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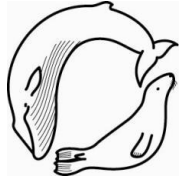
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This report presents the results of marine and freshwater scientific work carried out for Marine Scotland under external commission.

Modelling Harbour Seal Movements

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Executive Summary

1. Both the quantification and modelling of harbour seal movement are required to predict the consequence of environmental change on population distribution and connectivity.

2. Two modelling approaches were considered. The first is an empirical Inter-Haulout Transition Rate (I-HTR) model which estimates the population probability of an individual moving from one haulout site to another. The second is a mechanistic Individual Based Model (IBM) of movement which uses seal physiology in a simulated quasi-realistic environment to predict movement patterns. The scope of the IBM development is to demonstrate its 'proof of concept'.

3. In the I-HTR model, data from harbour seals tracked in Orkney and the Pentland Firth (22 GPS / GSM tags and 19 Argos tags) are used to populate a transition matrix (TM) showing the frequency of movement from one haulout site cluster to another. The TM is statically adjusted to represent the likely transitions of the local population of seals. It is then transformed to represent the probability of movement per unit time. The TM can now be used as the basis for a time-based simulation of seal movement and connectivity. However, the I-HTR model is empirical and as such does not consider the causes of movement, and so is not well suited to predict the consequence of environmental change.

4. A prototype individual based model (IBM) of harbour seal movement over time scales of days/weeks has been developed for the Pentland Firth / Orkney area. Many of the parameters in the model are place-holders (albeit realistic ones), with values that will be refined in the next stage of model development. The prototype IBM has a simple structure but it nonetheless captures the basic movement patterns and behaviour that are observed in harbour seal telemetry data.

5. To become a useful management tool, an IBM of appropriate complexity must be developed and tested, with the best possible estimates of parameters used to construct the model, e.g. from bioenergetic studies of captive seals or realistic estimates of habitat preference. The validation and checking of IBMs in general is an area of active research and for the seal IBM, appropriate checks may include comparison of model predictions in terms of summary properties and emergent properties of observational data, e.g. general patterns of spatial distribution.

6. The prototype IBM has proven the concept and development work should continue to test whether the available data (seal and environmental), statistical selection and fitting techniques can ultimately progress to producing a robust management tool. However, an important future challenge is to sufficiently map and quantify the dynamics of the geographical resources that seals require, such as haulout sites and foraging areas. Approaches could include the use of synoptic physical and biological data to predict those regions that may be preferred for foraging.

Contents

1   Introduction

Harbour seal (*Phoca vitulina*) movements are driven by the need to seek out geographically dispersed resources (haulout sites and foraging areas) within a dynamic environment and according to the changing demands of their annual life cycle. Movements result in two emergent properties that are relevant to conservation management. The first is geographic seal distribution, both hauled out on land and at sea. This distribution (also known as usage) is important for both near-shore and offshore planning (Jones *et al.*, 2016). The second is connectivity, or the flux of seals from one haulout site to another. An example of the importance of connectivity is the need to know the impact of disturbance at one haulout site on a distant Special Area of Conservation (SAC) haulout site. Connectivity also influences the transmission and persistence of disease.

To predict the consequence of change (natural or anthropogenic) on harbour seal movement patterns, it is necessary to quantify and model their movement patterns in a way that is representative of the local population. The aim of this study was to examine what modelling approaches are best suited to provide a robust management tool that can predict the consequences of 'what if' scenarios on harbour seal movement.

The scope of the study was limited to movement patterns and consequent distribution and connectivity. The population consequences (in terms of survivorship and fecundity) are outside the study scope. However, application of the models will assist the ability of expert opinion to predict population consequences (Harwood *et al.*, 2014).

Two modelling approaches are presented. The first approach, Inter-Haulout Transition Rate (I-HTR) modelling, is an empirical one. Telemetry data from a sample of tagged harbour seals in Orkney and the Pentland Firth are used to create inter-haulout movement transition matrices which are adjusted to reflect the local harbour seal *population* movements. The second approach is a mechanistic Individual Based Model (IBM) of movement. IBMs predict emergent behaviour from physiological capabilities and constraints using a set of biologically realistic yet simple rules within a simulated environment. Given that these rules can be sufficiently guided and tuned by data, IBMs offer the potential to present robust and biologically plausible scenarios to explore the effect of environmental change on seal movements. The scope of this exercise is limited to the construction of a prototype IBM as a 'proof of concept'.

2 Inter-Haulout Transition Rate Modelling

2.1 Introduction

Inter-Haulout Transition Rate (I-HTR) modelling is an empirical approach to summarise the connectivity within a network of harbour seal haulout sites. The approach is based on harbour seal telemetry data to determine the location of, and sequential use of, haulout sites. A haulout site can comprise a single seal on an isolated rock, or hundreds of seals hauled out within a square kilometre. To make the modelling tractable, geographically close haulout sites used by the tracked seals were clustered together. The transition between haulout sites requires the codification of what constitutes a trip (which may or may not include a foraging bout). A transition matrix (TM) is then constructed. However, this represents the movements of a sample of the population of seals, and then only up to nine months while telemetry tags functioned and remained attached to the seals. The TM is statically adjusted to represent the likely transitions of the local population of seals. The TM at this stage represents the probability of movement after each identified trip. However, trips may be of variable duration, so the TM must be expanded to include this variation. The TM would then describe the probability of transition per unit time. The TM may be further modified to restrict hauling out to the lower part of the tidal cycle.

2.2 Methods

Data collection

The study area used in the project was the Pentland Firth and Orkney Islands. The study area limits were 4.1° W to 1.8° E and 58.6° N to 59.9°N) (see the blue box in Figure 1). Telemetry data were compiled for tagged seals using this area (n=46) using data from 2003 to 2015. Because this study focuses on seal movements among haulout sites, only animals with ten or more haulout events within the study area were retained for the analysis (n=41). In total, 22 GPS/GSM tags (2011:13, 2012:6, 2015:3) and 19 ARGOS tags (2003:5, 2004:4, 2007:1, and 2012:9) were included in the analysis (Table 1). The study area is not a closed system in terms of movement. Thus, the entire extent of the tracks of the seals that used the study area is shown in Figure 1. Similarly, Figure 2 extends to all haulout sites used by the seals used in the analysis.
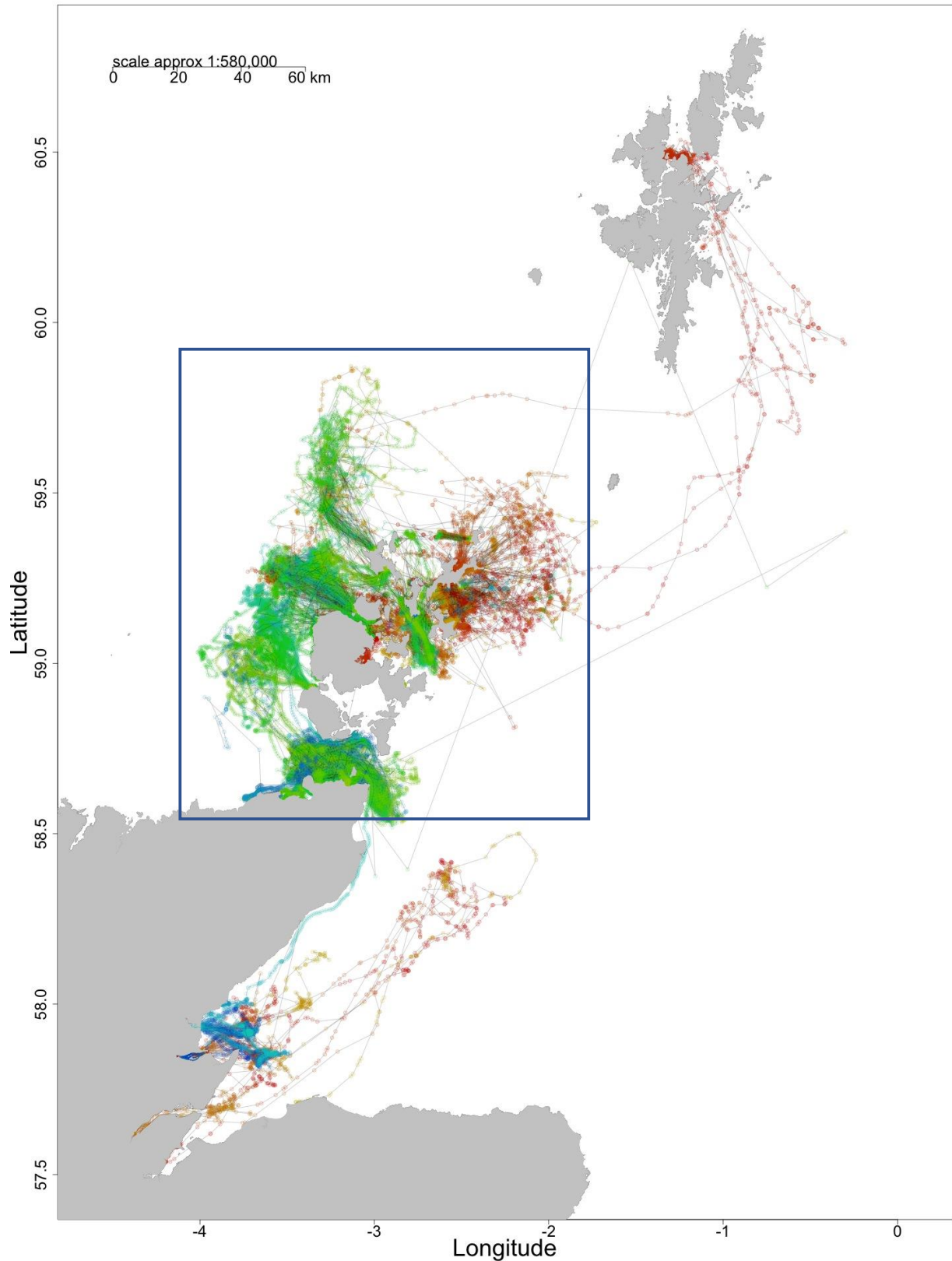
Figure 1. Tracks from 41 harbour seal tags: 19 ARGOS and 22 GPS. Each ARGOS track is coloured from red to orange (beginning to end) and each GPS from blue to green, to show the progression of each animal. The blue box represents the study area.

Table 1. Details of the 41 harbour seals included in the study. Longitude (Lon) and Latitude (Lat) indicate the approximate location of capture and tagging.

Tag ID	Type	Lon	Lat	Year	Start	End	Sex	Mass
pv1-ali-03	ARGO	-2.55	59.	2003	02/10	06/04	F	87.0
pv1-bo-03	ARGO	-2.55	59.	2003	02/10	03/04	F	83.5
pv1-cat-03	ARGO	-2.55	59.	2003	02/10	06/05	F	66.0
pv1-dot-03	ARGO	-2.55	59.	2003	02/10	01/07	F	85.0
pv1-erin-03	ARGO	-3.02	59.	2003	02/10	15/03	F	82.5
pv6-pat-04	ARGO	-2.60	59.	2004	15/03	08/07	F	83.0
pv6-queenie-	ARGO	-3.02	59.	2004	16/03	23/06	F	93.5
pv6-sally-04	ARGO	-3.12	59.	2004	18/03	31/05	F	78.0
pv9-dory-04	ARGO	-4.01	57.	2004	17/10	09/03	F	60.0
pv12a-181-	ARGO	-4.40	57.	2007	01/03	13/06	F	61.0
pv24-112-11	GPS	-3.16	58.	2011	24/09	09/03	M	92.8
pv24-148-11	GPS	-3.16	58.	2011	24/09	14/02	M	76.2
pv24-150-11	GPS	-3.16	58.	2011	26/09	17/01	F	86.6
pv24-151-11	GPS	-3.16	58.	2011	25/09	06/12	M	84.8
pv24-153-11	GPS	-3.16	58.	2011	26/09	25/01	F	72.0
pv24-165-11	GPS	-3.16	58.	2011	30/03	17/05	M	90.6
pv24-394-11	GPS	-3.16	58.	2011	30/03	26/06	M	49.6
pv24-541-11	GPS	-3.16	58.	2011	30/03	10/08	M	96.8
pv24-580-11	GPS	-3.16	58.	2011	29/03	01/07	F	89.0
pv24-590-11	GPS	-3.16	58.	2011	30/03	09/06	M	49.8
pv24-598-11	GPS	-3.16	58.	2011	29/03	17/07	F	84.6
pv24-622-11	GPS	-3.16	58.	2011	31/03	15/06	M	91.4
pv24-x625-	GPS	-3.16	58.	2011	31/03	23/06	M	98.6
pv44-003-12	ARGO	-2.77	59.	2012	18/06	29/07	F	92.8
pv44-004-12	ARGO	-2.77	59.	2012	14/06	25/07	F	100.0
pv44-005-12	ARGO	-3.12	59.	2012	19/06	09/08	M	107.0
pv44-007-12	ARGO	-2.77	59.	2012	16/06	26/07	F	67.8
pv44-011-12	ARGO	-3.12	59.	2012	19/06	09/08	M	106.0
pv44-014-12	ARGO	-3.12	59.	2012	19/06	02/08	M	112.4
pv44-017-12	ARGO	-2.77	59.	2012	18/06	29/07	M	99.0
pv44-018-12	ARGO	-2.77	59.	2012	18/06	14/07	M	110.0
pv44-020-12	ARGO	-2.77	59.	2012	16/06	18/07	F	80.2
pv47-392-12	GPS	-3.12	59.	2012	11/10	29/01	M	NA
pv47-427-12	GPS	-3.12	59.	2012	10/10	27/10	M	NA
pv47-539-12	GPS	-2.77	59.	2012	09/10	01/03	M	NA
pv47-583-12	GPS	-3.12	59.	2012	10/10	17/01	M	NA
pv47-585-12	GPS	-2.77	59.	2012	09/10	09/03	M	NA
pv47-588-12	GPS	-3.12	59.	2012	11/10	12/01	M	NA
pv59-05-15	GPS	-4.07	57.	2015	25/02	26/06	F	89.7
pv59-07-15	GPS	-4.07	57.	2015	27/02	18/07	F	73.1
pv59-12-15	GPS	-4.07	57.	2015	26/02	04/07	F	94.0

Data Filtering

The raw tag data required filtering. The lower accuracy and rate of location data provided by Argos tags compared to that provided by GPS tags meant that different filtering was required for the two types of tag data.

GPS Tag Data

The median time that GPS tags transmitted data whilst attached to seals, or lifespan of the tags, was 87 days (range: 16 days to 176 days. Each location was assigned a 95 % C.I., the distance between the given location and the true location of the animal. This distance was modelled (using a Gamma distribution) as a function of the number of satellites, using a large published dataset on GPS error (Dujon *et al.*, 2014).

Using the track data, each time-stamped haulout was assigned a location. If there were any valid GPS locations during a haulout, the maximum likelihood coordinates were used for the haulout. If there were none, the GPS locations immediately preceding and immediately following the haulout were used to interpolate (linearly) the haulout location. These locations were then 'snapped' to the nearest coastline. The distance between the estimated and snapped location was termed the 'snap distance'.

ARGOS Tag Data

The median lifespan of the ARGOS tags was 94 days (range: 32 days to 284 days). A Speed-Distance-Angle filter was applied to exclude unfeasible locations (Freitas *et al.*, 2008). A maximum speed of 5m/s [1], threshold angles of 5/10 degrees and distances of 5/10 km were used. The remaining locations were then Kalman filtered (Jones *et al.*, 2015).

However, some locations appeared (erroneously) on land. These were snapped to the coastline by the following method. Land locations were first snapped to the nearest coastline. The shortest path at sea between the locations at sea immediately preceding and following the landlocked location was then calculated, and the landlocked location was then interpolated along this path.

Using the track data, each time-stamped haulout was assigned a location. If there were any valid ARGOS locations during a haulout, the median coordinates were used for the haulout. If there were none, the ARGOS locations immediately preceding and immediately following the haulout were used to interpolate (linearly) the haulout location. For some haulouts, locations used for interpolation were distant

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[1] This speed threshold may be low in areas of high tidal current. However, a lesser speed would tend to allow some locations with a large error to pass through the filter.

in time. Interpolated haulout locations with the longest time intervals (top 5 %) were excluded. The remaining locations were then snapped to the nearest coastline. Some interpolated haulout locations remained distant from the coast. This could be due to location error, the linear interpolation being carried out on locations that occurred long before and long after the seal had hauled out, or to extended surface intervals (ESI) at-sea that can appear as haulout events (Ramasco *et al.*, 2014; Russell *et al.*, 2015). Haulout locations over 2 km from the nearest coastline were assumed to be ESI events and were therefore excluded.

Defining Haulout Site Clusters

Haulout sites determined from the seal tracks were grouped using a clustering algorithm (R package 'hclust', with the centroid method). The minimum distance between the centroid of haulout clusters was set at 3 km. This threshold was selected to identify as many distinct haulout sites as possible while staying outside the likely location error of ARGOS haulouts. Seventy haulout clusters were produced and their coordinates were snapped to the nearest coastline (Figure 2).

Trip assignment

A trip was defined as 'not hauled out for at least ten minutes', and having moved at least 2 km away from the last haulout cluster, as smaller changes in locations could be simple location error. The entire track of a seal was thus divided into mutually exclusive trip and haulout states.

Construction of Transition Matrices

Maximum Likelihood Estimates

The trip events were used to construct matrices of transition probabilities among haulout clusters. These probabilities are shown in matrix form (Figure 3), where each cell illustrates the probability of transition from rows to columns. The maximum likelihood estimates for transition probabilities from each starting haulout cluster (row) are simply the number of trips to each destination divided by the total number of trips starting at that cluster. To preserve individual variability, a transition matrix was obtained for each animal.
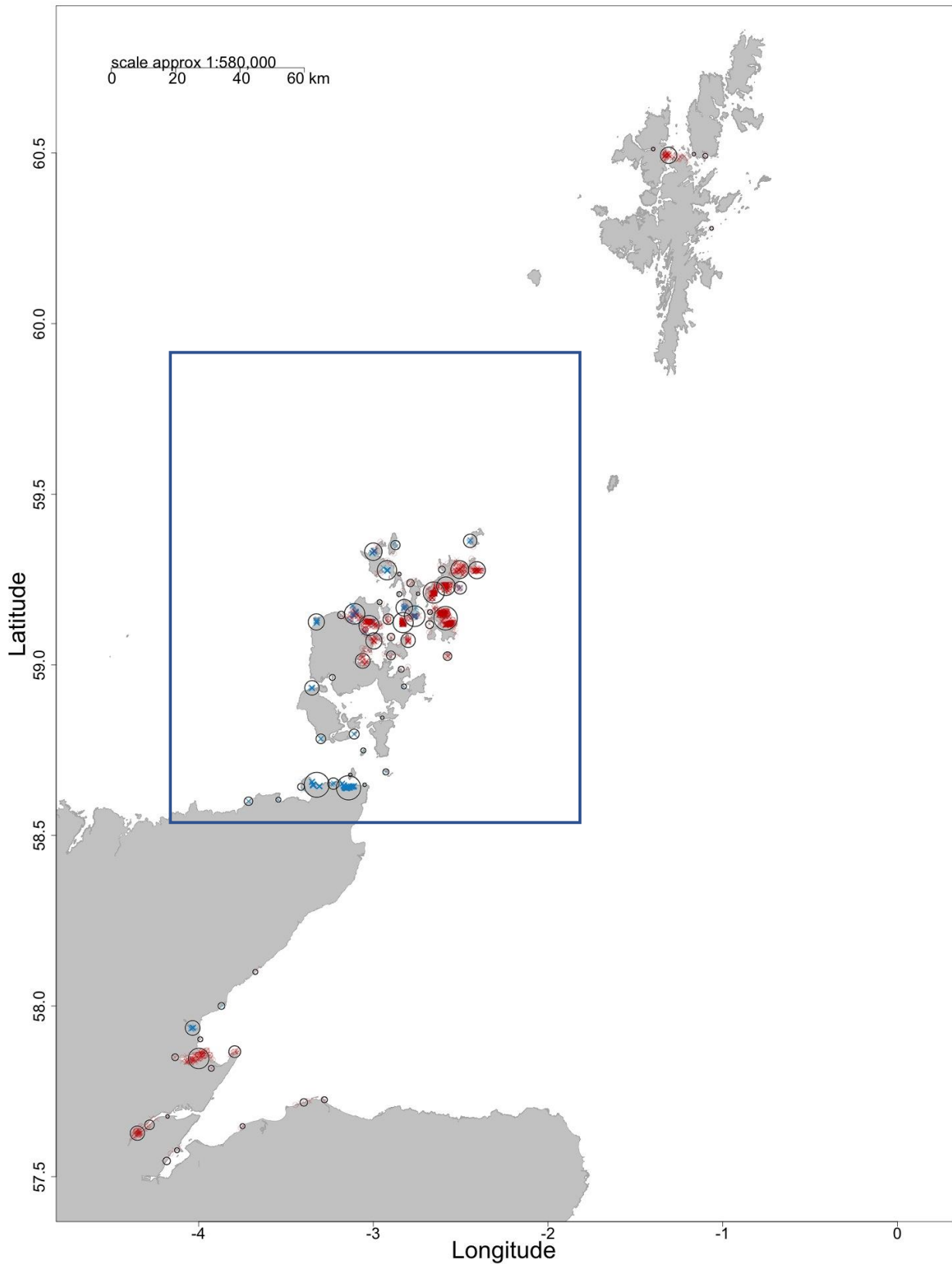
Figure 2. Haulout site clusters derived from 41 harbour seal tags. Individual haulout events from ARGOS tags are shown in red (N=1485) and those from GPS tags in blue (N=1800). Black circles show the centroids of haulout sites after clustering, and the size of circles shows the number of haulout events assigned to each cluster.

The blue box represents the study area.
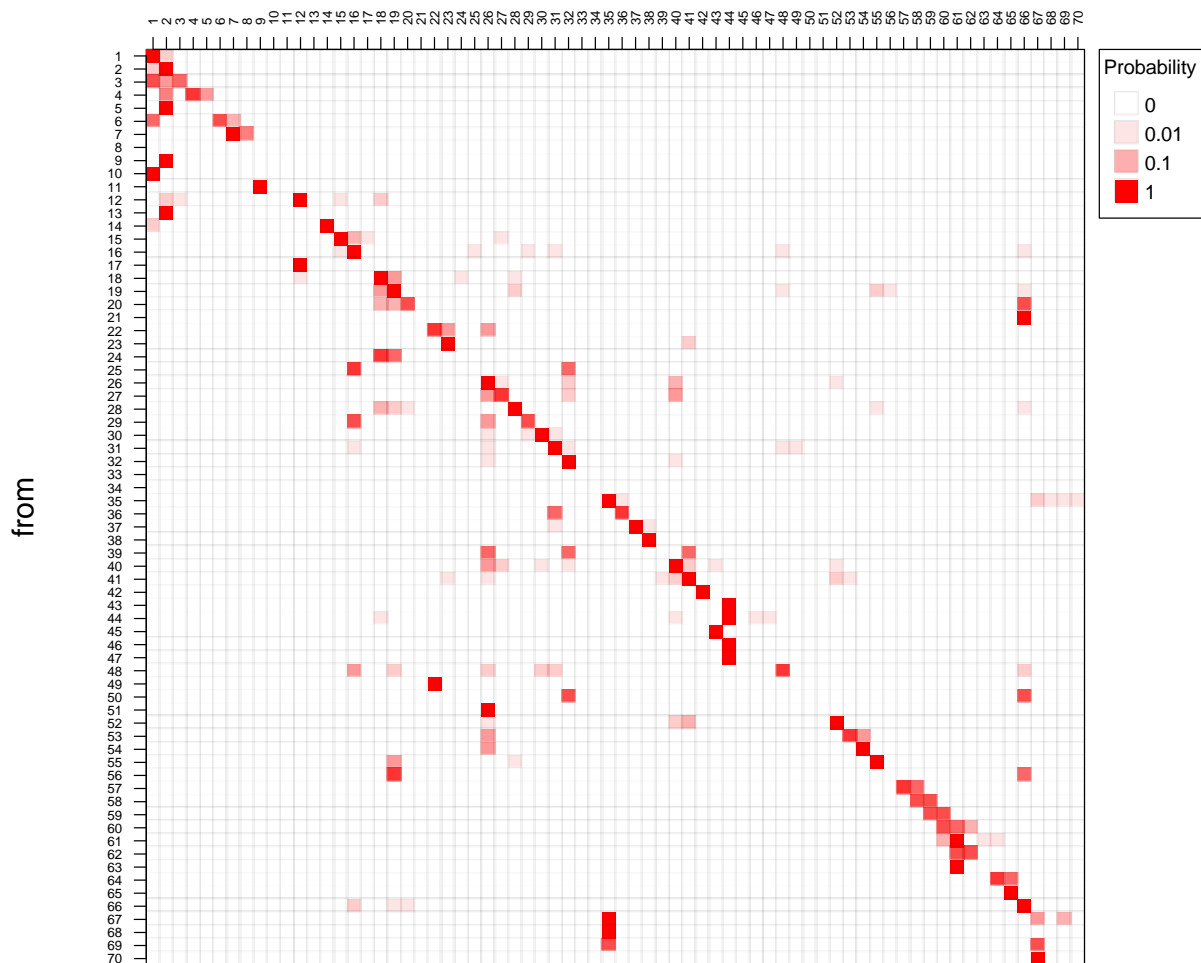
Figure 3. The probability of transitions from one haulout cluster (rows) to another (columns) using data from 41 harbour seal tracks. These are the maximum likelihood estimates. The model only has a first-order memory. This means that where a seal hauls out next is only influenced by its previous haulout site.

Modelling Transition Probability

The transition matrices contain many zero probabilities – trips between haulout sites that were never observed. While some may correspond to trips that will never occur, many are likely to happen given a longer observation period. In addition, historical aerial survey data reveal seals hauled out at sites from which no trips were observed. To fill in these gaps, the transition probability was modelled as a function of distance between sites (shortest sea route) and averaged historical aerial counts of hauled-out harbour seals (1996 to 2014: Duck *et al.*, 2015). The aerial counts within 1.5 km of a haulout site were counted for each year, and the median count for

all available years was calculated. Transition probability was modelled with a zero-one inflated beta distribution (R package 'zoib') using the population level trips. The model explained 49% of the variance. The modelled transition probabilities were used to fill in gaps in the next step.

As tracks only covered a limited time (~ two months), only a sample of the haulout sites visited by each seal were observed. If the animals had been tracked for longer, the number of unique haulouts and trips would almost certainly be higher than that observed during the study period. The number of unique haulout sites visited by each seal over longer time periods was estimated by fitting a discovery curve, which models the rate at which new haulout sites are visited. The number of unique haulout sites (N_{unique}) was modelled as a function of the number of haulout events (N_{events}) using the non-linear equation:

$$N_{unique} = \beta_0 - e^{(-\beta_1 * N_{events})}$$

where β_0 is the maximum number of unique haulout sites that an animal visits and β_1 is the rate of discovery. For each seal, haulout clusters were resampled with replacement 500 times and the curve was fitted to each bootstrap sample. This yielded a distribution of β_0, the expected number of unique haulout site clusters visited and was summarised by a log-normal distribution for each animal. At the start of each simulation iteration the number of missed unique haulout site clusters (N_{missed}) was drawn randomly from this distribution, with the constraint that at least one haulout site was missed. The identity of each new unique haulout site was drawn from a multinomial distribution, where the probability of a haulout cluster being selected equalled the sum of the modelled transition probabilities for each haulout cluster used by an individual tracked animal.

A trip ending at the new haulout cluster (E) was then added. The starting haulout cluster (S) was drawn from among the observed haulouts. The probability of S being selected was proportional to the modelled probability of transition from S to E and the matrices of transition probability were then recalculated. As there were no data for trips originating from a new haulout cluster, the modelled probability of transition was used for each new haulout cluster.

Converting the TM to a Time-Base

To account for variable haulout and trip durations, at-sea states indexed by the haulout cluster of departure were added to the transition matrices. For each of the 41 individual seal track transition matrices, the median duration of haulouts and at-

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sea trips were used to estimate the hourly probability of remaining in each state. These *time-based* transition probabilities were then used to populate a haulout/trip transition matrix as illustrated in Figure 4. The upper left quadrant of the matrix refers to the probability of remaining at a haulout (diagonal with probabilities close to 1). The upper right quadrant refers to the probability of leaving a haulout and entering an at-sea state. The lower right quadrant refers to the probability of remaining in an at-sea state. The lower left quadrant refers to the probability of hauling out at a haulout cluster given its previous haulout cluster. Seals cannot directly transit from one haulout cluster to another without first having transitioned via an at-sea state (indexed by its departure haulout cluster).

In most areas, seals haulout more frequently at low tide. To reproduce this tendency, a tidal modifier (11h cycle) was added to the probability of starting and ending a trip: the right half of the transition matrix (Figure 4). The maximum difference in the probability of hauling out (low vs high water) was set to 2 on the logit scale; an approximation from time lapse photos obtained at two haulout sites (SMRU, unpublished data).
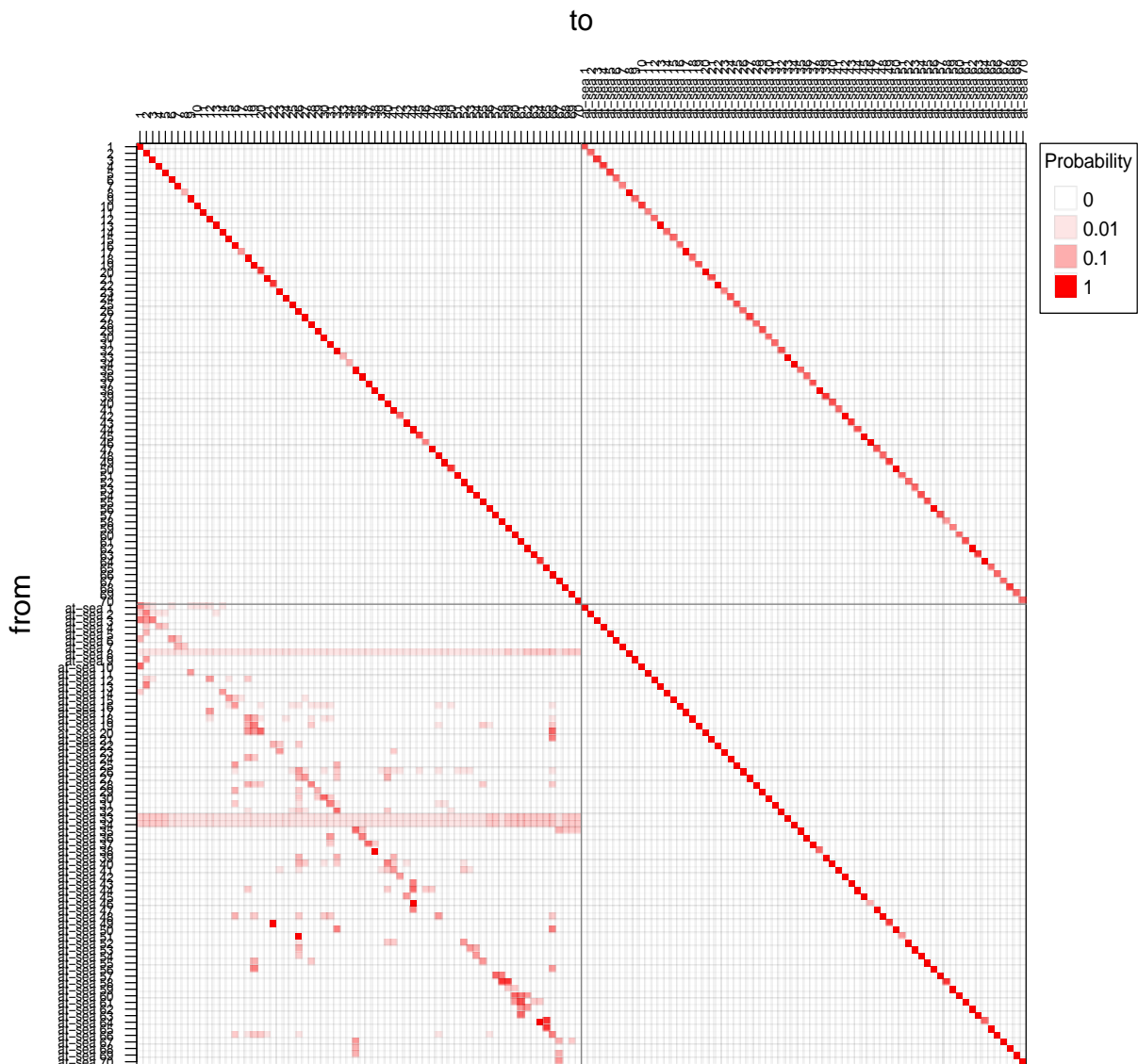
Figure 4. Example of a two-class (haulout and at-sea) transition matrix. The elements represent the hourly probability of transitioning 'from' one state 'to' another. The upper left quadrant shows the probability of remaining at a haulout site. The probability of the alternative event (ending a haulout and entering the 'at-sea' state indexed by that haulout site) is shown in the upper right quadrant.

The lower right quadrant shows the probability of remaining in an 'at-sea state'. The probability of the alternative event (ending a departure-specific 'at-sea' state and choosing where to haulout next) is shown in the lower left quadrant.

The TM illustrated may now be used to quantify the connectivity of any one haulout site with other sites.

2.3 Discussion

This movement model has two novel features. The first is that it infers which new haulout sites might have been used if the tagging duration of individuals had been longer. This was achieved by modelling a discovery curve. The second is that an inference is made about movement patterns of the *population* of seals (from which the sample of tagged animals are drawn).

Connectivity is an important consideration for marine regulators. Consider a haulout site designated as a Special Areas of Conservation (SAC) under the EC Habitats Directive - knowledge of inter-haulout connectivity with other haulout sites is needed to maintain such a discretely-delineated site at a favourable conservation status within a larger network. The degree of connectivity also impacts the interpretation of haulout count surveys by identifying the geographic scale of individual's movements patterns.

Whilst outside the scope of this methodological study, the I-HTR model may be used to test for the effect of age, sex, and seasonality on inter-haulout connectivity where sufficient telemetry data are available to consider these factors. The TM may also be used to predict the dynamics of haulout site usage. This could be achieved by initially assigning (either randomly or informed by survey data) the population of local seals over the set of haulout sites. This vector of seal 'location states' could then be repeatedly multiplied by the TM. After a suitable run-in period, this vector would indicate the dynamics of population haulout site usage over periods of weeks. The emergent distribution may be stable, or cyclical. This theoretical prediction of population variability in haulout site usage can be tested against a time series of observations of a set of haulout sites, and then used to generalise the variability associated with single survey counts.

The I-HTR model is based on telemetry track data and the framework compliments extensive pelage recognition mark-recapture studies that can persist over many years. The I-HTR model is inherently empirical, thus, whilst useful for modelling the existing or historical dynamics of inter-haulout movement (the model does not predict where animals will be located at-sea), the I-HTR model is limited in its ability to explore scenarios involving environmental change. Such changes may be natural (such as the changing distribution of prey fields and on-shore wind patterns) or anthropogenic (such as the disturbance of a haulout site due to industrial activity, or the establishment and operation of marine energy generation schemes). In addition, the model's 'memory' is limited to the location of the previous haulout site. These limitations, resulting from the empirical nature of the model, are the main drivers to

explore the feasibility of a mechanistic individual based model of harbour seal movement based on physiology, energy and information.

3 Individual Based Modelling

3.1 Introduction

This section explores the feasibility of constructing and populating a scalable, mechanistic harbour seal individual based model (IBM) to model harbour seal movements and ultimately to predict changes in their distribution in relation to man-made or natural environmental change. This compliments the I-HTR approach above. A limitation of the I-HTR approach is that modelled animals can only remember one step (transition) back and this is unlikely to be true in real seals. In addition, the I-HTR approach is purely empirical; that is, the model is not based upon individual seals' strategies to achieve their energetic requirements through foraging and resting in a variable biological and social environment.

An IBM is a set of simple, biologically-derived rules that are applied to a population of simulated animals. The resulting patterns of movement and behaviour are referred to as the IBM's *emergent properties*. Examples of such properties include various summary statistics of movement, distribution and activity budgets. These properties may be compared with similar summary statistics (Thiele *et al.*, 2014) of real data to assess the model fit and to guide changes to the model structure. The IBM rules should be comprehensive enough to realistically predict seal behaviour under a number of 'what if' scenarios. On the other hand, too many rules will produce an over-complex, computationally demanding model. Recent developments in IBM methodology have provided tools to determine optimal model complexity for a given purpose and to estimate model parameters (Railsback and Grimm, 2011; Thiele *et al.*, 2014).

Whilst IBMs are challenging to build and data hungry to parameterise, they do offer an opportunity to synthesise environmental and biological processes and data over a spectrum of temporal (from dive behaviour to seasonal trends) and spatial scales, thus offering the prospect of more credible and defensible predictions of the effect of natural or anthropogenic change. It is important to note that the aim of an IBM is not to reproduce the exact behaviour of individuals, rather it is to validate its emergent properties compared with data, to check the credibility of the underling rules.

An IBM[2] has been developed in Denmark to explore the effect of noise on the movements of harbour porpoises (*Phocoena phocoena*) (Nabe-Nielsen *et al.*, 2013; 2014). However, there are basic differences in the movement behaviour of harbour seals and porpoises which must be reflected in changes to this model structure. On the positive side, the quantity and quality of data available for model validation and parameter estimation is far greater for harbour seals than was available for construction of the porpoise IBM.

The aim of this study is to identify the components of a plausible harbour seal movement model and to identify the data that would be required to tune it into a useful predictive model. In addition to establishing 'proof of concept', the research requirements for full model development are discussed.

3.2   Harbour Seal Biology

An IBM should be based upon the known physiology and behaviour of the target species. The pertinent features of harbour seal biology are summarised here.

Harbour seals need to maintain both short-term condition (through foraging–resting cycles) and long-term condition (for females sufficient to produce a viable pup each year). The strategy seals use to attain these goals is both enabled and constrained by their physiology, for example, ingestion/digestion rates (Sparling *et al.*, 2007).

Harbour seals haul out on land at a variety of haulout sites, forming groups of various sizes. Some haulout sites may not be available during high water tides. Most haulout events last between 6 and 12 hours. This is followed by a foraging trip of between one and five days, typified by a directed travelling phase, an area restricted search (ARS) or foraging phase, and a return phase of directed travel (Cunningham *et al.*, 2008). Few foraging trips extend further than 50 km from the departure site. Usually the seal will return to the same haulout site and the 'central place' foraging pattern is repeated. This implies both navigational skills and the use of a spatial memory map. However, harbour seals occasionally move to alternative (sometimes distant) haulout sites, resulting in a larger total area being used. Interruption of at-sea foraging with a terrestrial haulout may be ultimately driven by a seal's ability to ingest food faster than it can digest it (Sparling *et al.*, 2007). Within the general behavioural pattern described above, there may be considerable variability. Whilst an individual may carry out repeated activity in one location, there can also be a high degree of inter-individual variability.

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[2] http://depons.au.dk/currently/news/nyhed/artikel/new-depons-model-released/

In summary, the activity of harbour seals may be grouped into three mutually exclusive states: resting (both ashore and at sea), directed travelling and searching, and foraging (Russell *et al.*, 2015). This central-place movement contrasts with the nomadic foraging of porpoises (Nabe-Nielsen *et al.*, 2014).

3.3 Model Structure

The biology of harbour seals is mapped onto a prototype IBM according to the scheme illustrated in Figure 5. The types of variable assignments, the decision rules and parameters outlined below describe the current status of a simple prototype IBM. The development, testing and parameterisation of these rules are discussed below.

The following typographic convention is used below. Variables and variable classes are shown in *italic*. Occasionally the plural version of a variable name may be used. There are three variable classes: global (*g*) referring to all individuals, individual-specific (*seals*), and landscape (*lscape*) which refer to the location and quality of physical (e.g. haulout sites) and biological (e.g. prey) resources. Variable and parameter values are indicated in courier font. Values have been chosen based on published estimates and on unpublished SMRU data.

IBM Currencies

The IBM is based on two currencies: energy and information (Nabe-Nielsen *et al.*, 2013). Activity indexed energy assimilation and expenditure is based on information in Sparling *et al.* (2007). Energy intake is based on a plausible (though speculative) maximum of one 200 g fish caught every second dive during foraging (FO) *activity* and subject to an energy assimilation factor. Each foraging patch has a *quality* index which decrements this maximum rate. Such energy budget estimates are placeholders to get the prototype IBM up and running, however, they are amenable to parameterisation, albeit with large confidence intervals.

The other currency, information, comprises the quality of resources previously visited and the navigational routes to get to them. This information is seal-specific and decays through time.

Physiological Urges and Behavioural Activities

Each seal in the IBM has physiological *urge* that alternates between foraging at sea (*urge* = FO) and hauling out ashore (*urge* = HO). Whilst, in reality, both urges may

coexist and compete, the model only considers *urge* as a binary outcome, based primarily on the recent condition and experience of an individual.

A physiological *urge* is potentially satisfied by the appropriate behavioural activity (HO or FO). However, foraging patches at sea and haulout sites on land are frequently geographically separate. Thus, a change in the dominant physiological *urge* will frequently require movement. Two types of movement *activity* are considered: directed travel (DT) to a specifically chosen geographic target in a spatial memory map (SMM), a concept which is supported by observed high inter-individual variation but low intra-individual variation in foraging patterns (Sharples *et al.*, 2012), and searching (SE) for a generic target/resource.

In summary, there are two *urges* (HO and FO) which results in one of four behavioural *activities* (HO, FO, DT and SE).

Movement

The IBM has four types of movement, each described by an activity-specific mean speed and mean turning angle (and their variability). During haulout *activity* (HO) there is no movement. During foraging *activity* (FO), there is a local area restricted search (ARS) movement. The remaining two movement patterns involve directed or searching transition (Nabe-Nielsen *et al.*, 2013) from one resource to another. Directed travel *activity* (DT) is based on the ability of a seal to store route information to resources (haulout sites or foraging patches) in a SMM, and the ability to navigate such routes. Prior to IBM simulation, these routes are pre-computed as raster layers at a granularity of 1 km^2, comprising vectors of the shortest sea-route to the target from any starting-point raster cell. An example raster is shown in Figure 6. There is one raster layer per target destination. In the model, these shortest sea-routes are currently not influenced by tidal currents.

Before initiating directed travel, a geographical target destination is required. The choice of target destination (either a foraging patch or a haulout site) is drawn from possible destinations within an individual's SMM. The choice is influenced both by the shortest sea-route distances to each candidate target, and the individual's perception of the historical quality of each target. For a haulout, target quality is enhanced by the previous co-occurrence of other seals, but is not currently influenced by temporally varying factors such as tidal height, air temperature and on-shore wave action. For a foraging patch target, the quality is enhanced by the perceived historical efficiency of energy assimilation (prey accessibility). In this

prototype IBM, the actual choice is stochastic, with the destination randomly drawn using a multinomial distribution based on the modelled preferences.

The information in each individual's SMM is forced to decay through time[3]. This reflects the fact that old information may be less relevant to current conditions, for example the historical location of transient shoals of pelagic fish in a different season. The seal then travels the shortest sea route to the chosen destination target. In the IBM there is no feeding during this travel phase.

The fourth movement pattern is searching *activity* (SE). This movement mode is selected if the memory mode has failed to maintain a satisfactory energy balance over a prolonged period (weeks). Search strategy is useful if a seal has an incomplete or significantly decayed SMM. In the prototype IBM, each seal is initiated with complete and recent knowledge about haulout site and food patch location and quality. Currently the search *activity* is not activated in the IBM, but it will take the form of moving to a recently used foraging patch and then initiating a variant of a correlated random walk search.

Assessment of Physiological Urge

During haulout (HO) or foraging(FO) *activities* the prevailing physiological *urge* is continually reassessed to determine whether it is still appropriate. During the transitional *activities* (DT and SE) there is no reassessment of *urge*.
The *urge* assessment in the prototype IBM takes the general form:

current *urge*	rule
FO	If 3 days have elapsed since the start of foraging, or an extra 3% of initial blubber energy has been gained since the last haulout then switch *urge* = HO.
HO	If 1 day has elapsed since the start of being hauled out, or a 3% of initial blubber energy has been lost during the haulout then switch *urge* = FO.

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[3] Each seal has two SMM structures: one for haulout sites and one for food patches. These take the form of geo-referenced rasters, at a granularity of $1 \ km^2$. For each cell visited, each map contains a pair of values representing the perceived quality of the targeted resource and the date of the observation. The rate of decay (blurring of spatial and quality data) is set to $10 \ days$.
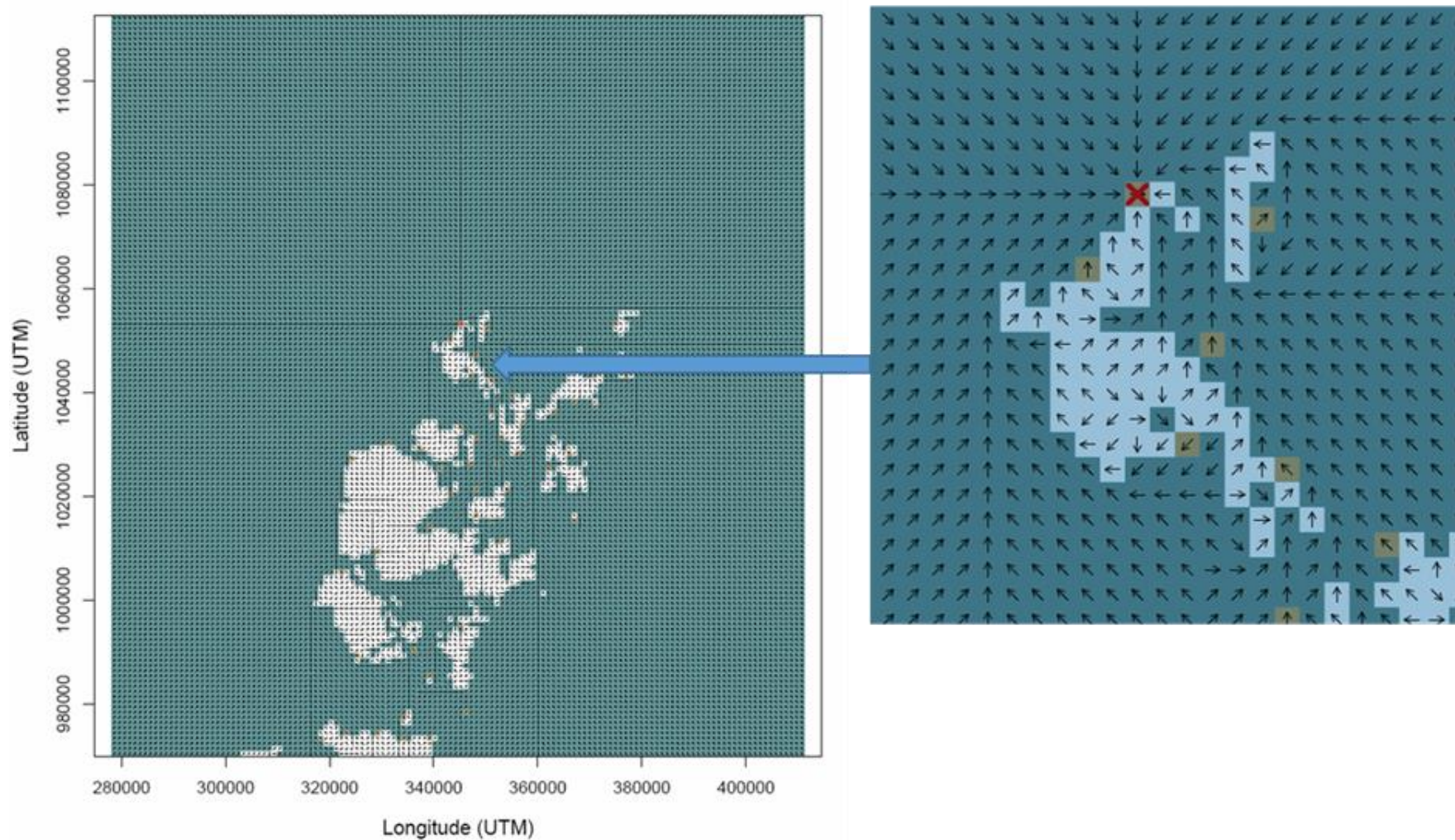
This is a very simplistic rule. Also, there is no distinction between waiting nearshore for a tidal haulout site to become available (current included in FO *activity*) and being hauled out on land. Approaches to select and parameterise more complex rules are considered in the Discussion.

Resources: Placement and Assessment

For the prototype IBM, a subset of 10 of the Orkney/Pentland Firth haulout clusters identified by the I-HTR model were used (see Figure 2). They were assigned uniform quality. Five foraging patches (restricted to only one 1 km^2 raster cell each) were derived from visual inspection of the tracks used in the I-HTR model (see Figure 1). They were assigned a random quality.

Figure 5. Simplified summary of prototype IBM structure. The following operators are used: ++ increment; = assignment; = = equality. The typographic style is: *variable*; value. See text for details.

Figure 6. Example of a shortest-sea-routes raster. The arrows show direction vectors routing the seals to a target (here specified by the red cross). Vectors on land have no meaning.

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3.4 Model Simulations

The IBM scheme shown in Figure 5 was coded in the R language (R Core Team, 2017)[4]. The prototype was run over the same geographical extent as the I-HTR model in the previous section, and at a spatial granularity of 1 km^2 and temporal resolution of 20 minutes. In each model run, the seal is provided with perfect knowledge of the locations and qualities of haulout sites and forage patches. The starting mass of each seal is set at 100 kg, and starting blubber mass is set at 25 kg. Assuming that 65% of the blubber is lipid and that lipid has an energy density of 3700 Jg^{-1}, the starting blubber energy of each seal is calculated to be 481 MJ.

An example of a 10-day run with a single seal is shown in Figure 7. It commenced in a hauled-out state (*activity* = HO) at a randomly chosen haulout site. As part of the modelling process, no consideration was given to potential barriers to seal movement at sea, such as causeways or bridges. Future modelling could incorporate such barriers. Figure 8 shows the sequences of *energy* storage, physiological *urge* state and behavioural *activity* state*.
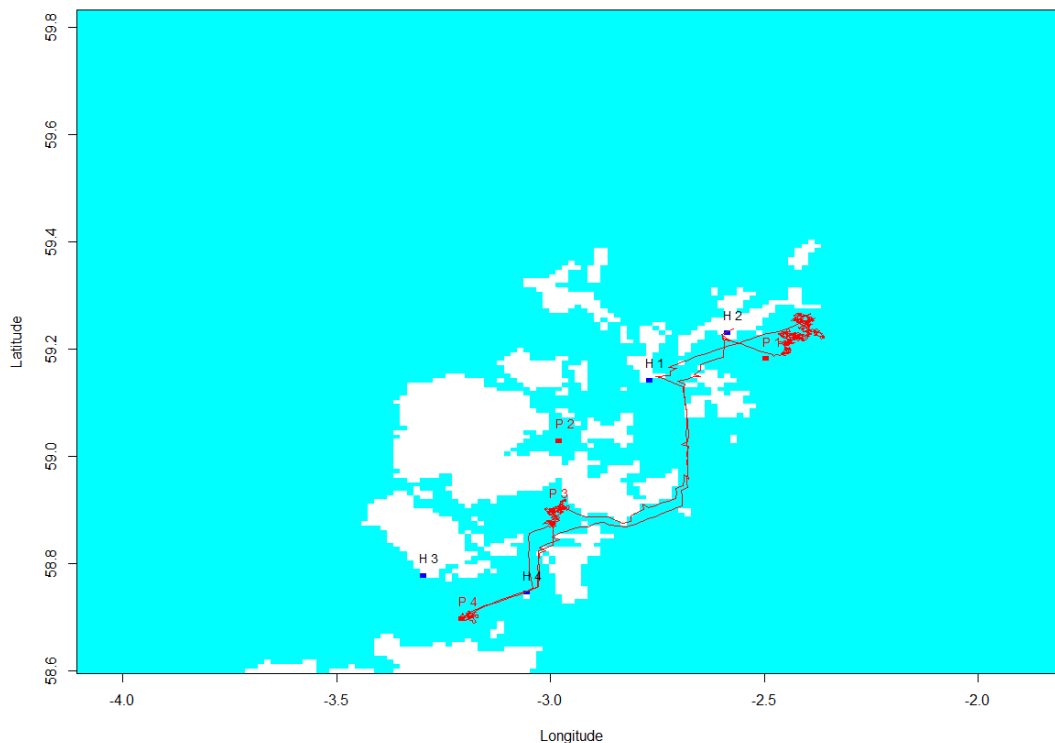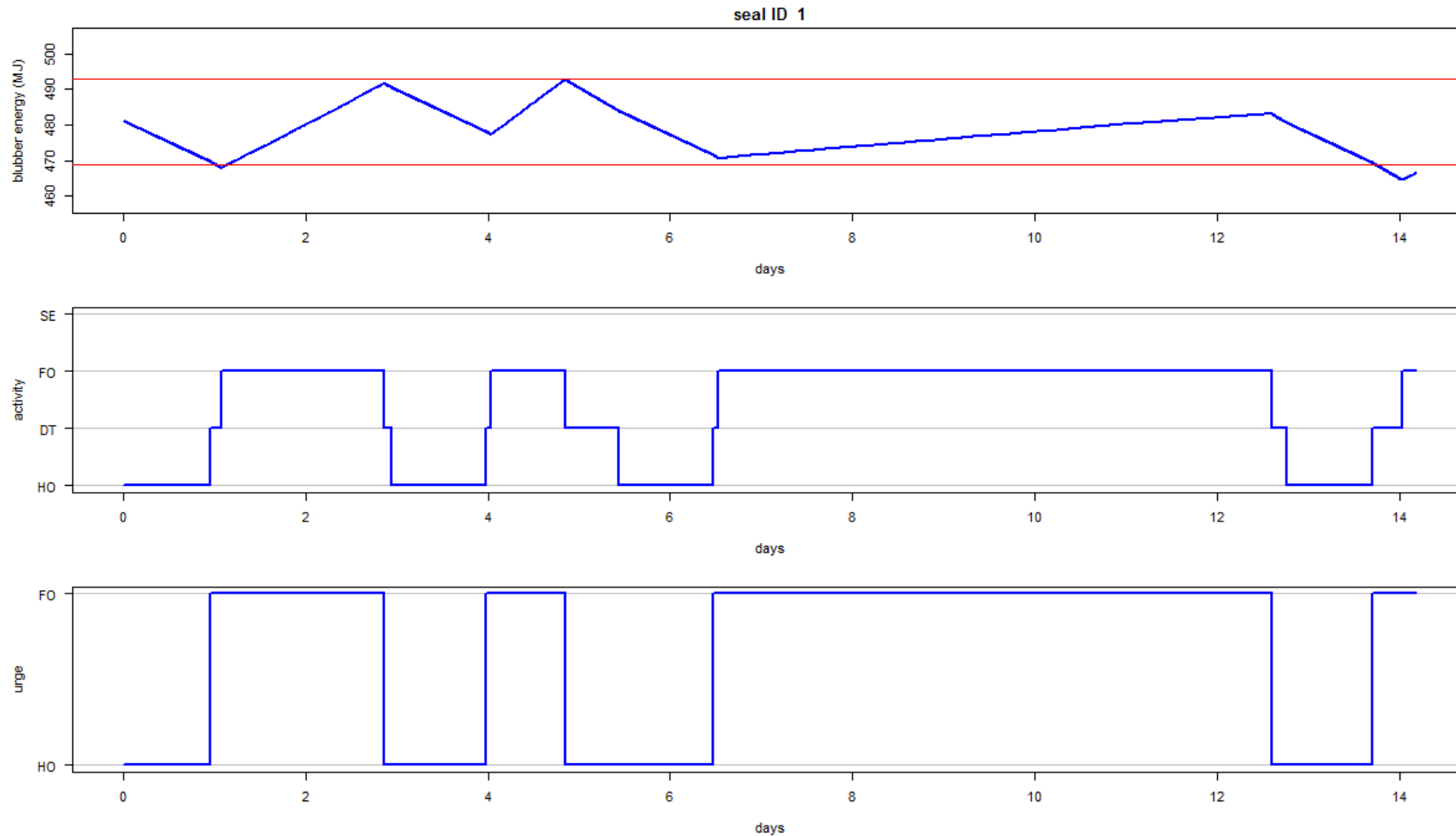

Figure 7. Map showing the simulated track of one seal over approximately 14 days. Haulout sites and foraging patches are shown in black and red respectively.

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[4] As a scripted language, R is not particularly fast. However, its popularity means that it is accessible for use or development by many researchers. The model is currently structured (via the 'lapply' function) to facilitate fast multi-core parallel processing.

Figure 9 shows four seals run for a period of 140 days and Figure 10 shows the energy and state timeline for the first of the four seals.

The physiological *urge* alternates between HO and FO. This results in the corresponding behavioural *activity*, lagged by the time needed to travel to and from offshore foraging patches. The resulting total blubber energy budget, in turn, influences the assessment of the dominant physiological *urge*.

The resulting tracks, whilst perhaps a little unvarying in bearing angle, qualitatively capture the movement and behaviour patterns shown by the real tracks in Figure 1.

Figure 8. Status timeline of the simulated seal shown in Figure 7. The top plot shows the total energy content of the blubber. The red lines show the thresholds that influence a change of *urge*. The middle plot shows the changes of behavioural *activities* (HO = hauled out, DT = directed travel, FO = foraging and SE = search (not currently supported)). The lower plot shows the changes in the underlying physiological *urges* that drive *activity* (HO = haulout, FO = forage).
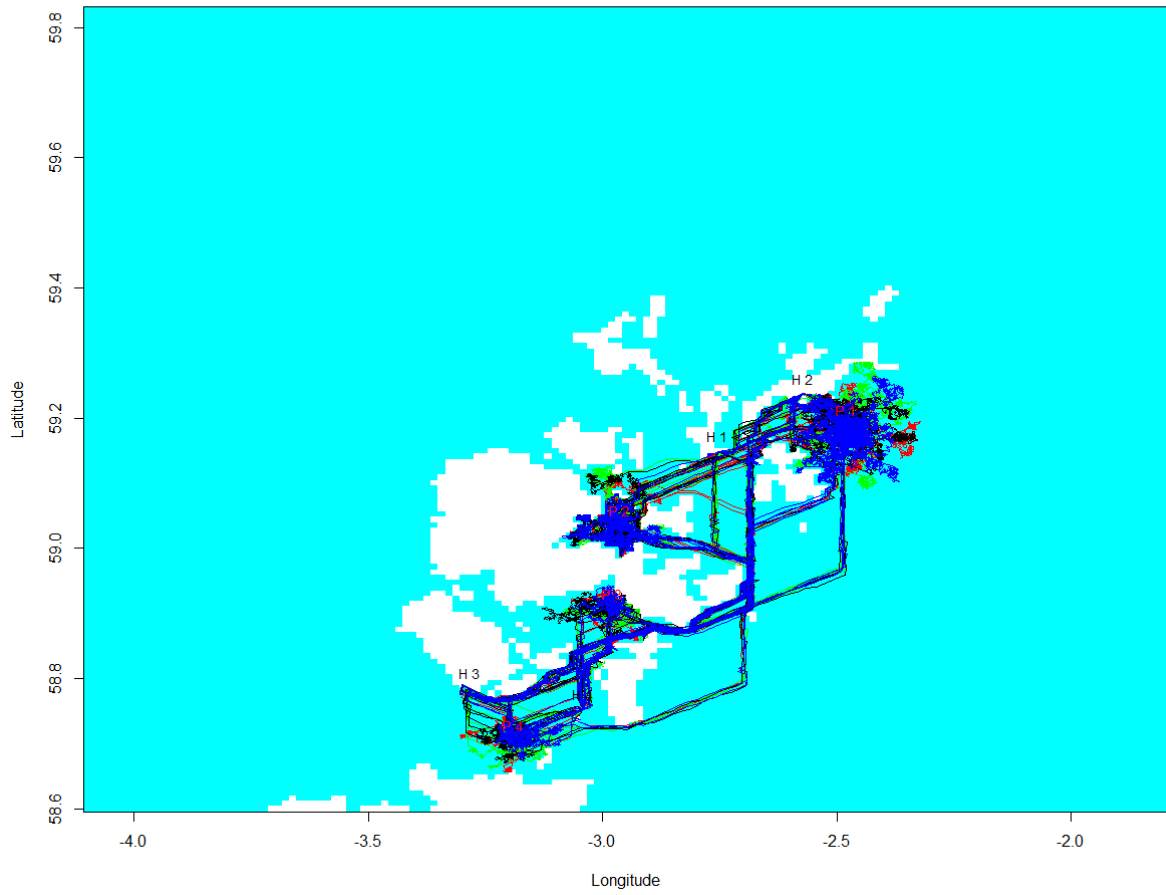
Figure 9. Map showing the simulated track of four seals over approximately 140 days, coloured by individual. Haulout sites and foraging patches are shown in black and red respectively.
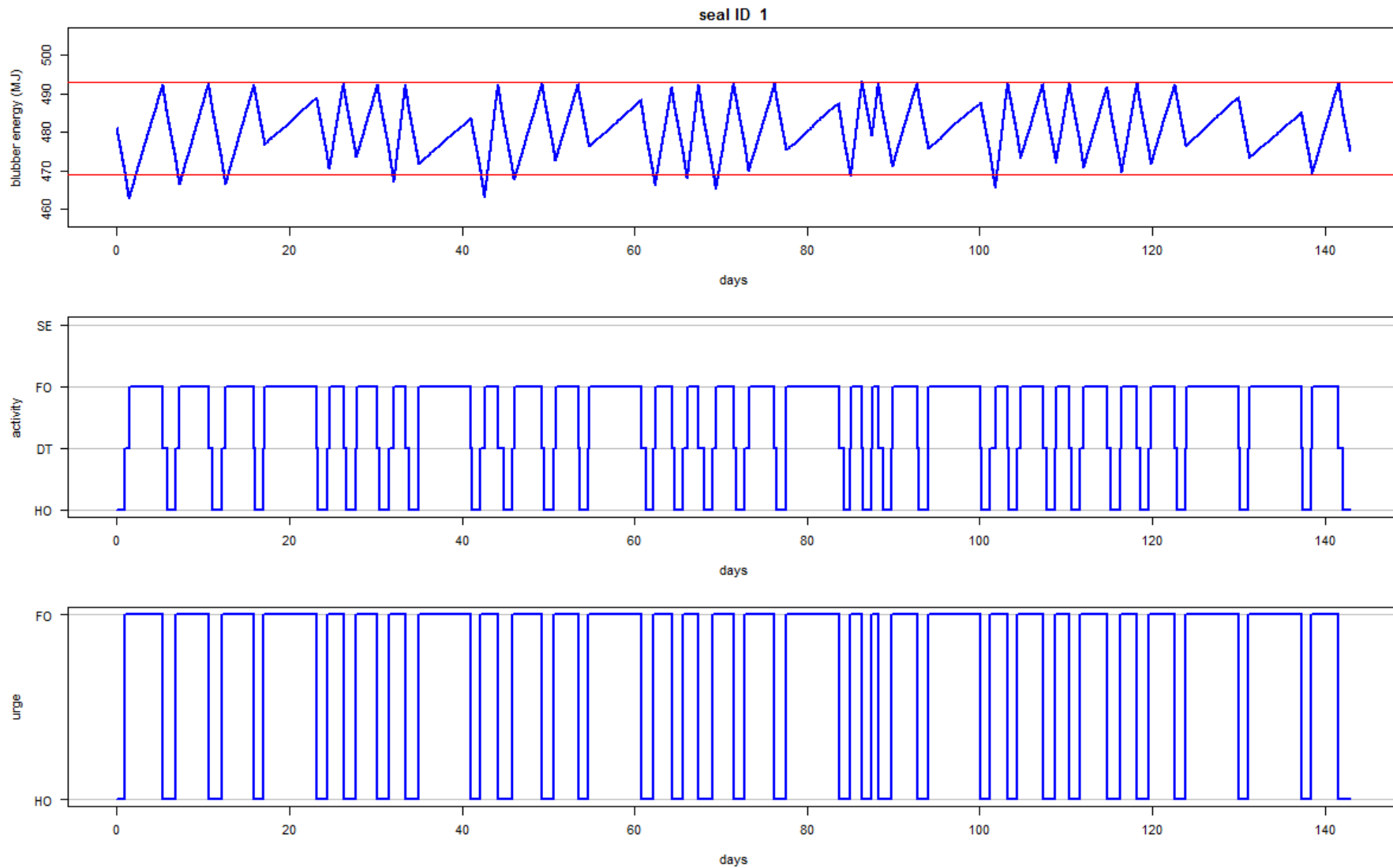
Figure 10. Status timeline of the first of four simulated seals shown in Figure 9. The top plot shows the total energy content of the blubber. The red lines show the thresholds that influence a change of *urge*. The middle plot shows the changes of behavioural

activities (HO = hauled out, DT = directed travel, FO = foraging and SE = search (not currently supported)). The lower plot shows the changes in the underlying physiological *urges* that influence *activity* (HO = haulout, FO = forage).

3.5 Discussion

There are three particularly important challenges in the development of a predictive harbour seal movement IBM (Thiele, 2014). The first is to adequately map and quantify the dynamics of the geographical resources that seals require, in this case haulout sites and foraging areas. The second is to construct and select an IBM of the appropriate structure and complexity. The third is to validate the predictions of the preferred IBM using observational data. Confronting these challenges depends on the data available and the results presented above show a reasonable resemblance to real track and behavioural data. Such a qualitative judgement is a necessary first step, but not sufficient to defend the IBM as a robust predictive tool. It is therefore necessary to carefully assess the current prototype harbour seal IBM, understand its potential development and judge whether such developments are practicable.

Mapping Foraging Patches and Estimating Gross Energy Intake

The foraging patches used to illustrate the current IBM are a subset of those that were extracted from the track data. These, in turn, are probably a subset of the patches that are available to the seal population. The state space approach of Russell *et al.* (2015) could be used to defensibly classify track segments, and thus locations, that suggest foraging. Those preferred locations could then be characterised in terms of synoptic bio-physical information (e.g. distance from haulout site, depth, sediment type, tidal energy and water temperature). Such a preference model could be used to predict potential foraging regions, and foraging patches could be randomly spread over such regions, their local density being influenced by the degree of preference. Currently the patches are single, isolated 1 km^2 cells. The track data suggest that they would be better represented as clusters of varying degrees of preference. Boat-based, sonar surveys, or seal-borne video tags could also be used to survey prey fields.

The primary currency of the IBM is energy; therefore, indices of spatial preference must be transformed to metrics of the gross foraging energy income. The gross energy gained during the *forage* activity may be estimated based on information from tagged harbour seals from populations that, unlike those modelled here, are not in decline. Movement and behavioural data from such tagged seals can used in state-space models to infer behavioural activity (Russell *et al.*, 2015). It may be cautiously assumed that seals tagged in the months preceding breeding will, at the very least, not lose body condition on average. Using this conservative assumption and the mean proportion of time classified as *foraging* from the state-space model, the mean

(or minimum) gross energy gain rate during foraging may be estimated, if realistic estimates of energy expenditure in wild harbour seals become available. It should be possible to rank the energy gain from different patches based on a) repeated consecutive visits and b) the simulations use of a set of foraging patches by several individuals[5]. Again, this analytical approach does not obviate the need to carry out fine-scale energy consumption measurements on free-swimming seals.

Behavioural Choice

Behavioural *activity* in the IBM is driven by the dominant physiological *urge*. Currently, the IBM uses a simplistic rule, based both on duration of current activity and energy balance, to determine the dominant urge. This generic rule avoids the fundamental question of which factor(s) drive and moderate a seal's desire to haulout on land. Note that it is probable that in some circumstances these factors result in an ESI at sea (Ramasco *et al*., 2014; Russell *et al*., 2015). Whilst ESI activity is not currently included in the IBM it could be included in future revisions.

There are two classes of biotic factor that may drive haulout behaviour. The first class is time-driven. For example, increased time hauled out may minimise the probability of being attacked by a marine predator, or a certain amount of time may be needed for fur maintenance[6]. The second class is event-driven. For example, following a successful foraging event, however long it may take, a seal may choose to defer digestion until it is hauled out (Sparling *et al*., 2007). This does not exclude the possibility that haulout activity is multi-causal, nor does it exclude the hauling out activity being moderated by season, tide and weather. However, inspecting the track data for time- or event-driven haulout behaviour can assist in formal IBM selection.

IBM Selection and Parameter Estimation

To be a useful predictor of behavioural response to environmental change, an IBM of appropriate complexity must be validated and its parameters must be estimated as realistically and defensibility as possible.

In both model validation and parameter estimation, it is the <u>emergent properties</u> of multi-individual simulations that need to be fitted to corresponding properties (also known as summary statistics) of data obtained from tagged seals and haulout

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[5] The latter data should form a set of simultaneous equations whose solution could estimate relative gross energy gain from different patches.

[6] The seasonal moult period and the breeding period is currently excluded from the prototype IBM

counts. This does not require the fitting of predicted tracks, point by point, to individual tracks from real animals.

IBM selection and parameter estimation is challenging, but recent developments have made the problem more tractable (Beaumont, 2010; Grimm and Railsback, 2012; van der Vaart *et al.*, 2016). For a harbour seal IBM, candidate summary statistics (Thiele *et al.*, 2014) of data that may be useful as fitting metrics include:

- foraging trip duration patterns and auto-correlation[7]
- foraging trip extent patterns and auto-correlation
- proportion and variability of activity budgets (rest, directed travel, foraging, hauled out)
- proportion and variability of haulout duration
- patterns of inter-haulout movement transitions (as derived from I-HTR modelling above)
- intra-individual synchrony in haulout site and foraging patch usage

Although physiological urges for each seal are generated in the IBM, these urges are latent (not directly observable) in conventional tracking data. However, specific studies that measure energy maintenance in wild or captive seals could usefully inform the IBM.

IBM Management Applications

IBMs offer the prospect of a biologically plausible and defensible framework to explain natural variability in behaviour and distribution and to predict the impact of environmental change. They seek to model the underlying processes from which distribution and connectivity emerge, rather than just describe the patterns themselves (O'Sullivan and Perry, 2013).

IBMs can assist in the identification and monitoring of a network of protected areas (SACs and MPAs). Whilst the underlying conservation goal is to identify and protect environments that are *crucial* to a species welfare, this is often condensed to identifying areas of high and persistent *usage*. An IBM offers the potential to consider what other areas could also support a species, and at what (if any) extra cost. Thus, they can identify what environments are, in fact, crucial. IBMs also offer

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[7] For example, the repeated use of a particular foraging patch (temporal and spatial auto-correlation) would tend to suggest that an animal is using memory rather than carrying out multiple independent searches.

the potential to inform monitoring strategies. A typical question might be what is the expected magnitude and geographical extent of disturbance resulting from some anthropogenic (e.g. piling activity). By running a number of IBM simulations, the intensity, geographical extent and power of a proposed monitoring strategy to detect change could be assessed *a priori*. IBMs also offer the opportunity to simulate the efficacy of mitigation strategies.

The limited aim of this prototype harbour seal IBM is to predict movement, and thus the dynamics of their at-sea and terrestrial distribution. Currently, this prediction is restricted to outside the breeding season. However, as and when data permit, the framework could be extended to the breeding season. Ultimately, an IBM could inform population processes estimates. Although the effect of seal condition on the factors that control population dynamics (survivorship, fecundity and immigration/emigration) is currently sparse or non-existent for harbour seals, the effect of environmental change on movement patterns will assist the ability of expert option to predict population consequences (Harwood *et al.*, 2014).

4   Summary and Recommendation

4.1   Inter-Haulout Transition Rate model

An inter-haulout transition rate model has been developed that quantifies the probability of a harbour seal travelling from one haulout site to another. This model takes sample track data and makes inferences about where the tagged seals would move over longer periods, and also where the larger population of seals would move. This quantification of inter-haulout site connectivity can inform the geographical extent of proposed haulout surveys required to census a local population to answer questions such as over what geographical area can a non-breeding season harbour seal population be considered as closed? It can also assist in predicting the consequence of infectious disease. However, it is essentially an empirical model and as such is does not consider the causality of movement and so is not well suited to predict the consequence of environmental change. This latter task is better approached using an individual based model that is based on the physiological causality of movement.

4.2   IBM

The construction of the prototype IBM serves two purposes. First, it demonstrates a framework that produces qualitatively credible approximations of track movement and behavioural data, based upon simple biological rules. Second, it focuses

attention on a future IBM development strategy and the data that would be required to progress the model to a useful management tool.

Most of the data required for model selection and parameterisation exist; but some are sparse or non-existent and demand further bespoke studies. The advantage of an IBM, with all the caveats mentioned above, is that uncertainty can be incorporated throughout and will transfer to the emergent results. Sensitivity analysis can be used to identify which parameters create the most uncertainty, and thus point to where more data are needed. A secondary advantage of the IBM approach is that it is essentially simple to understand and to demonstrate. Thus, it can be readily communicated to non-expert stakeholders.

Considerable work is required to develop the current, naive IBM into a useful and defensible management tool. However, the authors recommend that the benefits of success outweigh the risks of failure, and that further development is worthwhile
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5   Acknowledgements

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