For example, telemetry data arising from different individuals are subject to stochastic variation at the level of the individual animal. Observations from the same animal are likely to be more similar than observations from different animals due to individual behavioural characteristics. If this effect is ignored, it leads to violations of the assumptions that need to be met for models to be valid. Regression models that account for this type of stochastic variation in the effect of a covariate on the response are called mixed effects regression models. In addition, the fact that telemetry data form time-series often results in non-independence of observations through time, which requires the use of methods that can account for that. Relatively complex regression models can be fitted in a frequentist framework because the software is more developed and readily available for standard formulations, though this advantage can be at the expense of computation time. In general, regression models fall under the umbrella of empirical or data-driven models because they quantify relationships between covariates without making assumptions about the way covariates interact to produce the observed relationships.

Bayesian methods have only come into mainstream use relatively recently in ecology as a result of the increase in computational power that has made computationally intensive methods more accessible (Clark 2005). The form of the posterior distribution of a parameter of interest is not usually known in Bayesian models, so probabilities cannot be derived analytically. This is what motivates the use of this framework for such cases. There are some special cases when the form of the posterior is known, but they do not often correspond
with useful models. Hence, computer intensive methods are required, that extend the special cases. These methods make it possible to analyse large, complex datasets and incorporate uncertainty and missing information into the modelling process (Hobbs and Hilborn 2006). This is an attractive feature regarding the analysis of animal telemetry datasets since they are often large and made up of patchy and irregular data from a relatively small number of individuals from which inferences are made about populations (Morales et al. 2004, Forester et al. 2007, Aarts et al. 2008, Johnson et al. 2008). As for the availability of prior information, it could be argued that the researcher always knows something about the system under study and could therefore provide prior information for the parameter of interest, even if it is vague (Clark 2005). Bayesian methods lend themselves to mechanistic models when it is desirable to make explicit, probabilistic statements about the mechanisms that generate observations, such as state-space models (described below).

A more descriptive approach to the analysis of animal movement data, not used here, is to characterize movement paths based on their summary properties. It has been argued both that movement characteristics are scale-dependent, and scale-invariant (e.g., Kareiva and Odell 1987, Fauchald and Tveraa 2003, Nams 2005, and, Sims et al. 2008, Humphries et al. 2010, Sims et al. 2012, respectively). Advocates of scale-dependence have used empirical, parameterized models to describe the way animals concentrate their time along a movement trajectory and relate it to characteristics of the environment (Kareiva and Odell 1987, Fauchald and Tveraa 2003). Examples include fractal dimension, Area Restricted Search (ARS) and First Passage Time analyses (FPT) (Fauchald and Tveraa 2003, Nams 2005, Tremblay et al. 2007). These methods rely on the assumption that behavioural changes indicative of animals attempting foraging are reflected in the movement path as increased search effort. Increased search effort has been measured either as high track tortuosity (fractal dimension, ARS) or increased time spent in an area (FPT). Although these are mostly descriptive approaches, they can be useful in identifying areas of possible successful foraging. Studies investigating scale-invariance in animal movement (i.e. that measurements of movement at all spatial scales have similar statistical properties) have sought to find a unifying and potentially optimal, with regard to foraging strategies, pattern of movement (e.g, Viswanathan et al. 1996, Sims et al. 2008, Humphries et al. 2010, Sims et al. 2012).
Although this kind of finding would have important implications for the evolution of mechanisms of search strategies and the study of animal movement, the evidence so far has been shown to be weak or lacking (e.g., Edwards et al. 2007, Reynolds 2010, Edwards 2011, James et al. 2011, Kawai and Petrovskii 2012).

In this thesis, movement of diving animals in the third spatial dimension (depth) is analysed using empirical and mechanistic models to make inferences about behaviour. Both Bayesian and frequentist methods are used to address questions regarding depth use. A generalized additive regression model (GAM) with a random effect for the effect of individual on maximum dive depth is used to investigate the relationship between maximum dive depth and covariates in chapter 2, and the dive reconstruction models in chapters 4 and 5 are built as mechanistic models and fitted using Bayesian methods.

1.7 State-space models for animal movement

1.7.1 State-space models

State-space models (SSMs) are powerful tools for analysing time-series (Jonsen et al. 2003), such as time-depth dive profiles, and can be implemented in both frequentist and Bayesian frameworks. A SSM predicts the future state of a system based on its previous states, using a probabilistic model for the true process, and describes the way observations of the state arise in an observation model (Patterson et al. 2008). A useful feature with regard to telemetry data is that SSMs recognize two levels of structure in a time-series and allow it to be modelled as two components: the observation process and the true process. Conceptually, this treatment acknowledges the fact that the data collected by the tag are only a representation of the true, unobserved dive, and that the two dive profiles (true and observed) are generated by different processes. As a result, the error arising from the sampling process in the form of measurement error, and the uncertainty in the biological process of interest can be modelled separately and combined appropriately (Patterson et al. 2008, Schick et al. 2008).

Here, the model for the true, biological process is a movement model: a collection of rules by which successive depths are generated within a seal dive. In the context of this work, the
purpose of the process model is to represent a dive the way the tag records it before it is abstracted (truth as we perceive it through observation), rather than the continuous-time movement of the seal while it is diving. This is because we cannot obtain movement information without measuring it, which imposes constraints on the way we perceive the diving process. The information that we have on which to base the process model, all come from telemetry. For this reason, and the practical advantages of interpretability of results, the process model is formulated to predict future depths at regular, discrete time intervals, corresponding to the sampling resolution of the tag, rather than in continuous time.

The observed data are the abstracted dive data generated by the BSm and are, by definition, discrete and consist of six points (in all dives, irrespective of their duration) that are sampled at different time points in each dive. To overcome the mismatch between the frequency of observations in the true and the observed data, the observation time-depth trajectory from the dive zone for each dive was imputed to match that of the true dive profile, at the sampling resolution of the tag (see Appendix I for details).

1.7.2 Random walk models
Random walk movement models are often used for modelling movement trajectory of an individual animal (e.g., Turchin 1998, Jonsen et al. 2005, Codling et al. 2008, Johnson et al. 2008). They allow for stochasticity in movement parameters (hence random walk), have well-understood properties and are expandable (Turchin 1998, Colding et al. 2008). Four models are developed in this thesis and are described here in the context of diffusion in the vertical dimension. All four models are developed in a state-space framework, using Bayesian methods to reconstruct a two-dimensional time-depth trajectory of the abstracted dive within the limits of the dive zone, and infer distribution in water column during a single dive.

An isotropic random walk dive model is equivalent to a simple diffusion model whereby movement is truly random, without bias or persistence in direction of movement. The simplest model implemented in chapter 4 is an isotropic random walk with a general prior distribution of inertia for all dives.
To make a diffusion model case-specific, the prior distribution for the movement parameters can be tailored to each dataset the model is fitted to. This is also a simple random walk but with an informative prior on the movement parameters, specific to each dive, and it is used as the second model in chapter 4.

To add biological realism, two elements were added to the movement model: a) a time-dependent bias was introduced into the direction of diffusion relative to the maximum depth in the dive, and b) a tendency to maintain the direction of movement from one time step to the next. This was the third model developed in chapter 4, a biased correlated random walk.

In chapter 5 the movement model is also a biased correlated random walk, whose characteristics change depending on the behavioural state of the animal. Behavioural state was determined probabilistically at each time step, choosing from three possible states, based on behavioural covariates. The behavioural state at one time step determined the parameter values within the movement model.

It is convenient to fit this type of behavioural model in a Bayesian framework, where it is possible to estimate the probability of a number of competing outcomes, because it makes it possible to build models in which animals can switch between behaviours depending on which one is more likely. The advantage of fitting Bayesian SSMs is that it is also possible to estimate the probability of transition between different movement states (Patterson et al. 2008), thus bringing behavioural information into the movement analysis (e.g., Jonsen et al. 2003, Morales et al. 2004).
1.8 PhD Objectives

The objective of this thesis is to develop analytical methods for improving our current understanding of how long-lived, wide-ranging marine predators use the vertical dimension of the ocean. I use data from three abundant top predators with contrasting diving behaviour, foraging ecology and life-history: elephant seals (*Mirounga leonina*, Linnaeus 1758 and *Mirounga angustirostris*, Gill 1866) and grey seals (*Halichoerus grypus*, Fabricius 1791).

In chapter 2, I explored the usefulness of a simple metric of depth use, the maximum depth in each dive, in an empirical model framework for a dataset of dive records from seven grey seals using a spatially explicit GAM with a random effect at the level of the individual. Grey seals forage on benthic and demersal prey so the maximum dive depth is likely to be a good indicator of the depth at which they find prey. Spatial, temporal, individual and environmental covariates were used to describe the conditions that explain maximum dive depth.

In chapter 3, I studied the implications of collecting dive data with CTD-SRDLS, specifically the use of the BSm for abstracting dive profiles, using detailed and abstracted dive profiles from northern and southern elephant seals, respectively. A consequence of having a user-specified abstraction algorithm is that it can be reversed. This means that even though the data returned from these instruments are sparse, additional information can be gained *post hoc*, regarding the detailed dive profile before it was abstracted. This information can be used to determine a confidence zone (termed the “dive zone”) about any BSm profile, within which the true profile occurred.

In chapter 4, I developed three Bayesian mechanistic models of diving, using state-space random walk movement models to reconstruct individual dive profiles, in terms of the time-depth trajectory and the depth use profile. I used a case study of ten high-resolution dives from northern elephant seals to assess the performance of each model. The observation model was based on the dive zone developed in chapter 3, and three different movement models were explored.
In chapter 5, I extended the random walk models developed in chapter 4 to include information regarding the behaviour of the seal during a dive. In this model the seal can be in one of three behavioural states at each time step. Behavioural covariates help determine the probability of switching from one state to another and the state determines the movement characteristics of the seal at that time step mediated by having a state-specific movement model.

A final chapter contains a synthesis of the conclusions from the analysis and methods I have developed, and presents ideas for future directions.
1.9 References


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What influences maximum dive depth in grey seals *Halichoerus grypus*? Inferences using spatially explicit Generalized Additive Models
2.1 Introduction

Seals are aquatic mammals whose vital resources are split between the sea surface, where they have to return to breathe, and the water depths at which they forage. When foraging, a seal is expected to maximise the amount of time it will spend at a depth where it is likely to find or has found food (Thompson et al. 1991), while spending only the time required at the surface, to replenish oxygen stores and fulfil other metabolic requirements, such as resting and digesting (Sparling et al. 2007a). A single dive paired with its subsequent surface interval can be regarded as a behavioural and physiological foraging unit (Sparling et al. 2007a). Multiple attempts have been made to characterise the depth in the water column that animals target while diving (Fedak et al. 2001, Davis and Weihs 2007). The maximum depth visited in a dive is a statistic commonly returned by telemetry devices and used to describe a species' diving behaviour. This is often useful, especially for species that feed benthically, but might not be an informative measure of how an animal apportions its effort in the water column throughout the dive, especially if swim speed and body angle are not constant. It also does not indicate how much time an animal spent at the maximum depth or at intermediate depths between the surface and the maximum depth. However, in some cases, maximum dive depth can hold information about where in the water column diving species go to locate prey. Since seals are limited in the time they can spend underwater by having to return to the surface to breathe, deep dives are typically longer and more energetically expensive, but only in absolute terms. In relative terms, the rate at which oxygen is consumed per unit of time has been shown to drop in longer dives (Sparling and Fedak 2004). This is presumably a result of adjustments involved in the physiological dive response (Davis et al. 2004), which makes it possible to extend the time diving animals can spend submerged.

Because diving involves expenditure of time and energy, the deepest depth visited during a dive should be a profitable one in terms of accessing resources. There is evidence that grey seals feed on benthic and demersal prey throughout the year (Prime and Hammond 1990, Hammond, Hall and Prime 1994a and 1994b, Bowen and Harrison 1994, Beck et al. 2007), so in this species, maximum dive depth should correspond to the geographic and environmental space in which grey seals obtain prey at least some, if not most, of the time.
The analysis in this chapter has been based on that premise. To investigate what influences the maximum depth of dives of grey seals during trips to sea, maximum dive depth of individual dives was used as a response variable in a logistic regression with individual, spatial, temporal and physical environmental covariates as explanatory variables.

The availability of animal-borne telemetry devices to study animals’ use of the water column is a development of the last few decades (Kooyman 1964, Kooyman 2004). This type of instrument has made it possible to monitor previously unobservable underwater behaviour of large marine vertebrates, and has provided insights into the marine environment and behaviour of marine animals. The first dataset on the movement and behaviour of free-ranging grey seals on the east coast of northern England and southern Scotland was collected in 1986 using focal follows of animals instrumented with a VHF radio tag and sonic tag (Thompson et al. 1991). Direct observations showed that the behaviour of grey seals in this area can be described using three nominal categories: “hauled out”, “at-sea” and “resting in the water” adjacent to haulout sites. While at sea, seals either visited offshore areas or travelled between haulout sites. Telemetry data collected in subsequent studies have confirmed these behavioural patterns and show that although animals spend a large proportion of their time relatively close to a haulout site, they can also engage in long-distance travel (McConnell et al. 1999), also seen in this study (Figure 2.1, female 915). Trips to sea observed by Thompson et al. (1991) were assumed to be foraging trips, because seals were seen in association with other marine predators. During these trips, seals swam slowly and near the seabed, and the predominantly flat-bottom time-depth dive profiles suggested that animals were trying to maximise the time spent at the greatest depths visited during the dive, where they were presumably foraging.

Grey seals are thought to be flexible, generalist and opportunistic predators (Hammond, Hall and Prime 1994a), so foraging is likely to occur throughout the time spent at sea, including during transit phases of dedicated foraging trips and travel between haulout sites. Dietary studies based on scat analysis have shown that grey seals forage mainly on sandeels (Ammodytes spp.), gadids such as cod, haddock, whiting and pollock (Gadus, Melanogrammus, Merlangius and Pollachius spp.), flatfish and sculpins (Solea and Platicthys spp., and members of the Cottidae family) as well as squid (Illex spp.) (Prime and
Hammond 1990, Hammond, Hall and Prime 1994a and b, Bowen and Harrison 1994). This method for reconstructing diet is likely to provide an incomplete assessment of prey species composition, particularly far from haulouts and on multiday trips. The UK population of grey seals has been increasing since monitoring began in the 1960s but recently there is evidence that population growth is levelling off. The whole UK population was estimated at approximately 106,200 (95% CI 82,000 to 138,700) at the beginning of the 2009 breeding season (SCOS 2010). Population growth has been maintained, despite the collapse of the commercial cod fishery in the 1990s and its slow recovery (ICES 2009) and a possible reduction in sandeel abundance, evident in the decrease in landings since the late 1990s (ICES 2009). Stock assessment, recruitment and length-at-age data for both stocks are subject to uncertainty, particularly for sandeels in the western North Sea (ICES 2009) where most of the data considered here were collected.

Theoretical studies of foraging by diving animals have focused on identifying strategies that maximise the time a diver spends submerged (e.g. Thompson et al. 1993). If prey encounter is assumed to be a cumulative function of the time spent searching, the longer divers spend at depths likely to be profitable, the more prey they are likely to encounter and potentially consume. This suggests that air-breathing divers should make foraging dives as long as possible, but the observed diving behaviour of a seal is a product of the interaction of several internal and external factors (Thompson and Fedak 2001). Some of these include the resources available to the animal at the time of the dive (oxygen, energy), short term locomotory implications of body composition (buoyancy), the dietary requirements of the animal, availability of resources in the environment, features of the physical environment both in space and time (light/dark conditions, water temperature and stratification, bathymetry, season), and the hormonal and metabolic status of the animal (Beck et al. 2000, Beck, Bowen and Iverson 2003, Beck et al. 2003a, Beck et al. 2003b, Sparling, Speakman and Fedak 2006, Beck et al. 2007, Thompson and Fedak 2001). Despite the theoretical advantage to routinely extending dive time, the frequency distribution of dive durations was found to be right-skewed for shallow divers, such as grey and harbour seals, and symmetrical for deep divers. In other words, grey and harbour seals dive for less time than they could, which suggests that “giving up” might lead to more prey encounters under certain conditions in the long term (Thompson and Fedak 2001).
The idea about the relationship between patch quality and residence time has been tested in captive grey seals. Seals tended to leave a patch before reaching their aerobic dive limit (ADL) for low and high quality patches, both for short and long distance travelled, but stayed at high quality patches for longer when the distance travelled was long (Sparling et al. 2007b). This strategy increased net energy gain, compared to if they had remained in a low quality patch up to their ADL. This suggests that observed diving behaviour might indicate relative prey availability, so that specific areas where grey seals perform long, deep dives could be flagged as potentially “high quality” patches, though local conditions need to be taken into account. In captivity, the mass of the animal had a negative effect on bottom duration (time spent at depth below 90% of max dive depth for that dive; Thompson and Fedak 2001) in low quality patches, but this could be an effect of larger, older seals having greater experience in knowing when it is worth abandoning a patch. The dive patterns observed in the captive study by Sparling et al. (2007b), where seals were seen to give up early in low quality patches, resulting in more V-shaped dive profiles, and remain in high quality patches, resulting in flat-bottomed dives, are consistent with observed dive shapes in free-ranging seals (Thompson et al. 1991). This suggests that dives in which seals concentrate their effort (in terms of time spent) at the deepest depths might also be the most profitable ones in terms of acquisition of those prey species that occur there.

The aim of this analysis was to identify and describe some of the spatial, temporal and physical environmental features that explain maximum dive depth in time-series of dives from grey seals, as recorded by GPS phone tags (McConnell et al. 2007). This was done by analysing dive records from seven animals in a mixed-effects regression framework using spatially explicit Generalized Additive Models. The strength of this approach is that it combines a complex set of environmental variables and a highly resolved response variable, thanks to the quality of locations obtained from the tags and the improved availability of bathymetric information on a finer scale.
2.2 Methods

2.2.1 Exploratory data analysis and data processing

This dataset was collected using GPS phone tags, deployed on eight grey seals at Abertay Sands (56° 26.17 N, 02° 47.10 W) in April 2008. The dataset consisted of approximately 335,000 dives in total (see technical specifications of the tag program in Appendix I, deployment data in Table 2.1). Telemetry data commonly feature high spatial and temporal autocorrelation. This can be present in locations, aspects of behaviour or properties of the movement trajectory, and environmental variables collected in association with locations.

The dive record of each individual was checked for spatial and temporal autocorrelation in maximum depth of consecutive dives using the autocorrelation function (ACF) (acf function, base package, R Development Core Team 2010). The ACF is a standard tool for exploring the evolution of a process through time (Chatfield 2004). It calculates the similarity (correlation coefficient) of pairs of observations with a lag. The first pair to be considered are the first and second observation, and the last pair are the first and second to last observation. The similarity is expected to drop away quickly with increasing distance between the observations in each pair and remain close to zero if there is no autocorrelation in the time-series. Plots of the temporal autocorrelation revealed a persistent cyclic pattern in all individuals, with successive increases and decreases in similarity between dive depths. This is likely the result of the systematic changes in available depth during onshore-offshore movement of animals performing successive trips, and possibly individual intrinsic rhythms.

Two ways to address the issue of autocorrelation are a) to take account of it in the model framework, or b) remove it from the data. The autocorrelation itself was not of interest within the scope of this analysis and the large size of the dataset hindered model fitting using the approach chosen here, so the dataset was subsampled, using every tenth dive from the track of each individual, which resulted in the disappearance of the autocorrelation.

The behaviour of interest within the tracks was depth use in areas where animals were likely to be foraging. Grey seals split their time between being at sea and hauled out on land, with an increased proportion of time spent hauled out during the moult and breeding season. While at sea, animals use nearshore and offshore areas, but also show directed movement...
between haulout sites, as observed by Thompson et al. (1991). To isolate the dive data that were directly relevant to the objective of the study, track data were classified into segments of “trip”, “transit” and “haulout”. To do this, the track and dive record of each individual was visually inspected in MamVIS AD (Fedak et al. 1996) and Google Earth (Google Inc. 2009), and segments of the time series that corresponded to trips to sea were selected for analysis. A trip started at the first at-sea location of a direct trajectory away from a haulout site, and ended at the first on-land location of a haulout period. A haulout period started at the first dry, on-land location of a dry period lasting at least three hours to make trips clearly distinguishable, and ended at the onset of a trip. A transit was a trip that started and ended at different haulout sites and showed directed movement between the two without excursions into offshore areas. There were few transits identified in this dataset and they were included in the maximum dive depth analysis as trips since foraging cannot be ruled out during this type of travel. Tracks were classified manually according to these criteria for seven out of eight individual tracks and associated dive records. For one of the individuals it was not possible to reliably classify trips using the same criteria so it was excluded from the analysis. This track consisted of many short excursions returning to several haulout sites, making trips indistinguishable from transits and not comparable to the trip definition for the rest of the individuals in the dataset. This individual (gp13-888-08) was blind when captured (although in good body condition), so it may be that its navigational and foraging strategies were altered to cope with lack of visual ability.

The number of trips identified per individual ranged from 6 to 24 (Table 2.1). Exploratory analysis of the trip data showed that animals that made more trips, had a bigger proportion of shallow maximum dive depths than animals with few trips, because animals that made fewer and longer trips seldom came within close range of the shore to encounter depths of <20m. The dataset of trips and transits consisted of over 200,000 dives, which was reduced further by taking every tenth dive from each individual as described above, which effectively removed serial autocorrelation from the response data. The resulting dataset consisted of 21,986 dives from all trips from seven individuals (Fig 2.1). Some individuals reliably returned to the same areas and by similar routes during different trips (e.g., 897, Fig 2.1) while others interspersed trips to regularly used areas, with long trips to distant or different
areas (e.g., 915, Fig 2.1). On the whole, all individuals used a small number of geographic regions frequently, with some overlap between individuals.

2.2.2 Statistical modelling

The explanatory variables included in the model were selected from the available variables on the basis that they characterise some aspects of the spatial, physical and temporal environment that seals experience while at sea, the two-dimensional (latitude and longitude) movement characteristics of a trajectory of a track, behavioural or physiological processes, and individual characteristics. Sex and morphometrics were not used as explanatory variables due to the small sample size of individuals and the expected lack of power to identify true differences. Knowledge of the diet of this population is incomplete and distribution data on known prey species is sparse. Instead, sediment type was used as a proxy for the potential presence of sandeels, known to form a substantial part of seal diet on the east coast of the UK from scat sample analysis (Prime and Hammond 1990, Hammond, Hall and Prime 1994a and b, Bowen and Harrison 1994). The variables used to explain maximum dive depth were bathymetry (range -4.0 to 200.9 m, source: DigBath250 dataset, scale 1:250 000, British Geological Society), longitude in WGS84 decimal degrees (range 3.04 to 9.10), latitude in WGS84 decimal degrees (range 54.7 to 59.0), rate of horizontal displacement between surface locations (range 0.00 to 2.20 m/sec), dive duration (range 12 to 954 sec), temperature structure of the water column (range 0.00 to 0.16 ΔC°/m, explained below), Julian day (range 100 to 334), percentage gravel in the sediment (range 0.00 to 83.0), percentage sand in the sediment (16.7 to 99.8), percentage mud in the sediment (range 0.02 to 48.29), a binary variable for light conditions (daylight/darkness) and an individual identification code.

Longitude, latitude, horizontal displacement rate, dive duration, temperature structure, Julian day and light conditions were taken directly from the data delivered by the tag or derived from those data. Temperature structure of the water column at the location of a dive was derived from the 2-hourly average temperature profiles (casts) collected by the tag. Each dive was matched with its temporally closest temperature cast and the difference between the minimum and the maximum temperature in the cast, divided by the depth of the cast in metres, was used to describe the temperature structure of the water column at
the location of that dive. This gave rise to a coarse index of the temperature structure of the water column measured in the change in degrees centigrade per meter depth ($\Delta C^\circ/m$). Light conditions at the time of the dive were calculated as a binary variable (light or dark), based on the timing of local sunrise and sunset, using the sunriset function in the maptools library in R (Lewin-Koh and Bivand 2011).

The bathymetry and sediment data were processed as per Aarts et al. (2008), resulting in values on a 1 km grid for both variables. Bathymetry and sediment type were matched to dive locations using bilinear weights to interpolate values on a rectangular grid to irregular locations, so that interpolated values at dive locations were interpolated along the $x$ and $y$ axes (latitude and longitude) from the four nearest points in the grid of bathymetry and sediment values. This was carried out using the interp.surface function in the fields package in R (Furrer et al. 2011).

Non-linear relationships between the response and many of the explanatory variables were apparent, so a model that accommodates non-linearity was used. Although the structure of the response data was such that there were two levels of nesting, dives from trips within individuals, a single random effect was included for individual, because trips from the same animal were found to have similar depth characteristics. A mixed model framework was employed to account for potential systematic variation in model residuals for dives by the same animal, by including an individual random effect on maximum dive depth. Non-linearity and random effects can both be accommodated in a generalised additive model (GAM) framework. The GAM was implemented with the gam function in the mgcv library in R (Wood 2000, 2003, 2004, 2006, 2008, 2011) using fast restricted maximum likelihood (fREML) as the fitting method. The random effect for individual was implemented using the “re” smoother option, which is appropriate for simple, independent random effects (Wood 2011). Under this formulation random effects are implemented by applying a penalty to the model matrix in the form of a scalar multiple of the identity matrix, hence assuming that the coefficients associated with the penalty are independent and normally distributed (Wood 2008). More specifically, this assumption requires that the sample of individual seals is representative of the population and that their behaviour is not more similar than would be expected by chance. The “gamma” parameter of the gam function, which is the degrees of
freedom inflation factor, (Wood 2006) was set to 1.4. This acts to reduce the model degrees of freedom, favouring a smoother model, and reduces the chance of overfitting. Latitude and longitude entered the model as a spherical smooth function of the response using the “sos” two-dimensional isotropic smoother option in the mgcv library, with a first derivative penalty, as is default, and 100 knots. All other continuous variables were fitted as smoothed functions with a minimum of 6 (k = 6) and a maximum of 10 knots (k = 10) and the variable for daylight or darkness entered the model as a factor. The appropriate number of knots in each case was chosen using the routines outlined in the mgcv package manual and Wood (2006). Cubic regression splines were used as the basis functions for all continuous variables. Since the response variable was maximum dive depth, and the North Sea is shallow relative to the known physiological diving capacity in greys seals (e.g., Beck et al. 2003c), and fairly uniform in depth, bathymetry was the only physical environmental variable expected to limit potential dive depth.

Maximum dive depth recorded by the tag is a strictly positive real-valued response variable, so a Gamma error distribution was initially considered to be the most appropriate for the model residuals. However, the Gamma distribution assumes that errors will be small near zero, and has a log link function. This might not be appropriate for modelling the distribution of the residuals in a model where maximum dive depth is a response and bathymetry is likely to be an important predictor. The rationale for this is that depth measurements recorded by the tags are precise to 0.1 m throughout their range, but the bathymetry measurements used have been averaged over a 1 km grid. Dive locations are temporally interpolated between surface locations along the track, so they are also subject to some degree of spatial measurement error. Bathymetry measurements are averaged to obtain a single estimate for a grid cell, and within coastal grid cells that overlap with land, estimates can sometimes be above sea level. This spatial mismatch resulting from measurement error in maximum dive depth and bathymetry estimates can result in a mismatch between dive depth and apparently available bathymetry. The use of GPS tags with more precise location estimates ameliorates this problem, but it is still common for dive depths to be greater than bathymetry estimates. This will be most common for dives within coastal grid cells where water depth is shallow as well as potentially biased by overlap of the grid cell with the land. Consequently, a model with a Normal error
distribution and an identity link function was seen to be more appropriate to describe the model residuals.

In order to compare the performance of the model with each error structure, GAMs with Gamma and Normal error distributions were fitted and compared. Predictions were found to be similar enough to justify using the Normal and the AIC score suggested that this was a better model. As a result, the Normal model was chosen, in favour of interpretability of the results and a reduction in the number of parameters estimated by the model. Using the Normal distribution, predictions are directly interpretable, compared to the Gamma model, where predictions are on a log scale, though this is easily back-transformed. The two important advantages of using a Normal error structure are shorter fitting time (Normal: 80 sec, Gamma: 793 sec), and that estimation of confidence intervals becomes exact, rather than approximate, in the Normal case (Wood 2006).

2.2.3 Variable selection
Variable selection was done automatically by using a smoothing function modification technique known as shrinkage. A GAM can be thought of as a generalized linear model (GLM) whose linear predictor has smooth functions of covariates in the place of linear functions. The smooth functions used in GAMs are regression spline bases, which need to be penalized to prevent over-fitting and excessive “wiggliness”. This is done automatically in the mgcv library in R and can also be specified by the user in the number of knots used to construct the spline (Wood 2006, 2008, 2011). Although a strict penalization of a spline for a given smooth component can shrink (i.e. lessen) its effect, that component remains in the model. Shrinkage smoothers allow smooth components to be shrunk to zero during smoothness selection, effectively extinguishing their effect from the model (Wood 2008). This is brought about by adding a small multiple of the identity matrix to the smoothing penalty of a covariate (Marra and Wood 2011). If penalization is strong enough, shrinkage smoothers will shrink all the coefficients of the smooth to zero, cancelling out its effect (Wood 2008). The appeal of shrinkage approaches is that 1) they have the consistency of methods that explore the combination of all possible subsets of covariates (subset selection), and 2) with them variable selection can be achieved in a single step, and 3) they
do not suffer from the variable selection uncertainty inherent in stepwise variable selection procedures and model subset selection (Marra and Wood 2011).

There are two smooth modification or smooth component selection techniques implemented in the mgcv library that employ a shrinkage approach: double penalty and shrinkage. The double penalty approach is used here because of its stability in prediction, and the advantage of being able to use it with any spline basis, including spherical splines. Despite it requiring double the number of smoothing parameters to be estimated (Marra and Wood 2011), model fitting with the double penalty approach was still quick. Once the model was fitted, the strength of effect of each of the explanatory variables on the response was assessed by comparing their individual values with the sum of Wald statistics (F) from all variables in the model, returned by calling the anova function (car library in R) for the model object. This was done to compare the relative importance of terms and avoid using p-values, since they are approximate for smooth terms (Wood 2006).

There was negligible autocorrelation in the residuals of the final model, based on ACF plots of the residuals and a visual check of the Pearson residuals. Concurvity of the explanatory variables included in the model as smooths was checked using the concurvity function in the mgcv library in R. The problem of concurvity is equivalent to that of collinearity in GLMs, whereby the information provided by one covariate could be approximated by another. Estimates of concurvity range from 0 to 1, with 1 indicating lack of identifiability between covariates. Like collinearity, concurvity is a common problem when dealing with multiple covariates that vary in space and time, as is the case here. The mean concurvity for the ten smooth covariates in the model was 0.68 (standard error 0.08). Of the three values returned by this function (worst, observed and estimated), the highest “worst” value was for the individual id, suggesting that in some individuals’ maximum dive depth was very similar. No covariates were excluded from the model on account of high concurvity because all of them were seen as biologically relevant in explaining the response.

2.2.4 Predictions
Seven prediction maps were generated for each individual in the dataset: a) two maps of predicted maximum dive depth, during light and dark conditions, b) two maps of relative
maximum depth used by the individual, during light and dark conditions, c) a map of the percentage of gravel at dive locations, d) a map of the percentage of sand at dive locations, and e) a map of the percentage of mud at each location. Predicted proportional use of the water column was calculated as the ratio of predicted maximum dive depth to bottom depth at the dive location. Where the predicted maximum dive depth was greater than the bottom depth measurement the ratio was set equal to one.

To facilitate valid comparisons between individuals, given the different spatial coverage and, in particular, longitudinal extent of their tracks and dive records, the prediction grid for each individual was set up to have a resolution of 1 km². Each map was scaled appropriately for the longitudinal and latitudinal extent of the track of the animal. Predictions were always within the observed latitudinal and longitudinal extent of the observed data. The spatial extent of predictions with respect to data points was limited using the “too.far” argument when plotting predictions from the model. The value provided determines when a location is considered too far from the data relative to the spatial range of the data (Wood 2006). Here, prediction was limited to being within 90% of the latitudinal and longitudinal range of the data (too.far = 0.1). Prediction matrices were constructed for the spatial variables, bathymetry and sediment, at the resolution of the prediction grid, 1 km². For the remaining covariates, the mean value was used to predict maximum dive depth.

Individual-level maps were combined to produce a population-level map for predicted maximum dive depth and proportional use of the water column. This was done by making predictions of maximum dive depth for each individual animal over a region containing the majority of track data, scaling each prediction matrix by the proportional contribution of each individual to the dataset, in terms of numbers of dives. The seven scaled prediction matrices were then summed to produce seven maps, as described above.

2.3 Results

2.3.1 Predictions

The plots of the component smooth functions (Fig 2.2) show the overall relationship between maximum dive depth and each of the covariates under the model. Maximum dive
depth has a negative relationship with bathymetry at the shallow end of the range and also at high values, where the standard error was also higher. The smooth for horizontal displacement (speed) suggests a slightly positive but stable trend at low values, followed by a drop in maximum dive depth, reaching a minimum at horizontal displacement of approximately 1.4 m/sec. Dive duration had a strong positive relationship with maximum dive depth up to 400 sec (6.6 min), with very small standard errors, and decreased thereafter with more uncertainty. Similarly for temperature structure, maximum dive depth peaked at 0.04 ΔC°/m and turned negative in more structured water columns but with large standard errors. The relationship with Julian day was variable, with maximum dive depth decreasing from the beginning of the tagging period in early April until late July (day 230), increasing rapidly in the middle of September (day 260) and decreasing after that until the end of October (day 300). There was a positive relationship between maximum dive depth and the percentage of gravel in the sediment up to 20% and a negative relationship with large standard errors, with increasing gravel content, thereafter. The relationship between maximum dive depth and the percentage of sand in the sediment was negative at low sand percentages and increased above approximately 60% with large standard errors. The relationship with mud was positive up to 3-4% mud and turned negative after that, with large standard errors. The plot for the random effect for individual shows that although five out of seven animals had similar maximum dive depth characteristics, under the model, two of these had more extreme effects than the rest. The partial residual plot for light conditions shows that dives made in daylight were deeper than those made during the hours of darkness. The two-dimensional smooth function for the relationship between latitude and longitude and maximum dive depth is shown in two (Fig 2.3a) and three dimensions (Fig 2.3c). In Fig 2.3c the origin of all tracks is the shallowest depth in the surface located at the centre of the range for latitude on the y-axis.

The observed maximum dive depth for the whole data set had a median of 47.2m compared to 56.3m for the predicted maximum dive depth, suggesting that in general the model over-predicts maximum dive depth. The shape of the density function for the observed and predicted data can be seen for each individual separately in Fig 2.4. The model predicts better for some individuals than others and on the whole, the predictions contained less variability than the observations. The data suggest that all individuals dived to the deepest
available depth some of the time, and focused on individual-specific depths, but that they also performed shallow dives over deep water throughout the bathymetric range they encountered (Fig 2.5, upper row). The model failed to explain this relationship between maximum dive depth and bathymetry, resulting in over-prediction at low values and under-prediction at high values of the response (Fig 2.5, lower row). In spite of this, the model described 67.2% of the variability (deviance) in the data. Under the model, maximum dive depth was predicted correctly at the median values of bathymetry for each individual’s track. Both observed and predicted values are shown for this covariate because it was the only one for which a potential shape was known for its relationship with maximum dive depth. The observed relationship between each of the other covariates fitted as smooth terms in the model is shown in Appendix III (Fig 2.6 to Fig 2.12). The shape of the density function for the observed maximum dive depth under light and dark conditions and seen for each individual separately in Fig 2.13.

By far the strongest predictor based on the comparison of Wald statistics for each term in the model (Table 2.2) was dive duration, also evident in Fig 2.2. Light condition (daylight/darkness) was the next strongest predictor, followed by rate of horizontal displacement, the random effect for individual and bathymetry (although this could be an artefact of having interpolated the data over a coarser grid) (Table 2.2). The model predicted maximum dive depth in the range of 20.0 to 80.0 m while the range of the observed maximum dive depth was 1.5 to 121.0 m (for maps of individual predictions Appendix III: Fig 2.14a to Fig 2.20a). The prediction maps for the proportional depth use showed that almost all individuals dived to, or near to the seabed (0.8 to 1.0 of available depth) in areas up to 50 m depth (Appendix III: Fig 2.14b to 2.20b).

In all individuals, predictions of maximum dive depth in dives performed during hours of darkness were shallower than those performed during daylight (Appendix III: Fig 2.14a (Light and Dark), 2.14b (Light and Dark) to Fig 2.20a (Light and Dark), 2.20b (Light and Dark)). This slight effect can also be seen in the smooth density distribution of light and dark maximum dive depths (Fig 2.2).
An area used by three of the seven individuals during the deployment period (two males, 902 and 908, and the largest of the four females, 915, Fig 2.1) was Dogger Bank, to the southeast of Abertay Sands, at approximately 55° N 02° W (Appendix III: Fig 2.15b, 2.16b and 2.18b), where the model predicted that all three seals dived to the seabed. Two females (897 and 910, Fig 2.1) used an area approximately 100 km west/northwest of Abertay Sands, and were also predicted to dive to the seabed, although predicted dive depth for 910 was slightly greater than the observed dive depth, and with less variability (Fig 2.4).

The composite map of maximum dive depth predictions shows a vertical band spanning the latitudinal range of the tracks, in which all seals appear to dive deeper both in light and dark conditions (Fig 2.21a (Light) and 2.21a (Dark)). Overall, dives made during darkness were predicted to be shallower across the whole area (Fig 2.21a (Dark)). An irregular pattern of depth use is present in Fig 2.20a (Dark). This is likely a result of combining the seven individual prediction matrices and may represent individual variation in patterns of depth use. The pattern of proportional depth use of the water column showed consistent dives to 70 to 100% (0.7 to 1.0) of the available depth during daylight (Fig 2.21b (Light)). Overall, dives made during darkness utilized proportionally less of the available depth as well as being shallower in absolute terms (Fig 2.21b (Dark)), but this pattern varied spatially. Dives carried out on the Dogger Bank had little diurnal variation in depth.

2.4 Discussion

A regression model was constructed to explain the conditions under which grey seals in the western North Sea dive to different maximum depths, based on a dataset of dives from seven individuals that were instrumented on the east coast of the UK in April 2008. The model explained a large proportion of the variability in the data (67.2 %) overall, but the predictions it generated were limited to an often narrow range around the median of the observed depth distribution for each individual. The median prediction was close to the median of observed dive depths, so in this sense predictions were not biased. Nonetheless, the model failed to predict shallow dives and very deep dives. It has been shown that grey seal diving behaviour occurs in bouts (groups of dives with similar characteristics) and that there are different types of dive bouts (Beck et al. 2003c, Austin et
Only one temporal scale of diving was considered in this analysis, that of trips, so it is likely that this lack of acknowledgement of a more fine-scale structure to diving behaviour lead to poor predictive power.

Data with inherent spatial and temporal structure, such as consecutive dive depths, are most often correlated in space and time. Fitting a model with an autocorrelation structure to large datasets can be computationally intensive, especially when the form of the autocorrelation structure is unknown. Although it is wasteful to discard data because this leads to loss of information, it is often a workable if not ideal solution to large autocorrelated datasets, and remedied the problem in this case. The observed periodic pattern in the raw data and model residuals from the full dataset was probably due to the onshore-offshore movement, as a result of multiple trips during the tracking period. Another possible source of periodicity in dive depth, especially given the different pattern present in each individual, is an inherent periodicity in the behaviour of each animal, e.g., due to digestion times and individual diet, which was not captured by the explanatory variables used here.

Only some of the internal and external factors that could contribute to the observed diving behaviour of a seal were considered in this study. External features of the physical environment both in space and time (light/dark conditions, water temperature and stratification, bathymetry, season, geographic coordinates) were considered to be adequately represented in the model, although tidal effects and currents were not included. Of the explanatory variables that were included, dive duration can be considered a proxy for oxygen availability during a dive and, given the strong association of sandeels with coarse sand and fine to medium gravel (Wright et al. 1998, van der Kooij et al. 2008), sediment type can be considered as a proxy for the availability of resources in the environment. Van der Kooij et al. (2008) found no clear relationship between bottom depth and sandeel abundance because they found sandeels at all but the deepest depths sampled during surveys carried out in 2005 and 2006 (maximum 48.5 m). In the same study, high surface salinity and temperature stratification were found to be predictor of sandeel abundance in areas where they were present, so it is possible that the simple index of temperature structure of the water column used here was not a relevant proxy for sandeel abundance.
However, it was worth including since sandeels are not grey seals’ only prey, based on scat sample analysis. The grey seals in this study used primarily three water masses, as defined by Ehrlich et al. (2009): Scottish Coastal Water, North Atlantic Water and Northern North Sea Water. Prey types represented in scat samples from the east coast of Scotland are probably only representative of prey taken by seals in Scottish Coastal Water. Trawls carried out in North Atlantic and Northern North Sea Water found that haddock and whiting dominated their catches (Ehrlich et al. 2009). As generalist and opportunist predators, it is likely that grey seals exploit these prey types in these water masses though they might not be adequately represented in scat samples.

Individual, internal factors that were not considered here include hormonal and metabolic status of the individuals, body mass, body condition, and the associated locomotory implications (i.e., buoyancy). A potentially important omission in the variables included in the model is information about the time-series of dive depths immediately prior to a dive. One of the shortcomings of the current model is that it did not accurately predict shallow dives made over deep water. Such dives could be resting or digesting dives, since it has been documented for grey seals in captivity to delay food processing for many hours after a feeding event (Sparling et al. 2007a). The strong positive effect of daylight, and associated negative effect of darkness on dive depth found here, ties in with the diurnal behaviour of sandeels, which feed in the water column in the day and bury themselves in the sediment at night (van der Kooij et al. 2008). It is possible that when targeting sandeels or other vertically migrating prey, grey seals dive deeper in the day and spend the hours of darkness carrying out shallower dives during which other metabolic functions can be carried out. The lack of effect of light conditions on maximum dive depth and proportional use of the water column on the Dogger Bank, a known fishing ground for lesser sandeels (Ammodytes marinus) (van der Kooij et al. 2008), in this analysis contradicts this. Seals consistently dive to the seabed in this area according to model predictions, suggesting that they might be feeding on other prey that are available when sandeels are not, or that this area is shallow enough to continue to dive to the bottom and carry out metabolic functions while diving to the seabed. The relationship between dive duration and light conditions was not investigated here, but given the diurnal effect on dive depth, dive duration may follow a
similar pattern. Irrespective of dive depth, longer dives might suggest more profitable, higher quality patches in the wild as has been found in captivity (Sparling et al. 2007b).

Light conditions were found to be an important explanatory variable in the model, but still did not successfully predict conditions under which seals dive shallowly over deep water. This suggests there might be an intrinsic variable that is missing from the model. Although there are more hours of daylight than darkness at the latitudes over which the seals ranged for most of the deployment period (roughly one third of dives were carried out during darkness), it seems unlikely that this pattern in dive depth is an artefact, due to the large sample size. Composite maps of maximum dive depth and also proportional depth use during darkness, combining predictions for all individuals, showed irregular patterns. This might be due to the limits placed on prediction with regard to proximity to data points, different densities of data across the prediction matrices, individual and/or spatial variability in diurnal dive patterns. A different method for combining the individual predictions might prevent this.

At the other end of the prediction range, the fact that dive depths were over-predicted at shallow depths might be due to the trip classification routine adopted here. The three-hour haulout definition used to make separate trips more distinct is likely to have excluded short trips in the vicinity of the haulout, during which opportunistic foraging should not be ruled out. The individual that carried out the most trips in this study (Fig 2.1, 897) and whose dive depth at shallow depths was best represented, were also most accurately predicted by the model. A solution to this would be to reduce the threshold time for haulouts between trips, to include near-haulout trips. A further improvement would be to increase the sample size of individuals to enable comparison of maximum dive depth between males and females as well as morphometric comparisons.

The findings of this study with respect to the relationship between maximum dive depth and mud are similar to those reported by Aarts et al. (2008), though this variable accounted for a very low proportion of the variability in the current dataset. Aarts et al. (2008) found that the grey seals in their study showed a preference for habitat characterized by approximately 3% or less mud content in the sediment. In the current dataset, although the
sample size of individuals was much smaller, a weak positive relationship with maximum dive depth was found for areas with approximately 3-4% mud content.

The effect of environmental, behavioural and individual characteristics on maximum dive depth was investigated using a dataset of dives from seven animals. The strongest predictors identified here were dive duration and light conditions. None of the variables were extinguished from the model (i.e., no relationship found with the response), despite using the double penalty approach for automated variable selection, which allows for it. The link between dive depth and its strongest predictor, dive duration, might warrant further investigation. This relationship will depend on speed of travel and might help to describe the mechanism via which dive depth occurs. The model fitted here explained a large proportion of the variability in the data, revealed a light-dependent dive pattern and suggests that seals dive to or near to the seabed in most areas up to 50 m. The poorer performance of the model at both extremes of the range of the response, suggests that there are important covariates missing from the model, one of which might relate to dive bouts.

The lack of information about what triggers shallow or deep dives, i.e. the mechanism that drives the alternation between shallow and deep dives, is likely to be the main reason maximum dive depth is not predicted accurately by this regression model. An alternative explanation for the model’s lack of predictive power is that the maximum dive depth is not an appropriate response variable, and does not always adequately describe the behaviour of the animals or their use of the water column. This provides motivation to develop models that contain more information about the behaviour of the animal, both in terms of its vertical use of the water column throughout a dive, and in terms of the time-series of behaviour at a time scale that considers multiple dives, possibly in bouts. One such method for producing information about seals’ depth use throughout the water column is developed in the following chapters.
2.5 References


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Fedak MA, Lovell P and Grant SM. 2001. Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Marine Mammal Science* 17(1): 94-110


Sparling CE, Speakman JR and Fedak MA. 2006. Seasonal variation in the metabolic rate and body composition of female grey seals: fat conservation prior to high-cost reproduction in a capital breeder? *Journal of Comparative Physiology B* 176: 505-512


2.6 Figures and Tables

Table 2.1. Individual deployment information and diving behaviour summary statistics (mean ± standard error) for the seven adult grey seals studied here. Length is nose-to-tail length, AxGirth is the axial girth of the animal, Deployment Period refers to the operational lifetime of the tag, Study Period refers to the period for which whole trips could be identified according to the criteria specified.

<table>
<thead>
<tr>
<th>Individual</th>
<th>897</th>
<th>902</th>
<th>908</th>
<th>910</th>
<th>915</th>
<th>916</th>
<th>921</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>F</td>
<td>M</td>
<td>M</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>Mass (kg)</td>
<td>79</td>
<td>113</td>
<td>135</td>
<td>98</td>
<td>129</td>
<td>96</td>
<td>137</td>
</tr>
<tr>
<td>Length (cm)</td>
<td>157</td>
<td>171</td>
<td>188</td>
<td>166</td>
<td>164</td>
<td>164</td>
<td>174</td>
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<tr>
<td>AxGirth (cm)</td>
<td>112</td>
<td>124</td>
<td>133</td>
<td>114</td>
<td>131</td>
<td>120</td>
<td>136</td>
</tr>
<tr>
<td>Study period</td>
<td>11 Apr - 1 Nov</td>
<td>09 Apr - 28 Sep</td>
<td>09 Apr - 13 Aug</td>
<td>14 Apr - 19 Oct</td>
<td>9 Apr - 3 Oct</td>
<td>14 Apr - 29 Nov</td>
<td>13 Apr - 14 Aug</td>
</tr>
<tr>
<td>Trips (of which were transits)</td>
<td>24 (0)</td>
<td>16 (4)</td>
<td>6 (2)</td>
<td>18 (0)</td>
<td>15 (2)</td>
<td>23 (2)</td>
<td>6 (0)</td>
</tr>
<tr>
<td>(days)</td>
<td>6.36±0.30</td>
<td>6.46±2.06</td>
<td>14.17±4.19</td>
<td>8.52±1.42</td>
<td>7.80±2.41</td>
<td>7.09±0.60</td>
<td>15.43±1.08</td>
</tr>
<tr>
<td>No. of dives</td>
<td>3968</td>
<td>2470</td>
<td>2123</td>
<td>4097</td>
<td>2601</td>
<td>4219</td>
<td>2508</td>
</tr>
<tr>
<td>MaxDep (m)</td>
<td>40.85±0.08</td>
<td>33.65±0.13</td>
<td>38.99±0.13</td>
<td>42.95±0.08</td>
<td>44.26±0.12</td>
<td>44.99±0.12</td>
<td>53.67±0.18</td>
</tr>
<tr>
<td>DiveDur (min)</td>
<td>3.94±0.01</td>
<td>3.38±0.01</td>
<td>3.90±0.01</td>
<td>3.89±0.01</td>
<td>4.77±0.01</td>
<td>3.59±0.01</td>
<td>3.69±0.01</td>
</tr>
<tr>
<td>SurfDur (min)</td>
<td>1.49±0.04</td>
<td>1.85±0.05</td>
<td>1.49±0.05</td>
<td>1.26±0.03</td>
<td>1.58±0.04</td>
<td>1.68±0.04</td>
<td>1.34±0.04</td>
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</tbody>
</table>
Table 2.2. The relative importance of explanatory variables in the model ranked according to the Wald statistic for parametric and smooth terms. The row labelled “F” shows the Wald statistic for each term in the model, obtained from output of the anova function in R, applied to the GAM model object. The row labelled “Prop.” shows the proportion of the sum of Wald statistics accounted for by each term. “Light” is the binary variable for light conditions: light (1) and dark (0). All terms of the form “s( )” are smoothed terms in the model. “s(Lat, Lon)” is the two-dimensional term for latitude and longitude. “s(Bathy)” is the term for bathymetry or bottom depth. “s(DiveDur)” is the term for dive duration. “s(TempStr)” is the term for temperature structure in the water column. “s(JulianDay)” is the term for Julian day. “s(Gravel)” is the term for percentage gravel in the sediment. “s(Sand)” is the term for percentage sand in the sediment. “s(Mud)” is the term for percentage mud in the sediment. “s(Ind)” is the random effect term for individual animal.

<table>
<thead>
<tr>
<th>Term:</th>
<th>Light</th>
<th>s(Lat, Lon)</th>
<th>s(Bathy)</th>
<th>s(HorizSpeed)</th>
<th>s(DiveDur)</th>
<th>s(TempStr)</th>
<th>s(JulianDay)</th>
<th>s(Gravel)</th>
<th>s(Sand)</th>
<th>s(Mud)</th>
<th>s(Ind)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>444.3</td>
<td>15.0</td>
<td>29.9</td>
<td>57.8</td>
<td>2132.4</td>
<td>9.8</td>
<td>19.7</td>
<td>7.9</td>
<td>1.6</td>
<td>3.6</td>
<td>38.3</td>
</tr>
<tr>
<td>Prop.</td>
<td>16.1</td>
<td>1.1</td>
<td>0.5</td>
<td>2.1</td>
<td>77.3</td>
<td>0.4</td>
<td>0.7</td>
<td>0.3</td>
<td>0.1</td>
<td>0.1</td>
<td>1.4</td>
</tr>
</tbody>
</table>
Figure 2.1. Map of the dive locations during trips to sea of seven grey seals instrumented in 2008. Map coordinates are in latitude and longitude (WGS84 projection).
Figure 2.2. The relationship between maximum dive depth and each explanatory variable in the model except latitude and longitude, including smooth terms, the random effect for individual and factor variable for light conditions. The grey shading in plots of smooth functions extends two standard errors above and below the estimate of the smooth being plotted. Each plot has different limits on the x and y axes corresponding to the scale of the variable in question. The dashed vertical lines and letters in the plot for Julian day show months April (A) to November (N). The numbers in the plot for Individual effects relate to the individual id number (where 1 to 7 correspond to 897 to 921).
Figure 2.3. The relationship between maximum dive depth and latitude and longitude, plotted in two dimensions, a) with standard errors, and c) as a surface.
Figure 2.4. Smooth density plots for observed (upper row) and predicted (lower row) maximum dive depth (m) for each individual (columns).
Figure 2.5. Smooth density scatterplots for the observed relationship between maximum dive depth and bathymetry (upper row), and the predicted relationship between maximum dive depth and bathymetry (lower row) for each individual (columns). The points in each plot represent the first 100 points in the areas of lowest density.

(For Figures 2.6 to 2.12 see Appendix III)
Figure 2.13. Probability density functions for the observed distribution of the maximum depth of dives carried out during daylight (black) and darkness (grey), for each individual (columns).

(For Figures 2.14 to 2.20 on individual prediction maps see Appendix III)
Figure 2.21. Map of model predictions for all individuals combined on a 1 km^2 grid, the blue circles represent dive locations from all individuals. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show interpolated sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each dive location.
Figure 2.21 (continued)
Figure 2.21 (continued)
Figure 2.21 (continued)
3

Performance and uncertainty of the broken-stick model applied to dive profile abstraction
3.1 Introduction

The rapid development of animal telemetry devices over the last three decades has made it possible to study marine animals remotely using animal-borne sensors. The collection and delivery of telemetry data is constrained in its quantity and resolution by the battery life of the telemetry device, the bandwidth of the communication system used to relay data to the ground station, the behaviour of the animal, and the software specifications of the device. This imposes a trade-off, between the temporal resolution of the resulting data, the rate of data sampling and delivery, and the operational longevity of the telemetry device (Appendix I: Fig 7.2), and has driven the development of efficient software and memory-saving processing routines, one of which is data abstraction.

For many migratory or wide-ranging marine species that return to the same location to breed, obtaining a complete annual time-series of locations and behaviour is more biologically interesting than detailed information over short periods. Specifically, questions about the behaviour and movement of large vertebrates at sea, and the innovative concept of recording near real-time, in situ oceanographic data on the environmental conditions the animals’ are experiencing, have spearheaded the development of purpose-built satellite-linked animal telemetry devices. One such device, the Conductivity Temperature Depth Satellite Relay Data Logger (CTD-SRDL), was pioneered by the Sea Mammal Research Unit (SMRU) for deployment on seals. The strength of the CTD-SRDL is that it records in situ hydrographic information (Boehme et al. 2009), complementing the behavioural information that is collected simultaneously, relating to the animal platform itself, and relays the information in real time (Fedak 2004). The advantage of obtaining the hydrographic information in real time is that it can be incorporated into the World Ocean Database and used to improve forecasting (e.g., Roquet et al. 2011).

When the priority is to collect data remotely over long periods, as is commonly the case for deployments of CTD-SRDLs on wide-ranging phocid seals, the data collected by a tag need to be abstracted and compressed on-board before transmission (Fedak et al. 2002). Simply put, the main reason for this is the trade-off between how much information can be sent, how often and at what energy cost, but see Appendix I for more detail. The information of
main interest with regard to the movement behaviour of a seal at sea is a) its horizontal
movement trajectory, and b) in the vertical dimension, its diving behaviour. For CTD-SRDLs,
locations are obtained with an associated residual error, as estimated by System Argos
(Argos 1986, 1989), the satellite system used for data transmission. Two-dimensional time-
depth dive trajectories and CTD profiles are abstracted on-board the tag prior to
transmission. For dive profiles and CTD profiles, abstraction is carried out according to an
algorithm, which summarises the dive data using a reduced amount of information. This
chapter focuses on the consequences of the abstraction routine for dive profiles, but the
same principles will apply to CTD profiles. There have been several generations of
abstraction routines (Fedak et al. 2001). The algorithm implemented on-board CTD-SRDLs
that have been manufactured since 2007 uses a variation of the broken-stick model (BSm),
described in detail below. The aim of this chapter is to investigate the consequences and
implications of abstracting dives using the BSm, in order to extract as much information as
possible from existing and historical dive data, and to provide advice on the interpretation
of abstracted dive profiles. To do this, both detailed and abstracted dive profiles are used,
from northern and southern elephant seals, respectively.

Broken-stick models (BSm), also known as change-point models, belong to piecewise
approximation methodology and are used to identify points of abrupt change in time-series.
In ecology, BSm’s have been in use since MacArthur’s work on niche separation (MacArthur
1957, MacArthur and MacArthur 1961). This type of model is flexible and has seen
application in a range of fields, for example, in oceanography to reduce data volume (Rual
1989), to identify edge effects in plant communities (Toms and Lesperance 2003), to locate
ontogenetic shifts in southern elephant seal foraging using stable isotopes (Authier et al.
2012) and in a Bayesian context applied to allometric relationships between tree height and
diameter (Beckage et al. 2007). The performance of this algorithm in the context of dive
profiles has not been tested rigorously, neither in terms of the fidelity of the resulting
abstracted profile to the true dive path, nor in terms of the uncertainty associated with
depths along the trajectory between broken-stick points. Nonetheless, on the whole, this
method has been found to perform well at capturing biologically relevant aspects of time-
depth dive profiles, as well as being fast and memory-efficient (P. Lovell, pers. comm.).
Under the BSm abstraction regime, highly resolved time-depth information is processed to generate abstracted dive profiles which are made up of six time-depth points; two at the surface, and four at depth, at irregular times, which vary from dive to dive. Some information is permanently lost in the digitization, compression and decompression process involved in coding, transmitting, and decoding the information upon receipt. The data abstraction routines are fully user-specified, making it possible to reverse the steps in the deterministic part of the process and back-calculate some of the information lost. By reconstructing the recoverable information, a confidence zone can be constructed around the abstracted profile, within which the dive is known to have taken place with 100% certainty. This confidence zone is hereafter referred to as the dive zone.

Detailed dive profiles can be used to investigate the abstraction process and the relationship between the dive zone and the detailed profile of a given dive. Here, a sample of ten consecutive dives from high temporal resolution dataset from a northern elephant seal, collected using an archival tag, was used to used as a case study of the abstraction process and its performance. First, computer code was used to emulate the dive data abstraction process that is carried out on-board CTD-SRDLs and apply it to detailed dive data. Then, a method was developed to partially reverse the abstraction process for any given dive, using the information that is contained in the final abstracted profile and knowledge of the algorithm that produces it. The code written for both routines can be found in the electronic supplement to Appendix II (sections 8.1.1 and 8.1.2). The aims were 1) to study the process by which the BSm generates abstracted profiles, 2) to assess the performance of the BSm for dive profile representation overall, by comparing detailed and abstracted time-depth dive profiles, and 3) to develop a method for constructing limits on the true dive based on its BSm abstracted profile, and 4) to develop an index of goodness of fit of an abstracted dive when truth is not known, using detailed dive profiles to validate it.

In summary, these methods serve to evaluate the similarity of the piecewise linear BSm profile and the true dive profile, and to explore the relationship between measures of error (in the abstracted profile), which can be derived from detailed dives, and the area of the dive zone, which can be derived for any abstracted dive, in an attempt to link the two. The number of iterations of the BSm algorithm carried out on-board tags was chosen empirically during software development for CTD-SRDLs as the minimum sufficient number to convey...
the shape of the dive profile, while keeping the number of computations low. This analysis studies the consequences of this abstraction regime.

3.2 General methods

3.2.1 Abstraction of dive data with the broken-stick algorithm

An efficient abstraction method for time-depth dive profiles should minimize the sum of vertical residuals (i.e. the residual error in depth) between the abstracted profile and the true profile. However, an algorithm implemented on-board a CTD-SRDL needs to do more than maximize goodness of fit. It also needs to compute in a fixed amount of time, with a low number of operations, and encode information in a fixed, small number of bits (P. Lovell, pers. comm.). These are inflexible constraints imposed by the tags’ current hardware specifications, in terms of processing power and transmission. Other desirable features are that this algorithm is simple and reliable, encodes biologically relevant information such as the shape of the dive and its maximum depth, and uses the raw observations as the tag’s sensors sample them.

The BSm was adopted as the dive abstraction algorithm on CTD-SRDLs as a working solution, not due to optimal precision, but because it satisfies the constraints described above, and has been used as part of the data reduction method to calculate significant points in temperature-depth profiles recorded by XBTs (eXpendable BathyThermogrammes) (Rual 1989). It produces an abstracted profile made up of \( n \) line segments that approximate the true, non-linear time-depth trajectory travelled. This is achieved through \( n \) iterations of the algorithm (\( i=1, 2, \ldots, n \)). First, the process is initialized by proposing a linear representation of the movement trajectory, defined, at this first iteration (\( i = 1 \)), by the straight line joining the start and end points of the dive in time, along the surface at zero depth (Fig 3.1b).

Second, the difference in depth between the true and abstracted trajectories is measured at each time point through the dive and stored (Fig 3.1c, 3.1f, 3.1i, 3.1l). Third, the time point at which the \( i^{th} \) iteration of the piecewise linear abstracted profile deviates most from the true trajectory is then added to the abstracted profile. This step creates a new piecewise linear profile comprising \( i+1 \) points and the algorithm returns to the second step.
The point in the true trajectory with the biggest departure from the abstracted profile proposed at the first iteration will always be the maximum depth point of any given profile (Fig 3.1d). This is because the point in the true trajectory that is most inconsistent with a straight-line representation of the dive (a line joining the start and end of the trajectory at zero depth) will be the deepest point in the dive. After identifying the first breakpoint, the selected time-depth point is added to the abstracted dive profile, which until now consisted of a single segment. Now, two new line segments can be defined: dive start to breakpoint 1 and breakpoint 1 to dive end, creating a V-shaped dive (Fig 3.1e). The maximum vertical departure is recalculated for each line segment (Fig 3.1f) and the greater of the two is selected as the next breakpoint and added to the profile (Fig 3.1g, 3.1h).

This process is repeated until the desired number of breakpoints is reached, and the resulting piecewise linear abstracted profile has been constructed. Ordinarily, after \( n \) iterations, the profile would be made up of \( n \) time-depth points and \( n+1 \) line segments. In the case of the CTD-SRDLs programmed according to CTD_GEN_07B, there are four breakpoints in the abstracted profile, even though five iterations are completed (Fig 3.1n). The residual error of the abstracted profile with five points is calculated and stored (R5, the maximum residual error prior to the addition of the fifth point) but no further points are added to the profile. The time-depth point to which R5 corresponds is not stored. At full resolution, R5 is a measure of fit of the abstracted profile with four points to the true trajectory, since it is the maximum absolute discrepancy between the original samples and the transmitted profile, in decimeters (P. Lovell pers. comm.). R5 is not sent in full resolution, but is reduced to one of four depth bins for transmission (0 to 6m, 6 to 12m, 12 to 18m and > 18m) (P. Lovell pers. comm.). This leaves four complete iterations of the algorithm, although a fifth iteration needs to be carried out in order to obtain R5, even though the point to which it corresponds is not saved.

When the abstraction process is complete, a successful transmission of dive data includes four time points (T1:T4), the corresponding four depths points (D1:D4), and a binned version of the maximum residual error (R5) for the profile defined by the four time-depth points and the two surface points. The order in which the time-depth points were selected (Fig 3.1o) and the time-depth point to which R5 applies are not stored or transmitted.
The technical details of the data collection routines that are carried out on-board CTD-SRDLs programmed according to the tag program CTD_GEN_07B are described in Appendix I, and by Boehme et al. (2009) with particular focus on the hydrographic data collection.

3.2.2 Reversing the broken-stick algorithm

The reason memory has not been allocated to transmitting a measure of fit in high resolution is that it can to some degree, be calculated post hoc. This exercise had not been carried out systematically until now. The abstracted profile is undoubtedly an information-poor version of the true trajectory, but since the abstraction process is known exactly, abstracted profiles contain more information than the $n$ points selected by the BSm.

Constructing the dive zone involves several steps. First, the BSm is run on the detailed or abstracted dive trajectory (illustrated using both a detailed, Fig 3.1, and an abstracted, Fig 3.2, trajectory as would generally be the case) to produce an abstracted dive with four breakpoints. The profile segments that are proposed at each of the $n$ iterations and their resulting residual values are stored: at $i=1$, the first residual, $R_1$, is calculated (Fig 3.2d) and a 2-segment profile is constructed (Fig 3.2e), at $i=2$, $R_2$ is calculated (Fig 3.2f), and a 3-segment profile is constructed (Fig 3.2g), etc., up to $i=4$, $R_4$ and a 5-segment profile. This is done to identify the order in which the points where added, as a means of determining the magnitude of the final residual. When the $4^{th}$ and last iteration is completed, the abstracted profile is made up of 4 breakpoints and 5 line segments, and it is known with certainty that there were no points in the true trajectory that had a greater vertical residual value than the last point, $R_4$, added to the abstracted profile (Fig 3.2j). All other depth points in the true trajectory will now have a smaller vertical distance to the abstracted profile.

At each iteration a zone can be drawn around the dive reflecting the size of the biggest known residual (illustrated up to $n=9$ breakpoints and $n+1=10$ segments, to investigate the adequacy of $n=4$, Fig 3.3). However, the residual of interest, e.g., $R_4$, cannot be applied directly to the entire profile to obtain upper and lower bounds of the dive zone. The dive zone (the area enclosed by the limits defined by the profile with 4 breakpoints $\pm R_4$) should only be symmetric around 4 of the 5 line segments, between breakpoints. $R_4$ is calculated based on the difference between an abstracted profile with 3 breakpoints and the true dive
path. Therefore, the last two line segments, arising from the addition of the 4th breakpoint, should not have a symmetric zone about them. R4 is the biggest departure of the true trajectory from the abstracted one, but only around the segment that was “broken” at the time-depth location of the fourth breakpoint. At this stage, no information is available about the residuals with respect to the two new line segments arising from the addition of the 4th and final breakpoint and R4 can only be projected in one direction, towards the 4th breakpoint. The resulting effect is that the 4th breakpoint touches the limit of the dive zone, which was constructed based on the distance of the 4th point from the abstracted dive profile with 3 breakpoints (Fig 3.3d). For data received in abstracted form, R5 is not known at high enough resolution to be of use in the construction of the dive zone.

To construct a confidence zone around the abstracted dive profile, a number of equally spaced time points are selected at which to sample vertical sections of the time-depth space. For both detailed and abstracted dive data, the resolution of time points should match, at best, but not exceed, the resolution at which depth data were collected by the tag and this will give smoother limits to the zone in which the true trajectory must have occurred. At each of these chosen time points the estimated lower and upper depth bounds define the depth interval through which the true trajectory will have passed. The narrowing of the dive zone around the breakpoints is due to the fact that depth at these points is known with certainty (see Appendix I). Lastly, no point in the true profile will be deeper than the maximum depth recorded by the tag (within the limits of the tag’s software specifications and recording range, see Appendix I), so the dive zone is truncated at a depth corresponding to the deeper limit of the depth bin to which the maximum dive depth belongs (Fig 3.3, see Appendix I section 7.7 for details on why depths received from the tag are, effectively, binned).

3.2.3 Assessing goodness of fit

3.2.3.1 Abstracted dives: R4 and the dive zone index

For dives received in abstracted form, the only way to assess the goodness of fit of the abstracted profile with respect to the trajectory is the value of R4. The approximation of a non-linear path will improve as the number of points that are used to approximate it
increase. This should be reflected in a reduction in the size of the maximum vertical residual as the number of BSm iterations increases. In absolute terms, a small value for R4 means that the biggest vertical outlier in the true path was a small distance away from the abstracted path, which might be expected to suggest a better fit. In the absence of detailed dive data (when detailed dive data are not available), a reliable and unbiased way of measuring goodness of fit is required to assess the accuracy of abstracted profiles, irrespective of the depth and duration of a dive. However, the R4 value is not an objective way of assessing goodness of fit over the whole dive, since it refers to a single point, the maximum error in the profile. Furthermore, the same R4 value can result from many different dive trajectories. The way R4 manifests over the whole dive depends on the maximum depth of the dive and on the slopes and lengths of the segments that make up the abstracted profile (Fig 3.3). Only the effect of maximum dive depth on R4 is explored here. The area of the dive zone is a better measure of fit, since it does contain information on the whole dive, and features the geometric effects that result from the slopes and lengths of the segments that make up the abstracted dive (Fig 3.3). However, deeper and longer dives will have a bigger dive zone area (Fig 3.4, 3.5a) and these effects need to be removed before a valid comparison between dive zone areas can be made. An index was derived to objectively compare the area of the dive zone between dives, removing the effect of the duration and the maximum depth of each dive. To construct the dive zone index the distances between the upper, $u_{pi}$, and lower, $lo_{li}$, limits (heights) of the dive zone were calculated for each time step $i$ in a dive and summed over the number of time steps, $n$. The sum of heights was then divided by the product of the maximum dive depth, $maxdep$, and the dive duration, $divedur$.

\[ dz.index = \frac{\sum_{i=1}^{t_{\text{max}}} u_{pi} - lo_{li}}{maxdep \times divedur} \]

Equation 3.1

3.2.3.2 Detailed dives: R4, the dive zone index and RSS

For detailed dive data, goodness of fit could also be assessed using the sum of squared residuals (residual sum of squares, RSS) between the true and abstracted depths,
\[ RSS = \sum_{i=1}^{n} (T_i - A_i)^2 \]

Equation 3.2

where \( T_i \) is the \( i \)th depth in the true profile, \( A_i \) is the \( i \)th depth in the linearly interpolated abstracted profile, and \( n \) is the number of time steps in the dive (Fox 1997).

The dive zone index was calculated for the 10 detailed study dives from one northern elephant seal, and 4,000 abstracted dives from 45 southern elephant seals instrumented in four different field seasons (1,000 dives each from two post-moult deployments and two post-breeding deployments) over two years (ct40 and ct45 in 2008, ct49 and ct58 in 2009) at the island of South Georgia, South Atlantic (Table 3.1).

The relationship between the three measures of fit (R4, dive zone index and RSS) was investigated graphically for both types of data. For the abstracted data the size of the residual error at the fourth iteration (R4) was investigated in relation to the dive zone index, while for the sample of 10 detailed dives, the relationship between R4, the dive zone index and the RSS was investigated in relation to the number of iterations of the algorithm, from one to nine.

Computer code for all routines described was written in R (R Development Core Team, 2011) and can be found in Appendix II.

3.3 Results

3.3.1 Assessing goodness of fit

3.3.1.1 Abstracted dives: R4 and the dive zone index

As expected, there was a diffuse relationship between maximum dive depth and residual size (Fig 3.5a), suggesting that there are other aspects of the dive that influence the residual size, aside from dive duration. Above a threshold of depth, deep dives are longer, by necessity, while longer dives need not be deeper, which might explain the lack of
relationship between R4 and dive duration. There was also a diffuse relationship between maximum dive depth and the dive zone index (Fig 3.5b). The relationship between R4 and the dive zone index was more defined. A linear trend was apparent but with substantial variability, especially at lower R4 values (Fig 3.5c).

3.3.1.2 Detailed dives: R4, the dive zone index and RSS

The availability of dive data with high temporal resolution made it possible to study the relationship between R4 and RSS for the BSm profile with four points, as well as the evolution of the size of the residual error and RSS with increasing iterations. This provided a link between abstracted and detailed profiles. The observed relationship between the size of the residual and the number of iterations for this sample of ten dives confirmed this (Fig 3.6). It also supports the choice of four iterations to represent dives by BSm abstraction, while having to satisfy other constraints imposed by tag software and hardware since the gain in reduction of the residual is relatively small from the fourth iteration onwards.

The relationship between the dive zone index and residual size was linear between iterations, from iteration two to ten, and was consistent for all ten dives within a given iteration (Fig 3.7a). This relationship was considered to be representative of dives in general, because the ten dives used in this case study had a similar dive zone index for their maximum dive depths to dives collected from southern elephant seals (Fig 3.5b). The maximum dive depths and residuals from the study dives were consistent with the average values for R4 and maximum dive depth (Fig 3.5a), though the dive zone indices were on the lower end of the scale (Fig 3.5c) suggesting they were relatively well represented by the BSm.

The dive zone index changed in a similar way in increasing iterations for all ten dives, despite different maximum dive depths (Fig 3.8). The absolute size of the dive zone index for different dives varied at low numbers of iterations, but converged to similar values by the fourth iteration. The relationship between the dive zone index and the iteration number, viewed in order of increasing RSS at four iterations of the BSm, showed that dives with a smaller dive zone index at all iterations of the algorithm, tended to have a smaller RSS value.
at the fourth iteration (Fig 3.9). This can also be seen in the relationship between log-transformed RSS values and the dive zone index (Fig 3.10).

3.4 Discussion

Data abstraction is a necessary evil for many types of telemetry devices deployed on wide-ranging marine species such as seals, particularly when devices cannot be recovered and when geographic and temporal data coverage are of interest. This has been the case for deployments of CTD-SRDLs on southern and northern elephant seals, and datasets collected using this software configuration can consist of many hundreds of thousands of dives. Previous dive data analyses have examined the relationship between shape characteristics of time-depth profiles and the function of the dive (e.g., Schreer and Testa 1995, Schreer et al. 1998). Trying to deduce functional relationships from abstracted behavioural data can be challenging because much of the information is stripped away during the abstraction process. The incentive for this work has been to develop methods for extracting as much information as possible from existing and historical dive data and potentially, to inform future software design by identifying aspects of the current algorithms that can be improved.

The BSm was adopted in the context of dive abstraction as a working solution to the problem of linearly approximating a non-linear path in the vertical dimension with as little information possible, while retaining biologically relevant information. The software for CTD-SRDLs has been designed to collect and transmit information about in situ hydrographic conditions and several different aspects of the behaviour and ecology of the animal carrying the tag, of which diving is but one. With a finite budget for energy, memory and an upper limit to transmission rate, collection and transmission of different types of information is a multifaceted trade-off. Even without considering constraints on the amount of information used to represent an approximated dive, there exists a best approximation for a finite-dimensional linear space, such as depth (Powell 1981). It is clear that the BSm does not generate the best possible approximation of the true dive, but that is not its purpose. Nonetheless, in a comparison of methods for detecting abrupt changes in habitat-species relationships using simulated data, Ficetola and Denoël (2009) found that piecewise
regression or broken-stick models are most suitable for accurately detecting the position and probability of change-points, compared with Generalized Linear Models (GLMs) or Generalized Additive Models (GAMs). They also noted that the performance of broken-stick models is particularly good when the rate of change in the time-series being approximated is large, an effect also found in this analysis.

When using the BSm for dive abstraction, the number of iterations is critical to the quality of the abstracted dive. A preliminary investigation of the adequacy of different numbers of iterations resulted in the standard use of, effectively, four iterations of the algorithm, resulting in a total of six points (two surface points and four BSm breakpoints) and five linear segments, to each dive. In addition to the BSm breakpoints, the next largest residual error is also transmitted (R5), but not the location of point that this residual corresponds to. This value is sometimes of use if it is smaller than the residual at the fourth iteration. However, caution should be exercised when considering R5. It cannot always be preferred over R4, even when it is smaller. In some cases, particularly for short, shallow dives with rapid changes in depth, the use of R5 in the construction of the dive zone can result in parts of the abstracted trajectory falling outside the dive zone. This is because the fifth residual is being projected above and below the abstracted trajectory without knowing where the fifth point occurs. The lack of change in the shape of the trajectory creates a mismatch between the dive zone and the abstracted trajectory. The current investigation of the adequacy of four iterations of the algorithm confirms that it achieves a satisfactory result for a given amount of tag resources, in terms of the relative magnitude of the residual. This confirms that the information gained in the transmission of a fifth breakpoint would be small.

This analysis demonstrates that dive duration, maximum dive depth, R4, and the dive zone index developed here, do not fully explain the goodness of fit of the abstracted profile, as measured by RSS. In general, dives with smaller dive zone indexes had smaller RSS values but a bigger sample of detailed dives is required to illustrate the relationship further. It is likely that additional data regarding the sinuosity of the time-depth path, such as the variability in depth increments in the detailed dive data, is required to inform the construction of the dive zone. The exact mechanism by which maximum dive depth, dive duration and sinuosity interact to produce the area of the dive zone is not clear, but in
general, it seems that shorter dives with straighter paths, and smooth changes in depth are better represented by the BSm abstraction than “wiggly” or lengthy dives, although very deep dives can also produce small dive zones, based on their dive zone index. This is counter-intuitive in some ways since deeper dives tend to be longer dives, given a relatively narrow range of swim speeds for efficient transport during the descent and ascent phases of a dive (Davis and Weihs 2007). In addition, the ratio of the number of time steps to BSm points will be high for deep dives, but when variability in the change in depth is low, even depth deep dives can be well represented with four breakpoints. Because of the inverse relationship between sampling resolution and dive duration on-board SRDLs (see Appendix I), this could be an artefact of the fact that depths available to the BSm have a coarser temporal resolution for very long dives than for short dives. A worthwhile future direction would be the investigation of specific effects of R4 on the geometric shape of the dive zone (through segment lengths and slopes) and the way this affects its area.

In this chapter, the performance of the BSm was assessed and a relative index of the quality of abstracted profiles was developed. The size of the final residual for a given number of iterations of the BSm cannot be used in isolation to describe the goodness of fit of abstracted dive profile to the original dive trajectory. An index of the area of the dive zone that accounts for the maximum dive depth and the duration of a dive was found to generally be in keeping with the size of RSS value, but the relationship was not clear based on the small sample of study dives used here. These results suggest that additional estimates on the properties of the path may be required to improve the estimate of the dive zone index. With regard to telemetry devices, it may be that at the cost of a few extra bits being transmitted, a small amount of additional information on the sinuosity of the path could improve the post hoc estimation of dive path properties for dive profiles abstracted using the BSm.

This investigation has raised many interesting questions regarding the relationships between measureable aspects of abstracted dive profiles and their goodness of fit to the true profile prior to abstraction. By using a larger dataset of detailed dives from elephant seals, and quantifying the relationships that were identified here, it will be possible to develop a reliable, quantitative measure of how well abstracted dive profiles represent the
true profile. Considering that large numbers of abstracted dive profiles are collected from many different species and used to make biological inferences about the behaviour of the instrumented animals, it seems essential that a method for assessing the accuracy of these abstracted dives is made widely available. A way of doing that would be to make the R code for the generation of the dive zone and any measures of fit that are derived, available as an R package. Lastly, an investigation of alternative algorithms for the linear and non-linear approximation of time-depth dive profiles on-board CTD-SRDLs, given known energy and memory constraints, would be an interesting and worthwhile exercise.
3.5 References


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Fedak M, Lovell P, McConnell BJ and Hunter C. 2002. Overcoming the contraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integrated and Comparative Biology* 42: 3-10


### 3.6 Figures and Tables

Table 3.1. Deployment information for the detailed dataset from a northern elephant seal (*M. angustirostris*) from which the sample of 10 study dives were taken, and the abstracted dataset(s) from southern elephant seals (*M. leonina*) which were used as a comparison. For southern elephant seals axial girth was not available, and length is given as the mean ± standard error.

<table>
<thead>
<tr>
<th>Deployment</th>
<th>Species</th>
<th>Deployment location</th>
<th>Deployment period</th>
<th>Sampling regime</th>
<th>Morphometrics</th>
</tr>
</thead>
<tbody>
<tr>
<td>NA</td>
<td><em>M. angustirostris</em></td>
<td>Año Nuevo CA, USA</td>
<td>23/08/2008 to 16/02/2009</td>
<td>On three-day duty cycle</td>
<td>Length: 350.0 cm</td>
</tr>
<tr>
<td>ct40</td>
<td><em>M. leonina</em></td>
<td>Husvik, South Georgia Island</td>
<td>28/01/2008 to 09/12/2008</td>
<td>As per CTD_GEN_07B</td>
<td>Length: 250.5 ± 29.0 cm (Females)</td>
</tr>
<tr>
<td>ct45</td>
<td><em>M. leonina</em></td>
<td>Husvik, South Georgia Island</td>
<td>17/10/2008 to 01/02/2009</td>
<td>As per CTD_GEN_07B</td>
<td>Length: 248.7 ± 9.2 cm (Females)</td>
</tr>
<tr>
<td>ct49</td>
<td><em>M. leonina</em></td>
<td>Husvik, South Georgia Island</td>
<td>28/01/2009 to 12/01/2010</td>
<td>As per CTD_GEN_07B</td>
<td>Length: 240.5 ± 13.2 cm (Females)</td>
</tr>
<tr>
<td>ct58</td>
<td><em>M. leonina</em></td>
<td>Husvik, South Georgia Island</td>
<td>22/10/2009 to 05/02/2010</td>
<td>As per CTD_GEN_07B</td>
<td>Length: 249.5 ± 11.7 cm (Females)</td>
</tr>
</tbody>
</table>
Figure 3.1. A step-wise illustration of the time-depth dive profile abstraction routine, using the broken-stick model, implemented on-board SMRU CTD-SRDLs with the CTD_GEN_07B software specifications. The red line represents the true time-depth dive path and the solid black lines represent the proposed BSm abstracted dive path at each iteration of the algorithm. The numbers represent the order in which points are added to the abstracted profile. Points 0 and 5 are known from the start since they mark the beginning and end of the dive. The dashed black lines represent the residuals that are calculated at each time step between the true and abstracted dive paths (component figures labelled a to o from left to right).
Figure 3.1 (continued)
Figure 3.2. Reversing the broken-stick model for abstracted time-depth dive profiles received from CTD-SRDLS with CTD_GEN_07B software specifications. The black line represents the abstracted time-depth dive profile received from the tag. The red points represent known breakpoints. Here, the solid red lines the proposed BSm abstracted dive path at each iteration of the algorithm and the dashed red lines represent the residuals that correspond to known breakpoints (component figures labelled a to k from left to right).
Figure 3.3. Illustration of the construction of the dive zone and its evolution up to ten iterations of the BSm (component figures labelled a) where the dive zone is based on R1, to i) where the dive zone is based on R9, from left to right).
Figure 3.4. Graphical representation of the performance of the BSm for 10 consecutive dives, using the residual sum of squared differences (RSS) between the true depth and the abstracted depth at each time step (component figures labelled a) Dive 1 to j) Dive 10)
Figure 3.4 (continued)
Figure 3.5. a) The relationship between maximum dive depth and residual size (R4), b) the relationship between maximum dive depth and dive zone index, and c) the relationship between residual error (R4) and the dive zone index with the size of the dive label indicating the magnitude of the RSS for that dive. Data from the 10 detailed dives are compared with 4,000 abstracted dives.
Figure 3.6. The relationship between the maximum vertical residual and BSm iteration number for 10 dives.

Figure 3.7. a) The relationship between the dive zone index and residual size for 10 detailed dives, coloured by the number of iterations of the BSm algorithm (R1 corresponds to one iteration, R2 to two etc) b) The relationship between R4 and residual size labelled with the dive number 1 to 10.
Figure 3.8. The relationship between dive zone index and the iteration of the BSm (1:9) for 10 detailed dives in order of occurrence (left) and in order of maximum dive depth (right). The shade of the panels corresponds to the maximum depth of the dive, according to the legend.
Figure 3.9. The relationship between dive zone index and the iteration of the BSm (1 to 9) for 10 detailed dives in order of increasing RSS value at the 4th iteration. The shade of the panels corresponds to the maximum depth of the dive, according to the legend.
Figure 3.10. The relationship between dive zone index and log of the RSS for ten study dives for 1 to 9 BSm iterations. Labels include the dive number, the maximum dive depth (m) and R4 (m).
Using random walk models to reconstruct time-depth trajectories and depth use of diving elephant seals (*Mirounga* spp.)
4.1 Introduction

The previous chapter described the derivation of the abstracted dive profile, and the idea of reverse-engineering the broken-stick algorithm (BSm) to produce a time-depth space in which the dive is known to have occurred, termed the ”dive zone”. Apart from providing a confidence envelope around the BSm-derived dive profile, the dive zone also facilitates inference about a seal’s behaviour beyond the piecewise linear abstracted dive profile that is generated. In this chapter, I use a movement model to estimate the trajectory of an animal through the dive zone. With this approach, any abstracted dive profile can be restored to an estimated continuous two-dimensional time-depth profile from dive data delivered by CTD-SRDL.

One potential use of a more detailed estimated trajectory than the abstracted profile is to derive a scalar metric of depth use (one spatial dimension) within a dive. This makes it possible to estimate where in the water column elephant seals spend most of their time. Having a better way to quantify their vertical niche will make it possible to investigate where and when elephant seals exploit different resources and how their potential exposure to risk (natural or anthropogenic) changes in space and time. Deriving this estimate from a more detailed dive profile than the abstracted one will provide more accurate inferences on depth use.

The BSm itself is a model for the dive path, using the depth data recorded by the tag to produce an abstracted dive path without making assumptions about the process generating the path, or the uncertainty associated with it. It is employed deterministically on-board the tag and dictates the process by which a detailed dive profile arrives at its abstracted, observable form. Even though a BSm profile does not offer enough information to make it possible to propose different, true dive paths for a given abstracted profile, or to be able to judge how likely each one of those is, it defines the limits within which a mechanistic model for animal movement in the vertical dimension can operate, by means of the dive zone.

The time-series’ generated by CTD-SRDLs and other similar telemetry instruments provide discrete-time snapshots of a continuous-time process for an individual, in this case, a diving
seal. This is described as a Lagrangian dataset in the animal movement literature (Smouse et al. 2010, Nathan et al. 2008, Bartumeus et al. 2005, Royer et al. 2005), where the focus is on individual movement trajectories, rather than the density of space use by many individuals at a given point in time or over a set period. Random walk movement models form a flexible and widely used framework for modelling individual animal movement in two spatial dimensions (e.g., Turchin 1998, Jonsen et al. 2005, Codling et al. 2008, Johnson et al. 2008). They lend themselves to the analysis of telemetry data, which can be thought of as an empirical representation of the continuous movement path of the animal. The random part of the name of these models refers to stochasticity, and is a modelling convention (Turchin 1998), because it would not be helpful to model animal movement in a deterministic way, since we are trying to learn about the mechanisms driving it. Random walk models (RWs) are used extensively as a starting point in modelling movement because of their well-understood properties and expandability (Turchin 1998, Colding et al. 2008). An important advantage of RWs is that they can be combined with a model of how movement data are collected in a state-space framework (described below) to distinguish the biological mechanisms underlying observed data from the measurement error arising from the observation process.

A random walk is typically a continuous time stochastic movement process. It is often approximated in discrete time in the context of analysing animal telemetry data where the location of an animal in space at the following time step is proposed by drawing values from a statistical distribution that is thought to describe the movement variables, e.g. step length, direction etc. In its most basic form, a simple random walk model (SRW), the location of an animal depends only on its location at the previous time step. This minimalist approach (Lima and Zollner 1996) is often a suitable starting point for modelling individual movement, which is likely to affected by many intrinsic and extrinsic factors. Using this isotropic random walk to describe movement might not be realistic for long-lived marine top predators such as seals, where memory and previous experience are likely to be important. However, random walk models can include many different realistic aspects of animal movement, such as tendency to move towards a centre of attraction (drift), physical effects such as inertia, or intrinsic information regarding the internal state of the animal and extrinsic information regarding the animal’s environment (Morales et al. 2004, Schick et al. 2008). Drift or bias
(tendency to move in one direction) and persistence (tendency to maintain direction) can be incorporated to inform the model of the animal’s movement characteristics. In the case of dive data for which a dive zone can be derived, as described in the previous chapter, an additional component is that there are known constraints on the animal’s position in the water column, not based on biological aspects of behaviour, but known as a result of the data collection process, which could be viewed as an example of a random walk with barriers (Codling et al. 2008).

Under the B5m, all points within the dive zone at a given time point are equally likely to occur in a trajectory. This is dictated by the observation process. However, some combinations of points or realizations of dive trajectories will be more probable than others, given physiological limits and behavioural characteristics of the species under study. This introduces two plausible “depth” spaces (plausible state-spaces) for the dive. One is dictated by the data collection process, as defined by the limits of the dive zone, and one dictated by the physiology and behaviour of the diver. It is the combination of these two spaces that contains the most likely trajectories. This means that before fitting any model to the dive path, information is available from two different sources.

Some other features of the data and study species help form a modelling framework for a one-dimensional (i.e., depth only) dive path. Since the data come from an air-breathing diver, the point of attraction is the surface, where all dives begin and end. Unlike the case of movement in two spatial dimensions, movement in time and depth occurs in one direction away from the surface and the opposite direction towards the surface, so this is a special case of an Ornstein-Uhlenbeck process for terrestrial animals that might move in all (horizontal) directions from a central point (Blackwell 2003). In addition, diving is a biased movement process in which the bias is predictable in time relative to the duration of a dive, whereby some proportion at the beginning of the dive will always be biased downwards, away from the surface, and some, not necessarily equal, proportion at the end of the dive will be biased upwards towards the surface. To begin with, it is simplest to assume a random walk without including additional information, such as drift, about movement in depth. Drift is implicit in diving, as mentioned above and is included in the more realistic models developed here.
There are two components to consider in representations of dives generated by telemetry devices, such as CTD-SRDLs, where processing occurs on-board. One is the observed process, which in this case is generated by the abstraction algorithm implemented on-board the tag. The other is the unobserved biological process, which generates the true (as measured by the tag) time-depth profile prior to abstraction. State-space models (Patterson et al. 2008) which can link the observation process to the underlying diving process are ideal for the analysis of these data.

State-space models (SSMs) are effective tools for describing the evolution of movement processes through time (Jonsen et al. 2003). A useful feature is that with them it is possible to incorporate the error arising both from the sampling process in the form of measurement error, as well as the uncertainty in the biological process of interest (Patterson et al. 2008, Schick et al. 2008). The depths that make up the underlying, true dive trajectory form a time-series that we seek to predict using sparse data returned by the tag. Discrete-time state-space models require that the process be sampled at regular time points within the observation model. The nature of the dive profile abstraction by broken-stick is such that the four depth points are sampled at different time points for every dive. This is implicit to any method that is used to choose important points in a time-depth profile. In this case, the issue of irregular timing of the abstracted dive data can be overcome by imputing the observation process from the dive zone at the relevant resolution for each dive.

With these features of data and analytical options in mind, three mechanistic models of animal movement are developed here: i) diffusion in one spatial dimension (an isotropic random walk); ii) informed diffusion (a random walk with informative Bayesian priors); and iii) biased vertical diffusion (a biased correlated random walk). They are tailored to the characteristics of the data and the abstraction algorithm, using all available information about the diving process linking the observed (abstracted time-depth profile) and unobserved (true, detailed time-depth profile) components of a dive. The models are developed in a state-space framework, using Bayesian statistical methods to reconstruct a two-dimensional time-depth trajectory of the abstracted dive within the limits of the dive.
zone, and infer the animal’s (one-dimensional and within a single dive) use of the water column.

State-space models need not be implemented in a Bayesian framework, but given the availability of prior knowledge on diving, it is the most appropriate for this work. Under a Bayesian approach, observed data are combined with prior information to yield a posterior density distribution for the parameters of interest, which represents what is known about these parameters. Here, the aim is to estimate the movement parameters that result in the true depths visited during a given seal dive (e.g. the rate of vertical displacement) and make behavioural inferences based on the estimated time-depth trajectory. In this context, the rate of vertical displacement is not a single estimate with some variance, instead it is contained in a conditional probability distribution of estimates for the rate of vertical displacement given the observed data and prior distribution, and is known as the posterior distribution.

The shape and parameters describing a posterior distribution are not usually known but can be found analytically if the distribution is simple enough. This is seldom the case when dealing with ecological examples (Clark 2005). Alternatively, the distribution of estimates for the rate of vertical displacement can be approximated using a Markov chain, a memoryless random process that evolves through time (Gelman et al. 2003). If the Markov chain has been constructed so that at each step it will tend to get closer to the true distribution of the rate of vertical displacement, and is allowed to complete enough time steps, it is expected to converge on a good approximation of the target posterior distribution. There are many ways to construct the Markov chain. One of the most commonly used algorithms is the Gibbs sampler (Geman & Geman 1984). It is attractive because it can be quick to converge and has been implemented in a number of software packages, but it is less flexible than other methods in that only standard statistical distributions can be used for the priors (Gelman et al. 2003). The Metropolis-Hastings algorithm is a more general sampler for constructing a Markov chain but can take longer to converge.

Once the target distribution has been reached, the samples that make up the Markov chain contribute to the posterior density of the parameter of interest. This method for obtaining
the integral of a multi-dimensional distribution is called Monte Carlo integration (Gelman et al. 2003). The construction of a Markov chain and Monte Carlo integration (Markov Chain Monte Carlo, MCMC) are used together to make inference about unobserved processes. This is the method used here for the development of movement models for diving with Gibbs sampling.

In software for Bayesian analyses (including that used here, JAGS), variability is specified as the inverse of variance (precision) and called \( \tau \), where \( \tau = \frac{1}{\sigma^2} \). When linked to movement parameters, \( \tau \) describes the inertia of the moving particle (the diver), the inverse of its mobility, and is referred to throughout as inertia.

The piecewise linear trajectory resulting from interpolating between time-depth points selected by the BSm, and the model-reconstructed dive paths were compared with the detailed depth data for a case study sample of ten consecutive dives from one northern elephant seal to assess the performance of each of the three movement models. Prior information for these models was drawn from this high-resolution dataset of 3,251 dives at 4 sec resolution (for details see chapter 3: Table 3.1). This included all dives collected during the deployment of a prototype archival instrument on a 3-day duty cycle, except the 3-day file from which the case study dives were taken. The estimation process was validated by simulation and prior sensitivity analysis. The results of this study are two-fold: the reconstructed dive trajectory and the density distribution of depths were compared with the true trajectory and depth density profile from the data. The consequences of the BSm and each SSM model in terms of the emergent depth use profile are illustrated.

4.2 General methods

A one-dimensional isotropic random walk in depth was used as the starting point, based on the assumption that it is a good approximation of the true process (mechanism) underlying a single dive. Two further models were developed as extensions of the method to include more biological realism in the process model. The key ideas here were a) including an empirically derived relationship that tailors the prior for inertia in vertical displacement on a dive-by-dive basis, and b) introducing a bias to the movement model relative to the point of
maximum dive depth as a drift parameter that gives the animal a tendency to move
downwards until the maximum depth, and then upwards until the end of the dive. These
extensions to the simple random walk model resulted in a model where the prior for inertia
was selected as a function of the maximum dive depth for that dive, and a model where in
addition to having a tailored prior for overall inertia, the dive was considered to be the
product of a mixture of two processes, one with a downward drift and one with an upward
drift.

The models listed above are different versions of the process model, describing the
mechanism underlying a seal dive. The observation model was the same in all three
movement models, based on the dive zone, whose derivation was described in chapter 3.
Code for all models can be found in Appendix II (sections 8.2 to 8.4).

4.2.1 Process models

4.2.1.1 Simple Random Walk (SRW) model

For the isotropic random walk the model was initiated at the sea surface, where depth is
equal to zero, \( d_1 = 0 \). According to this model, successive depths through a dive were
generated from a Normal distribution centred on depth at the previous time step, with
inertia, \( \tau \), drawn from a Gamma distribution, to ensure it was positive valued.

\[
\begin{align*}
    d_{t+1} & \sim N(d_t, \tau) \\
    \tau & \sim \Gamma(k_\tau, \theta_\tau) \\
    k_\tau & = \frac{\mu_\tau^2}{\sigma^2_\tau}, \theta_\tau = \frac{\sigma^2_\tau}{\mu_\tau}
\end{align*}
\]

Equations 4.1

The shape, \( k \), and scale, \( \theta \), parameters for the Gamma distribution were selected to reflect
the distribution of the variance of inertia (the increments in vertical displacement) from the
high-resolution dataset (mean \( \mu_\tau = 0.25 \), variance \( \sigma^2_\tau = 0.03 \)). In this model the same prior
distribution was used for all dives so \( k \) and \( \theta \) were static (Appendix II: section 8.2).
4.2.1.2 SRW model with an informative prior

The main limitation of the SRW was that the prior on inertia of the dive path specified values that were too small for some dives and too large for others. This led to the investigation of this parameter with respect to other aspects of the dive, such as maximum dive depth and dive duration, in the high-resolution data. A strong inverse relationship between inertia and maximum dive depth suggested that the variability in vertical displacement per 4 sec time step was greater in deeper dives (Fig 4.1). This empirically derived relationship was included with the effect that the prior for inertia was tailored on a dive-by-dive basis (Appendix II: section 8.3). The relationship was formalized in a logistic regression model with the inverse of the variance of depth increments, i.e., inertia ($\tau$, range 0.028 to 1.611) as the response variable, and maximum dive depth ($maxdep$, range 9.45 to 1392.25) as an explanatory variable and with Gamma distributed errors and an inverse link function. The model was fitted in R using the glm function (R Development Core Team 2011).

The data for inertia were underdispersed ($\phi = 0.141$), which might be due to the fact that all dives in the dataset come from a single individual. In spite of the underdispersion, there was no evidence for a severe lack of fit of the model based the size of the residual deviance compared to the degrees of freedom ($\phi$ indistinguishable from 1) (Faraway 2006). The data and the line of fit are shown in Fig 4.1. Visual inspection of the standard errors of the fit revealed a positive relationship between the fitted values and the size of their standard errors. To account for this, a logistic regression model with Gamma distributed errors was fitted to the relationship between maximum dive depth and the standard errors (range $4 \times 10^{-4}$ to $36.9 \times 10^{-4}$) associated with the inertia predicted by the regression model. This provided a measure of spread of the predicted values of inertia for a dive with given maximum depth, and was converted to and used as the variance of the prior for inertia, $\sigma^2$, to appropriately regulate the mean of the prior distribution, $\mu$. The model for the errors was checked for goodness of fit as above, without evidence for any problems, but visual inspection of the predicted values suggested this was only a moderately good fit to the data. This was not seen as a cause for concern here since the fitted values are used as priors only.
Since the prior came from the data being modelled (excluding the file from which the ten case study dives were taken) it was expected to be appropriate, even if the signal was weak.

This depth-specific simple random walk model ensured that the prior for inertia was always tailored to the dive being reconstructed.

\[
\begin{align*}
  &d_{t+1} \sim N(d_t, \tau) \\
  &\tau \sim \Gamma(k_\tau, \theta_\tau) \\
  &k_\tau = \frac{\mu_\tau^2}{\sigma_\tau^2}, \theta_\tau = \frac{\sigma_\tau^2}{\mu_\tau} \\
  &\mu_\tau = \frac{1}{\beta_{0,\mu_t} + \beta_{1,\mu_t}(\text{maxdep})} \\
  &\sigma_\tau^2 = \frac{1}{\beta_{0,\sigma^2_t} + \beta_{1,\sigma^2_t}(\text{maxdep})}
\end{align*}
\]

Equations 4.2

The coefficients from the logistic regression models for inertia ($\beta_{0,\mu}$ and $\beta_{1,\mu}$) and the residual error standard errors associated with the predicted inertia ($\beta_{0,\tau}$ and $\beta_{1,\tau}$) were on the scale of the linear predictor (inverse link) and had to be back-transformed to obtain $\mu_\tau$ and $\sigma_\tau^2$.

4.2.1.3 Biased and Correlated Random Walk

As a third step, the model was developed further into a biased random walk, in which the direction of bias changes relative the point of maximum depth in the dive (Appendix II: section 8.4). No drift was assumed in the two previous models, so that the random walk was unbiased in its direction throughout the dive within the limits of the dive zone. Here, movement was given a downward bias, $\xi_1$, from the beginning of the dive until the time point where the maximum dive depth occurred, $t_{\text{maxdep}}$, followed by an upward bias, $\xi_2$, from the time of the maximum dive depth to the end of the dive, $t_{\text{max}}$.

These parameters were calculated on a dive-by-dive basis by assuming that the direction of vertical displacement increments (generally downwards until the maximum dive depth,
followed by a switch to generally upwards until the surface) was the result of a mixture of distributions of two drift parameters, \( \xi_1 \) and \( \xi_2 \), depending on the timing at which the maximum depth point was reached, \( t_{\text{max dep}} \), as a proportion, \( p \), of the duration of the dive, \( t_{\text{max}} \) (Matthiopoulos 2011). Given that the overall mean \( \mu_t \) and the variance \( \sigma_t^2 \) for the mixture were known from Equations 4.2, and the mean, \( \mu_{\xi_1} \), and variance, \( \sigma_{\xi_1}^2 \), for one of the mixture’s components could be estimated in a similar way, then the remaining two parameters, \( \mu_{\xi_2} \) and \( \sigma_{\xi_2}^2 \), corresponding to the mean and variance of the second drift component, could be calculated as follows.

\[
p = \frac{t_{\text{max dep}}}{t_{\text{max}}}
\]
\[
\mu_t = p\mu_{\xi_1} + (1 - p)\mu_{\xi_2}
\]
\[
\sigma_t^2 = p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + (1 - p)(\mu_{\xi_2}^2 + \sigma_{\xi_2}^2) - \mu_t^2
\]

Finding \( \mu_{\xi_2} \):

\[
\mu_{\xi_2} = \mu_t - p\mu_{\xi_1}
\]
\[
(1 - p)\mu_{\xi_2} = \mu_t - p\mu_{\xi_1}
\]
\[
\mu_{\xi_2} = \frac{\mu_t - p\mu_{\xi_1}}{(1 - p)}
\]

Finding \( \sigma_{\xi_2}^2 \):

\[
\sigma_{\xi_2}^2 = p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + (1 - p)(\mu_{\xi_2}^2 + \sigma_{\xi_2}^2) - \mu_t^2
\]
\[
(1 - p)(\mu_{\xi_2}^2 + \sigma_{\xi_2}^2) = \sigma_t^2 - p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + \mu_t^2
\]
\[
\left(\mu_{\xi_2}^2 + \sigma_{\xi_2}^2\right) = \frac{\sigma_t^2 - p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + \mu_t^2}{(1 - p)}
\]
\[
\sigma_{\xi_2}^2 = \frac{\sigma_t^2 - p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + \mu_t^2}{(1 - p)} - \mu_{\xi_2}^2
\]

(Using \( \mu_{\xi_2} = \frac{\mu_t - p\mu_{\xi_1}}{(1 - p)} \))

\[
\sigma_{\xi_2}^2 = \frac{\sigma_t^2 - p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + \mu_t^2}{(1 - p)} - \left(\frac{\mu_t - p\mu_{\xi_1}}{(1 - p)}\right)^2
\]
\[
\sigma_{\xi_2}^2 = \sqrt{\frac{\sigma_t^2 - p(\mu_{\xi_1}^2 + \sigma_{\xi_1}^2) + \mu_t^2}{(1 - p)} - \left(\frac{\mu_t - p\mu_{\xi_1}}{(1 - p)}\right)^2}
\]

Equations 4.3
The prior for the mean of first drift parameter, \( \mu_{\xi_1} \) (beginning of the dive until the maximum depth point), its inertia \( \sigma_{\xi_1}^2 \), and the mean and variance of the overall inertia, \( \mu_r \) and \( \sigma_r^2 \), were calculated for each dive individually using regression models, as for the SRW with an informative prior. The model for the prior on \( \mu_{\xi_1} \) was a linear regression model with normally distributed errors, with the increments in vertical displacement in the first part of the dive as the response. The model was fitted with the \texttt{lm} function in R (R Development Core Team 2011). The full model had maximum dive depth, the proportion \( p \) and the interaction between maximum dive depth and \( p \), as explanatory variables. Model selection was carried out using the \texttt{dredge} function in the \texttt{MuMIn} library in R that compares models with all possible subsets of the covariates and ranks them according to AIC (Bartón 2011), and the full model was found to be the best fit (Akaike weight=1), with an adjusted \( R^2 \) value of 0.72 suggesting the model captured most of the variability in the “descent” drift, \( \mu_{\xi_1} \).

There was no systematic relationship between the response and the standard errors of the fitted values for this component so the square of the mean standard error of the predicted values, \( s^2 \), was used as the variance of \( \mu_{\xi_1} \), \( \sigma_{\xi_1}^2 \), in its prior distribution.

First drift component:

\[
\sigma_{\xi_1}^2 = s^2
\]

\[
\mu_{\xi_1} \sim \Gamma(k_{\xi_1}, \theta_{\xi_1})
\]

\[
k_{\xi_1} = \frac{\mu_{\xi_1}^2}{\sigma_{\xi_1}^2}, \theta_{\xi_1} = \frac{\sigma_{\xi_1}^2}{\mu_{\xi_1}}
\]

\[
\mu_{\xi_1} = \beta_{0,\xi_1} + \beta_{1,\xi_1}(\text{maxdep}) + \beta_{2,\xi_1}(p) + \beta_{3,\xi_1}(\text{maxdep})(p)
\]

Equations 4.4

The coefficients from the models described above were used to calculate an appropriate prior for \( \xi_1 \), its inertia \( \sigma_{\xi_1}^2 \), and the overall mean and inertia of depth increments throughout the whole dive. These were then used to calculate the second drift parameter \( \mu_{\xi_2} \) and its inertia \( \sigma_{\xi_2}^2 \) deterministically within the model, according to Equations 4.3 to inform the movement model appropriately.
Second drift component:

\[
\mu_{\xi_2} = \frac{\mu_\tau - p\mu_{\xi_1}}{(1 - p)}
\]

\[
\sigma^2_{\xi_2} = \frac{\sigma^2_\tau - p(\mu^2_{\xi_1} + \sigma^2_{\xi_1}) + \mu^2_\tau}{(1 - p)} - \left(\frac{\mu_\tau - p\mu_{\xi_1}}{(1 - p)}\right)^2
\]

Equations 4.5

This relationship was tested with a small sample of detailed dive data (four dives) and was found to be highly accurate (Table 4.1).

The addition of these two drift components introduced bias to the random walk model to reflect the descent and ascent phase of dives, as well as having a tailored prior on inertia. Using the mixture distribution to determine the relative point at which the bias should change from downward to upward made the model flexible enough to predict the variability between different dive profiles.

4.2.2 Observation model

Based on the data-collection process, described in chapter 3, all dive paths within the limits of the dive zone are equally plausible, so the observed data were imputed as the depth midpoint of the dive zone at each time-point. This imputed path together with the distance above and below each midpoint to the dive zone boundary represents the data that were observed.

\[
D_t \sim U(d_t - \frac{1}{2} \Delta d, d_t + \frac{1}{2} \Delta d)
\]

Equation 4.6

As a result of the unusual situation of knowing the boundaries to any dive path for a given abstracted dive it was necessary to implement interval censoring of the depths generated by the process model. Censoring was implemented by specifying that the depth proposed by the process model for the next time step, \(d_{t+1}\), be uniformly distributed within the range
of depths resulting from adding to and subtracting from it half the height of the zone at that time step.

If this condition did not hold true, the likelihood was invalid, resulting in another depth being drawn from the normal distribution as the depth at the next time step (see Appendix II: section 8.2). This setup allowed depths proposed by the movement model to be accepted conditional on being in agreement with the observation model. This condition was implemented in all versions of the process model.

4.2.3 Estimation

All data processing and model fitting was carried out in R (R Development Core Team, 2011). The state-space models were written and implemented in R using the rjags package for JAGS 2.1.1 (Plummer 2003, Plummer 2011). All models were run for 100,000 updates of the Gibbs sampling algorithm using two Markov chains. The initial values for each Markov chain were sampled from a uniform distribution between the upper and lower limits of the dive zone at each time step. The first 10,000 iterations were discarded as burn-in. Posterior estimates were thinned to every 10th value resulting in 9,000 estimates of depth at every time step. Models were initialized at depth of 0 m using the mean values of the prior distributions as initial parameter values for the drift parameters and inertia. Mixing between the two chains and convergence were checked visually. The performance of the models in terms of trajectory reconstruction was assessed using sum of squared residuals (RSS) between the true dive profile and the posterior mean reconstructed dive profile, as described in the previous chapter.

4.2.4 Validation with simulated data

Before using these SSMs to reconstruct real dives, a simulation study was carried out to validate the estimation process for the basic model, the SRW. Validating the models’ ability to correctly estimate the movement parameters of a dive trajectory generated by a random walk process verifies that if the true underlying dive process is well approximated by a random walk then it will be possible to correctly estimate the parameters that describe it. In addition, exploring the behaviour of the model under different prior condition helps assess its robustness to mispecified or highly variable prior distributions of the parameters.
An isotropic random walk was used to simulate a time-depth dive profile with known movement parameters. Depth at the first time step was set to -0.001 m depth. Conditional on depth values being negative (below the sea surface), depth at the next time step was drawn from a Normal distribution centred on depth at the previous time step and with a standard deviation of 3.16 (inertia 0.1). This value was chosen because it represented the highest density in the distribution of the high resolution data. The simulation was terminated when a positive depth value was drawn. This last value was replaced with a zero and the time-series of depths was saved as a simulated dive (Appendix II: section 8.5).

The simulated dive was subjected to the abstraction routines that would have been carried out on-board a CTD-SRDL (chapter 3) and the SSM model was run using the resulting dive zone data, monitoring inertia. The posterior estimates of the inertia parameter were compared with the value used to generate the data and the effect of different prior parameter distributions on the model’s ability to estimate movement parameters was investigated.

The performance of the SSM was assessed based on whether the inertia parameter for depth used in the simulation was estimated correctly. Two dives were chosen, one short dive (54 time steps) and one long dive (290 time steps). In this context, the sampling resolution was the same whether the dive was short or long even though this is not the case for dives abstracted on-board the tag. Either way, by using a fixed number of time and depth points to represent abstracted dives, a bigger proportion of information will inevitably be lost during the abstraction of longer dives. Four different prior parameter distribution scenarios were investigated for inertia to find out what the effect of prior information was on the estimation procedure and the posterior estimates for this parameter. The model was run using each of the following prior distribution setups for inertia for the short simulated dive and the long simulated dive: accurate and precise (mean 0.1, variance 0.001), accurate and imprecise (mean 0.1, variance 0.003), inaccurate and imprecise (mean 0.3, variance 0.01) and inaccurate and precise (mean 0.3, variance 0.0005).
4.2.5 Application to real data

Each of the three models described above was applied to detailed depth data from a sample of ten consecutive dives. Depth measurements in this ground-truthing dataset were sampled at 4 sec resolution with 10cm (1 dm) accuracy, recorded by a prototype logging device which incorporated a standard SRDL and a three-axis accelerometer, deployed on a male northern elephant seal (*Mirounga angustirostris*) at Año Nuevo, Santa Cruz in August 2008 (for deployment information and morphometrics see chapter 3: Table 3.1). The prior distributions for movement parameters were drawn from a dataset of 3,251 dives from a single northern elephant seal, all dives recorded by the accelerometer-SRDL apart from the three-day depth record from which the sample dives were drawn (chapter 3: Table 3.1). For the SRW and the SRW with an informed prior, the only parameter to be estimated was inertia. For the BRW overall inertia, drift and its inertia during the first phase of the dive (beginning of the dive to maximum depth point) were estimated stochastically and used to calculate drift and its inertia in the second phase of the dive (from the maximum depth point to the end of the dive) deterministically according to the mixture equation (Equations 4.3).

A by-product of reconstructing the dive path in a Bayesian setup is that it is possible to reconstruct a profile of depth use during the dive, as an image, using the density of the posterior distribution of depth estimates. This was done for the true profile, the abstracted (BSm) profile, and the posterior estimates from each of the three SSMs. For the true profile, densities were generated based on the raw depths using the same number of depth bins for each dive, based on achieving a 5 m depth resolution for the deepest dive considered, Dive 2. For the BSm, densities were generated using 10,000 depth values drawn from a uniform distribution between the lower and the upper boundary of the dive zone for each dive. Finally, for the three movement models, densities were generated based on the 9,000 posterior estimates of depth at each time step of each dive.
4.3 Results

4.3.1 Validation with simulated data
On the whole, the estimation procedure of the precision for depth was robust. Inertia was estimated more or less correctly for both the long and short dive, with some variability, for all but the fourth prior distribution scenario (inaccurate and precise prior on inertia) where the posterior estimate was drawn towards the inaccurate prior and away from the truth (Fig 4.5, Fig 4.9). There was more bias in the case of the shorter dive, even with an accurate and precise prior (Fig 4.2 short dive: mean estimate 0.087 ± 0.020, Fig 4.6 long dive: mean estimate 0.106 ± 0.021), but the standard deviation was the same in both cases.

4.3.2 Application to real data
The simplest model, the simple random walk with a general prior, performed worst, and in some cases (e.g., Dive 5, 6, 8, 10) had a higher RSS score than the BSm (Fig 4.10, Fig 4.11). The biased random walk performed best, on average, in terms of absolute similarity to the true path. This can be seen in terms of the decrease in RSS score compared to the BSm (Fig 4.10, Fig 4.11). Even though the posterior distribution of depth estimates from this model was narrowest, the true path sometimes fell in the lowest density band of the posterior distribution (Fig 4.10). The most consistently reliable model for reconstructing the dive path was the simple random walk with an informative prior, since the posterior almost always contained the true path (Fig 4.10). The RSS for this model was on a par with the biased random walk and sometimes lower (Fig 4.11).

The depth use profiles for the BSm and the simple random walk model were similarly broad and diffuse, bearing little similarity to the true depth profile of the dive (Fig 4.12). The random walk model with an informative prior for inertia, selected as a function of the maximum depth of the dive, and the biased random walk performed much better than the other two methods. The latter produced the narrowest focal depth use estimates and both methods sometimes missed the finer details in the true depth use profile. The sequence of dives and their depth-use profiles according to the best-performing of the SMMs are shown in Fig 4.13.
4.4 Discussion

A dive by an air-breathing mammal can be represented by a time-series of depths, at a given time resolution, and can be thought of as a random walk in the vertical dimension, generated by an interaction of biological processes. This is the rationale for the modelling framework that has been developed in this chapter and the following one. The process models were specified in discrete time continuous space to simplify model estimation and interpretation (McClintock et al. 2012) even though the biological dive process is continuous both in space and time.

The estimation procedure for reconstructing dive paths using a simple random walk model was found to be sensitive to inaccurate and imprecise priors, insofar as the values used here are concerned, though more simulated dives are required to validate this more rigorously. This was addressed in the modelling framework by incorporating an empirical relationship between the magnitude of the inertia for change in depth, and the maximum depth of that dive, as a more appropriate prior. Maximum dive depth is a statistic that is commonly returned by telemetry instruments so if this relationship can be verified with more high-resolution dive data from other individuals, it will prove a useful tool for informing the process model for more accurate estimation.

This observed relationship is likely to be a manifestation of the fact that when seals carry out deep dives, the proportion of the dive that is taken up by traveling from and to the surface is increased. Seals and other marine animals have a minimum cost of transport speed that is used to reduce the energy expenditure during travel (Thompson et al. 1993). The way in which vertical speed corresponds to actual swim speed depends on the angle at which the animal is swimming. As the swimming angle approaches vertical, the observed vertical speed should approach actual swim speed. Hassrick et al. (2007) found that swim speed in elephant seals increased with depth of the dive. In contrast, Gallon et al. (2007) found that for captive grey seals swim speed approached the minimum cost of transport in deeper dives of increased duration. If the objective during a dive is to maximize time at the deepest depth reached during a dive, while maintaining a speed that minimises energetic costs (Thompson et al. 1993), then deeper dives should have steeper descent and ascent.
angles. Le Boeuf et al. (1992) found that dives with flat bottom time-depth profiles had similar angles of descent but steeper angles of ascent than other dives. Presumably, the combination of relatively invariant, high transit speeds, steeper angles of descent and ascent, and shorter phases of little change in depth in deeper dives, interact to produce the relationship between maximum dive depth and inertia that was found for this dataset.

The addition of the empirical relationship between inertia for change in depth and the maximum dive depth dramatically improved the model’s ability to estimate dive depth, an effect which was also reflected in the depth use profiles produced by the second and third model. The visual representation of results showed that the simplest movement model consistently underestimated inertia, which resulted in the posterior distribution containing the whole dive zone, without providing any extra information about the true dive profile. None of the models were able to faithfully reconstruct the dive path at a resolution higher than that of the BSm in terms of the small-scale depth changes. This might suggest that the abstracted dive path with four points at depth simply does not contain enough information to identify these small-scale features of a dive. Additionally, it could be that the model formulation itself is one that does not adequately capture the diving process. This could be due to a random walk being unsuitable for describing movement during a dive, or a lack of appropriate behavioural information to inform the process. The addition of this sort of information is explored in the following chapter.

The examination of the performance of these models could be carried out more rigorously by computing Gelman-Rubin-Brooks ratios to evaluate the relationship of the variability within and between Markov chains (Gelman et al. 2003). In future development of these models, the Markov chains should be initiated at different depth points to make it possible to rigorously check for convergence.

Trajectory reconstruction aside, the potential applicability of a dive’s depth use profile is substantial. There is an increasing demand for maps of spatial usage for marine animals as part of environmental impact assessment exercises and conservation initiatives. Being able to quantify depth use and add a third dimension to usage maps will increase our
understanding of the ecology of marine species, and their potential prey and contribute to the ability to mitigate impacts by anthropogenic activities.
4.5 References


Clark JS. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8: 2-14


4.6 Figures and Tables

Table 4.1. Constituents of the mixture distribution for the BRW model for a sample of five dives (Dive 1 to Dive 5) from the ten study dives. Parameters $\mu_t$ (overall mean vertical displacement), $\sigma_t^2$ (variance in overall mean vertical displacement), $p$ (proportion of dive duration at which maximum dive depth occurs), $\mu_{\xi_1}$ (mean vertical displacement from the beginning of the dive to the point of maximum dive depth), and $\sigma_{\xi_1}^2$ (variance in vertical displacement from the beginning of the dive to the point of maximum dive depth) interact according Equation 4.3 to generate estimates of $\mu_{\xi_2}$ (mean vertical displacement from the point of maximum dive depth to the end of the dive) and $\sigma_{\xi_2}^2$ (variance in mean vertical displacement from the point of maximum dive depth to the end of the dive). True values for $\mu_{\xi_2}$ and $\sigma_{\xi_2}^2$, calculated from each dive, are also provided for comparison.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Dive 1</th>
<th>Dive 2</th>
<th>Dive 3</th>
<th>Dive 4</th>
<th>Dive56</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_t$</td>
<td>0.007</td>
<td>0.001</td>
<td>-0.005</td>
<td>-0.013</td>
<td>-0.007</td>
</tr>
<tr>
<td>$\sigma_t^2$</td>
<td>11.920</td>
<td>12.332</td>
<td>13.324</td>
<td>12.309</td>
<td>13.434</td>
</tr>
<tr>
<td>$p$</td>
<td>0.367</td>
<td>0.373</td>
<td>0.785</td>
<td>0.374</td>
<td>0.756</td>
</tr>
<tr>
<td>$\mu_{\xi_1}$</td>
<td>-2.957</td>
<td>-3.603</td>
<td>-1.452</td>
<td>-3.329</td>
<td>-1.409</td>
</tr>
<tr>
<td>$\sigma_{\xi_1}^2$</td>
<td>3.979</td>
<td>4.493</td>
<td>6.144</td>
<td>5.166</td>
<td>7.230</td>
</tr>
<tr>
<td>ESTIMATED</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\mu_{\xi_2}$</td>
<td>1.724</td>
<td>2.149</td>
<td>5.279</td>
<td>1.968</td>
<td>4.345</td>
</tr>
<tr>
<td>$\sigma_{\xi_2}^2$</td>
<td>14.395</td>
<td>14.774</td>
<td>25.539</td>
<td>14.684</td>
<td>23.521</td>
</tr>
<tr>
<td>TRUE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\mu_{\xi_2}$</td>
<td>1.728</td>
<td>2.150</td>
<td>5.282</td>
<td>1.975</td>
<td>4.360</td>
</tr>
<tr>
<td>$\sigma_{\xi_2}^2$</td>
<td>8.429</td>
<td>4.587</td>
<td>3.741</td>
<td>6.012</td>
<td>7.408</td>
</tr>
</tbody>
</table>
Figure 4.1. The relationship between inertia (inverse of variance) and maximum dive depth for 3,251 detailed dives (described by a GLM with a Gamma error distribution). Different colours represent dives from different three-day records of continuous data. Deeper dives have lower precision (higher variance) in depth increment than shallow dives.
Figure 4.2. A simulated short dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an accurate and precise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.3. A simulated short dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an accurate and imprecise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.4. A simulated short dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an inaccurate and imprecise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.5. A simulated short dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an inaccurate and precise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.6. A simulated long dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an accurate and precise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.7. A simulated long dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an accurate and imprecise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Simulation
Long dive
Inaccurate, imprecise prior

Figure 4.8. A simulated long dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an inaccurate and imprecise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Simulation
Long dive
Inaccurate, precise prior

Figure 4.9. A simulated long dive path, its abstracted dive profile and dive zone (top row). The reconstructed posterior mean dive trajectory from the SRW with an inaccurate and precise prior for inertia, and central credible intervals for its posterior distribution, and a comparison of the prior and posterior distribution for inertia (bottom row).
Figure 4.10. The dive zone and reconstructed mean dive paths for dive 1 to dive 10 and posterior distributions for the three movement models: the simple random walk with the same inertia prior for all dives, the simple random walk with an informative prior tailored to each dive individually according to its maximum depth, and the biased random walk with two drift components.
Figure 4.10 (continued)
Dive 3

Figure 4.10 (continued)
Dive 4

Figure 4.10 (continued)
Figure 4.10 (continued)
Dive 6

Figure 4.10 (continued)
Dive 7

Figure 4.10 (continued)
Dive 8

Figure 4.10 (continued)
Dive 9

Figure 4.10 (continued)
Dive 10

Figure 4.10 (continued)
Figure 4.11. A comparison of the RSS values between the true dive path each of the four dive reconstruction methods for ten study dives: the broken-stick model (BSm), the simple random walk (SRW), the simple random walk with an informative prior on inertia (SRWinf.prior), and the biased random walk (BRW). The BSm profile and model-reconstructed profiles were based on an abstracted profile with six time-depth points (four iterations of the BSm abstraction algorithm) as would be the case for data received from CTD-SRDLs.
Figure 4.12. Detailed dive profiles and depth use profiles for dive 1 to dive 10 generated from the detailed dive data (TRUTH), the BSm dive zone (BSm), the simple random walk movement model with a general prior (SRW), the simple random walk model with specific prior, based on the relationship between precision and maximum dive depth (SRW inf. prior) and the biased random walk model (BRW).
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.12 (continued)
Figure 4.13. Detailed dive profiles in sequence (upper panel) and depth use profiles generated from the biased random walk model (lower panel).
Developing movement models for diving elephant seals
(*Mirounga* spp.) with state switching
5.1 Introduction

There is a sustained interest in determining at-sea body condition and identifying behaviours in widely-ranging marine species in areas where they cannot be directly observed (e.g. Biuw et al. 2003, Bailleul et al. 2007, Biuw et al. 2007, Thums et al. 2008, Biuw et al. 2010, Dragon et al. 2010, Robinson et al. 2010, Simmons et al. 2010, Aoki et al. 2011, Thums et al. 2011). The world oceans remain a partially understood biological, geochemical and oceanographic system. The mechanisms by which large, abundant marine predators, such as elephant seals, exploit their environment provides links to the conditions that they find favourable, which in turn are manifestations of the way biotic and abiotic features of the environment interact to generate biological productivity in the upper trophic levels. Depths routinely visited by air-breathing divers who forage at depth indicate potentially profitable regions in vertical space. The conditions or resources found at the targeted depths, at the geographical and temporal location of a dive, provide information about what resources predators might be exploiting. Detailed information about within-dive behaviour might also make it possible to infer foraging strategies and foraging success over multiple dives, which could be linked to and compared with estimates of relative changes in body condition (Biuw et al. 2003, Aoki et al. 2011). The modelling framework described here introduces a Bayesian, mechanistic approach to modelling diving using a multi-state random walk model with behavioural covariates, which both inform the estimation process and make it possible to make inference about the parameters they approximate. This state-space model incorporates a biased random walk with state switching and the observation model described in chapter 4.

In the previous chapter, three random walk models were developed to reconstruct the time-depth trajectory of abstracted dives, recorded by CTD-SRDL telemetry devices, and make inferences about depth use during a dive. These models use behavioural parameters, such as directional bias, to reconstruct the time-depth trajectory but do not estimate behaviour itself during the dive. In this chapter the framework is developed further to make it possible to estimate behavioural parameters during the dive using a state-space model in a Bayesian framework. Here, movement is classified into three behavioural modes; “descent”, “bottom”, “ascent”, corresponding to movement phases within a dive, and each
state has associated with it state-specific behavioural parameter values. At each time step, the behavioural parameters are estimated, and determine the behavioural mode, which is used to inform the movement model through which estimates of the state variable, depth, are generated. The coefficients for the behavioural parameters also determine the probability of transition between behavioural modes.

The aim of this analysis is to develop a modelling framework with which to make inferences about the behaviour of seals at the temporal scale of individual dives and eventually over a sequence of dives to encompass whole migrations. Four covariates were identified as relevant and informative for modelling a dive: oxygen availability, degree of satiation, potential active foraging and potential prey encounter. The modelling framework is described in terms of all four covariates as a concept model, and the applicability of this type of model is illustrated by implementing a model with a single covariate, a proxy for oxygen availability, as a proof of concept with real data.

5.2 Methods

5.2.1 Model description

5.2.1.1 Concept model

Conceptually, the model developed in this chapter is based on those described in the previous one. The observation model is identical and the movement model is similar, based on a random walk in the vertical dimension (depth) with a prior for inertia in depth increments, selected on a dive-by-dive basis, according to an empirical relationship between maximum dive depth and inertia, from high-resolution time-depth data (see chapter 4). Throughout this chapter the term inertia is used to describe how much a variable is able to change from one time step to the next, defined as the inverse of its variance. High inertia means a parameter can only change slowly, in small increments, whereas low inertia means that a parameter can change quickly, in large increments. This model differs from those developed in the previous chapter in three ways, 1) each time-depth pair during the dive is described in terms of one of three behavioural modes, 2) the mode the animal is in at a
given time step will determine its movement characteristics, 3) transition between
behavioural modes is determined by four behavioural covariates.

The behavioural modes within the dive are considered distinct from each other, both in
their movement characteristics and their biological function. Descent and ascent phases are
considered to be transit phases to and from a favourable foraging depth. Especially in deep
divers like elephant seals, where the descent and ascent phases are typically long,

movement during these phases is characterized by relatively constant vertical speed and
bias in the direction of movement (on the vertical axis) and little foraging is expected to
occur, until past some depth threshold. High-resolution dive data collected in the context of
a stomach temperature study on southern elephant seals suggest that feeding events are
commonly associated with rapid changes in speed (Horsburgh et al. 2008), which supports
the idea that feeding during descent and ascent is rare. Visual inspection of high-resolution
time-depth data suggests that the bottom mode is better defined in some dives than others,
but is generally characterized by a reduction in vertical speed initially, and variable
direction. In some dives depth in the bottom mode is constant and with few excursions and
in others movement is erratic and vertical speed can be high. In both cases the tendency is
to maintain depth, with some variability, which makes this mode distinct from the
consistent downward or upwardly biased movement typical of descent and ascent. These
behavioural modes are termed behavioural states throughout this chapter. Movement in
each state is modelled as a biased random walk with its own drift and bias. The state the
animal is in determines its movement through state-specific movement parameters that
inform the movement model.

The behavioural parameters, described below in detail, interact to produce the probability
of transition from one state to the next, through the multinomial logistic distribution (MNL).
This formulation allows for the prediction of the probability of entering a given state based
on the values of the behavioural parameters in the current state, which allows us to use the
model to learn about the transition from one state to another and the relationship between
states, in addition to the resulting state. If the animal is currently in state $i$ the probability of
transition from state $i$ to state $m$, is $P_{m,i}(t)$, where $t = 1, ..., tmax$. This is written as a
continuous function of time and can be expressed as a MNL function. Terms $L_{im}(t)$ and
\( L_{jm}(t) \) are linear predictors comprising the intercept term, covariates \( X_k(t) \) of movement and their coefficients \( \beta_{k,i,m} \).

\[
P_{m,i}(t) = \frac{e^{L_{mi}(t)}}{\sum_{j=1}^{3} e^{L_{mj}(t)}}
\]

\( m, i \in \{1, 2, 3\} \quad t = 1, \ldots, t_{max} \)

\[
L_{mi}(t) = \beta_{0,i,m} + \sum_{k=1}^{4} X_k(t) \cdot \beta_{k,i,m}
\]

\[
L_{mj}(t) = \beta_{0,j,m} + \sum_{k=1}^{4} X_k(t) \cdot \beta_{k,j,m}
\]

Equations 5.1

The subscript \( m \) denotes behavioural state. The behavioural state at the current time step can be defined as \( M(t) \) and is used in place of \( m \).

\[
M(t + 1) \sim \text{Multinomial} \left( 1, P_{m,i}(t) \right)
\]

Equation 5.2

Once the probability of staying in the current state or entering one of the remaining two states has been calculated, the transition process from the state at one time step to the state at the next time step is modelled as a 1\textsuperscript{st} order Markov process.

The coefficients of each of the behavioural parameters exist as constants in a 3 x 3 transition matrix (Box 5.1). Each column of the matrix represents the state the animal is currently in, the state of origin, and each row in the matrix represents the states the animal can move to. Depending on which the current state is, \( M(t) = 1, 2 \text{ or } 3 \), the corresponding column in the transition matrix is used to calculate the vector of probabilities in the MNL distribution, according to which the next state is generated. The code used to implement this model can be found in Appendix II (section 8.6). A numbered overview of the concept state-space model is given in Box 5.1.

5.2.1.2 Parameters
The four behavioural parameters considered here were selected on the basis of measurable biological relevance to depth during a dive, using only its reconstructed time-depth profile and the time-depth profiles of previous dives. These were oxygen availability, degree of satiation of the animal, potential active foraging and potential prey encounter. Oxygen availability, potential for active foraging and potential prey encounter evolve within a dive whereas degree of satiation pools information across several dives. Because direct information on these parameters was not available, proxies were used in their stead. A bullet-point rationale for selecting these variables can be found in Box 5.2.

The proxy used for oxygen availability was time elapsed since the beginning of a dive. This is an index of an animal’s oxygen availability, or tendency to resurface, because diving capability varies from individual to individual, and the rate of oxygen consumption during a dive will depend on physiological parameters as well as activity level and has been shown to drop in longer dives (Sparling and Fedak 2004). Furthermore, in some species it has been shown that dive duration also depends on the quality of the patch encountered during a dive (Sparling et al. 2007b). Whatever the capability of a given individual, there is an upper limit to the distribution of dive durations it is capable of, and an observed mean dive duration for the sample of dives from an animal’s dive record.

The proxy for satiation was chosen as the cumulative number of time steps over a number of previous dives. As discussed in chapter 2, captive grey seals were found to extend bottom time in profitable patches (Sparling et al. 2007b), which suggests that the amount of time spent in the bottom phase of a dive might correspond to successful resource acquisition. A potential problem with this is that the inverse is not necessarily true, if a very profitable prey item is caught in a short amount of time spent in bottom state. The lack of a means of validation of successful prey capture or measure of the quality of a prey item for data collected using CTD-SRDLs means that it is still not entirely clear how bottom time relates to successful prey acquisition.

The proxy used for foraging was the number of consecutive time steps in the bottom state in a given dive. Based on the same premise as satiation, the longer an animal remains in
bottom state, where it is presumably searching for prey, the more likely it is to have been successful in capturing prey.

Lastly, the proxy used for prey encounter was depth at each time step. Dietary information on the prey of southern elephant seals from a wide range of samples and analytical techniques suggests that they feed on fish and squid species with some evidence for differences between sexes and age classes (Green and Burton 1993, Sinclair 1994, Brown et al. 1999, Daneri et al. 2000, Daneri and Carlini 2002, Cherel et al. 2008, Newland et al. 2009, Bailleul et al. 2010, Newland et al. 2011). Based on this, seals are more likely to be targeting some depths compared to others, depending on the prey type they are most likely to be exploiting and its distribution. This depth is expected to change on the scale of days, weeks, months, years and geographically (e.g. Biuw et al. 2010).

The state-specific drift parameter informs the movement model of how the animal is expected to move in each state, by introducing a bias to the random walk. A negative, downward bias is used for drift in the descent state, a zero drift in the bottom state, and a positive, upward bias is used in the ascent state. The inertia of each drift parameter in the movement model determines how variable the speed and direction of movement are likely to be.

5.2.1.3 Assumptions
The assumptions made here are that behavioural states are mutually exclusive and conditionally independent, that the proxies for behavioural covariates are good, and that the movement during diving in elephant seals can in fact be approximated by a random walk model in the vertical dimension. This model incorporates the conditional relationship between inertia and maximum dive depth, introduced in the previous chapter, so the assumption that that relationship holds also applies here. This framework is illustrated here using the time elapsed within a dive.

5.2.1.4 Example model
The process leading to the observed pattern of diving in elephant seals on a timescale of hours to days is poorly understood, both from a motivational and physiological perspective.
This makes it challenging to envisage the effect of all four behavioural covariates simultaneously and what values of their coefficients would achieve a realistic outcome, even within a single dive. However, considering the effect of each behavioural covariate on a dive and across several dives is conceptually tractable. A reduced version of the model was fitted to investigate how a proposed effect of one of them, the time elapsed since the beginning of a dive, can be implemented in the model as a proof of concept. For the purpose of simulating artificial test data, combinations of intercept and slope coefficients were explored manually (Appendix II: section 8.7) to achieve realistic-looking transition probabilities between states as a function of time through a dive and used as priors in the model (Fig 5.1). The empirically derived values for the nine intercept coefficients and nine slope coefficients (Appendix II: section 8.8) were used in the linear predictor of the MNL model (Equations 5.1) to generate the vector of three probabilities, one for each of the candidate states at the next time step.

5.2.2 Model priors
The model was provided with normally distributed priors for each of the nine intercept coefficients and nine time coefficients in the transition matrix. These were Normally distributed and centred on the empirically derived plausible values, with an arbitrary value for inertia for the first dive in the sequence of ten dives. The posterior distribution of each of the parameters was used as the prior in the following dive so that models were run sequentially. This was done to incorporate the information accumulated each time the model was run on a different dive.

Prior distributions for each state-specific drift parameter and its inertia selected based on a high-resolution dataset of 3,251 dives from one individual (see chapter 3 for details). Descent, bottom and ascent phases were identified for each dive based on change in vertical displacement. All dives were assumed to begin in the descent phase. The algorithm for identifying the end of the descent phase calculated a moving average of ten steps either side of each time-point in a dive, starting from the beginning of the dive. The end of descent was selected as the time-point where mean vertical displacement of the previous ten steps was smaller than -0.5 times the standard deviation of the mean rate of displacement over the whole dive, and the mean of the following ten steps was smaller than -0.3 times the
standard deviation. The algorithm for identifying the beginning of the ascent phase calculated a moving average of twenty steps either side of each time-point, starting from the beginning of a dive. The beginning of the ascent was selected as the time-point where mean vertical displacement of the previous twenty steps was greater than 0.3 standard deviations of the mean displacement over the whole dive, and the mean of the following twenty steps was greater than 0.7 standard deviations. The time steps between the end of descent and the beginning of ascent were assigned to the bottom phase. These rules were derived empirically and checked by eye for most dives, to produce a reasonable segmentation of dives into the three phases. The mean vertical displacement during each phase for each dive, and its variance were used in the model as the prior for drift in each behavioural state, specified as a Normal distribution (Appendix II: section 8.9).

The prior distribution for inertia of the state variable, depth, was chosen on a dive-by-dive basis through its relationship with maximum dive depth, as described in chapter 3.

5.2.3 Model estimation
The model was implemented using JAGS (Plummer 2003) in R, using the rjags (Plummer 2011) and MCMCpack libraries (Martin et al. 2011). A model was run using data from each of the ten case study dives used in chapter 3. Models were run for 100,000 updates of the MCMC sampling algorithm using two Markov chains. The first 10,000 iterations were discarded as burn-in and the rest were thinned to every 10th value resulting in 9,000 posterior estimates of depth at every time step. The model was initialized in the descent state, at depth of 0.5 m at the first time step, and 1.0 m at the next time step, using the mean values of the prior distributions as initial parameter values for state-specific drift (descent 3.34 m/4 sec, bottom 0 m/4 sec, ascent -3.37 m/4 sec) and each of the coefficients for the state transition matrix (Table 5.1). Mixing between the two chains and convergence were checked visually and no problems were identified.

5.2.4 Application to simulated data
A simulation study was carried out to validate the estimation process for this model (Appendix II: section 5.8). This exercise tested whether the parameters could be correctly estimated by the model when the process model was correct. The performance of the
model was investigated under four scenarios for the priors for the state-specific drift parameters: 1) accurate and precise priors, 2) accurate and imprecise priors, 3) inaccurate and imprecise priors, 4) inaccurate and precise priors. For the purpose of this exercise the behavioural coefficients for the intercept term, and time through the dive were fixed, to investigate the estimation of behavioural state.

The movement model used was a biased random walk with state-switching and known movement parameter values. In the simulation, depth was set to 0.5 m at the first time step and 1.0 m at the second time step, state was set to 1 (descent). Conditional on depth being below the sea surface (here, positive), mean depth at the next time step was calculated by adding the state-specific vertical drift to the depth value at the previous time step. A value for depth at the next time step was then drawn from a Normal distribution centered on this projected mean time step with a standard deviation of 2.00 (inertia: the inverse variance of the increments in vertical displacement), based on the detailed dive data. The behavioural coefficients were set to the values in Table 5.1. As in chapter 3, the simulation was terminated when a negative depth value was drawn (i.e. above the surface). This last value was replaced with a zero and the time-series of depths was saved as a simulated dive (Appendix II: section 8.8).

The simulated time-depth series was subjected to the abstraction routines that would have been carried out on-board a CTD-SRDL (chapter 3) and the SSM model was run using the resulting dive zone data, monitoring inertia in vertical displacement, state-specific drift, state and each of the nine coefficients for the two behavioural parameters, the intercept and time through a dive. The prior for state-specific drift in descent was specified as a Gamma distribution with shape and scale parameters selected to reflect the distribution of the descent and ascent drift components, selected from each dive in the detailed data as described above (descent drift 3.34m/4sec ± 1.56, ascent drift -3.37m/4sec ± 1.72). For vertical drift in the bottom state a Normal prior distribution was used to allow for drift to be positive or negative (bottom drift 0.01m/4sec ± 1.05). The posterior estimates of the inertia, the three drift parameters and behavioural coefficients were compared with the value used to generate the data and the effect of different prior parameter distributions on the model’s ability to estimate movement parameters was investigated. State estimation was checked
by comparing the timing of switches between estimated states with the switch points selected by the algorithm described above.

Four different prior parameter distribution scenarios were investigated for the coefficient of the parameter for time elapsed within a dive to find out what the effect of prior information was on the estimation procedure and the posterior estimates for this parameter. The model was run using each of the following prior distribution setups for the time coefficient: 1) accurate and precise, 2) accurate and imprecise, 3) inaccurate and imprecise, and 4) inaccurate and precise. The values used for the accurate and inaccurate priors are shown in Table 5.2 and the inertia of the coefficients was set to 0.022 standard deviations in the precise scenarios and 0.028 in the imprecise scenarios. The difference between precise and imprecise priors was small because the precise value was realistic and the imprecise value was the lowest possible inertia while ensuring convergence of the SSM.

5.2.5 Application to real data

Models were run sequentially on a sample of ten consecutive high-resolution dives made by a northern elephant seal (chapter 3: Table 3.1), the same dives used in the SMMs in the previous chapter. Here, the first dive in the sequence was provided with the Normally distributed accurate and precise priors used in the simulation, and Normally distributed priors for the intercept coefficient with inertia of 0.045 standard deviations. Thereafter the posterior distributions for the intercept and time coefficient from one dive were used as the priors for the next dive in the sequence, to provide the model with information regarding real dives. The state specific drift priors were the same for all dives and inertia in vertical displacement was chosen on a dive-by-dive basis (chapter 4).

5.3 Results

5.3.1 Application to simulated data

On the whole, the model estimated state correctly for the simulated data. The state switch points selected by the algorithm were 3.3 min for the end of descent, and 12.6 min for the start of the ascent. The model estimated state to be 1.38 ± 0.57 (mean ± standard deviation)
from the beginning of the dive until 3.3 min into the dive, \(1.90 \pm 0.49\) from 3.3 min to 12.6 min and \(2.80 \pm 0.40\) from 12.6 min till the end of the dive at 16.2 min.

State determination was robust in all four prior distribution scenarios (Fig 5.2 to 5.9). There was more variation in the estimation of state in the middle section of the dive with an inaccurate and imprecise prior (Fig 5.6). The reconstructed dive path was almost identical in all cases as were the estimates of state-specific drift parameters, which is unsurprising since the priors were the same. The standard deviation of the drift parameters was underestimated in all three cases, and the mean posterior estimates were different from but not inconsistent with the priors.

5.3.2 Application to real data

The performance of the SSM in terms of path reconstruction was variable. In two cases (dive 1 and 2, Fig 5.10, 5.11 and 5.12, 513) the SSM performed worse than the BSm judging by the RSS value of each trajectory, and almost identically in one case (dive 7, Fig 5.22 and 5.23). In the remaining seven cases the SSM performed substantially better than the BSm, halving the RSS value. A notable characteristic of the reconstructed trajectories of this SSM, which likely accounts for the improved RSS scores produced here, is that they are curvilinear, and hence more similar to the true path.

The descent and ascent drift parameters for all dives were estimated to be more extreme than the priors, with faster descent and ascent rates than the mean values from the detailed data. The posterior distribution for drift in the bottom state was variable but not as extreme as for descent and ascent and never wholly inconsistent with the prior (odd figure numbers between Fig 5.11 and 5.29). As for the simulated data, the model underestimated the variability of all drift parameters.

It is not possible to say whether state estimation was correct, since true states were not known for each dive. However, the model assigned sensible states to different segments of each dive, similar to the way I would have classified segments by eye.
5.4 Discussion

This chapter extended the state-space dive models developed in the previous chapter to facilitate the estimation of behavioural state within the dive and draw inferences about four different aspects of the diver’s behaviour. In practice, a reduced version of the model was fitted to a set of ten consecutive dives, with just one behavioural covariate, illustrating that it is possible to fit such models to data. It is possible that the full concept model is too computationally intensive to implement since the example model took over 17 hrs to run for a dive of approximately 400 time steps at a 4 sec interval (approximately 27 min). As mentioned in chapter 4, convergence of the Markov chains should be carried out more rigorously in future applications by computing Gelman-Rubin-Brooks ratios (Gelman et al. 2003).

The example model, though a reduced version of the concept model, provides proof of that fact that it is possible to incorporate behavioural parameters into a dive model with state switching, but also demonstrates that a model that only considers time elapsed though a dive is capable of producing sensible state estimates. The ability to reconstruct dive trajectories, often improving on the BSm trajectory, and gaining information about the variability of depth increments within a dive, was demonstrated in chapter 3, and confirmed here in the context of a more complex SSM. Although time elapsed through a dive was discussed in the introduction as being used as a proxy for oxygen availability through a dive, it cannot be interpreted as such in the example model. In the current, reduced model formulation, the coefficients for this covariate are scaled to account for the duration of each individual dive. This means that dives of different duration are treated as equal by the model so a switch to ascent state cannot be directly interpreted as reduced oxygen stores. In spite of this, the model performs well at identifying when the diver switches from state to state, and switch points selected by eye by a trained observer would be, in most cases, almost identical. That said, manual dive classification is an objective exercise.

This method offers a means of estimating the depths at which elephant seals focus their time while diving. It is assumed that this depth corresponds to biologically “interesting” areas where seals focus their searching, prey-finding and, ostensibly, their foraging effort. A
probabilistic view of this depth, and the way it evolves through time, can be obtained by forming a probability density distribution of the depths which the model assigned a “bottom” state to. The advantages of a probabilistic approach to depth use is that with it the need for using summary data stored on-board telemetry instruments, or describing depths with a simple scalar value can be avoided.

The computation time currently required for this model is greater than desired. With telemetry datasets often consisting of many thousands of dives, this method needs to be accelerated in order to be a practical option for processing abstracted dive data to obtain biological insight into long time-series of dives. One way of doing this would be to re-write existing code models in a lower level programming language.

Though reduced in biological realism compared to the concept model, the example model implemented here is a simplified but valid representation of the diving process in elephant seals. It incorporates a movement model to account for the observation process, and a process model that combines a movement model to describe and learn from the time-depth observations with state determination for making inferences about the behaviour of the animal in-dive. Behavioural aspects that were not considered in this framework are a more direct measure of satiation or cumulative foraging success over a time window of previous dives, and how to deal with non-foraging dives. Obtaining an independent measure of foraging success during a trip to sea, e.g. using relative measures of body condition derived from drift dives (Crocker et al. 1997, Webb et al. 1998, Biuw et al. 2003, Biuw et al. 2010, Thumbs et al. 2011), would make it possible to assess whether there is a signal for successful foraging in the time-depth profiles of dives. The issue of non-foraging dives is less readily tractable.

Functional classification of dives has been carried out for many seal species based on characteristics of the time-depth profile of their dives (Hindell et al. 1991, Schreer et al. 1998, Lesage et al. 1999, Photopoulos 2007, Thums et al. 2008), but validation of these functions and identification of one-to-one correspondence between dive shapes and dive functions is difficult (Kuhn et al. 2009). Dive shapes derived from low resolution telemetry data (e.g. from CTD-SRDLs) might be masking subtle differences in true shape, and further
to that, the same shape might correspond to more than one behavioural function (Tinker et al. 2007). Both preclude the identification of biological function of a dive based only on its time-depth trajectory. For many species including elephant seals, it is not clear if there are discrete traveling or other non-foraging periods within the dive record of an individual. This is in part because the complete picture of seal diet is not known so potential prey and potential foraging areas cannot be ruled out with confidence. In addition, it is not yet possible to identify foraging from time-depth information in the dive record arising from CTD-SRDLs without examining other aspects of diving and horizontal movement behaviour. In the context of trying to infer foraging from dives without knowing if foraging actually took place, the potential for travel or rest dives in which foraging is not “planned” or is opportunistically engaged in, should be noted.

This state-space dive model with state switching introduces a new approach to the analysis of abstracted dive data, such as those collected by CTD-SRDLs, and movement modelling in general. The ability to reconstruct a realistic, near-continuous dive trajectory from abstracted data is useful in itself, and a feature that is improved compared to the models in chapter 3. However, the strength and novelty of this SSM is that with it we are able to learn about aspects of the behaviour of a diver on dive-by-dive basis, based on the sparse observations and a representation of the diving process. The aspect of behaviour used to demonstrate the functionality of the example model developed in this chapter is vertical direction of travel as a function of time spent diving, represented by three states: decent, bottom, ascent. This is a quantitative representation of the time-depth dive profile, describing how the animal apportioned its time in the dive according to the three states. The timing of entry and exit from each state, the vertical speed of the diver during each state and the overall variability of vertical displacement are estimated by the model. More than making it possible to extract more information out of abstracted time-depth dive data, this approach offers an expandable, theoretically sound, and hopefully workable solution to the behavioural analysis of dive data from elephant seals, with application to any diving species on which CTD-SRDLs and standard SRDLs (Appendix I) are deployed.
5.5 Text boxes

Box 5.1. Step-by-step model description

1. Movement model for movement through zone, where

\[
d_{proj}(t) = d(t) + sState(t - 1) \\
d(t + 1) \sim N(d_{proj}(t), \tau)
\]

- \(d_{proj}\) is the projected depth of the animal
- \(sState\) is the true underlying mean vertical velocity for each movement state
- \(\tau\) the inertia parameter that controls the spread of the distribution from which depth at the next time step will be generated
- \(d\) is depth, or cumulative vertical displacement

2. Three movement modes were defined, each modelled as a biased random walk with its own drift and bias.

   1. Descending state: tendency to increase in depth
   2. Middle state: tendency to maintain depth
   3. Ascending state: tendency to reduce in depth

3. The probability of moving between modes was modelled as a 1\textsuperscript{st} order Markov process according to a 3 x 3 transition matrix. A multinomial logistic probability density function was used to estimate the probability of moving from one state to another, using a vector of parameter values for each of the behavioural covariates and a matrix of their coefficients (see Equations 5.1 and 5.2).

\[
M(t + 1) \sim \text{Multinomial}(1, P_{m,i}(t)) \\
P_{m,i}(t) = \frac{e^{L_{mi}(t)}}{\sum_{j=1}^{3} e^{L_{mj}(t)}}
\]
Box 5.1 (continued)

4. Behavioural covariates that characterize the multinomial probability of being in a state are defined. We would like each of these parameters (number of parameters is 4+1 for the intercept) and their coefficients (3 x 3 matrix) to be estimated by the model.

\[ td \] Proxy for oxygen availability: Time in dive \\
\[ tf \] Proxy for probability of foraging: The number of consecutive time steps in middle state \\
\[ cpf \] Proxy for satiation: Cumulative proportion of dive time spent in a sequence of successive, uninterrupted flat segments over some time window of previous dives \\
\[ d \] Proxy for prey encounter: Depth

5. Possible effects of covariates on transition probabilities

The transition probabilities are functions of the behavioural covariates defined above. These are not known but serve as proxies for oxygen availability, actual or expected prey encounter, potential for satiation, and potential for foraging.

<table>
<thead>
<tr>
<th></th>
<th>from D</th>
<th>from B</th>
<th>from A</th>
</tr>
</thead>
<tbody>
<tr>
<td>to D</td>
<td>-satiation -O₂ -prey enc</td>
<td>+satiation +O₂ -foraging</td>
<td>-satiation -O₂ +prey enc</td>
</tr>
<tr>
<td>to B</td>
<td>±satiation +O₂ +prey enc</td>
<td>-satiation -O₂ +foraging</td>
<td>-satiation +O₂ +prey enc</td>
</tr>
<tr>
<td>to A</td>
<td>+satiation +O₂ -prey enc</td>
<td>+satiation -O₂ -foraging</td>
<td>+satiation +O₂ -prey enc</td>
</tr>
</tbody>
</table>

- Satiation will be an index of the likely degree of satiation of the animal. Could be measured by cumulative segments in bottom mode, or change in buoyancy over a time window of previous dives.
- O₂ will be an index of the animal’s likely degree of oxygen depletion, measured as time through a dive. This could have a prior distribution of the observed distribution of dive durations.
- Foraging will be an index of the likelihood of the animal actually foraging, based on how long it has maintained a certain position in the water column.
- Prey encounter will be an index of the likelihood of the animal having encountered prey, based on the depth at which prey is found.
Box 5.2. Rationale for choosing behavioural covariates that might influence position in the water column during a dive

What might make you exit descent
- You encounter prey and change course to handle or pursue it
- Your prey item escapes and you pursue it
- You don’t encounter any prey so you give up and change course
- A prey item you were handling or chasing escapes and you return to a favourable depth to continue searching
- You’ve reached a depth where you expect to find prey
- You’ve reached a depth you want to travel at, or one that makes most sense for traveling dives which don’t really have dedicated bottom time
- Your oxygen stores are running low and you decide to return to the surface
- You’ve reached the bottom
- You stop travelling and rest/sleep
- Buoyancy (not clear how a rule might be derived for how this might affect movement, but worth keeping in mind)

What might make you want to leave a depth you are maintaining
- You encounter prey and change course to handle or pursue it
- You don’t encounter any prey so you give up and change course
- Your oxygen stores are running low and you decide to return to the surface
- You encounter a physical bathymetric feature that forces you to change course
- You perceive a threat (again, not clear how an animal would respond to perception of threat but as an air-breathing mammal it seems unlikely it would go downwards)
- You stop active swimming to rest/sleep and your buoyancy (almost always negative in adult elephant seals, as far as we know) dictates a bias to your passive drifting

What might make you exit ascent
- You encounter prey and change course to handle or pursue it
- Your prey item escapes and you pursue it
- A prey item you were handling or chasing escapes and you return to a favourable depth to continue searching
- You’ve reached a depth where you expect to find prey
- You’ve reached a depth you want to travel at
- You perceive a threat (again, we don’t really know how an animal would respond to perception of threat but as an air-breathing mammal I doubt it would go downwards)
- You stop active swimming to rest/sleep and your buoyancy (almost always negative in adult elephant seals, as far as we know) dictates a bias to your passive drifting
5.6 References


Brown DJ, Boyd IL, Cripps GC and Butler PJ. 1999. Fatty acid signature analysis from the milk of Antarctic fur seals and southern elephant seals from South Georgia: implications for diet determination. *Marine Ecology Progress Series* 187: 251-263


Newland C, Field IC, Nichols PD, Bradshaw CJA and Hindell MA. 2009. Blubber fatty acid profiles indicate dietary resource partitioning between adult and juvenile southern elephant seals. *Marine Ecology Progress Series* 384: 303-312


5.7 Figures and Tables

Table 5.1. Intercept and time coefficients used in the simulation and as starting values in the model. See Figure 5.1 for the resulting relationships between states and the probability of transition between states as a function of time (D=descent, B=bottom, A=ascent).

<table>
<thead>
<tr>
<th>Intercept</th>
<th>Time</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
</tr>
<tr>
<td>D</td>
<td>7</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
</tr>
<tr>
<td>A</td>
<td>-4</td>
</tr>
</tbody>
</table>

Table 5.2. Accurate and inaccurate coefficients used in the prior for the time coefficient in each state (D=descent, B=bottom, A=ascent).

<table>
<thead>
<tr>
<th>Accurate</th>
<th>Inaccurate</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>B</td>
</tr>
<tr>
<td>D</td>
<td>-0.055</td>
</tr>
<tr>
<td>B</td>
<td>0.020</td>
</tr>
<tr>
<td>A</td>
<td>0.055</td>
</tr>
</tbody>
</table>
Figure 5.1. Empirically and conceptually derived profiles for the probability of transition from one state to another for a dive of 17 min. The coefficients used to generate the profiles can be found in Table 5.1. Each profile shows the way the probability of leaving the current state (descent, bottom and ascent, from left to right) and entering another state (descent, bottom or ascent, coloured black, red and green)
Figure 5.2. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on a simulated dive with an accurate and precise prior on inertia of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.3 Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on a simulated dive with an accurate and precise prior on inertia of the coefficient for time through the dive.
Figure 5.4. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on a simulated dive with an accurate and imprecise prior on inertia of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.5. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on a simulated dive with an accurate and imprecise prior on inertia of the coefficient for time through the dive.
Figure 5.6. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on a simulated dive with an inaccurate and imprecise prior on inertia of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.7. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on a simulated dive with an inaccurate and imprecise prior on inertia of the coefficient for time through the dive.
Figure 5.8. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on a simulated dive with an inaccurate and precise prior on inertia of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.9. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on a simulated dive with an inaccurate and precise prior on inertia of the coefficient for time through the dive.
Figure 5.10. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 1 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.11. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 1.
Figure 5.12. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 2 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.13. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 2.
Dive 3

Figure 5.14. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 3 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Dive 3

Figure 5.15. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 3.
Figure 5.16. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 4 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.17. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 4.
Figure 5.18. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 5 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.19. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 5.
Figure 5.20. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 6 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.21. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 6.
Figure 5.22. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 7 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.23. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 7.
Dive 8

Figure 5.24. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 8 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Dive 8

Figure 5.25. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 8.
Figure 5.26. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 9 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.27. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 9.
Figure 5.28. The BSm dive zone and reconstructed posterior mean dive paths (upper row) for the multi-state random walk movement model run on dive 10 with a prior on inertia selected according to the maximum dive depth (see chapter 4 models) of the coefficient for time through the dive. The posterior estimates for behavioural state are shown as different colours on the time-depth profile of the dive and compared with the true behavioural state each time step (lower row). State 1 is descent, state 2 is bottom, state 3 is ascent.
Figure 5.29. Prior and posterior distribution of the drift parameter for each state for the multi-state random walk movement model run on dive 10.
6

Synthesis
6.1 Summary of work

With this collection of analyses I have investigated the use of space in the vertical dimension with respect to dive depth in three seal species, elephant seals and grey seals. Because diving and depth use are measured remotely using animal telemetry devices, there are practical difficulties relating to 1) knowing what information to record for studying depth use and how to summarize it, 2) getting information back at a relevant resolution, and 3) knowing how to interpret that information in the absence of independent observations. The methods developed in this thesis make use of dive data that have been collected using CTD-SRDLs, GPS phone tags and a prototype archival accelerometer tag, and address point 3), in order to make the analysis of existing data more effective and improve methods of data collection in future studies of diving and depth use in seals.

6.2 Conclusions

6.2.1 Maximum dive depth in grey seals in the UK

The depth-use maps generated using predictions from a GAM for maximum dive depth in grey seals show that individuals have different patterns of dive depth even when they are in the same geographical area and have the same depth available to them. The dominant patterns in the maps of the proportional use of the water column, where zero means the seal was diving very shallowly and one means the seal was diving to the seabed, is that use of the water column varies spatially in three dimensions (geographically and with water depth), and also temporally, according to light conditions. The relationship between maximum dive depth and dive duration, the strongest predictor of dive depth in the model, is likely an important one for understanding the activity budgets of seals in different areas in combination with dive depth.

The diurnal variation in maximum dive depth was present in all individuals, but the effect also varied spatially within individual. One area in which there was no light effect on maximum dive depth was the Dogger Bank. The diurnal effect is apparent across the study area except for very close inshore, and this suggests that there is some characteristic of the environment on the Dogger Bank that makes it better to dive to the bottom irrespective of...
daylight or darkness. This result is counter-intuitive with respect to sandeel behaviour, a known grey seal prey type that has high relative abundance on the Dogger Bank and are found in the water column during the day and bury themselves in the sediment at night. If the seals were tracking this behaviour they might be expected to dive shallower at night when they are less likely to encounter sandeels. However, there might be other benthic or demersal prey to exploit at night. In addition, the Dogger Bank is the biggest shallow bank in this part of the North Sea so it might be that the depth to which seals would dive to during darkness in other deeper areas corresponds to the maximum available dive depth on the Dogger Bank.

Shallow dives and extended surface intervals have been linked to food processing in grey seals and found to occur most often at night after feeding (Sparling et al. 2007a). The presence of more shallow dives during darkness might be responsible for the reduced average night time dive depth in this dataset, but does the lack of shallower night time dives on the Dogger Bank suggest that seals do not perform processing dives when they are in this area or that the depth of processing dives is indistinguishable from foraging and travelling dives? Data on successful foraging and heart rate from seals on the Dogger Bank would help answer this question. Maps of sediment type at dive locations revealed an association with gravel patches, as in previous studies (McConnell et al. 1999, Aarts et al. 2008), which can be found throughout the North Sea as well as on the Dogger Bank. However, it could also be that high percentage of gravel and high density of sandeels on the Dogger Bank means that this effect is more pronounced since other sediment types are not available in this area.

The presence of a diurnal variation in dive depth might also signal towards the type of activity or the type of foraging that animals engage in in an area. The areas with the least diurnal variation in maximum dive depth after the Dogger Bank and inshore areas is a latitudinal corridor at approximately 0 degrees longitude. Many of the seal tracks traverse this area rapidly and directly, which suggests that they might be travelling through it, and if so, that dive depth does not vary diurnally during travel, at least in this area. This could be related to the probability of encountering prey at different depths in different areas.
Although the regression model for maximum dive depth in grey seals illustrates these aspects of depth use on the east coast of the UK that had not previously been directly addressed, the model failed to capture the finer details of why seals dive to different depths under what conditions and in certain areas. A reason for this is likely to be the lack of information on fine-scale temporal variation in diving behaviour, such as dive bouts. Though this could be incorporated into the kind of regression model fitted here, a preferable approach would be to build a model that uses information about what triggers shallow or deep dives, i.e., the mechanism that drives the alternation between shallow and deep dives.

6.2.2 Using the BSm to represent dives

The consequences of using different numbers of points (1 to 9 breakpoints) to represent abstracted dives were investigated as a case study using a sample of 10 detailed dives from archival data. This showed that the four iterations of the BSm algorithm currently used (4 breakpoints), achieve an appropriate balance between the information gained by sending an additional point (in terms of the reduction in residual error) and the energy cost onboard the tag of sending more points. However, a small residual error (the point at which the abstracted profile is furthest vertically from the true path) cannot be directly interpreted as an indication of the abstracted profile being a good representation of the true profile. The relationship between the vertical residual and an index of the time-depth area enclosed within the dive zone (the dive zone index) were visually compared with the RSS for the abstracted profile (the squared sum of vertical distances between the abstracted and true paths) but neither consistently explained the fit of the abstracted profile based on a sample of ten dives. This suggests that abstracted profiles may not contain the necessary information to assess fit post hoc. Nonetheless, being able to construct a dive zone and derive limits about abstracted dives proved to be an essential step in quantifying the process by which abstracted dive data are collected, and ultimately in building a model of diving behaviour in depth and time.

6.2.3 Simple and multi-state SSMs for reconstructing dive trajectories and depth use profiles

The three single-state SMMs developed here illustrate that even a relatively simple movement model can be useful in reconstructing the depth use profile of a single dive. The
only obstacle to making the biased random walk model a tool for use on large datasets of many dives is computation time, so this is the priority for future work to make it a user-friendly and practical method. The performance of these models was not as good with regard to the reconstructed dive trajectories, which did not consistently outperform the piecewise linear BSm trajectory. This highlights the importance of biological information when modelling animal movement at fine scales in the vertical dimension.

The need for biological information was addressed here by introducing multiple behavioural states, and a behavioural covariate to the movement model. This multi-state model provides a method for estimating the distribution of depths at which elephant seals focus their time while diving and can potentially estimate values of behavioural covariates at those depths. This depth distribution is assumed to represent areas in geographical and environmental space where seals search for and, potentially, acquire prey, which are of interest regarding ecology and conservation (Biuw et al. 2007). This model formulation is a new approach to the analysis of abstracted dive data, such as those collected by CTD-SRDLs. With it, it is possible to reconstruct a realistic, near-continuous dive trajectory from abstracted data and learn about aspects of the behaviour of a seal on dive-by-dive basis. The strength of this approach is that it is expandable and theoretically sound. Once the fitting process has been accelerated it will be a workable solution to the behavioural analysis of dive data from elephant seals.

These four state-space movement models incorporate three of the four elements that contribute to understanding the drivers behind animal movement according to Schick et al. (2008). These include having a likelihood-based framework and an adequately complex process model, and addressing the behavioural patterns that are present in dive data. The element that is not addressed in the context of this work is a means of distinguishing between intrinsic and extrinsic drivers of inferred behaviour.

One criticism of random walk models for movement is that they may be well suited to describing a movement process at one scale but ill-suited to another (Schick et al. 2008). A realistic and feasible extension to these dive models, once fitting time is accelerated, will be to model the diving behaviour of an animal along a multi-dive track, maintaining a within-
dive treatment of movement but also using information from previous dives to estimate movement and behavioural covariates for the current dive. This will preserve the relevant scale for modelling individual dives but will place them in context at a scale that is also relevant to the overall movement ecology of the animal. The manifestation of dives as building blocks of behavioural bouts, trips, or whole migrations is a much-needed expansion to the treatment diving behaviour, one that incorporates multiple scales simultaneously and deals with them appropriately.

6.3 Future research

The movement model framework developed here represents an attempt to formulate biology-driven process models that incorporate what we already know about diving behaviour in deep-diving seals, fully account for the observation process, the measurement error therein, and to exploit the fact that the process by which the observations and associated measurement errors arise are deterministic and known. What these models do not do at this stage is incorporate environmental covariates, though it is a natural extension made possible by the existence of in situ environmental data collected by CTD-SRDLs and other SRDLs under development to incorporate new sensors.

The relatively poor predictive power of the regression model developed in chapter 2 and its inability to accurately predict changes in behaviour of a time-series of dives highlights the need to develop models that contain more information about the mechanisms of behaviour at multiple time scales. Integrating of the kind of framework developed by McClintock et al. (2012) for modelling movement in two spatial dimensions as a collection of movement strategies, and the methods developed here to model depth use, would provide a powerful tool with which to study the at-sea behaviour of seals and other marine divers in all four dimensions, and make inferences about mechanisms of behaviour.

This body of work goes some way to increasing our understanding of where, when, and why seals dive to different depths. A clearer understanding of the distribution and behaviour of seals in the vertical dimension will contribute to what is known about other aspects of their biology, as well as their vulnerability to human activity in the water column.
6.4 References


Appendices
Appendix I: The generalized data collection protocol for SMRU CTD-SRDL and GPS phone tags

*aka “A day in the life of a SMRU CTD-SRDL”*
The protocol for data collection by SMRU CTD-SRDL and GPS phone tags has not been previously documented in detail. The information presented here is the result of study of the existing documentation and software specifications made available by SMRU for tag-users, and interviews with Phil Lovell, SMRU, who has been primarily responsible for the development of this software.

7.1 Introduction

The development and manufacture of animal telemetry devices (hereafter, tags) by the Sea Mammal Research Unit (SMRU) started in the late 1980s. Research and development are on-going, but a tag that has been routinely deployed, particularly on wide-ranging polar marine mammals, since its inception in the early 2000’s, is the Conductivity-Temperature-Depth Satellite Data Relay Logger, or CTD-SRDL (Fig 7.1). The niche of this instrument in the rapidly expanding field of animal telemetry is to remotely and autonomously collect and transmit simultaneous hydrographic and behavioural data from air-breathing marine vertebrates. CTD-SRDLs are particularly relevant for animals, which long-term dataset are required, and from which archival tags can seldom, if ever, be recovered. These devices have been developed specifically for the remote collection and satellite transmission of long-term behavioural and hydrographic data from wide-ranging migratory marine vertebrates. CTD-SRDLs have been deployed on a wide range of animals (Fedak et al. 2002).

CTD-SRDLs are designed, built and programmed in-house by a small team of soft- and hardware engineers in collaboration with marine mammal scientists. The tags’ program specifications are adjusted on a case-by-case basis specifically for each deployment and in accordance with user requirements, within the limits of the capabilities of the tag, given known constraints. This system combines a logger and a transmitter. The operation of the logger is managed by a controller (chip), which interfaces with the sensors to handle data inputs and is programmed in C. When activated, the UHF transmitter relays the information that is compiled by the controller, according to a time schedule it dictates. The consequence of finite battery life of the telemetry device, and the limited bandwidth of the satellite system used to relay data to the ground station, is that data must be reduced in size prior to transmission. It should be noted however, that even when longevity of the device is
forfeited for higher resolution data, there is still an upper limit to the throughput and rate of information transfer this device is capable of.

The limiting factor in terms of energy is the balance between the rate of data collection and the transmission of the data (Fig 7.2). Routine sampling of the instrument’s sensors requires little energy (Boehme et al. 2009). The satellite system used by CTD-SRDLs to transmit the information they record consists of six polar orbiting satellites operated by Argos (Argos, 1989, 1996). Information is sent from the tag to the satellite in units, or messages known as uplinks. Uplinks can be up to 960 msec in duration and require a minimum of 40 sec between attempted transmissions. The prescribed message length accepted by System Argos is fixed at 256 bits, of which 28 bits are used to identify the PTT number of the instrument. This leaves 228 bits per message for behavioural and hydrographic data, which are transmitted using several separate messages (5 according to tag program CTD_GEN_07B). As a result, the software and processing routines implemented on-board CTD-SRDLs have been developed over many years to try to maximise the amount of biologically and hydrographically relevant information that can be sent, while using the least possible amount of bandwidth (Fedak et al. 2001). Within this framework instruments can be individually programmed to collect and transmit information according to the behaviour of the target species, the questions of interest, and the range of hydrographic conditions the animal is expected to encounter. The collection and compression routines for the behavioural and hydrographic data have already been described by Fedak et al. (2002 and 2006) and Boehme et al. (2009), respectively.

The aim of this Appendix is to provide a detailed description of the order of events that take place on-board a CTD-SRDL, primarily to illustrate the way the dive data analysed throughout this thesis arise, but also to highlight the strengths, limitations and potential applications of the data returned by the instruments. Two types of instruments were used in the collection of the dive data analysed here; GPS phone tags (chapter 2) and CTD-SRDLs (chapter 3, 4 and 5). CTD-SRDLs incorporate hydrographic sensors for measuring temperature and conductivity whereas GPS phone tags used to collect the data in this study only have a temperature sensor. The CTD-SRDL software specification CTD_GEN_07B, developed in 2007 for deployments on southern elephant seals is used as a working
example to illustrate the data collection, abstraction and compression routines carried out on-board a CTD-SRDL. Where the operation of CTD-SRDLs differs substantially from GPS phone tags, with regard to the collection of dive data according to the GPS-GSM SRDL software specification MONK_08A used for the grey seal dataset analysed in chapter 2, both processes are described and the differences highlighted in Box 7.1.

7.2 General housekeeping

CTD-SRDLs incorporate a number of sensors as well as an internal clock, a transmitter, a battery cell and a USB interface port socket. The sensors include a wet/dry sensor, pressure sensor, temperature sensor and conductivity sensor (Boehme et al. 2009). Sensors are checked routinely and the readings are used to schedule data collection, processing, storage and transmission tasks according to user-specified criteria. The sequence of events according to which data are accumulated by CTD-SRDLs programmed with CTD_GEN_07B is described and illustrated. The year-counter in the internal clock can take values between 0 and 3, where year 0 is expected to be a leap year. The clock is set to the appropriate year value at the time of programming for deployment, to prevent errors in date and time resulting from the different number of days present in a leap year. Should tags that are more than 4 years old be refurbished for re-deployment, both the internal clock and year-counter will need to be reset to the appropriate year at deployment.

After initial activation, the default state of a CTD-SRDL is to be idle. The instrument becomes active for routine sampling of the wet/dry and pressure sensors (Box 7.1) every 4 sec according to its internal clock. This is the tag’s basic heartbeat. This clock can drift up to 0.1 sec per day due to temperature fluctuations. The controller determines if the tag is submerged in water by inducing a potential across two copper lugs on the outside of the tag and measuring the resulting current. The force exerted on the pressure sensor is the sum of physical and electrical changes in response to temperature (hysteresis), the weight of the water column above the instrument and the atmospheric conditions, and is measured in dbar. The effect of atmospheric variation (average 1013.25 bar) is expected to be negligible compared to hysteresis since 1mbar of pressure is exerted by 1cm of water and the animals on which tags are deployed can routinely dive to many hundreds of meters. As a result,
pressure readings taken at successive surfacing’s may vary by 0.1% of FSD (full scale deflection, or measurement range of the sensor). To avoid negative pressure readings a deliberate 10 dbar offset is added to the pressure sensor calibration. These pressure readings are corrected using a surface pressure measurement, which is obtained whenever the wet/dry sensor reads dry, and is known as the zero-offset. The corrected pressure readings are used to calculate depth. The instrument can deal with depth in two ways, depending on the context. The hydrographic data uses the corrected pressure measurement itself, while for behavioural samples pressure is converted to depth and stored with a resolution of 1 decimeter (1 dbar ≡ 0.1 m) until further processing.

7.3 Behavioural states and the samples buffer

The 4 sec samples are stored in a dedicated memory space called the “samples buffer”. The information held in the samples buffer is used to decide the behavioural state of the tag. Behavioural state is modeled on a three-state, simplified description of seal behaviour. Standard behavioural states for seals are “hauling out”, “diving” or “at the surface”. States “hauling out” and “diving” are defined by a set of criteria, including constraints on one or more sensors, and a time limit for which these constraints must hold true for a behavioural state to qualify (Box 7.1i). State “at the surface” is the complement of “hauling out” and “diving”. The tag program designed for elephant seals includes a fourth behavioural state, called a “cruise”, which describes expended periods “at the surface”. Information about behavioural states is used to construct summaries of behaviour over a set time period. Summary data are assembled every 6 hrs according to CTD_GEN_07B (MONK_08A: 2 hrs). The 4 sec samples are processed and dictate what actions should be carried out next. For example, if the animal is at the surface, a transmission should be attempted, if the animal is in the descent phase of a dive, then dive information should be collected, if the animal is in the ascent phase of a dive, then CTD data may need to be collected.

The size of the samples buffer is dictated by the number of 4 sec samples collected during the longest of the qualifying periods for a behavioural state, for example the start of a haulout (Box 7.1i). Processing of the information in the “samples buffer” is scheduled to happen approximately every minute, when the tag will work through the stored samples
trying to allocate each sample in turn to one of the behavioural states. If this coincides with other activity on-board the tag, e.g. a transmission, processing is deferred until after the next 4 sec sample. Furthermore, the entry and exit criteria for some behavioural states are time-dependent, so, as the each 4 sec sample is considered, it may be necessary to “look ahead” through subsequent samples to work out which state applies to the time of sampling. Sometimes there will not be enough samples to determine which state applies. In these cases processing is deferred until the appropriate information is available.

7.3.1 The dive shape buffer

Once a number of samples is encountered that satisfy the dive start criteria (Box 7.1i), subsequent samples are transferred to a “dive shape buffer”, which is ready to receive time-depth information about a dive. This dive shape buffer can hold up to 256 entries (500 since 2010). As processing continues through the samples buffer, depth samples are added to the dive shape buffer until the criteria for the end of the dive are met.

If all 256 entries are filled before the end of a dive (i.e. when dive duration exceeds \(4 \times 256 = 17\) min), alternate entries are discarded, leaving 128 entries, 8 sec apart. Only every other 4 sec sample is added from then on. If the buffer is filled with entries that are 8 sec apart (up to dive duration 34 min), alternate entries are again discarded leaving 128 samples, 16 sec apart. Only every fourth 4 sec sample is added from then on. For practical purposes, it holds true for the transmitted dive data that this process continues indefinitely up to maximum possible dive durations. The implication of this data collection regime is that a) the internal time resolution differs for dives of different duration: 4 sec for dives up to 17.1 min long, 8 sec for dives up to 34.1 min, 16 sec for dives up to 68.3 min, 32 sec for dives up to 136.5 min, as dive duration increases, and b) that the time resolution is implicit for a dive of given duration.

The resulting information stored in the dive shape buffer includes a sequence of depths of known sampling resolution, e.g. 230 samples taken every 8 sec gives an approximate dive duration of 31 min. Dive duration is stored at a 4 sec resolution regardless of the duration of the dive. Irrespective of the number of time-depth sample points that are collected during a dive (e.g. 150 time-depth points for a dive duration of 20min, at 8 sec sampling rate) each
time point is represented as a proportion of the dive duration with the corresponding depth value associated with it. If an 8-bit value is used to transmit this proportion, it will have a resolution of 1/256 (0.39%).

For short dives, the 4 sec sampling regime will be the limiting factor in terms of temporal resolution, whereas for long dives, the successive reduction in resolution due to memory constraints, that is described above, will be what limits the temporal resolution of time information. This topic is reiterated below, in the “Representing time in dive profiles” section.

7.4 The broken-stick model

7.4.1 Dive data

Once the dive end criteria are met (Box 1.1), the “dive shape buffer” is submitted for further processing by abstraction, according to the broken-stick model (BSm) \(^1\). Four iterations of the algorithm are carried out for CTD_GEN_07B resulting in four time-depth pairs (T1:T4 and D1:D4) as well as the maximum residual error (R5) between the true profile and its abstracted profile after the last iteration is complete, represented by the four time-depth pairs and two surface points. This procedure is described in chapter 3. At this stage, BSm depths are still stored at the device’s internal resolution of 1 decimeter and the time resolution (4 sec or multiples) is known implicitly since it is linked to dive duration.

Dive data recorded by GPS phone tags (MONK_08A) are not submitted to the BSm. They are made up of nine time-depth pairs spaced equally in time through the duration of the dive, and two surface points, resulting in eleven points per profile.

\(^1\) Used as the abstraction algorithm on-board SRDL for dive data and hydrographic data on Argos tags from 2007 onwards.
7.5 Hydrographic data

The CTD sensor is programmed to measure conductivity, temperature and pressure every 1 sec between the deepest point in the dive and the surface, on the ascent, as the animal swims up through the water column. This yields a CTD “upcast”, a slice through the water column, providing a cross-sectional view of the physical environmental conditions at the location of the dive. Salinity is calculated on-board the instrument (using temperature, conductivity and pressure) and stored for transmission, while conductivity is discarded. Temperature is not measured instantaneously so measurements are lagged according to the lag time constant of the temperature sensor. To avoid a temporal mismatch between temperature and salinity measurements conductivity is lagged accordingly and smoothed logarithmically to match temperature. Both measurements are then added to a depth bin. A completed upcast consists of three vectors with 1 sec resolution; temperature, salinity and pressure.

Real time does not feature in transmitted CTD upcasts. The time resolution of the data collection regime is fixed at 1 sec, and the end date and time of the dive during which the upcast was completed places it in real time. Instead, the independent variable according to which temperature and salinity are stored is pressure. For hydrographic samples, 1000 temperature bins and 1000 salinity bins are made available for storing data during an upcast. Each temperature and salinity reading is added to one of these bins according to the pressure at which it was sampled. There are normally 1000 pressure bins available, each 1 dbar wide, which is suitable for animals that do not dive deeper than approximately 1000 m. On instruments programmed for deployment on deep diving animals, such as southern elephant seals, which are likely to experience a larger range of pressures, resolution is sacrificed to ensure the whole range is captured. In these cases 1000 pressure bins are still made available and pressure resolution drops to 2dbar. This is effectively rounding the pressure to the nearest 2 dbar.

Typically, end-product CTD profiles are made up of 17 sets of points; 9 of these are collected at fixed depths during a dive and the remaining 8 are selected using the BSm as for dives. In the context of dive abstraction, the first iteration of the BSm constructs the proposed profile
as a straight line between the start and end points of the dive. For CTD upcasts, the first iteration of the BSm is taken as the piecewise linear profile made up of the deepest point, the surface point and the intermediate fixed depth points. Eight points are added to this profile as per the BSm algorithm described in chapter 3. Short summaries of hydrographic data collection, and technical information regarding the sensors themselves, can be found in Box 7.1.ii and Box 7.2, respectively. A comprehensive and detailed description of the hydrographic data collection and compression can be found in Boehme et al. (2009).

On instruments designed for deployment on deep-diving species like southern elephant seals, upcasts are measured between 2,000 and 6 dbar, in 2 dbar bins, as mentioned above. Collection of a CTD cast is triggered by a pressure measurement exceeding the user-specified threshold for the collection of hydrographic data. This threshold is time dependent. For CTD_GEN_07B, the aim is to collect one CTD cast every 6 hours. The depth threshold that will trigger the collection of an upcast becomes shallower as time moves through a 6 hour window (1,000 m in hour 1, 600 m in hour 2, 300 m in hour 3, 100 m in hour 4, 50 m in hour 5, 25 m in hour 6). In addition, if a dive occurs in a given 6 hour window, with a maximum depth exceeding the depth of the upcast currently stored for that period by 20% or more, then the shallow upcast is discarded in favour of the deeper one. If no dive has qualified for the collection of an upcast by the final hour in a 6 hour period, then the threshold could be as shallow as 25m. This routine ensures that a) at least one CTD upcast is collected for every 6 hour period, provided the animal is diving, and b) that the upcast is collected for one of the deepest possible dives in that period so that maximum coverage of the water column is achieved, without wasting energy collecting samples that are later discarded.

For GPS phone tags (MONK_084) temperature is collected continuously, every 4 sec, and construct a single average profile for each 2-hour summary period (Box 7.1.iii).

7.6 Representing time in dive profiles

Dives are stored in groups for transmission. Only one timestamp is transmitted per dive group, and each group typically contains three dives (MONK_08A: eight). The timestamp for
a group is the dive-end date and time (DE_DATE) for the last of the three dives in a dive group, corresponding to the date and time when the dive end criteria were met. The DE_DATE associated with the remaining two dives, can be obtained by subtracting the appropriate dive durations (DIVE_DUR) and surface durations (SURF_DUR) from the dive group's timestamp, and is carried out by the decoding software that the dive data are submitted to once they are received at SMRU. This date is exact but truncated, to further trim down the amount of memory used. Each of the DIVE_DUR and SURF_DUR values are subject to some degree of rounding error, meaning that the accuracy of the DE_DATE for the first and second dives in a dive group is reduced. For the most part, actual time is irrelevant and individual dives are only put in real-time context retrospectively, as described above.

Time information is reduced for transmission by allowing only 5 bits to represent each time point within a dive. This means that each dive is allowed 32 equally spaced points to represent time, irrespective of its duration. Each of these points corresponds to a percentage relative to the total dive duration, in increments of 3.125%. This is the consequence of the 5 bit quota per time point, and means that time within a dive can be represented economically, using only 160 bits in total (32 x 5 = 160 bits). These percentage time points relate back to real time using the timestamp of the dive group to which the dive in question belongs. Of these 32 discrete time points, the ones closest to the BSm time points are stored for transmission. So for any time point within the received time-depth information for a given dive, time could have an associated error of up to 1.563% of that dive’s duration, half of the 3.125% increment, if the time point lies exactly half way between two of the 32 values used to represent time. Representing times as proportions of each dive’s duration gives the best resolution for a fixed number of bits.

The consequence of the 4 sec (or multiples thereof) sampling regime dictated by the fixed size of the dive shape buffer, and the digitization procedure described above, is that for very short dives (< 2 min) the internal (4 sec) sampling resolution is limiting, but in longer dives it is the successive reduction in resolution due to memory constraints and the fact that only 32 values can be transmitted which limits the resolution of the time information delivered by the instrument.
7.7 The transmission buffer

Once processed, abstracted and compressed data are added to the transmission buffer ready for transmission at the first opportunity. In the case of dive data, dives are grouped, typically into three’s, and sent as a unit. The BSm depth points (and the equally spaced depth points, for MONK_08A) are coded before transmission according to a pseudo-logarithmic mantissa and exponent representation. With this representation resolution can be made proportional to the scale of the number being represented, making it useful for depth, but less useful for temperature where a constant resolution would be better. For more detail on this digitization method see Fedak et al. (2002). The length of time for which dives remain in the transmission buffer (“sell-by” date), and are available to be sent, depends on their time resolution (number of bits used to represent time) and is usually set to approximately 5 days. Older dives are displaced in the transmission buffer by newer dives, so at times of high diving activity when dives are rapidly being accrued in the transmission buffer, or when transmission is difficult, some dives may be displaced from the transmission buffer before they get the chance to be selected for transmission, and are permanently lost. Once in the transmission buffer, dive groups are sampled randomly with replacement for transmission, so that all dive groups are equally likely to be transmitted. However, as is inevitable when sampling with replacement from a small population, some dives are transmitted twice, and others not at all. For behavioural states “hauled-out” and “cruise”, state entry and exit times are stored and relayed as is, in digitized form, and no processing is required. Newer software versions for CTD-SRDLs can store all data ever scheduled for transmission, or in some cases all raw temperature and salinity data, on a separate memory card, from which data can be downloaded directly if the CTD-SRDL is retrieved after a deployment.

7.8 Obtaining locations for dive profiles and CTD upcasts

Satellite uplinks are only possible when the animal is at the surface and the wet/dry sensor reads dry. All uplinks received by the System Argos satellites are used to calculate a geographic location estimate for the tag based on changes in Doppler shift as uplinks are received by different satellites. Consequently, geographic locations can only be obtained
during surface intervals and haulout periods. The movement trajectory of an animal in geographic space is often interesting in its own right, but dive profiles provide information about the behaviour of the animal along this movement trajectory. The hydrographic data collected during dives are increasingly becoming the priority in deployments, as the role of animal platforms in the collection of environmental data is becoming more widely recognized (Boehme et al. 2008, Boehme et al. 2009). Given that behavioural and hydrographic information is collected at depth, and locations can only be obtained at the surface, this creates a mismatch. This is overcome by linearly interpolating the location of the dive using the locations obtained on either side of it; the location just before the onset of a dive, and the location directly after the dive-end criteria are met. An estimate of location error is calculated by ARGOS for each location along a track, which then needs to be filtered to remove locations with large errors. The choice of location filter will affect the location of dives. The filtering procedure that has been used extensively for tracks arising from CTD-SRDLs and behaviour-only SRDLs is described in McConnell et al (1992).

The way locations are obtained for GPS phone tags is described by McConnell et al (2007).

7.9 Missingness

Dive records resulting from most telemetry tags using the Argos satellite system will almost always be incomplete, i.e. have some missing dives, locations and CTD upcasts. This is exacerbated by the lack of acknowledgement when transmitted information is received, or “handshake” between the platform and the satellite. Even though two of the six Argos satellites (Argos-3) are now able to send a “downlink” to the platform (Argos 1989, 1996), acknowledging receipt of a message, implementation is too slow to be of use for marine mammal platforms, and uses up an impractical proportion of the message being sent. This lack of handshake, creates the need for a stochastic transmission strategy of the information accumulated in the transmission buffer. The proportion of dive data that is lost will depend on a number of factors, including the geographic region in which the instrumented animal operates (e.g. polar regions have better coverage by Argos satellites than equatorial regions because they are polar orbiting), the animal’s diving ecology, how long the animal spends at the surface where transmission is possible, and the frequency
with which that transmission window occurs. For elephant seals, there are two main reasons why data are lost. Firstly, as for all species, there will be periods during deployment when conditions for satellite transmission are poor, and secondly, there may be periods when data accumulate at a higher rate than the tag can transmit them, for example periods of high diving activity that exceed the size (in terms of time) of the transmission buffer. Southern elephant seals are a species that spend very little time at the surface (mean surface time $2.18 \pm 0.0019$ min, SMRU unpublished data), providing a narrow window for transmission. The consequences of elephant seal surfacing behaviour on the number of messages sent and the quality of the locations are shown in Boehme et al. (2009, Fig. 4). The transmission buffer in CTD-SRDLs designed for deployment on southern elephant seals is made large enough to hold many days worth of dives, to minimize the proportion of information lost during low Argos coverage, and to avoid data return being biased in favour of data collected during high Argos coverage (Box 7.1iii). In addition, as mentioned above, stored data are selected randomly from the transmission buffer. Information remains in the transmission buffer either until its “sell-by” date expires or it becomes displaced by newer information being added to the buffer.

7.10 Numerical accuracy and measurement error

Data are truncated during the decoding process, once information is received. This involves a look-up table linking a short, coded number that is transmitted, to a truncated version of the true number. Using a depth example, a true depth of 111.4 m, recorded with a resolution of 1 dm, will fall into the 110.0-112.5 m bin when coded for transmission, and will be represented as the smallest number in that bin, 110.0 m. This process is performed for all numbers (dive duration, surface duration, depth profile) recorded and transmitted by the instruments. The information available for analysis is therefore, effectively binned (Boehme et al. 2010, unpublished). As a consequence, knowing the exact bounds to each received number is not realistic, since there is some stochasticity in the way information is degraded during processing and transmission. To work backwards from the transmitted depth to the true depth, one would have to add some amount to the transmitted value, to account for the rounding down, and this amount will depend on the size of the bin at that depth point,
which in turn depends on how large the true number recorded by the pressure sensor actually was.

When instruments are recovered after deployment, abstracted dive profiles for all dives that the instrument ever collected can be found stored in memory. This means that a complete dive and hydrographic profile record can be obtained from recovered instruments since they hold information that passed through the transmission buffer before transmission could be attempted. The advantage of retrieving instruments, from a data resolution point of view, is that the tag stores the original, abstracted information at the internal depth resolution of the tag and without the extra coding that is required to fit the values into a transmission. With this information it would be possible to compare pre- and post-compression abstracted profiles to gain a better understanding of how the compression procedure affects the shape and resolution of dive profiles.

7.11 End products

Finally, five types of messages are produced and stored in the transmission buffer, ready for transmission by Argos, each of length 256 bits. The two types of message (labeled here: 1a and 1b) contain detailed information about dives, one message containing the summary data (2) including behavioural information regarding any haulouts and cruises for a 6 hour period, and two messages each containing part of a CTD profile (3 and 4) since the hydrographic data are spread over two separate messages (fixed points and BSm points). Messages are selected for transmission in a prescribed sequence according to their type (for CTD_GEN_07B the sequence is 1a 1b 2 3 4 3 4), and some messages are sent more often than others. This sequence of selection repeats indefinitely cycling through the information in the transmission buffer. When it is time for a transmission, the next item of the appropriate type is taken from the transmission buffer. An item may remain in the transmission buffer for many of these cycles before being transmitted (e.g. the summary message is transmitted 40 times on average to achieve a 95% probability of being received). Independence of the insertion (as the data are collected and processed) and extraction processes (as the data are selected from the buffer and transmitted), has the effect of randomizing the buffer so that all information is equally likely to be received.
Figure 7.1. Photograph of a CTD-SRDL, with visible hardware components labelled. Photo Lars Boehme.
Figure 7.2. An illustration of the relationship between the rate of data collection (sampling rate) and transmission.
Box 7.1. Data collection and transmission summaries

i. Behavioural state definitions

CTD_GEN_07B
Enter “hauled out” if dry for 10 min, exit if wet for 40 sec.
Enter “diving” if wet and depth is greater than 6m for 8 sec, exit if depth is less than 6m for
any length of time (0sec), or dry at any time.
“At the surface” is the complement of “hauled out” and “diving”. If this state persists, and
there is no dive for 9min, it is called a “cruise” treated as a separate state. Entry and exit
information is stored and transmitted.
Dives are transmitted in groups of 3.

MONK_08A
Enter “hauled out” if dry for 10 min, exit if wet for 40 sec.
Enter “diving” if wet and depth is greater than 1.5m for 8 sec, exit if depth is less than 1.5m
for any length of time (0sec), or dry at any time.
“At the surface” is the complement of “hauled out” and “diving”. Entry and exit information
is stored and transmitted.
Dives are transmitted in groups of 8.

ii. CTD data collection in summary

CTD profiles collected on-board CTD-SRDLs according to the CTD_GEN_07B software
configuration are made up of 17 sets of 3 points; pressure, temperature and salinity. Nine of
these are collected at fixed depths during a dive and the remaining 8 are selected using the
BSm. 1000 pressure bins are normally made available. For deep divers like elephant seals
each pressure bin is 2 dbar wide, allowing CTD data to be collected down to approximately
2000 dbar pressure. For more details see Boehme et al. (2009). The valid temperature range
for the deployments considered was -2.5 to 30.2 °C and the valid salinity range was 28.9 to
37.1 psu.

Temperature casts collected on-board GPS phone tags according to the MONK_08A software
specification are made up of 12 sets of 2 points, pressure and temperature. The only fixed
points are the deepest point in the profile and the surface and the remaining 10 points are
selected using the BSm. 250 pressure bins are available in 2 dbar bins, giving a maximum of
500 dbar pressure. The valid temperature range for this deployment was -5 to 35.95 °C in
steps of 0.01 °C.
Box 7.1. (continued)

iii. Transmission buffer

**CTD_GEN_07B**

Dive profiles 1200 bytes are made available for dives, which are stored in groups of 3. If we assume average dive duration of 10 min this results in a 6.25 day buffer with capacity for 300 dives.

Haulouts and cruises 120 bytes each are available for haulouts and cruises. Since only the entry and exit times are stored for haulouts and cruises this means that 30 haulouts and 30 cruises can be stored in the buffer.

6-hour summaries 40 bytes are made available for 6-hour summaries, which are stored in groups of 3. This results in a 7.5 day buffer.

**MONK_08A**

Dive profiles 5600 bytes are made available for dives, which are stored in groups of 8. If we assume average dive duration of 10 min this results in a 77.78 day buffer with capacity for 1400 dives.

Haulouts 200 bytes are available for haulouts (no cruises recorded by MONK_08A). Since only the entry and exit times are stored for haulouts this means that 50 haulouts can be stored in the buffer.

2-hour summaries 240 bytes are made available for 2-hour summaries, which are stored in groups of 12. This means that 60 summaries can be stored in the buffer.

Temperature profiles 1200 bytes are available for CTD casts which results in a 25 day buffer.
Box 7.2. Hydrographic sensors

i. Pressure (Depth)
The nominal accuracy of the pressure transducer is in the area of 20 m for the entire range of temperature and pressure it is designed to sample (from 2000 m at -40°C until 0 m at +80°C). In practice, it has been found that the error in surface pressure following a deep dive can be about 0.5-1.5 m rather than zero (P. Lovell, pers. comm.). To minimize the pressure measurement error as much as possible, the instrument updates the zero-offset at every opportunity, when the wet/dry sensor reads “dry”. The exact value of the zero-offset will vary according to the hydrographic conditions, which is why the instrument is programmed to update this value whenever the sensor reads “dry”. The pressure reading is deliberately shifted away from zero to avoid interference from electrical noise generated by the tag.

Depth within a dive is calculated as follows: 1) pressure is collected, 2) the zero-offset is subtracted from the pressure measurement, 3) pressure is rounded to the nearest dbar (or nearest 2 for deep diving species) throughout the measurable depth range, and 4) the resulting value is converted to depth. The resulting depth measurements are processed by the instrument at its internal resolution of 1 decimeter (= 10 cm) for behavioural samples such as the dive shape buffer.

ii. Temperature (for non-CTD SRDLs)
Temperature data is collected by measuring the changes in resistance that the thermistor incurs in response to temperature changes in the surrounding medium. The response of the thermistor itself is well understood, however the behaviour of the thermistor once it has been incorporated into the instrument is not completely known. Each instrument is calibrated at room temperature before deployment with high-precision resistors, but many unknowns remain about how the whole device performs in the field. Two issues that need to be addressed with dedicated experiments are, a) the time constant of the temperature sensor once embedded in the instrument, and b) how temperature changes affect the instrument’s ability to measure temperature change. For details regarding temperature collected by CTD-SRDLs see Boehme et al. (2009).

Upcasts performed by the current generation of CTD-SRDLs yield 17 values each for temperature and conductivity. Temperature is collected at a resolution of 0.001 K within a valid range of -2.5 to 30.2°C. For non-CTD tags (e.g. GPS/Gsm with temperature sensors) the accuracy is hopefully in the range of 0.05°C, however this has never been systematically measured.
Only minimum and maximum temperature within an upcast are sent, and each of the 17 temperature values is expressed as a percentage of the range (0=Tmin, 100=Tmax), in units of 1/1000. The resolution of the temperature measurements will be 0.001 (or 0.1%), if the temperature range of the profile is less than 1°C, or (Tmax-Tmin)/1000 if the range is greater than 1°C. For CTD-SRDLs accuracy of the temperature measurement is at least 0.01 °C.

iii. Salinity
Salinity is treated in the same way as temperature. Conductivity and temperature are used to calculate salinity, then conductivity is discarded. Salinity is stored at a resolution of 0.001 within a valid range of 28.9 to 37.1 in psu. Only minimum and maximum salinity within an upcast are sent and each of the 17 salinity values is expressed as a percentage of the range (0=Smin, 100=Smax), in units of 1/1000. Therefore, the resolution of the salinity measurements will be 0.001 (or 0.1%), if the salinity range of the profile is less than 1psu, or (Smax-Smin)/1000 if the range is greater than 1psu. Minimum and maximum salinities are sent with resolution 0.02 psu.
7.13 References


Fedak MA, Lovell P and Grant SM. 2001. Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Marine Mammal Science* 17(1): 94-110


Appendix II: Computer code for computational routines and statistical models
8.1 Broken-stick model for dive abstraction and dive zone construction

Code for abstracting detailed dives and constructing their dive zone, as well as for constructing the dive zone for already abstracted dives is provided electronically. All code was written in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011).

8.1.1 Finding the order of BSm points and the last residual, and constructing the dive zone for abstracted dives

Script file diveAbstr.diveZone_6point.R

8.1.2 Dive abstraction and dive zone reconstruction for dives with 4 sec depth measurement resolution

Script file diveSim.diveAbstr.R

8.2 Simple Random Walk model

This model was implemented using JAGS (Plummer 2003) in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011), using the rjags (Plummer 2011) and MCMCpack libraries (Martin et al. 2011).

```r
model{

d[1] <- 0

for (t in 1:(tmax-1)) {

d[t+1] ~ dnorm(d[t], tau)

mids[t+1] ~ dunif(d[t+1]-halfwids[t+1], d[t+1]+halfwids[t+1])
}

tau ~ dgamma(2.03009, 1/0.1255819)
}
```
8.3 Random Walk model with an informative prior on inertia

This model was implemented using JAGS (Plummer 2003) in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011), using the rjags (Plummer 2011) and MCMCpack libraries (Martin et al. 2011).

model{

d[1]<- 0

b0tau1 <- 0.8101287
b1tau1 <- 0.0194938

b0setau1 <- -1.507417
b1setau1 <- 2.824999

tau1mean <- 1/(b0tau1 + b1tau1*maxdep) # inverse Gamma link
tau1se <- 1/(b0setau1 + b1setau1*maxdep) # inverse Gamma link
tau1var <- tau1se^2

k <- tau1mean^2/tau1var # shape
theta <- tau1mean/tau1var # rate

for (t in 1:(tmax-1)) {
  d[t+1]~dnorm(d[t],tau)
  mids[t+1] ~ dunif(d[t+1]-halfwids[t+1], d[t+1]+halfwids[t+1])
}

tau ~ dgamma(k, theta)
}
8.4 Biased Random Walk with drift

This model was implemented using JAGS (Plummer 2003) in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011), using the rjags (Plummer 2011) and MCMCpack libraries (Martin et al. 2011).

model{

d[1]<- 0

# prior for tau0: overall precision for speed
b0tau0 <- 0.8101287
b1tau0 <- 0.0194938

b0setau0 <- -1.507417
b1setau0 <- 2.824999

tau0mean <- 1/(b0tau0 + b1tau0*maxdep) # inverse Gamma link
tau0se <- 1/(b0setau0 + b1setau0*maxdep) # inverse Gamma link
tau0var <- tau0se^2

tau0.k <- tau0mean^2/tau0var # shape
tau0.theta <- tau0mean/tau0var # rate

# prior for drift1: coefficients of linear regression model for speed on descent
b0drift1 <- 2.05485903
b1drift1 <- 0.00678982
b2drift1 <- -2.46710437
b3drift1 <- -0.00583909

p <- tmaxdep/tmax

drift1mean <- b0drift1 + b1drift1*maxdep + b2drift1*p + b3drift1*maxdep*p
drift1var <- (0.01748783^2)

drift1.k <- drift1mean^2/drift1var # shape
drift1.theta <- drift1mean/drift1var # scale

# prior for tau1: precision for speed on descent
tau1mean <- 0.4729253
tau1var <- 0.1312162
tau1.k <- tau1mean^2/tau1var # shape
tau1.theta <- tau1mean/tau1var # rate

# deterministic relationships for drift2 (speed on ascent) and tau2 (precision for speed on ascent)
drift2 <- (0-p*drift1)/(1-p)
tau2 <- 1/(((1/tau0)*p*(drift1^2+(1/tau1))-0-p*drift1))/(1-p))^2

for (t in 1:(tmax-1)) {

  mu[t] <- d[t] + step((tmaxdep+0.001)-t)*(-drift1)+step((t+0.001)-tmaxdep)*drift2 # in JAGS step checks for x>=0

  tau[t] <- step((tmaxdep+0.001)-t)*tau1+step((t+0.001)-tmaxdep)*tau2

  d[t+1] ~ dnorm(mu[t], tau[t])

  mids[t+1] ~ dunif(d[t+1]-halfwids[t+1], d[t+1]+halfwids[t+1])
}

tau0 ~ dgamma(tau0.k, tau0.theta)

  drift1 ~ dgamma(drift1.k, drift1.theta) # to give mean of descent speeds

tau1 ~ dgamma(tau1.k, tau1.theta) # to give mean of descent speed precision
}
8.5 Random walk dive path simulation

Dive path simulation by unconstrained random walk in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011).

d <- 0
t <- 1
d[1] <- -0.001
tau <- 0.1

while(d[t] < 0){
    d[t+1] <- rnorm(1, mean=d[t], sd=1/sqrt(tau))
    t <- t+1
}

d[t]<0
8.6 Multi-state random walk dive model

This model was implemented using JAGS (Plummer 2003) in R version 2.13.1 (2011-07-08) (R Development Core Team, 2011), using the rjags (Plummer 2011) and MCMCpack libraries (Martin et al. 2011).

model{

Dstate[1]<-1
DDstate[1]<-1
state[1]<-1

sw[1]<-0 # Multiplier for tf in DESCENT (state 1)
sw[2]<-1 # Multiplier for tf in BOTTOM (state 2)
sw[3]<-0 # Multiplier for tf in ASCENT (state 3)

d[1]<-0 # Depth at time step 1
d[2]<-0.1 # Depth at time step 2
d.proj[1]<-0.11 # Temporary carrier for depth

td[1]<-1 # Starting value for time
tf[1]<-0 # tf at beginning of time step 1
tf[2]<-0 # tf at beginning of time step 2
cpf<-10 # Cumulative time in state 2 as a proxy for satiation. The idea is for this to be calculated over a moving time window eventually.

# Priors on movement parameters
dummy1 ~ dgamma(4.5963, 1/0.7273975) # mean 3.343337, var 2.431935: descent drift from all dives, all three-day accelerometer depth records - accel.dive.R
dummy2 ~ dnorm(0.007497271, 0.9087327) # mean 0.007497271 var 1.100434; bottom drift from all dives, all three-day accelerometer depth records - accel.dive.R
dummy3 ~ dgamma(3.849741, 1/0.8761762) # mean 3.373051, var 2.955387: ascent drift from all dives, all three-day accelerometer depth records - accel.dive.R

sState[1]<- dummy1
sState[2]<- dummy2
sState[3]<- dummy3

# prior for tau0: overall precision for speed
b0tau0<- 0.8101287
b1tau0<- 0.0194938
b0setau0<- -1.507417
b1setau0<- 2.824999

tau0mean <- 1/(b0tau0 + b1tau0*maxdep) # inverse Gamma link
tau0se <- 1/(b0setau0 + b1setau0*maxdep) # inverse Gamma link
tau0var <- tau0se^2

tau0.k <- tau0mean^2/tau0var # shape
tau0.theta <- tau0mean/tau0var # rate

tau ~ dgamma(tau0.k, tau0.theta) # prior for precision on speed related to the maxdep of the dive

# Priors on coefficients for state transition matrix
# intercept
betazero[1,1] ~ dnorm(7, 500)
betazero[2,1] ~ dnorm(2, 500)
betazero[3,1] ~ dnorm(-4, 500)

betazero[1,2] ~ dnorm(10, 500)
betazero[2,2] ~ dnorm(5, 500)
betazero[3,2] ~ dnorm(-10, 500)

betazero[1,3] ~ dnorm(10, 500)
betazero[2,3] ~ dnorm(5, 500)
betazero[3,3] ~ dnorm(-10, 500)

# time in dive

betatwo[1,1] ~ dnorm(-0.055, 2000)
betatwo[2,1] ~ dnorm(0.02, 2000)
betatwo[3,1] ~ dnorm(0.055, 2000)

betatwo[1,2] ~ dnorm(-0.08, 2000)
betatwo[2,2] ~ dnorm(0.0, 2000)
betatwo[3,2] ~ dnorm(0.08, 2000)

betatwo[1,3] ~ dnorm(-0.06, 2000)
betatwo[2,3] ~ dnorm(-0.0, 2000)
betatwo[3,3] ~ dnorm(0.09, 2000)

for (t in 2:(tmax-1)){

td[t] <- td[t-1]+1 # Update to the next time step by incrementing time index by 1
i[t] <- Dstate[t-1] # Let state at the previous time step determine the value of i. State can take on values 1:3 so we are using it here as a column index

# State transition matrix - Transition 3 always a complement of 1 and 2
mu[1,t] <- exp((betatwo[1,i[t]]/(tmax/250))*td[t]+betazero[1,i[t]]*1)
mu[2,t] <- exp((betatwo[2,i[t]]/(tmax/250))*td[t]+betazero[2,i[t]]*1)
mu[3,t] <- exp((betatwo[3,i[t]]/(tmax/250))*td[t]+betazero[3,i[t]]*1)

# row 1, column 1
m[1,t] <- mu[1,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 1
# row 2, column 1
m[2,t] <- mu[2,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 2

# row 3, column 1
m[3,t] <- mu[3,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 3

# State determination

p1p2[t] <- m[1,t]+m[2,t] # Joint probability of state 1 and state 2, given they are independent
mbin1[t] ~ dbin(p1p2[t],1) # TRIAL 1 - generate a random outcome based on the sum of probabilities of states 1 and 2

mvec[t,3] <- 1-mbin1[t] # mvec[t,3] is the complement of the mbin1[t] outcome, because if it wasn’t in state 1 or 2 it must have been in state 3

pdummy[t] <- mbin1[t]*m[1,t]/max(p1p2[t],equals(p1p2[t],0))) # Did the random draw yield a success given the joint prob of state 1 and state 2?
# if yes (1), then the first part becomes 1, and the conditional probability of m[t,1] is turned on, and
# pdummy[t] <- m[1,t]/(m[1,t]+m[2,t])
# if no (0), then the first part becomes 0, and the conditional probability of m[t,1] is turned off, and pdummy[t] <- 0

mbin2[t] ~ dbin(pdummy[t],1) # if pdummy[t]=0 then mbin2[t]=0, otherwise carry out a binomial trial with probability m[1,t]/(m[1,t]+m[2,t]) - TRIAL 2

mvec[t,2] <- (1-mbin2[t])*(1-equals(mbin1[t],0)) # use the complement of mbin2[t], the conditional trial for state 1 : if mbin2[t]=1 then the outcome for state 2 will automatically be 0. If mbin2[t]=0 and the trial for state 1 gave a failure (0) then state 2 is automatically a success
# This is implemented by checking whether pdummy[t]=0 :
# if yes (1) then the second part becomes 0
# if no (0) then the second part becomes 1 and mvec[t,2] is the complement of mbin2[t]

mvec[t,1] <- mbin2[t]

DDstate[t]<-max(1,min(3,mvec[t,1]*1+mvec[t,2]*2+mvec[t,3]*3)) # Dstate is determined using the vector of outcomes, mvec, and vector of state values, v

state[t] ~ dnorm(DDstate[t], 10) # checks whether the state I am providing (state) agrees with the state I am estimating (Dstate)

Dstate[t] <- max(1,min(3,round(state[t]),)))

tf[t+1]<-sw[DDstate[t]]*(tf[t]+1) # This controls whether tf is incremented or not in the given time step. The dummy variable, sw, controls when this happens. If not in state 2, the number of time steps spent in flat mode is re-zeroed by being multiplied by zero, otherwise one time step is added to it.

# Movement model

d.proj[t]<- d[t]+sState[DDstate[t-1]] # Projected mean for depth at time t is defined as the depth at the
previous time step plus the vertical speed calculated above

d[t+1]~dnorm(d.proj[t],tau) # Depth at time t+1 is drawn from a Normal distribution centered on the
acceleration the projected mean for depth at time t with a depth precision, tau.

mids[t+1] ~ dunif(d[t+1]-halfwids[t+1], d[t+1]+halfwids[t+1]) # data dictate that d[t+1] is bound above and
below by the halfwidth of the dive zone at t+1

} # closes t loop
}
8.7 Priors for behavioural coefficients


zones <- matrix(c(1,2,3,4),ncol=4,byrow=F)
layout(zones, widths=c(2/7,2/7,2/7,1/7),heights=c(1,1,1,1)); layout.show(4)
cex.axis <- cex.lab <- 1.8

# zone 1: DESCENT
t<-1:250
b1<- -0.055
b2<- 0.02
b3<- -0.055
mu1<-exp(7+b1*t)
mu2<-exp(2+b2*t)
mu3<-exp(-4+b3*t)
p1<-mu1/(mu1+mu2+mu3)
p2<-mu2/(mu1+mu2+mu3)
p3<-mu3/(mu1+mu2+mu3)

par(mar=c(4,5,0,0))
plot(t,p1, ylim=c(0,1), lwd=1.2, type="l", xaxt="n", xlab="Time (min)", ylab="P(transition FROM Descent)"
, cex.axis=cex.axis, cex.lab=cex.lab, bty="n")
lines(t,p2, lwd=1.2, col="red")
lines(t,p3, lwd=1.2, col="green")
xmax <- ceiling(250*4/60)
xmax/5
axis(1, at=axTicks(1, axp=c(0,250,4)), labels=seq(0,xmax,length.out=5), cex.axis=cex.axis)

# zone 2: BOTTOM
t<-1:250
b1<- -0.08
b2< 0.0
b3<- -0.08
mu1<-exp(10+b1*t)
mu2<-exp(5+b2*t)
mu3<-exp(-10+b3*t)
p1<-mu1/(mu1+mu2+mu3)
p2<-mu2/(mu1+mu2+mu3)
p3<-mu3/(mu1+mu2+mu3)

par(mar=c(4,5,0,0))
plot(t,p1, ylim=c(0,1), lwd=1.2, type="l", xaxt="n", xlab="Time (min)", ylab="P(transition FROM Bottom)"
, cex.axis=cex.axis, cex.lab=cex.lab, bty="n")
lines(t,p2, lwd=1.2, col="red")
lines(t,p3, lwd=1.2, col="green")
xmax <- ceiling(250*4/60)
# zone 3: ASCENT

t<-1:250
b1<- -0.06
b2<-0.0
b3<-0.09
mu1<-exp(10+b1*t)
mu2<-exp(5+b2*t)
mu3<-exp(-10+b3*t)
p1<-mu1/(mu1+mu2+mu3)
p2<-mu2/(mu1+mu2+mu3)
p3<-mu3/(mu1+mu2+mu3)

par(mar=c(4,5,0,0))
plot(t,p1, ylim=c(0,1), lwd=1.2, xlab="Time (min)", ylab="P(transition FROM Ascent)",
cex.axis=cex.axis, cex.lab=cex.lab, bty="n")
lines(t,p2, lwd=1.2, col="red")
lines(t,p3, lwd=1.2, col="green")

xmax <- ceiling(250*4/60)
xmax/5

axis(1, at=axTicks(1, exp=c(0,250,4)), labels=seq(0,xmax,length.out=5), cex.axis=cex.axis)

# zone 4: Legend

par(mar=c(4,4,0,0))
plot(t,p1, ylim=c(0,1), type="n", xaxt="n", yaxt="n", xlab="", ylab="", bty="n")
legend(x=.3, y=0.2, legend=c("TO Descent", "TO Bottom", "TO Ascent"), col=c(1,2,3), lty=c(1,3,1,3),
bty="n", cex=cex.lab)
8.8 Multi-state random walk dive path simulation


Dstate <- 0
sw <- 0
d <- 0
d.proj <- 0
tau2 <- 0
sState <- 0
betazero <- matrix(NA, nrow=3, ncol=3)
betatwo <- matrix(NA, nrow=3, ncol=3)
td <- 0
tf <- 0
i <- 0
mu <- matrix(NA, nrow=3, ncol=1000)
m <- matrix(NA, nrow=3, ncol=1000)
mvec <- matrix(NA, nrow=1000, ncol=3)
DDstate <- state <- Dstate <- 0
t <- 1

# simulation

Dstate[1]<-1 # You start the dive in DESCENT (state 1) so you wont have accumulated any time in flat mode so
# tf starts at zero
DDstate[1] <-1
mvec[1,] <- c(1,0,0)
state[1] <- 1

sw[1]<-0 # Multiplier for tf in DESCENT (state 1)
sw[2]<-1 # Multiplier for tf in FLAT (state 2)
sw[3]<-0 # Multiplier for tf in ASCENT (state 3)

d[1]<-0.5 # Depth at time step 1
d[2]<-1.0 # Depth at time step 2
d.proj[1]<-0.11 # Temporary carrier for depth

td[1]<-1 # Starting value for time
tf[1]<-0 # tf at beginning of time step 1
tf[2]<-0 # tf at beginning of time step 2
cpf<-10 # Cumulative time in state 2 as a proxy for satiation. The idea is for this to be calculated over a moving
time window eventually.

# state-specific rate of vertical displacement
sState[1]<- 3.343337
sState[2]<- 0.007497271
sState[3]<- -3.373051
tau1 <- 0.25 # inertia on speed from 18 three-day accelerometer depth records

# Coefficients for state transition matrix

# intercept
betazero[,1] <- c(7,2,-4)
betazero[,2] <- c(10,5,-10)
betazero[,3] <- c(10,5,-10)

# oxygen
betatwo[,1] <- c(-0.055,0.2,0.055)
betatwo[,2] <- c(-0.08,0,0,0.08)
betatwo[,3] <- c(-0.06,0,0,0.09)

while(d[t] > 0){
  t <- t+1
  td[t]<-td[t-1]+1 # Update to the next time step by incrementing time index by 1

  i[t]<-Dstate[t-1] # Let state at the previous time step determine the value of i. State can take on values 1:3 so we are using it here as a column index

  # State transition matrix - Transition 3 always a complement of 1 and 2
  mu[1,t] <- exp(betazero[1,i[t]] + betatwo[1,i[t]]*td[t])
  mu[2,t] <- exp(betazero[2,i[t]] + betatwo[2,i[t]]*td[t])
  mu[3,t] <- exp(betazero[3,i[t]] + betatwo[3,i[t]]*td[t])

  # row 1, column 1
  m[1,t] <- mu[1,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 1

  # row 2, column 1
  m[2,t] <- mu[2,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 2

  # row 3, column 1
  m[3,t] <- mu[3,t]/(mu[1,t]+mu[2,t]+mu[3,t]) # Linear predictor for state 3

  # State determination
  mvec[t,] <- rmultinom(n=1, size=1, prob=m[t])
  Dstate[t] <- max(1,min(3,mvec[t,1]*1+mvec[t,2]*2+mvec[t,3]*3)) # Dstate is determined using the vector of outcomes, mvec, and vector of state values, v
  state[t] <- rnorm(1, Dstate[t], 1/sqrt(10)) # checks whether the state I am providing (state) agrees with the state I am estimating (Dstate)
  Dstate[t] <- max(1,min(3,round(state[t])))
# Dstate[t]

tf[t+1] <- sw[Dstate[t]]*tf[t]+1) # This controls whether tf is incremented or not in the given time step. The dummy variable, sw, controls when this happens. If not in state 2, the number of time steps spent in flat mode is re-zeroed by being multiplied by zero, otherwise one time step is added to it.

# Movement model

d.proj[t] <- d[t]+sState[Dstate[t-1]] # Projected mean for depth at time t is defined as the depth at the previous time step plus the vertical speed calculated above

    d[t+1] <- rnorm(1, d.proj[t], tau1)
# Depth at time t+1 is drawn from a Normal distribution centred on the projected mean for depth at time t with inertia, tau1.

) # closes t loop
8.9 References


Appendix III: Supplementary figures for chapter 2
Figure 2.6. Smooth density scatterplots for the observed relationship between maximum dive depth and horizontal displacement (speed, m/s) for each individual (columns).

Figure 2.7. Smooth density scatterplots for the observed relationship between maximum dive depth and dive duration (sec) for each individual (columns).
Figure 2.8. Smooth density scatterplots for the observed relationship between maximum dive depth and temperature structure of the water column (°C/m) at the dive location, for each individual (columns).

Figure 2.9. Smooth density scatterplots for the observed relationship between maximum dive depth and Julian day, for each individual (columns). Month boundaries are delineated with vertical dashed white lines and month initials listed at the top of each figure (April to November, A to N).
Figure 2.10. Smooth density scatterplots for the observed relationship between maximum dive depth and percentage gravel in the sediment at the location of the dive, for each individual (columns).

Figure 2.11. Smooth density scatterplots for the observed relationship between maximum dive depth and percentage sand in the sediment at the location of the dive, for each individual (columns).
Figure 2.12. Smooth density scatterplots for the observed relationship between maximum dive depth and percentage mud in the sediment at the location of the dive, for each individual (columns).
Figure 2.14. Maps of model predictions for female 897 on a 1 km² grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.14 (continued)
Figure 2.14 (continued)
Figure 2.15. Maps of model predictions for female 902 on a 1 km$^2$ grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.15 (continued)
Figure 2.15 (continued)
Figure 2.16. Maps of model predictions for female 908 on a 1 km$^2$ grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.16 (continued)
Figure 2.17. Maps of model predictions for female 910 on a 1 km² grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.17 (continued)
Figure 2.17 (continued)
Figure 2.18. Maps of model predictions for female 915 on a 1 km$^2$ grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.18 (continued)
Figure 2.18 (continued)
Figure 2.19. Maps of model predictions for female 916 on a 1 km$^2$ grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.19 (continued)
Figure 2.19 (continued)
Figure 2.20. Maps of model predictions for female 921 on a 1 km² grid, the blue circles represent the track of the animal. Map a) shows maximum dive depth predictions during daylight (Light) and darkness (Dark). The colour legend and contours denote predicted depth in meters. Map b) shows predicted relative maximum dive depth (maximum dive depth divided by available depth) during daylight (Light) and darkness (Dark). The colour legend shows the maximum dive depth relative to the available depth, and the contours show actual depth in meters. Maps c) to e) show sediment distribution: c) the percentage of gravel at dive locations, d) the percentage of sand at dive locations, and e) the percentage of mud at each location.
Figure 2.20 (continued)
Figure 2.20 (continued)