TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaluation"), which provides supporting evidence that our model is thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows (Schmolke et al. 2010, Grimm et al. 2014) and uses the updated standard terminology and document structure in (Grimm et al. 2010, 2014, Augusiak et al. 2014, Nabe-Nielsen et al. 2018)

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1. Model description

This TRACE element follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006, 2010).

Throughout the text, we use phrases as defined in Box 1.

Box 1. Glossary

Phrase	**Definition**
Data	Measurements and observations of the **real** world
(Observed) pattern	A characteristic, clearly identifiable structure in **nature** itself or in the **data** extracted from nature. A pattern is anything that goes beyond random variation and thus indicates an underlying process that generates this pattern.
(Harbour) seal	Refering to this species of pinniped **observed** in nature
*M*seal	Seals (agents in the ABM terminology) **modelled** by AgentSeal
Haul-out and haul-out site	Onshore location of seals resting. This resting behaviour is called haul-out
(Foraging) trip	Seal movement at sea between two consequtive haul-out events >6h. See section 2.2.3 of SI for justification of this duration.
Patch	For the case study modelled, 1x1 km **grid cell** of the underlying landscape. Patch can be of a category land or water.

Summary:

Here we present the complete description of AgentSeal. It includes an overview of the underlying movement, and description of how simulated animals behave at sea and on land.

1.1 Purpose and patterns

We aim to build a relatively simple movement model of adult harbour seals which captures general fine- and large-scale harbour seal movements and reproduces their central place-foraging and general behaviour, except for the breeding and moulting seasons. The model is based on optimal foraging theory, assuming that seals adjust their behaviour based on their physiological state and foraging movements based on their knowledge of prey availability.

Specifically, the aims of the model presented here are to: i) build a relatively simple movement model of adult harbour seals outside their breeding and moulting season; ii) capture general fine- and large-scale harbour seal movements that are consistent with telemetry observations, energy balance and drivers behind central place foraging (hauling out and at-sea movement); iii) capture high variation between individuals but low intra-individual variability in movement and foraging behaviour; iv) identify which aspects of movement and general behaviour of this marine predator are having the strongest effects on the emergent patterns.

In order to evaluate whether our model results in realistic behaviour of *m*seals, we adopted the pattern-oriented modelling approach (POM) (Wiegand et al. 2003, Grimm and Railsback 2005, Grimm et al. 2005). The chosen patterns can be grouped into four categories: *energetics*: energy intake and expenditure, body reserves; *movement* and other *behavioural* *patterns*: spatial distribution of *m*seals, visual comparison of tracks, overlap of kernel densities, characteristics of foraging trips (Box 1) (duration and extent) and fine-scale movement (step length and turning angle), and proportion of different activities performed by *m*seal (resting, foraging) and at-sea foraging site fidelity. We also evaluate one *environmental* pattern: food depletion. Although there is no observed data on this pattern, we still use it to understand whether food depletion may be an important driver of seal movement and behaviour. We include a broad range of patterns to evaluate the performance of AgentSeal. We use POM in two phases of the modelling cycle. During model development it is used for parameterisation to check which combinations of parameter values resulted in realistic *m*seal behaviour; and in model evaluation to establish whether the model outputs are sufficiently realistic consistent with its intended application (Rykiel 1996). Table 1 summarises which patterns are used within the modelling cycle and description of the data sources used.

Spatial and fine-scale movement patterns are based on long term tagging programs and surveys of harbour seals along the East and North-East Coast of Scotland between 2007 and 2018 by University of St Andrews (Sea Mammal Research Unit, SMRU) and University of Aberdeen (Lighthouse Field Station, LFS) along east (study site) and north-east coast (Moray Firth) of Scotland. Only adult individuals deployed with GPS tags (providing frequent and accurate GPS location fixes) and transmitting in autumn-spring (September-April) are considered in order to avoid harbour seal moulting and breeding seasons when the drivers and nature of the movement are different compared with outside these two seasons. All together we analyse data from 48 seals tagged in Moray Firth, 11 from the Firth of Forth and St Andrews and 3 from Aberdeen summing up to 14 at the study site for the case study (East Coast of Scotland), and 62 altogether.

The observed locations are interpolated in time to 15 min to match temporal resolution of the model. Comparing movement data collected at different time resolution may result in mismatch in distribution of step and turning angles (Michelot 2019). For the calculation of observed turning angle and speed distribution and correlation (patterns 1.1 – 1.2, Table 1) and spatial patterns (patterns 2.6-2.9 and 3.2, Table 1), we removed locations when seals are hauling-out and when the duration between two consecutive locations before interpolation is >= 3h. Detailed description of the tagging, data cleaning and interpolation is given in (Russell et al. 2011, Mcclintock et al. 2013, Russell 2015). Number of tracked animals based on which a given pattern is established and collection period is given in Table 1. Patterns 2.5 and 2.9 are only calculated for seals observed at the study site and hence different number of seals used in the analysis.

Body condition data (pattern 2.3, Table 1) come from morphometrics (body length and mass) taken during tagging of adult harbour seals measured by SMRU and LFS and Wadden Sea (Royal Netherlands Institute for Sea Research, the Netherlands, NIOZ) in autumn between 1989-2012.

The remaining patterns are established from literature and detailed description is presented further in this document describing parameter selection (chapter 2) and model evaluation (chapter 5).

We do not have data on food depletion due to seal foraging. However, we incorporated this factor, to understand whether food depletion may be an important driver of *m*seals movement and behaviour.

Table 1. Summary of different patterns used in pattern-oriented approach during modelling of the *Case study*. Detailed descriptions of the use of the patterns is given in sections 2 and 5.

	Pattern	**Category/Scale**		**Source of data**
Parameterisation-fine scale movement	1.1 Frequency distribution of turning angles	Movement	Individual	Telemetry data of 62 adult harbour seals tracked in autumn-spring between 2007-2017 along East and North-east (Moray Firth) coast of Scotland by SMRU and LFS[1]
	1.2 Correlation in turning angle between steps	Movement	Individual	
Parameterisation– general movement and behaviour	2.1 Daily consumption of fish	Energetics	Individual	Literature: (Härkönen and Heide-Jørgensen 1991, Kastelein et al. 2005, Sharples et al. 2009, Wilson and Hammond 2016)
	2.2 Daily energy expenditure	Energetics	Individual	Literature on captive studies: (Markussen et al. 1990, Härkönen and Heide-Jørgensen 1991, Renouf and Noseworthy 1991, Rosen and Renouf 1998, Sparling 2003, Kastelein et al. 2005)
	2.3 Changes in proportion of blubber over model duration	Energetics	Individual	Literature (Renouf and Noseworthy 1991, Rosen and Renouf 1998) and data from 78 adult harbour seals measured along East and North-east coast of

[1] Lighthouse Field Station (LFS), University of Aberdeen, UK

				Scotland (SMRU, LFS) and Wadden Sea (NIOZ[2]) in autumns 1989-2012
	2.4 Daily proportion of time spent resting and hauling-out	Behavioural	Individual	Literature: (McConnell et al. 1999, Cunningham et al. 2009, Mcclintock et al. 2013, Ramasco et al. 2014, Russell et al. 2015)
	2.5 Frequency distribution of number of individually visited haul-out sites	Movement	Individual	Telemetry data of 14 adult harbour seals tracked in autumn-spring between 2008-2012 along East coast of Scotland by SMRU
	2.6 Frequency distribution of trip duration	Movement	Individual	Telemetry data of 62 adult harbour seals tracked in autumn-spring between 2007-2017 along East and North-east (Moray Firth) coast of Scotland by SMRU and LFS[1]
	2.7 Frequency distribution of trip extent	Movement	Individual	
	2.8 Frequency distribution of at-sea positions with distance from the departure haul-out site	Movement	Population	
	2.9 Overlap of kernel densities	Movement	Population	Telemetry data of 14 adult harbour seals tracked in autumn-spring between 2008-2018 along East coast of Scotland by SMRU
Evaluation	3.1 Food depletion	Environmental	Population	No data available
	3.2 Visual comparison of tracks	Movement	Individual/Population	Telemetry data of 5 adult harbour seals tracked in autumn-spring between 2008-2012 along East coast of Scotland by SMRU

[2] Royal Netherlands Institute for Sea Research, the Netherlands

	3.3 Site fidelity	Behavioural/Movement	Individual and Population	Telemetry data of 5 adult harbour seals tracked in autumn-spring between 2008-2012 along East coast of Scotland by SMRU

1.2 Entities, state variables, and scales

The model includes the following entities: *m*seals, landscape patches (Box 1) and on-land resting sites (haul-out sites). The entities can be characterised by static (fixed over the entire model duration) or dynamic (updated at each time step) state variables, or a combination of these, as listed in Table 2a-b.

Table 2a. List of entities, type and name of state variables attributed to each entity and the name of the process when these variables are updated. For description of processes see *Process overview and scheduling*.

Entity	Type of state variable	Name of state variable	Process in which the state variable is updated
***m*seals**	Static	Unique id	
		Age	
		Sex	
		Stomach capacity	
		Length	
	Dynamic	Location	FORAGE, GO TO HAUL-OUT SITE
		Speed	FORAGE, GO TO HAUL-OUT SITE
		Movement direction	FORAGE, GO TO HAUL-OUT SITE
		Mass (total and reserves)	ALL
		Behaviour (resting or foraging)	FORAGE, GO TO HAUL-OUT SITE, TIME TO REST?, TIME TO HAUL-OUT?
		Net energy level	ALL
		List of memorised patches	FORAGE, GO TO HAUL-OUT SITE
		List of memorised haul-out sites	FORAGE, GO TO HAUL-OUT SITE, HAUL-OUT
Patches	Static	Category (land or water)	
	Dynamic	Habitat suitability index (HSI)	FORAGE, GO TO HAUL-OUT SITE
Haul-out sites	Static	Location	
		Unique id	
		Proportion of the observed seals within model domain occupying a given site	

The model geographical domain can be based on any area defined by the user (see *Case study* for an example). One time step in the model represents 15 minutes and each patch in the model is 1x1 km in size.

The model is programmed in NetLogo 6.02 (Wilensky 1999) and analysed in R 3.5.2 (R Core Team 2018).

Table 2b. Full State variables, parameters used to calculate these variables, their value and procedure in which they are used in the Case study.

State variable and derivatives[3]	**Parameters used to calculate state variable and references to calculation**[4]	**Value and unit**[5]	**Description and references**[6]	**Constant (C) or varying (V) over model duration.**	**Procedure in which the state variable is used and updated/modified if applicable**[7]
General (global)					
n_of_seals		350	Initial number of *m*seals	C	All
time_step (time step)		900 s	Duration of one time step	C	All
Haul-out sites					
ho_id			Unique id of each haul-out site	C	Initialisation
perc10_16		%	Observed proportion of all *m*seals from East Scotland hauling-out on a given haul-out site based on annual counts between 2010-2016 (SMRU, 2017)	C	Initialisation
numberOfModelledSeals	perc10_16 * n_of_seals	#	Initial maximum number of *m*seals on a given haul-out site calculated from perc10_16 (SMRU, 2017)	C	Initialisation
Landscape patches					
patch_size		1000 m^2	Size of one patch	C	All
categ		-	Land, water, shore	C	Initialisation
HSI		0-1	Habitat suitability index (Grecian et al. 2018)	V	Initialisation and All

[3] Regular font: names used in the code; (): names used in TRACE

[4] Regular font: names used in the code; *Italic*: references to points in TRACE where detailed information on calculations can be found (): names used in TRACE. The more detailed description of parameters can be found in provided references and in the code. If the cell is empty state variable = parameter.

[5] Values as used in the final model simulations. More values are given in section 2 of TRACE and references given in column 2

[6] For detailed references see section 2 of TRACE

[7] See *Process overview and scheduling* for the description of the procedures

#Fish_m2,(N)	HSI, #Fish_hsi_multiplier, *section 0,* *Table* 4	#	Number of fishes per m^2	V, P[8]	Initialisation and All
#FishTotal	#Fish_m2, patch_size	#	Total number of fishes per patch	V	Initialisation and All
distance2shore		km	Distance from each water patch to land	C	Initialisation
distance_hoX		km	Distance from a given patch to each of the 16 haul-out sites (X)	C	Initialisation
km_5_id		-	Id of 5x5 km square to which a patch belongs	C	Initialisation/Forage
Nseals		#	Cumulative numbers of visiting *m*seals	V	All
Shortest path	*Section 1.7.4*	7 km	A network of points along the coast, which defines 'shortest' path along the coastline The shortest path is calculated along a set of points equally distributed within 7 km from the shore and linked with all such points within 2 km	C, SA[8]	Initialisation/Forage/Go to haul-out site
Mseals					
Energetic and physiology related state variables					
sex	*Table 4*	M | F		C	Initialisation
Blength	*Table 4*	cm	Body length (ref in Table 4)	C	Initialisation
Tmass	Blengt, *Table 4*	g	Total body mass (ref in Table 4)	V	Initialisation/Forage/Go to haul-out site/Calculate net energy
ResMass	Tmass, *Table 4, eq. 13 and 14*	g	Mass of blubber (reserves) (ref in Table 4). If this mass <= 5% of Tmass, *m*seal dies	V	Initialisation/Calculate net energy
BMR	Tmass, *Tables 4 and 6, eq. 12*	MJ	Basic metabolic rate (ref in Table 4)	V	Initialisation/Calculate net energy
stomachCap	Tmass, *Table 4*	g	Max mass of fish *m*seals can fit in their stomach before taking digesive break (ref in Table 4)	C, SA[8]	Initialisation/Time to rest?

[8] P – parameterised, SA – sensitivity analysis. For information whether the entire state variable or parameters used to calculate this variable is parameterised/used in sensitivity analysis refer to section 2 of TRACE.

ei	mean_kJ_per_gOffish, mean_kJ_per_gOffish, *eq. 6-7, Table 5*	MJ/s	Instant energy intake calculated from consumed fish	V, SA[8]	Forage/Go to haul-out site
daily_ei		MJ/day	Cumulative daily energy intake. Reset every 24h	V	Forage/Go to haul-out site
ee	BMR multiplier for each activity, *Table 6*	MJ/s	Instant energy expenditure	V	Calculate net energy
daily_ee		MJ/s	Cumulative energy expenditure. Reset every 24h	V	Calculate net energy
DailyNetEnergy	daily_ee - daily_ei	MJ	Daily net energy		Calculate net energy
fishConsumed_g	#Fish_m2, search rate (sr), mean_g_per_fish, *eq. 6-7, Table 5*	g	Cumulative amount of fish consumed between digestion resting breaks. Reset after each such break	V	Forage/Go to haul-out site/Time to rest?/Rest at sea/Haul-out
TotalfishConsumed_g		g	Consumed fish over the model duration	V	Forage/Go to haul-out site
durationOfResting; DurationOfDigestion	Mean_durHO, sd, b_prob, short resting, *Section 1.7.5, eq. 9*	s	Time which *m*seals are going to spend resting (rest at sea or haul-out)	V, P, SA[8]	Time to rest?/Time to haul-out?
durationSinceLastHa		min	Number of time steps since last haul-out	V	Time to haul-out?
Behaviour related state variable					
activity		-	*M*seal current behaviour (i.e. Foraging, haul-out, long-digest, short-digest, land avoidance)	V	All
Land avoidance state variable					
check-land-distances	*Table 7*	1.04 km	Distance used by *m*seals to evaluate whether there is land ahead	C, SA[8]	Forage/Go to haul-out site
my_path		-	List of points along which *m*seals go to the next haul-out site if this *m*seal encounter land on its way to haul-out site	V	Forage/Go to haul-out site
Fine-scale (BCRW) movement state variable					
speed	Vmin, Vmax, his, his_opt, sigK, shape, rate; *eq. 4, Table 7*	m/s	Speed	V, P[8]	Forage/Go to haul-out site
Turning angle	HSI, his_opt, sigK, b, dist2target, imp_dist; *eq. 1-3, Table 7*	degrees	Turning angle	V, P[8]	Forage/Go to haul-out site
target		-	Target point (patch or haul-out site) towards which *m*seal wants to move	V	Forage/Go to haul-out site

Memory related state variables					
patch-ei-5k-memory (M_{square})	ref-mem-decay-rate (r), *eq. 5*	-	Memory value of visited 5x5 km squares	V, P[8]	Forage/Go to haul-out site
NdaysWithNegativeNEB		7 days	Number of consecutive days with daily energy expenditure >= daily energy intake, after which *m*seals switch to large scale foraging	C	Forage/Go to haul-out site
patches_km25_maxhsi		-	List of 90% of patches with best HSI within 25x25 km^2. Such list is the same for all individuals	C	Initialisation
memory-hauls-list ($M_{haulOut}$)	haul-out_detection_distance, mem_level_passedBy_ho	-	Memory level of visited haul-out sites	V, P[8]	Forage/Go to haul-out site
my_next_patch	*eq. 11*	-	Foraging square towards which *m*seals move after hauling-out	V	Forage/Haul-out
my_next_ha	*eq. 10*	-	Next haul-out site	V	Forage/Go to haul-out site
patch-hsi-list		-	List of location of visited squares and their corresponding HSI, memory and energy intake	V	Forage/Go to haul-out site
memory-hauls-list, haul-ids		-	List of location of visited and memorised haul-out sites with memory value assigned to each site	V	Go to haul-out site

1.3 Process overview and scheduling

Processes: The processes are structured into six procedures as described below. They describe the central-place foraging and haul-out movements of adult harbour seals outside the breeding and moulting seasons.

Scheduling: The order of the procedures is the same for each time step but, as the model assumes no hierarchies among *m*seals, the order in which individuals execute a given procedure is randomised at each time step. For each *m*seal, each state variable is immediately assigned a new value as soon as that value is calculated by a procedure (Table 2a). The graphical description of the model flow is shown in Figure 1.

Names in **BLACK BOLD** refer to these procedures and **GREY BOLD** to Submodels of these procedures throughout TRACE document.

a) **FORAGE –** this procedure represents *m*seals' search for and capture of food. *M*seals move/forage according to a correlated random walk biased towards a destination food patch (BCRW). The step length and turning angle is related to habitat suitability index (HSI, see *Case study* for an example) – a measure depicting availability of food. BCRW enables *m*seals to slow down in areas of good habitat (habitat with large number of fish; high HSI) and travel faster and more directly through areas of low quality (low HSI). The bias (correction of *m*seals' heading 'pulling' it back on track towards the target) increases the closer to the patch. If *m*seals are too close to land, they avoid land (**AVOID LAND**). *M*seals remember visited patches and the amount of food captured on these patches (**REMEMBER PATCHES**). *M*seals also remember haul-out site which they passed by within certain distance during foraging (**REMEMBER HAUL-OUT SITES**). During foraging, *m*seals expend energy (**ENERGY EXPENDITURE**) and gain energy by consuming fish, the amount of which is related to fish availability in the foraged patches (**INTAKE ENERGY**). Number of caught fish is then corrected for level of *m*seals fat reserves based on the assumption that overweight seals have reduced diving capacity due to their increased buoyancy. The consumed fish are then subtracted from fish available at this patch (**FOOD DEPLETION**). There is no food replenishment in the model.

If the daily amount of consumed fish is not enough to cover daily energy expenditure for certain number of days in a row (7 days in the *Case study*), *m*seals swap to exploratory movement. There are two types of such movement and there is equal probability of choosing any by each mseal after the 'hunger' period: i) CRW not biased towards any previously visited patch, and ii) CRW biased towards one of the patches from initial memory list (see *Initialisation* in the *Case study* for details). In any of these cases, the previous memory of *m*seals is cleared.

b) **TIME TO REST?** – *m*seals evaluate if it is time to rest based on the amount of recently consumed food (digestive constraints). If it is, they further decide whether to rest at sea or go to a haul-out site to digest.

c) TIME TO HAUL-OUT? - Even if *m*seals do not have to rest due to digestive constraint, they further evaluate if it is time to haul-out if they haven't done so for a while (see Design concept for details).

d) REST AT SEA - *m*seals rest at sea to digest food and duration of this rest is defined by *m*seals' digestion capability. *M*seals also spend energy while resting (**ENERGY EXPENDITURE**).

e) GO TO HAUL-OUT SITE- this procedure is the very similar to **FORAGE**, *m*seals also memorise visited patches and get food. The target haul-out site is chosen based on distance between *m*seals' location and the sites and the memory values of these sites stored in *m*seals' memory (**CHOOSE NEXT TARGET HAUL-OUT SITE**). If *m*seals are not close to shore, they move according to correlated random walk biased towards the target haul-out site. The bias increases the closer to the haul-out site. If *m*seals are close to shore, they follow the shortest path along the shore to get to the haul-out site (**TAKE SHORTEST PATH TO HAUL-OUT SITE**). **REMEMBER PATCHES, REMEMBER HAUL-OUT SITES, INTAKE ENERGY, ENERGY EXPENDITURE** and **FOOD DEPLETION** also takes place in this procedure.

f) HAUL-OUT – *m*seals haul-out for a duration depending on the haul-out reason (digestive constrains or other, see section 1.4.4) chosen stochastically from a defined range given the reason. At the end of the haul-out, *m*seals evaluate what is the next food patch they head to, based on their memory of (and distance away from) previously visited patches (**CHOOSE NEXT TARGET PATCH**). *M*seals memorise all the previously visited haul-out sites (**REMEMBER HAUL-OUT SITES**). *M*seals also spend energy while resting (**ENERGY EXPENDITURE**).

At the end of each time step *m*seals calculate their net energy intake (NEI) as the difference between energy obtained from fish and expenditure. If NEI > 0, *m*seals convert the excess energy into storage (blubber), otherwise they lose weight (see section 1.7.6 in SI). If mass of blubber of *m*seals is <=5% of their total body weight, they die. *M*seals only change their body mass; growth (changes in body length) is not included in the model.

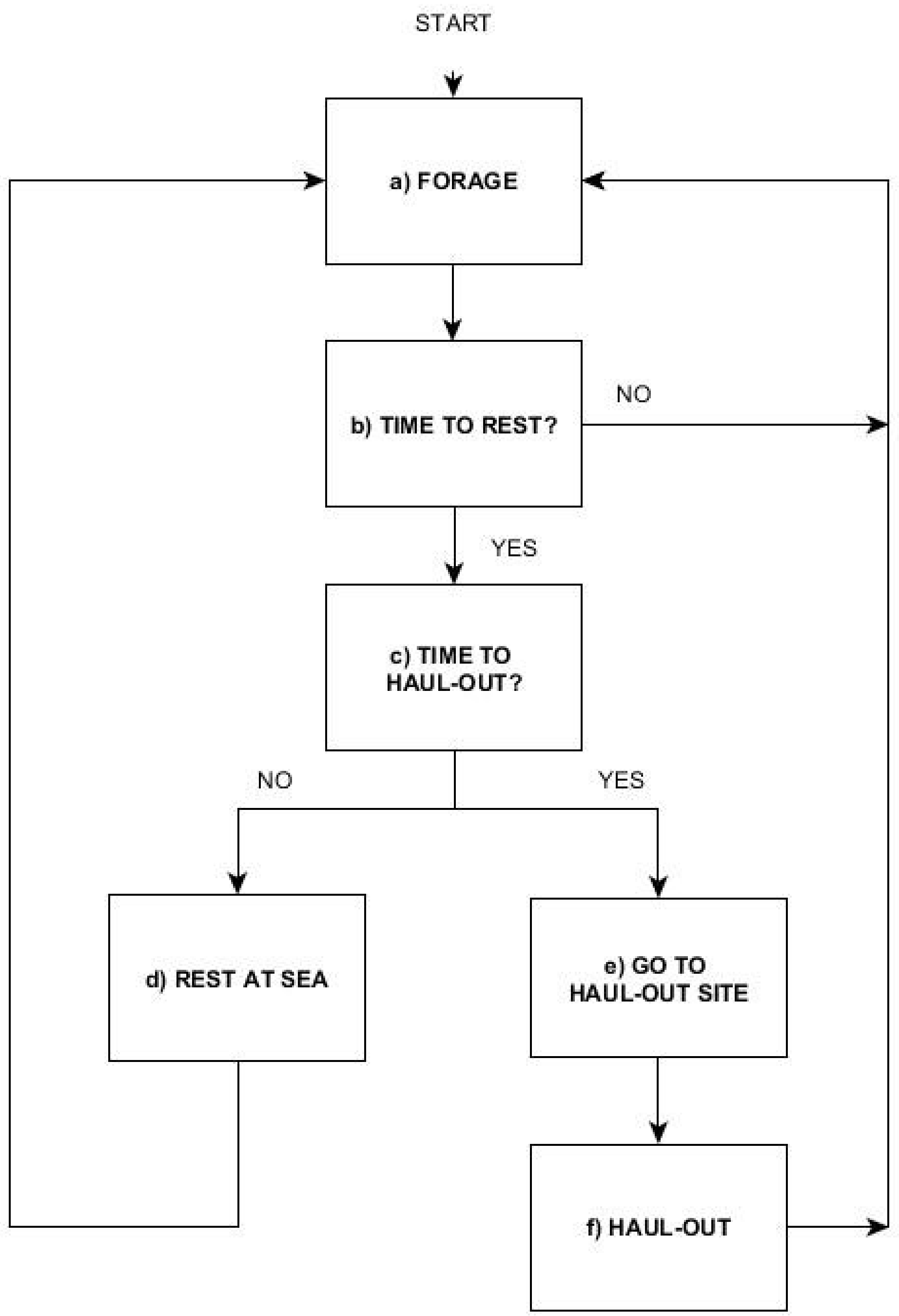


Figure 1. Graphical description of the model procedures, which apply to all mseals at each time step.

1.4 Design concepts

Underlined sections are not presented in the main text

1.4.1 Basic principles

*M*seals optimise their foraging movements by increasing the time spent in good quality habitat and minimising distance travelled by relating their movements towards good patches. They memorise visited habitat patches and are more likely to return to profitable ones. This memory decays with time. Digestive constraints and non-digestive reasons are the primary motives behind resting and haul-out behaviour.

1.4.2 Emergence

The movement patterns emerge from *m*seals' different movement characteristics (turning angle and speed) in relation to habitat quality, from their ability to memorise and return to good quality patches, their need to haul-out and their choice of haul-out sites. Energetic patterns emerge from a balance between energy needed for body maintenance (energy expenditure) and fish consumption (energy intake) and define changes in body mass and mass of reserves (blubber). Behavioural patterns (proportion of time spent resting at sea, foraging and hauling out) emerge from *m*seals' physiological constraints (e.g. digestive constraints), distance to the next haul-out site and energy intake, defining whether to take a digestive break or not. Site fidelity emerges from the fact that seals are more likely to revisit a patch which resulted in good energy intake when visited previously and is close to a frequently visited haul-out site. Finally, environmental patterns (food depletion) result from consumption of fish within the study site.

1.4.3 Adaptation

*M*seals react to food abundance (expressed as HSI) by slowing down in areas of good habitat and travelling faster through area of low quality. *M*seals are more likely to return to good quality habitat. In order to minimise energy expenditure, *m*seals choose their haul-out sites based on distance needed to travel to these sites. They decide when and where to digest food based on the amount of food consumed since the last digestive break and distance to haul-out site, as a possible site to take a break to digest.

1.4.4 Objectives and learning

The objective of *m*seals is to maximise their net energy intake, while taking their digestive constraints and need to periodically haul out into account. *M*seals increase their chance of finding fish by spending more time in good quality areas and returning to these if previous visits resulted in high food intake, while they will transit through areas of low quality. As marine environments are dynamic and heterogenous, it is not likely that animals can correctly learn and memorise the quality of all visited foraging patches over a long period of time and we therefore let memory decay logistically with time (Van Moorter et al. 2009). On the other hand, seals can remember and return to haul-out sites even after several years (Mackey et al. 2008, Cordes and Thompson 2015), and *m*seals therefore remember all the visited haul-out sites. This knowledge does not decay with time.

1.4.5 Prediction

*M*seals do not predict the future using proxies of current environment or their condition such as body condition.

1.4.6 Sensing

*M*seals can sense how far they are from land, which permits them to avoid going on it, unless they are about to haul-out. They can also sense the habitat suitability index of the patches they are on. Each *m*seal can also sense its own location, which is used to calculate distance and shortest way to a set of candidate food patches or haul-out sites (see **CHOOSE NEXT TARGET HAUL-OUT** and **CHOOSE NEXT TARGET PATCH** procedures).

1.4.7 Interaction

There is no direct competition between *m*seals but due to food depletion, *m*seals may compete indirectly.

1.4.8 Stochasticity

The key uses of stochastic processes and the name of procedures for which these rules apply are given in Table 3.

Table 3. List of key stochastic processes and the name of the procedure where they are included. See section 1.3 for description of each procedure.

Stochastic process	**Procedure name**
Initial haul-out site	Initialisation
Sex, body length, blubber %	Initialisation
Fine-scale movement (direction of land avoidance, biased CRW)	Forage, Go to haul-out site
Next site to haul-out	Go to haul-out site
Next patch to head to after hauling-out	Forage
Rules defining whether to rest and haul-out or not	Time to haul-out?, Time to rest?
Memorised haul-out sites	Forage, Go to haul-out site
Duration of haul-out, duration of resting	Rest at sea, Haul-out
Energy intake Energy expenditure	Forage, Go to haul-out site Calculate net energy

Stochasticity in the model is used to represent two situations: a) when there is a range of observed parameters instead of one value (i.e. initial body length), and b) when the given procedure/behavioural rule is likely to be inherently stochastic in nature (i.e. feeding rate).

1.4.9 Collectives

Social structure, grouping or any other direct interaction between *m*seals are not included in the model.

1.4.10 Observation used in the Case study

At the end of each time step, all dynamic state variables are saved for each seal. At the end of each simulation final HSI of the patches are saved as well as cumulative number of *m*seals visiting each water patch.

1.5 Simulation experiment: case study

1.5.1 Initialisation

We test the model for one case study: East coast of Scotland (Figure 2).

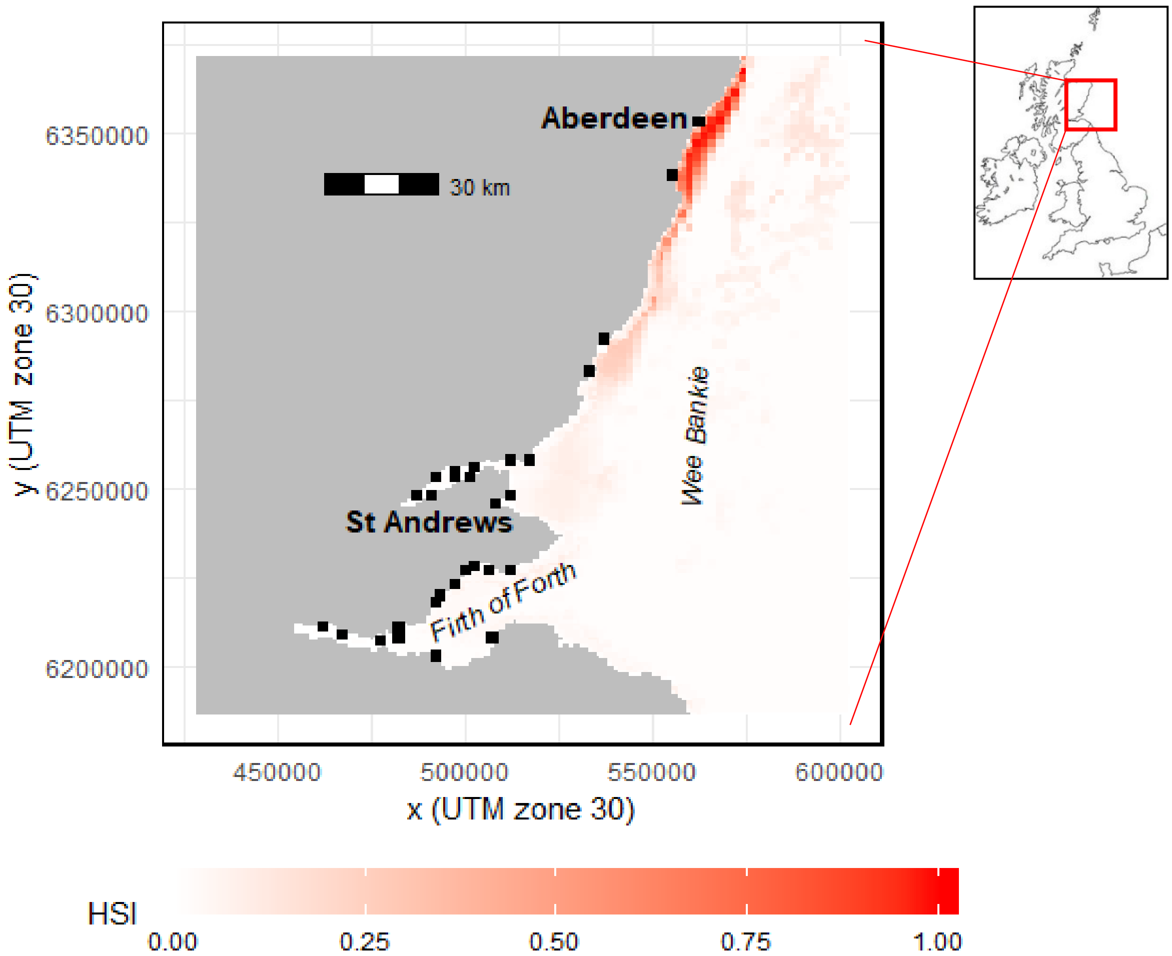


Figure 2. Model domain showing land (grey patches) and water. Habitat suitability index, a proxy for food availability, of water patches is represented by red colour palette. The higher the index the better the habitat suitability. Black squares represent haul-out sites, places where *m*seals rest on land, and are based on location of sites in reality. Cities and geographical locations mentioned in the text are marked in **bold** and *italic* respectively.

Creating the landscape

The landscape consists of 1x1 km grid patches with attributes of land and water (Box 1). Water patches have distance to land, distance to each predefined haul-out site and values of HSI which serves as proxy for food resources and, therefore, habitat quality. HSI is calculated by relating data of 55 tracked harbour seals around Scotland to a list of environmental covariates including depth, sea-surface temperature (SST), sediment type and distance to haul-out site (species distribution model (SDM); Grecian et al. 2018). The minimum adequate SDM retained all the above-listed covariates with distance to haul-out site being the most important predictor of seal distribution. However, to construct the suitability map (HSI), we used all the retained covariates from the SDM except distance to haul-out sites as we wanted the relationship between this distance and *m*seals' distribution to be an emergent property of the model and not enforced by the collinearity of the underlying habitat map. For simplicity, the results from the SDM are normalised to get HSI values between 0 and 1.

Each water patch is assigned an initial number of fish (*N*, [fish/m^2]) which is scaled to HSI. We parameterised (see section 2.3) the $N_{HSI=1}$ *(#Fish_hsi_multiplier*,

Table 4) and all the other patches had *N* = $N_{HSI=1}$ *HSI as HSI has values between 0 and 1, and number of fish is therefore expressed as proportional to number of fish in the best patches (with HSI=1). We tested various values of $N_{HSI=1}$ based on ICES transformed catchability data [kg/km^2] (Moriarty and Greenstreet 2017, Walker et al. 2017). The maximum value observed for ICES within the study area squares for the species occurring in seals' diet for the study site = 26386.09 kg/km^2. Assuming that an average fish weights certain amount based on seal diet from the study area (48g; Table 5*)*, $N_{HSI=1}$ = 0.5. However, as we have very little knowledge on actual fish abundance and seal search behaviour, as well as not all fish species from seals' diet are monitored by ICES, we varied $N_{HSI=1}$ as an integer number between 0.5 and 6 fish/m^2. The final value used in AgentSeal is $N_{HSI=1}$ = 4 fish/m^2 and see section 2.3 for details. The total number of fishes per patch is calculated as N * patch size. Most of the patches at the study site had HSI < 0.1 (Figure 4, Figure 2).

The water patches are also grouped into bigger squares 5x5km and 25x25 km and each 1x1km patch has an id of the bigger squares assigned. The 5x5km squares are used in memory procedures (**REMEMBER PATCHES**) and the 25x25 km squares are used to set up initial list of memorised patches (see *Creating mseals* below) and later in defining direction of large scale foraging (**LARGE SCALE FORAGING**) (Figure 2).

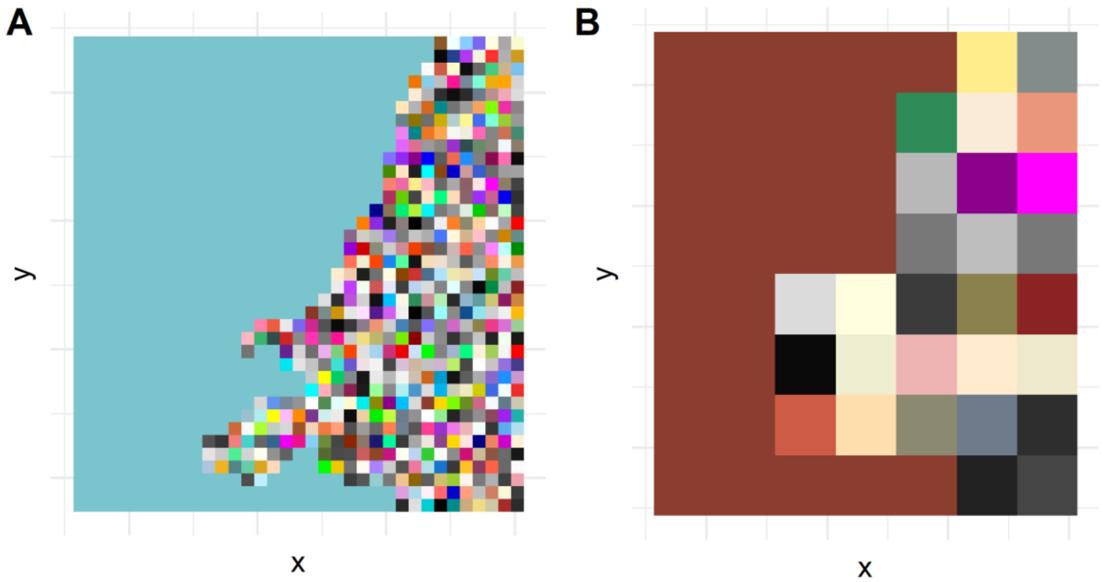


Figure 3. Division of the study site into (A) 5x5 km and (B) 25x25 km squares. The color scale is just for illustration.

The locations of modelled 16 haul-out sites is based on aerial surveys (SCOS 2018). Each haul-out site is assigned the proportion of overall seal population using this site, based on surveys during the moult season in 2010 – 2016 (SCOS 2018).

A network of points along the coast, which defines 'shortest' path along the coastline is created during Initialisation. The shortest path is calculated along a set of points equally distributed within 7 km from the shore (points are located in the middle of all patches adjacent to land) and linked with all such points within 2 km (see Figure 10, **TAKE SHORTEST PATH TO HAUL-OUT SITE**).

Creating *m*seals

The model is initialised by creating 350 *m*seals: the harbour seal population status for East Scotland (SCOS 2017, Thompson et al. 2019) for 2010-2016 and proportionally distributed over 16 haul-out sites to mean number observed during moult season surveys. There is little migration and exchange between subpopulations of harbour seals around Scotland (Sharples et al. 2012, Jones et al. 2015, Olsen et al. 2017). Thus, the model environment is considered as a closed system with no new *m*seals entering or exiting the model over the model duration.

Only adult individuals are modelled. *M*seals state variables: sex, body length, and initial total mass calculated from body length, initial mass of body reserves, basic metabolic rate (a function of total body mass) and stomach capacity (a function of total body mass) are assigned during initialisation (

Table 4). Sex influences initial body length and the relationship between body length and total body mass. Within the model there are no other processes which differ between sexes.

As the *Case study* is based on movement of adult seals, we assume that *m*seals are not naïve seals at the beginning of the simulations, but instead possess some knowledge about food distribution within the study site . To create the initial list of memorised patches, we created a list of patches with highest HSI within each 25x25 km square and then made a subset of this list with 90% highest values (referred to as 'omniscience'). This subset is the initial memory list for all individual[9]. The list of memorised haul-out sites contains all the haul-out sites within the study area. All sites receive memory level = 0.20, except site on which *m*seal is currently hauling-out. This site's memory = 0.99 (**REMEMBER HAUL-OUT SITES**). The memory level influences the likelihood of *m*seal to return to this site (see description **CHOOSE NEXT TARGET HAUL-OUT SITE**)

*M*seals' current energy expenditure, energy intake and mass of consumed fish are set to zero at initialisation.

[9] We also tested other options like burn-in time during which *m*seals would move freely within the study site and learn the environment, but this option did not significantly improve the results of the model in comparison to 'omniscience' option.

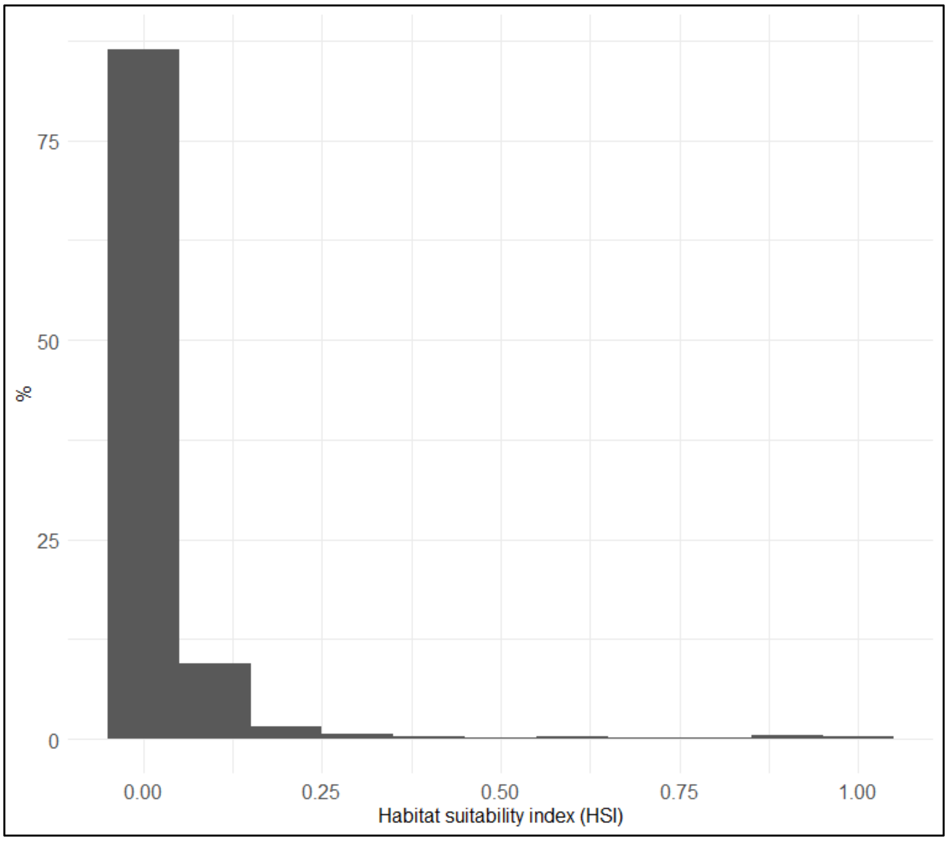


Figure 4. Frequency distribution of habitat suitability index assigned to water patches.

Table 4. Parameters related to model initialisation.

Parameters and state variables[10]	**Value and unit**[11]	**Description and values**	**Source**	**Reference**
Creating landscape				
perc10_16	%	Observed percentage of all seals from East Scotland hauling-out on a given haul-out site based on annual counts between 2010-2016	Observed	SCOS, 2017, 2018
numberOfModelledSeals	350	Initial maximum number of *m*seals on a given haul-out site calculated from perc10_16	Observed	SCOS, 201 7, 2018
HSI	0-1	Habitat suitability index	Observed	(Grecian et al. 2018)
distance2shore	km	Distance from each water patch to land	Observed	
distance_hoX	km	Distance from a given patch to each of the 16 haul-out sites	Observed	
#Fish_m2,(N), HSI, #Fish_hsi_multiplier ($N_{HSI=1}$)	fishes/m^2	Number of fishes per m^2 of a patch calculated as $N_{HSI=1}$ * his). Initial $N_{HSI=1}$ = 4)	Calibrated	Section 2.3

[10] Names of the parameters presented here are as used in the code; names used in the text, if different than in the code, are given in ()

[11] Value used in the final model simulation. If there is no value given, refer to references provided

Shortest path	7 km	A network of points along the coast, which defines ‘shortest’ path along the coastline The shortest path is calculated along a set of points equally distributed within 7 km from the shore and linked with all such points within 2 km	Sensitivity analysis	Section 1.7.4; Figure 10
Creating mseals				
sex	M,F	Drawn from binomial distribution with 50% chance of either sex	Observed	SMRU, unpublished data
Blength: mean, sd	cm	Body length Drawn from normal distribution (F: mean = 138.6, sd = 5.7; M: mean = 146, sd = 6.86)	Observed	Distribution for adults (> 5 years) seals – SMRU data (Hall et al. 2012, 2019)
Tmass	g	Total body mass F: 0.86*Blength - 49.67; M: 1.27* Blength - 102.67	Observed	Linear relationship for adults (> 5 years) based on SMRU data (Hall et al. 2012, 2019)
ResMass	g	Mass of blubber (reserves) Drawn from uniform distribution between 23 and 32% of Tmass	Observed	Markussen 1992, Sparling 2006, Beltran 2007; University of Aberdeen unpublished data
BMR	MJ	Basic metabolic rate 70 * Tmass^0.75 * 0.004184	Observed	Kleiber 1975
stomachCap	g	Max gram of fish seals can fit in their stomach (3.155 * Tmass + 132.93) * 800	Observed, Sensitivity analysis	Christiansen 2004

1.6 Input data

No time-series input is used in the model.

1.7 Submodels

1.7.1 FORAGE

1.7.1.1 AVOID LAND

In NetLogo animals are free to move within the entire model domain, unless movement restrictions are explicitly coded. The *m*seals would, therefore, frequently end up on land patches. Avoid land procedure is, therefore, not a behaviourally driven procedure but modelling practice. The design of the land avoidance procedure is based on the approach described by (Dalleau 2013) and implemented by (Liukkonen et al. 2018), where the procedure is thoroughly described. A summary is provided here.

During land avoidance procedure, *m*seals check if there is land ahead within certain distance (*check-land-distances* = 1.04 km, Table 7). If yes, they turn right or left depending on which direction has less land ahead. If there is an equal amount of land in both directions, the turning direction is chosen randomly.

1.7.1.2 BIASED CORRELATED RANDOM WALK

Fine-scale movements of *m*seals are simulated using a mixture of correlated random walk (CRW) behaviour and spatial memory resulting in movement biased towards profitable memorised places.

Movement vector of each *m*seal ($\vec{V}_{res}$) is the sum of the vectors $\vec{V}_{CRW}$ and $\vec{V}_{bias}$ and has two components: turning angle (TA) and step length (speed) (Figure 5). The TA of movement vector is calculated as the sum of these angles of $\vec{V}_{CRW}$ (related to previous turning angle and habitat suitability index of the patch) and $\vec{V}_{bias}$ (bias towards target foraging patch or a haul-out site also related to the habitat suitability index of the patch). The length of $\vec{V}_{res}$ is drawn from the observed (based of GPS tracking of seals, Table 1) speed distribution and is, therefore not related to speed in the previous time step. Details of calculation of $\vec{V}_{res}$ are presented below.

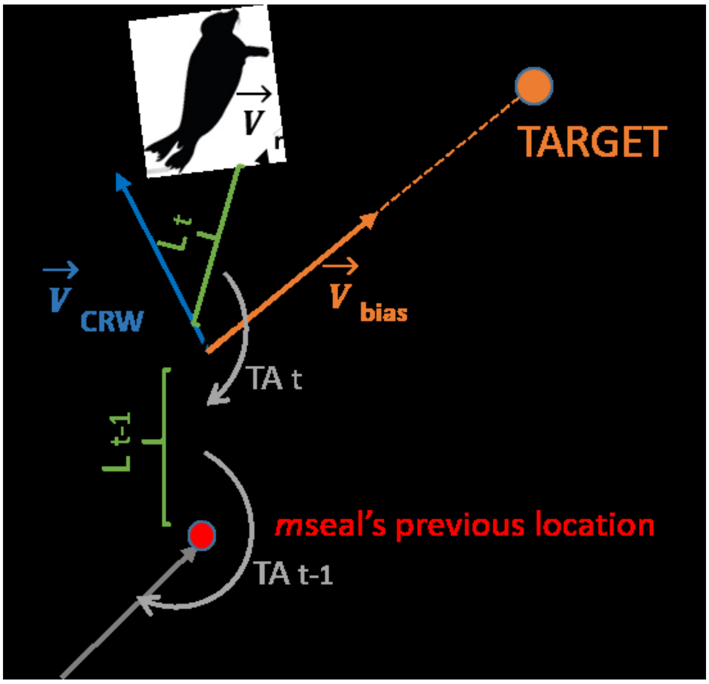


Figure 5. Schematic illustration of biased correlated random walk. Each vector has two components: turning angle (TA) and length (L, also referred to as step length or speed). The TA of movement vector $\mathbf{V}_{res}$ is calculated as the sum of these angles of $\mathbf{V}_{crw}$ (related to previous turning angle and habitat suitability index of the patch) and $\mathbf{V}_{bias}$ (bias towards target foraging patch or a haul-out site also related to the habitat suitability index of the patch). The length of $\mathbf{V}_{res}$ is drawn from the observed (based of GPS tracking of seals) speed distribution and is, therefore not related to speed in the previous time step.

$TA\ \vec{V}_{CRW}$ is as described in (Bartumeus et al. 2005) where directional persistence (i.e., the degree of correlation in the random walk) is defined via the probability distribution of turning angles as follow:

$$TA_{\vec{V}_{CRW}} = b * TA_{t-1} + N[0;\sigma] \qquad \text{Eq. 1}$$

where

- TA_{t-1} is turning angle at time t - 1 (in degrees),
- *b* is a coefficient defining 'wiggliness' of the movement. This value is calibrated (see section 2.2) and kept constant throughout the model run. *b* = -1 would result in zigzagging and b = 1 going in circles (Nabe-Nielsen et al. 2013).
- $N[0;\sigma]$ is a change in turning angle drawn from a normal distribution with σ = SD_{dir} * expHSI. If $N[0;\sigma]$> 180 -> $N[0;\sigma]$= $N[0;\sigma]$– 360. If $N[0;\sigma]$< -180 -> $N[0;\sigma]$= $N[0;\sigma]$+ 360
- SD_{dir} is fixed throughout the entire simulation. expHSI defines how distribution of changes in turning angles is related to HSI based on relationship set by (Humston et al. 2000: we used their parameter naming).

$$expHSI = \exp(-0.5) * \left(\frac{HSI_{on} - hsi_{opt}}{sigK}\right)^2 \qquad \text{Eq. 2}$$

where

- HSI_{on} is value of HSI of a patch *m*seal is currently on
- *his_opt* is optimal (maximum) value of HSI equals to 1 (HSI ranges between 0 and 1)
- *sigK* is a variance parameter controlling the strength of the relationship with HSI (Figure 12).

$\vec{V}_{CRW}$, therefore, causes *m*seals to have more tortuous movement in good habitat (habitat with high HSI) and in more straight line in bad habitat (habitat with low HSI).

$\vec{V}_{bias}$ is the difference between *m*seal's current heading and heading towards the target. The importance of bias component of $TA_{\vec{V}_{res}}$ is further proportional to HSI: the better the habitat quality the weaker the bias towards the target; and distance to the target:

$$TA_{\vec{V}_{bias}} = \frac{1}{Dist_{target} * expHSI * imp_{dist}} \qquad \text{Eq. 3}$$

where

- $Dist_{target}$ is distance to target (either haul-out site or patch)
- *imp_dist* - factor defining the importance of distance in the bias, ranging from 0 to 1

If *m*seals don't have any patch in their memory towards which they want to move (see **CHOOSE NEXT TARGET PATCH**), the bias vector is set to zero.

An example of movement of one individual moving according to biased CRW rules is shown on Figure 6.

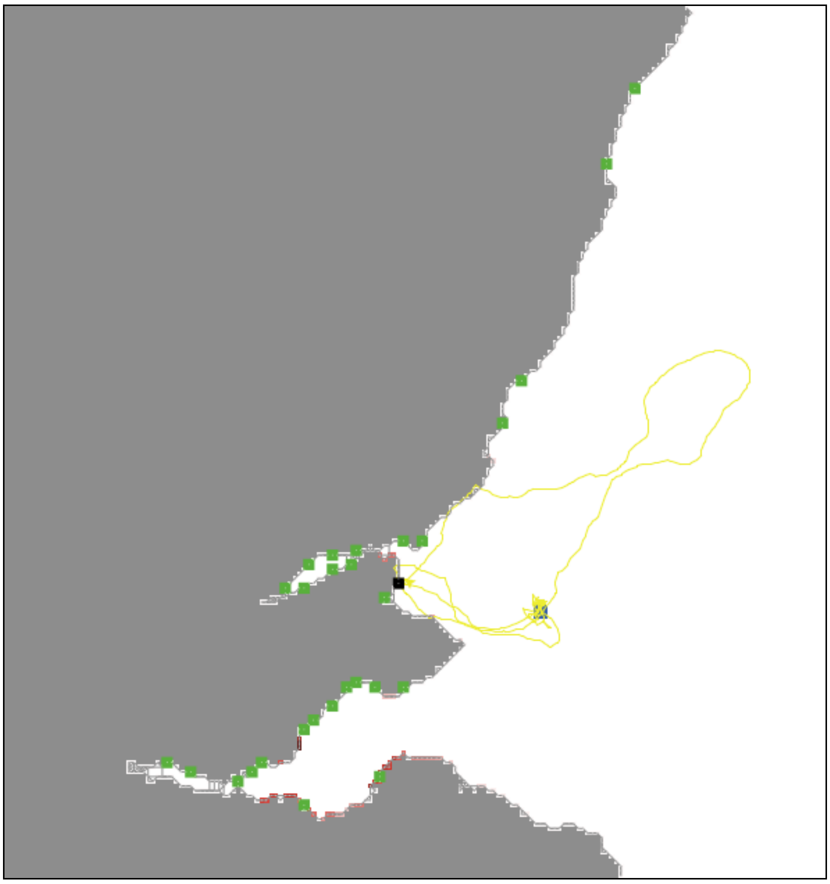


Figure 6. Example of movement: two consecutive foraging trips of one *m*seal moving according to biased CRW. For simplicity, the underlying HSI is reduced to values below 0.3, causing *m*seal to move in relatively straight line in the absence of bias. Black square indicates starting and, in this case, the next hauling-out site. The first foraging trip of this *m*seal (between the starting haul-out site and the next haul-out event) is towards open waters, in a relative straight line because HSI of the area is low and *m*seal has not memorised any patches yet and therefore has no target. Once it left the site, it starts memorising all the visited patches and the energy intake obtained on these patches. Once *m*seal 'decides' to return to haul-out site it turns back and heads towards the departure site and then haul-out. The blue square shows a habitat patch which is chosen as the next patch to visit during the second foraging trip from list of memorised patches (see **REMEMBER PATCHES** and **CHOOSE NEXT TARGET PATCH** procedures below). Close to the patch, *m*seal track during the second trip is very tortuous because bias 'pulls' it towards the target patch.

Speed (step length) is only related to HSI and not to the speed in the previous time step. The next speed (speed) of *m*seals is drawn each time step from a gamma distribution, as observed based on telemetry data (Table 1).

$$\text{SLt} = \text{gamma}\left(\frac{\text{shape}}{\text{expHSI}}, \text{rate}\right) \qquad \text{Eq. 4}$$

Shape and rate parameters are based on the observed values, calculated as described in section 1.4.10 for fine-scale movement (0.60 and 1.92 respectively).

The gamma distribution is right censored by the maximum observed swimming speed (V_{max}) and left censored by the minimum speed (V_{min}). If the values taken from the gamma distribution do not meet these criteria, a new value is drawn from the distribution based on Eq. 4.

1.7.1.3 REMEMBER PATCHES

For computation reasons, *m*seals memorise the location, id of the larger 5x5km square to which a visited 1x1km patch belongs as well as energy intake obtained at this patch at a given time step. Each visited square is also assigned a reference memory (M_{square}), which decays logistically over time based on equation by (Nabe-Nielsen et al. 2013), following (Van Moorter et al. 2009):

$$M_{square_t} = M_{square(t-1)} - \left(r * M_{square(t-1)} * \left(1 - M_{square(t-1)}\right)\right) \qquad \text{Eq. 5}$$

where the shape of the logistic curve is determined by the decay rate, r. This decay is a fixed value and does not change over model duration (r = 0.009/time step, see section 2.3 for details on calibration of r). Memory decays at each time step, regardless of *m*seals' activity. M_{square} can have a value between 0.99 and close to 0, but never 0. A newly visited square is assigned M_{square} = 0.99 and a square which has been visited previously, has M_{square} updated to 0.99. Square and their corresponding attributes (location and energy intake), for which M_{square} <= 0.01, are deleted from the memory list. With the current model settings of r = 0.009 [1/time step], seals forget a square if not revisited for approximately 10 days (Figure 7).

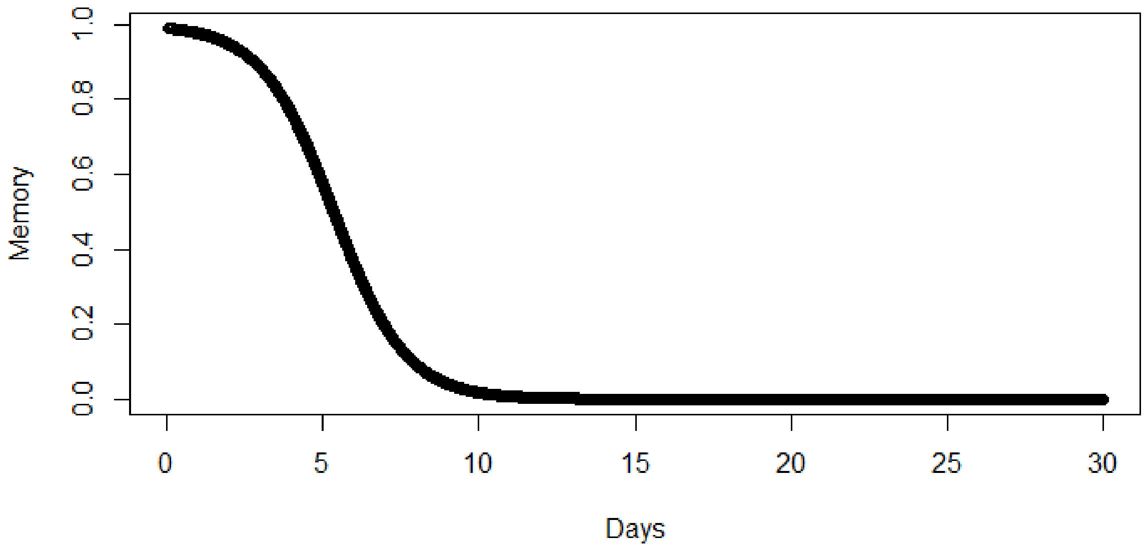


Figure 7. Memory decay of squares with rate *r* = 0.009 [1/time step].

Because the energy intake is not only function of HSI, but it is also determined by stochastic processes (see **INTAKE ENERGY** for details), *m*seals' fish consumption at the same patch may differ between visits, even if HSI of this patch does not change. To incorporate such changes, *m*seals do not store in their memory the energy intake obtained at the last visit within a given square, but a mean value of all visits at this square. The number of memorised intakes per square changes with time based on assigned memory which decays at the same rate as for patches (Eq. 5, Figure 7) and is removed if memory values falls below 0.01.

The memorised energy intake is later used to calculate which square is going to be visited in the next foraging trip (see **CHOOSE NEXT TARGET PATCH** in **HAUL-OUT** procedure). Because the energy intake on patches with low HSI, is usually close to zero, for computational simplicity, seals only store in their memory squares for which HSI>0.01.

1.7.1.4 REMEMBER HAUL-OUT SITES

*M*seals remember all haul-out sites within the study area but the memory value of each site differs between sites on which they have already hauled-out, sites passed by within a certain, calibrated, distance (*haul-out_detection_distance* = 2.1 km, see section 2.3 and Table 10) and sites which haven't been visited or passed by within the model duration. Each already visited haul-out site has memory value assigned to 0.99. Each haul-out site remembered by being passed by receive memory of *mem_level_passedBy_ho* = 0.5 following stochastic probability of 0.5. The memory value reflects *m*seals perceived attractiveness of a haul-out site: already visited sites are more attractive than sites which are passed by. The memory value is further used in calculating attractiveness of haul-out sites and therefore the next haul-out site of the seals (see **CHOOSE NEXT TARGET** and **HAUL-OUT**).

In contrast to memorising squares, the information about memorised haul-out sites does not decay with time. Tracking of harbour seals revealed that they can remember and return to haul-out sites on which they were born even after several years (Mackey et al. 2008, Cordes and Thompson 2015). Therefore, the memorised list is never cleared, and *m*seals therefore remember all haul-out sites over the entire model simulation.

1.7.1.5 INTAKE ENERGY

*M*seals obtain energy by foraging on fish while diving. The model time step (15 min) is longer than an average dive duration of harbour seals which is about 3 min (Bjørge et al. 1995, Suryan and Harvey 1998, Lesage et al. 1999). *M*seals' diving behaviour is, therefore, modelled in bouts with one bout lasting one time step. The number and type of fish eaten during one bout depends on number of fish available/encountered within a given patch, stochasticity and observed diet composition of the seals from the study area:

1. The number of available/encountered fish depends on search rate (*sr*, [m^2/time step]; this is a calibrated parameter with the same value for all individuals, see section 2.3 for details). For a single dive bout (time step), the number of available equals:

$$Prey_{available} = N * sr \qquad \text{Eq. 6}$$

where N is number of fish available within a given patch [fish/m^2] calculated as maximum number of fish available for best habitat (HSI=1) multiplied by HSI of a patch *m*seal is currently on (see section 0).

2. Number of available fish is then corrected for level of *m*seals fat reserves based on the assumption that overweight seals have reduced diving capacity due to their increased buoyancy. In AgentSeal we copied the approach used in DEPONS (Gallagher et al. 2020, in review). *M*seals with fat reserves approaching or exceeding maximum value observed (FR_{max} = 45 % (Beck et al. 2000, 2003)) reduce their number of caught fish exponentially as they reach this value. This fat reserves fish intake modifier (FI_{mod}, Eq. 8), is determined using the seal's level of fat reserve excess (FR_{over}, Eq. 7) over mean value observed for harbor seals in the autumn (FR_{mean} = 28 % REF). The $Prey_{available}$ is then augmented by multiplying by the FI_{mod}.

$$FR_{over} = \frac{FR_{curr} - FR_{mean}}{FR_{\max} - FR_{mean}} \qquad \text{Eq. 7}$$

$$FI_{mod} = \exp^{-5*FR_{over}} \qquad \text{Eq. 8}$$

3. The actual number of caught fish is drawn from the following Poisson distribution:

$$Prey_{caught} = poisson(Prey_{available}) \qquad \text{Eq. 9}$$

4. The energetic value and mass of the consumed fish is calculated as weighted mean mass and weighted mean of minimum and maximum energetic value of species observed in the diet multiplied by $Prey_{caught}$ (Table 5).

Table 5. Observed proportion of various fish in diet of harbour seals off the east coast of Scotland, their mass and caloric values and mean values used in the model. Proportion in diet is based on the report by (Wilson and Hammond 2016) for Harbour seals in East Scotland

Species	**Proportion in diet by occurrence [%]**	**Mean mass [g]**	**Sd mass [g]**	**Min kJ/g of wet mass**	**Max kJ/g of wet mass**	**Season at which caloric value is measured**	**Reference to caloric value**
Cod	3.8	133.3	12.1	3.68	4.4		(Murray and Burt 1977, Härkönen and Heide-Jørgensen 1991, Winship et al. 2002, Arnason et al. 2009)
Whiting	8.3	63.2	3.5	3	5		(Hislop et al. 1991, Winship et al. 2002)
Sandeel	18.4	10.5	0.5	4.6	7.5	Spring, summer	(Hislop et al. 1991)
Flat fish	44.6	45.0	3.0	2.5	5		(Murray and Burt 1977, Winship et al. 2002, Bayhan et al. 2008)
Mackerel	3.6	291.9	2.3	10.3	10.3	Summer	(Montevecchi et al. 1984)
Squid	8.4	10.0	1.0	2	6		(Van Pelt et al. 1997, Winship et al. 2002)
Sprat	4.4	20.0	1.0	5.06	8.2	Winter	(Hislop et al. 1991)
Weighted mean		**48**		**3.4**	**5.9**		**Mean energy value of fish used in the model is 4.7 kJ/g**

The energy intake from fish is not corrected for assimilation efficiency as energy expenditure related to digestion is calculated in ENERGY EXPENDITURE of **CALCULATE NET ENERGY** procedure (Table 6).

1.7.1.6 FOOD DEPLETION

$Prey_{caught}$ (Eq. 10) is subtracted from the total number of fishes from patch *m*seal is foraging and N of this patch is recalculated. There is no habitat replenishment in the model as we assume that major fish movement and recruitment occurs during spring and not autumn period (Dippner 1997, Henriksen et al. 2018).

1.7.1.7 LARGE SCALE FORAGING

If the daily amount of consumed fish is not enough to cover daily energy expenditure for seven consecutive days, *m*seals swap to exploratory, large-scale foraging movement. This procedure aims at mimicking situation when seals observed in nature would leave the unprofitable areas. There are two types of large scale foraging movement and there is equal probability of choosing any by each *m*seal after the ‘hunger’ period: i) CRW not biased towards any previously visited patch, and ii) CRW biased towards one of the patches from initial memory list (see *Initialisation* for details). In option i) current list of memories patches is emptied and seals start searching as they were naïve seals. In option ii) current list of memories patches is emptied and replaced by randomly chosen patch from initial memory list. This patch then becomes a target patch for a given *m*seal.

1.7.2 TIME TO REST? and TIME TO HAUL-OUT?

The *m*seals rest either to digest or non-digestive reasons (see section 1.4*)*. Digestive break can both take place at sea or at the haul-out site; resting for non-digestive reasons always takes place on land.

The schematic overview of decision process whether to rest and then haul-out or not is shown on the below flow chart (Figure 8). *M*seals go through four ‘checklists’ (NEED TO DIGEST?, CLOSE TO THE HAUL-OUT SITE?, NEED TO HAUL-OUT FOR NON-DIGESTIVE REASONS? and GENERAL CONDITION GOOD?.

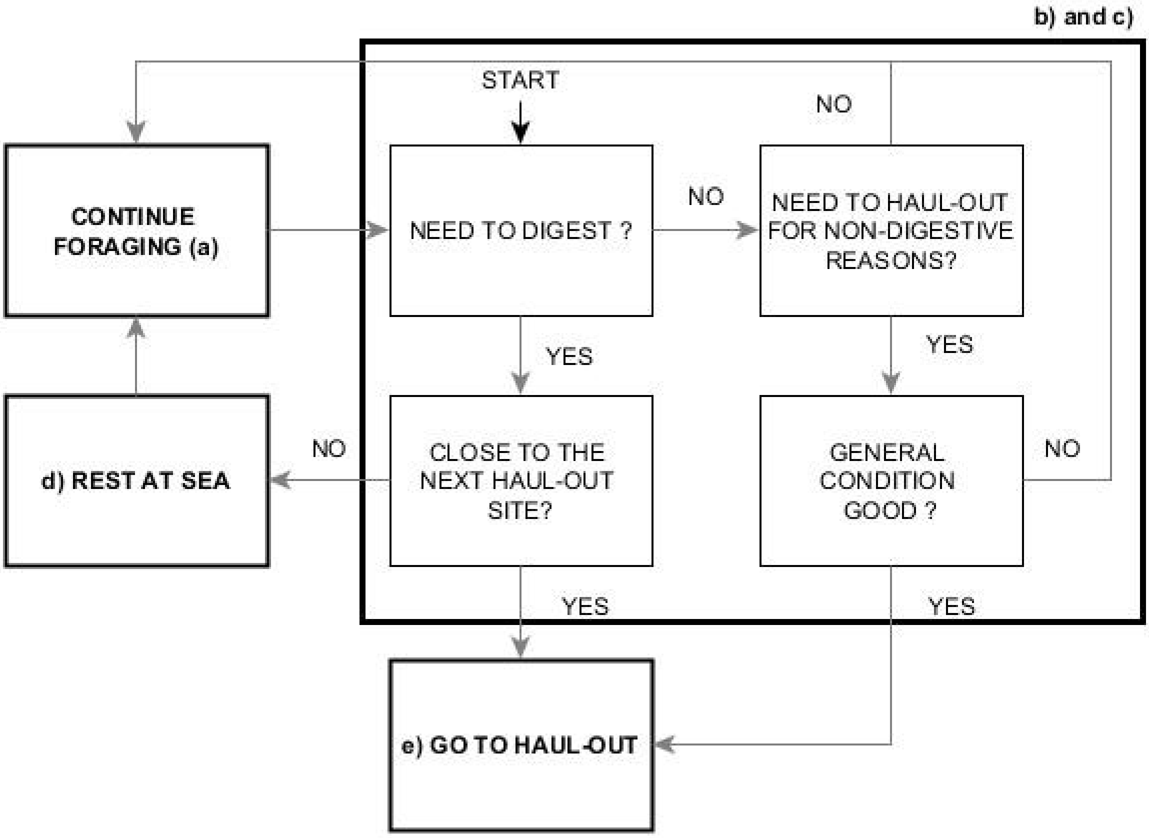


Figure 8. Flow chart showing decision process of *m*seals whether to rest or not and if yes whether at sea or to haul-out. Procedures and letters (a-d)in **bold** correspond to procedures in Figure 1.

NEED TO DIGEST? There are two digestive constraints which *m*seals may face: stomach capacity limits the amount of food which can be ingested (hereafter referred to as 'short-digestion'); and time it takes for food to pass through the digestive track (hereafter referred to as 'long-digestion').

*M*seals, therefore, take a break if the amount of consumed fish exceed 80-100% of their stomach volume (*stomachCap*„

Table 2) – . Short-digestion always takes place at sea.

Long-digestion takes place when *m*seals consumed 7 -14 % of their total body mass, reported as maximum daily food intake (Renouf and Noseworthy 1991, Rosen and Trites 2004, Kastelein et al. 2005). Long-digestion can take place at sea or at a haul-out site depending on the distance from the *m*seal's location when it has to rest, and the haul-out sites stored in its memory list (see **CHOOSE NEXT TARGET** and **HAUL-OUT**). If seals must digest, NEED TO DIGEST? is set to TRUE.

CLOSE TO THE NEXT HAUL-OUT SITE?: The further the distance away, the less likely *m*seals go to haul-out site but rest at sea instead. The distance / probability of the haul-out relationship is defined by logistic regression:

$$Prob_{haulOut} = \frac{1}{1 + a_{prob} * \exp\left(b_{prob} * x\right)} \qquad \text{Eq. 10}$$

x can be either distance to haul-out site, time since last haul-out or blubber % (see below and Figure 9). Coefficients are set to *a_prob* = 1000 and *b_prob* = -0.34 after calibration (see section 2.3).

First, selection between 0 and 1 is calculated with 50% of chance of either outcome. If this value is zero, *m*seals rest at sea (see **REST AT SEA**) and CLOSE TO THE NEXT HAUL-OUT SITE? is set to TRUE. Otherwise they go to a haul-out site (see **GO TO HAUL-OUT SITE**) and CLOSE TO THE NEXT HAUL-OUT SITE? is set to FALSE.

NEED TO HAUL-OUT FOR NON-DIGESTIVE REASONS? : Even if *m*seals do not need to take a long digestive break, they may have to haul-out for other than digestion-related reasons. The need of hauling-out increases, therefore, with time since last haul-out (*durationSinceLastHa*) according to logistic regression (Figure 9, Eq. 10) with x = time since last haul-out.

First, selection between 0 and 1 is calculated with 50% of chance of either outcome. 0 = NEED TO HAUL-OUT FOR SKIN RELATED REASONS? is set to TRUE, otherwise set to FALSE

GENERAL CONDITION GOOD? :

The blubber % (=*Tmass/ResMass*) / probability of haul-out relationship is defined by the logistic regression (Figure 9, Eq. 10) with x= blubber percentage.

First, selection between 0 and 1 is calculated with 50% of chance of either outcome. 0 = *m*seals continue foraging, GENERAL CONDITION GOOD? is set to FALSE, otherwise GENERAL CONDITION GOOD? is set to TRUE and *m*seals go to haul-out site.

The haul-out decision of *m*seals is therefore coded as a nested, hierarchical if-else condition. Digestion need has a priority over skin related reasons to rest:

If NEED TO DIGEST? TRUE

```
[rest]
else
        [
        if NEED TO HAUL-OUT FOR NON-DIGESTIVE REASONS? FALSE
        {
                If GENERAL CONDITION GOOD? TRUE
                [rest]
                else
                [forage]
        }
                        else
                        [forage]
        ]
```

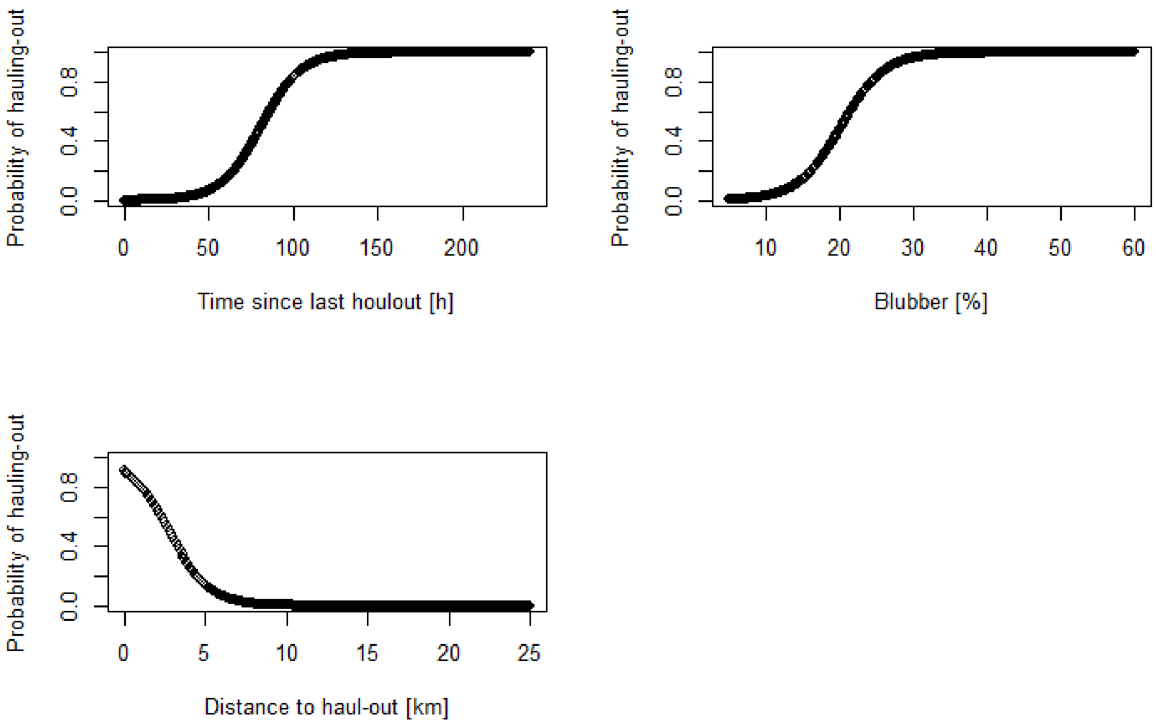


Figure 9. Probabilities of hauling-out with distance to haul-out site (upper left panel), time since last haul-out (upper right panel) and seal condition (Blubber, lower panel).

1.7.3 REST AT SEA

If *m*seals rest at sea due to short-digestion, duration of resting is a random number between 45-60 min (3 or 4 time steps) mimicking short-term resting at sea (Ramasco et al. 2014).

If *m*seals rest at sea due to long-digestion, the duration of rest is proportional to the amount of fish consumed from the last long-digestion ($Fish_{lastLongDig}$) in relation to their total body mass (*Tmass*) (Sparling et al. 2007):

$$\mathrm{DurationOfDigestion} = 47.3 + 12.72 * \left(100 * \frac{Fish_{lastLongDig}}{Tmass}\right) \qquad \text{Eq. 11}$$

*M*seals do not change location while resting at sea.

1.7.4 GO TO HAUL-OUT SITE

1.7.4.1 CHOOSE NEXT TARGET HAUL-OUT SITE

*M*seals ‘choose’ their next site to haul-out site based on the distance and memory value of the sites stored in their memory as also used in studies by (Mitchell and Powell 2007, Nabe-Nielsen et al. 2013, Liukkonen et al. 2018). The memory value ($M_{haul\text{-}out}$) is set to 0.99 for already visited sites and 0.50 for sites memorised while passing by (see **REMEMBER HAUL-OUT SITES** description in **FORAGE** procedure) and does not decay with time.

The attractiveness of each memorised haul-out site is calculated as below (Liukkonen et al. 2018):

$$Attract_{haulOut} = \frac{M_{haulout}}{D_{target}} \qquad \text{Eq. 12}$$

Attractiveness is multiplied by a random number between 0 and 1 and the next haul-out site to visit is then chosen as haul-out site with highest attractiveness after multiplication.

1.7.4.2 BIASED CORRELATED RANDOM WALK

While on their way to haul-out sites, *m*seals move according to correlated random walk biased towards the site as described in **BIASED CORRELATED RANDOM WALK** in **FORAGE** procedure. The difference is that the target is now a haul-out site, and not a patch.

1.7.4.3 TAKE SHORTEST PATH TO HAUL-OUT SITE

If *m*seals encounter land on their way to haul-out site, instead of moving as described in **AVOID LAND** in **FORAGE** procedure, *m*seals follow the coastline towards the haul-out site along the shortest path. While avoiding land *m*seals frequently change their moving direction as the direction in which *m*seals avoid land depends on the ‘amount of land’ ahead of *m*seal. In such a situation, *m*seals could never reach the haul-out sites. Harbour seals are very coastal phocids and it is quite likely that they use coastline to navigate as well. Spending time near-shore may also serve to avoid open-water predators.

NetLogo does not have implemented ‘shortest path’ function in its basic version. We, therefore, used ‘turtles-on-path-to’ primitive from bundled Networks extension. The shortest path is calculated along a set of points equally distributed along the shore (points are located in the middle of all patches adjacent to land) and linked with all such points within 2 km (Figure 10). *M*seals, then, take as many time-steps to get to the haul-out site as points along the calculated path.

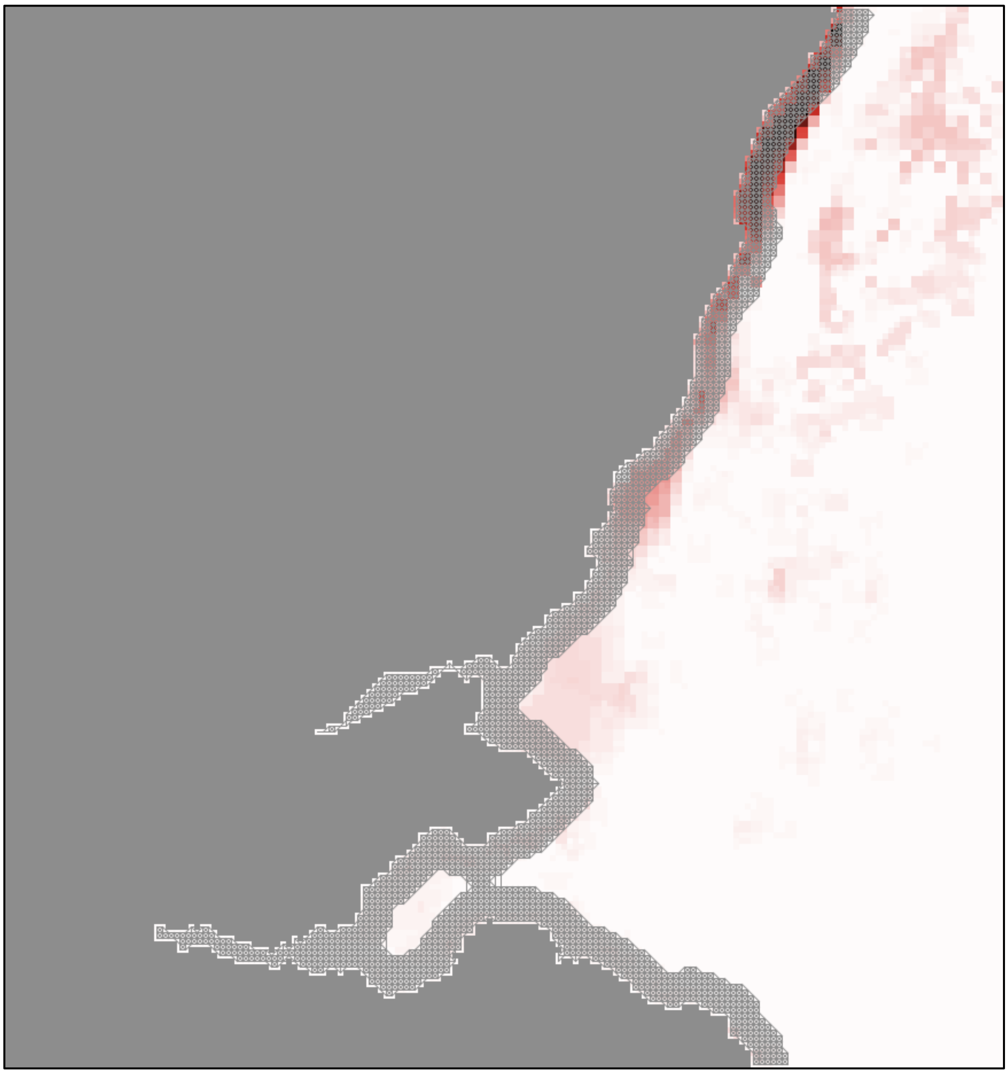


Figure 10. Example of a network of points (grey) along which shortest path to haul-out site is calculated. Habitat suitability index, a proxy for food availability, of water patches is represented by red colour pallet with grid cells with high index being darker.

1.7.5 HAUL-OUT

The duration of haul-out (*durationOfResting*) reflects the durations observed in reality and is drawn from log normal distribution with 7.37 ± 3.6 h (see section 2.3 for details on parameterisation of this value). Duration of haul-out cannot, however, be shorter than *DurationOfDigestion* if *m*seals haul-out due to long-digestion, and longer than 35h as observed.

1.7.5.1 CHOOSE NEXT TARGET PATCH

At the end of each haul-out event, *m*seals ‘choose’ a foraging patch towards which they will head after the haul-out. The choice is based on the mean energy intake *m*seals memorised for a given square (EI_{square}), distance to this square ($D_{target,}$ always >= 1) and the memory value (M_{square}, Eq. 5). Because *m*seals store in their memory the 5x5km square to which a given patch belongs, the distance is calculated as distance to the last visited patch within a given square. We, therefore, used the same approach as (Mitchell and Powell 2004, Van Moorter et al. 2009) and implemented by (Nabe-Nielsen et al. 2013):

$$Attract_{square} = \frac{M_{square} * EI_{square}}{D_{target}} \quad \text{Eq. 13}$$

Attractiveness is than multiplied by a random number between 0 and 1 and the next patch to visit is then chosen as patch with highest attractiveness after multiplication.

Due to numerous stochastic processes in AVOID LAND procedure, seals which haul-out in small bays, may not leave the bays to get to their next patch to visit located outside the bays before they go back to haul-out. In order to avoid such situations for seals hauling out in small bays (in case study Firth of Forth and Eden, Figure 2), seals leave the bays along the shortest path from the haul out site to a predefined points just outside the bays. This procedure is coded the same way as TAKE SHORTEST PATH TO HAUL-OUT SITE.

1.7.5.2 REMEMBER HAUL-OUT SITES

*M*seals add the haul-out site on which they currently are to their memory list and assign it $M_{haulOut}$ = 0.99 (see description of the same procedure in **FORAGE**).

1.7.6 CALCULATE NET ENERGY

1.7.6.1 ENERGY EXPENDITURE

*M*seals' energy expenditure over each step depends on their activity. Energy expenditure is calculated as activity-specific multiplier of BMR calculated as (Kleiber 1975) (Table 6):

$$BMR_{\left[\frac{MJ}{day}\right]} = 70 * (Tmass)^{0.75} * 0.004184 \quad \text{Eq. 14}$$

The value of BMR is calculated based on initial body mass and does not change over model duration, even if body mass changes.

Table 6. Values of BMR multipliers for various mseals' activities used to calculate energy expenditure.

Activity	**BMR multiplier (mean, sd)**	**Reference**
Haul-out	2.08, 013	(Sparling et al. 2006)**
Short-digestion	2.08, 014	(Sparling et al. 2006)
Long-digestion	7.28, 1.2	(Sparling et al. 2007)
Forage	1.8, 0.45	(Sparling 2004, Gallon et al. 2007)*

**M*seals' energy expenditure during foraging is assumed to equal energy expenditure during diving.

** If *m*seals haul-out due to long-digestion (see *Need to digest?* in **TIME TO REST?** procedure), and the haul-out time = time of long-digestion, then energy expenditure is calculated as for long-digestion. If haul-out time >

time of long-digestion, the energy expenditure during the time difference is calculated as energy expenditure of haul-out.

Although thermoregulation may be energy costly (Watts 1992, e.g. Beltran et al. 2017), we assume that the *m*seals are rarely outside their thermoregulatory neutral temperatures and that the main thermoregulation happens during haul-out and is, therefore, included in the BMR multiplier (Erdsack et al. 2012).

1.7.6.2 NET ENERGY AND CHANGES IN BODY MASS

Net energy (energy intake – energy expenditure) is only calculated once per modelled day at 8:00.

If net energy > 0 *m*seals turn the energy excess into fat reserves (we assume 100% conversion into blubber) assuming efficiency of fat synthesis (Fat_{synth}) to be 74 – 90 % (Malavear 2002, drawn as random number from this range, Beltran et al. 2017) and energy content of 1g of fat = 0.0394 MJ (Blaxter 1989), and therefore *m*seals gain mass ($Tmass_{[t-1]} = Tmass_{[t]} + ResMass$)

$$RessMass = \frac{Net_{energy} * Fat_{synth}}{0.0394} \qquad \text{Eq. 15}$$

If net energy < 0 seals, *m*seals burn fat reserves and loose mass ($Tmass_{[t-1]} = Tmass_{[t]} - ResMass$), assuming efficiency of fat catabolism to be 80% (Barboza et al. 2009):

$$ResMass = \frac{Net_{energy}}{0.0394 * 0.80} \qquad \text{Eq. 16}$$

If *ResMass/Tmass* <= 0.05, *m*seals die (Malavear 2002 in Beltran et al. 2017).

A list of state variable and entities which are updated/modified in all above procedures are given in

Table 2.

2. Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterise and calibrate the model, and of the observed patterns that are used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

There are 36 parameters in AgentSeal: 16 parameters related to model initialisation, 9 parameters related to fine-scale movement and land avoidance, and 11 parameters related to general movement, physiology and behaviour of *m*seals. Ten of these 36 parameters had to be parameterised (finding appropriate values of parameters which have a range of reported values in literature or data) or calibrated (finding appropriate values of parameters which are not measurable or have not been observed in reality). Due to the large number of parameters in the model, and possibly quite high interaction rate between parameters, the model parameter selection is divided into two stages. We first parameterise and calibrate fine-scale movement: biased correlated random walk by running simulations on an artificial environment (see 2.2 below). The remaining parameters are established in the second stage using fixed values of parameters parametrised and calibrated in the previous stage (section 2.3) and is based on running simulations on multiple parameter combination over 1 month.

The choice and values of remaining 26 parameters, for which values are taken from the literature or based on data collected by SMRU, is also described in the below sections.

2.1 Parameters related to model initialisation

There are 16 parameters related to model initialisation: seven related to landscape (patches and haul-out sites) and six related to *m*seals' morphometrics (

Table 4).

As the modelled landscape reflects the East Coast of Scotland, most parameters are directly taken from observed values and scaled to the modelled domain: location of haul-out sites and shape of coastline are modelled as in reality. Each patch has a pre-calculated distance to shore and distance to each of the 16 haul-out sites to speed up the model. Also, the initial distribution of seals across the haul-out sites is based on observed values (SMRU 2017).

Estimating and mapping seals' prey distribution and abundance is very logistically difficult. Creating a prey map in the model had to be, therefore, based on proxies or calibrated if such values are not reported. HSI of the patches is based on species distribution model for seals tagged by SMRU around Scotland (Grecian et al. 2018). Assigning prey availability and energetic to HSI for each patch has been parameterised and calibrated as described in section 2.3.

Creating the shortest path to haul-out sites along the coast (see section 1.7.4) required two subjectively chosen parameters: distance at which a network of points is created from the shore (7 km) and distance at which neighbouring points are connected to form a path (2 km). None of these values can be measured in nature and there is no pattern observed which could be used in POM. The coastline in this case-study has several bays and is convoluted. We chose 7 km as distance at which the network of points is created to cover shortest paths across the mouths of the smaller bays, rather than always hugging the coast. The effect of this threshold distance is tested in sensitivity analysis.

Initial *m*seals' morphometrics are based on extensive SMRU data for adult harbour seals, including only those which were measured during the same season as the current model temporal extent (autumn).

2.2 Parameters and data related to fine-scale movement: biased correlated random walk

2.2.1 Description of parameters

Fine-scale movements of seals are simulated using a mixture of correlated random walk (CRW) behaviour and spatial memory resulting in movement biased towards memorised places (see section 1.7.1). Seals also avoid land. This section describes parameters related to land avoidance and biased CRW (BCRW) (used in **FORAGE** (section 1.7.1) and **GO TO HAUL-OUT SITE** (section 1.7.4) procedures); parameters related to memory, general behaviour and physiology are described in the next session of this document (see section 2.3).

There is one parameter related to land avoidance: distance between mseal and land at which seals take decision to avoid it. Obviously, such a value is not possible to measure, and we chose a value which allowed *m*seals to 'smoothly' follow the coastline and not stuck in very small bays, common along the East Coast of Scotland. The effect of this distance is tested in sensitivity analysis.

There are eight parameters related to BCRW (Table 7). Five of these – parameters related to mseals' speed and speed distribution, are obtained from literature or based on observed data (Table 1), which shows speed distribution and characteristics of harbour seals from the same region as the modelled environment – East Coast of Scotland (Mcclintock et al. 2013, Russell et al. 2015). The remaining three parameters are calibrated and parameterised as described below.

Table 7. Model parameters related to fine-scale movement of seals: biased correlated random walk. The ‘code names’ are the names used in the NetLogo code in the current version of the model.

Parameters and state variables[12]	Value and unit[13]	Description	Source	Reference
check-land-distances	1.04 km	Distance used by seals to evaluate whether there is land ahead	Sensitivity analysis	Defined as distance *m*seals can travel within four time steps with average speed
his_opt	1	optimal, best habitat value	Set	Eq. 2
sigK	0.52	variance parameter controlling the strength of the relationship with HSI	Calibrated	Eq. 2
b	-0.70	wiggliness' coefficient	Calibrated	Eq. 1
imp_dist	0.015	factor defining the importance of distance in defining the bias	Calibrated	Eq. 3
Vmin	0.0002 m/s	minimum seals swimming speed	Observed	McCLintock 2013, Eqs (page 23)
Vmax	2 m/s	maximum seal swimming speed	Observed	Willimas and Koyman 1985 in Ramasco 2014, Eqs (page 23)
Shape, rate	0.60, 1.92	Descriptors of gamma distribution of speed	Observed	Eq. 4

2.2.2 Parameter selection: parameterisation and calibration – procedure

The parameter selection (parameterisation and calibration) of the fine-scale movement model is performed using a simulation model that included the biased correlated random walk (BCRW) behaviour, but without spatial memory behaviour and land avoidance movement. For this reason, we used an artificially created landscape and one target point as shown on Figure 11. We modelled *m*seal movement in an environment which had several, randomly distributed clusters of ‘good’ habitat (high HSI), and lower quality habitat in between. We tested three different modelled environments: as shown below, larger number of small clusters and completely random, not clustered, assigned of HSI values to patches. The type of environment did not affect the results.

[12] Names of the parameters as used in the code, names used in the text, if different than in the code, are given in ()

[13] Value used in the final model simulation

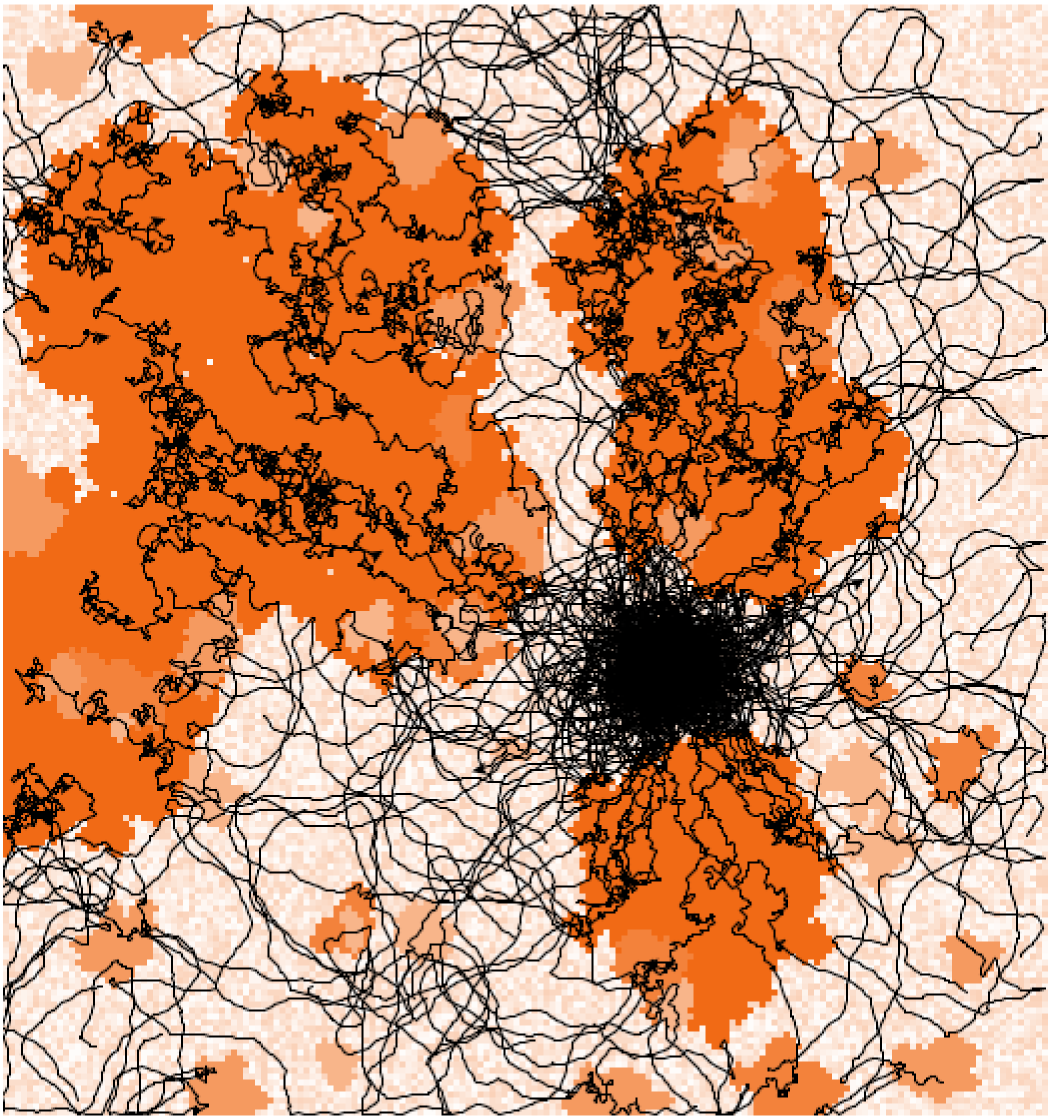


Figure 11. An artificial landscape used to parameterise biased correlated random walk. Habitat suitability index has a value from 0 to 1, as in the final model, and is depicted by different shades of orange: the darker the higher index. The target point is under the point with high concentration of tracks. The spatial resolution of this artificial environment is the same as in the final model with one patch = 1x1 km.

We calibrate values for *b*, *sigK* and imp_{dist} but used *his_opt* = 1 for all simulations, as this is the highest HSI value defined in our model.

Below is a graph depicting the relationship between *expHSI* (Eq. 2) and HSI defined by various values of *sigK*.

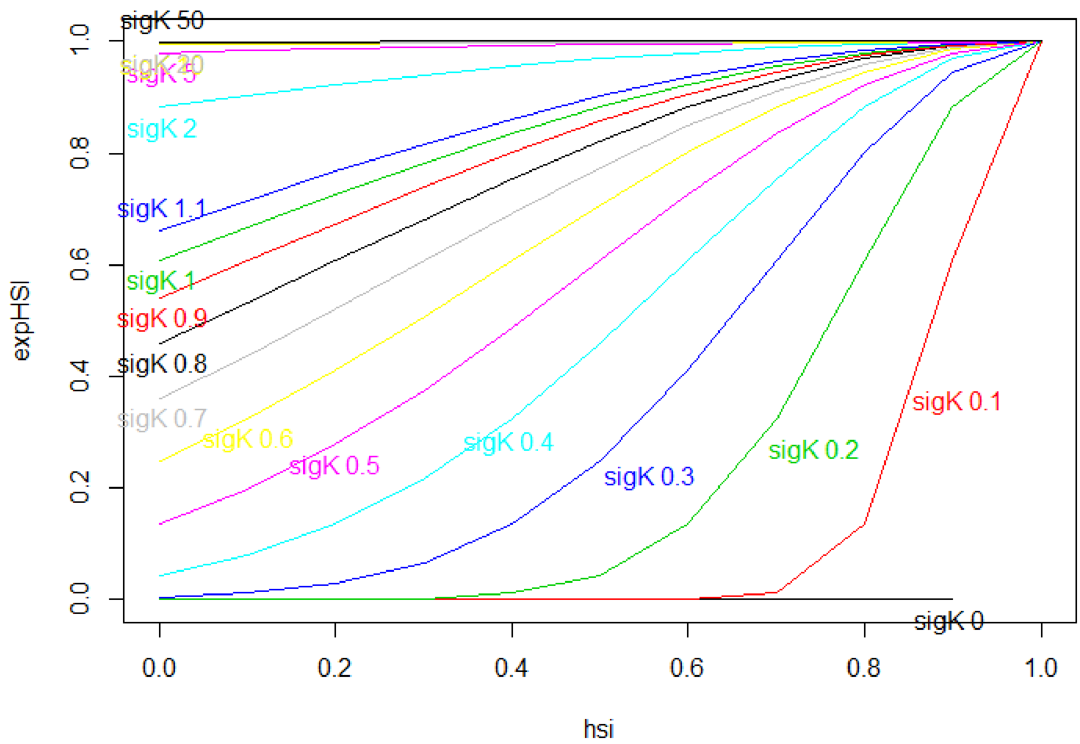


Figure 12. Relationship between habitat suitability index (HSI) and expHSI defined by various values of *sigK*.

For smaller the values of *sigK* (< 0.3), HSI will only increase the 'tortuosity' of CRW of seals in very good habitat (HSI > 0.7, Figure 12). Speed also will only change (reduce) substantially at high HSI. In other habitats seals will go almost straight (black line in

Figure 13). At larger values of *sigK*, however, seal movement is 'wigglier' regardless of HSI (Figure 12; red line in

Figure 13).

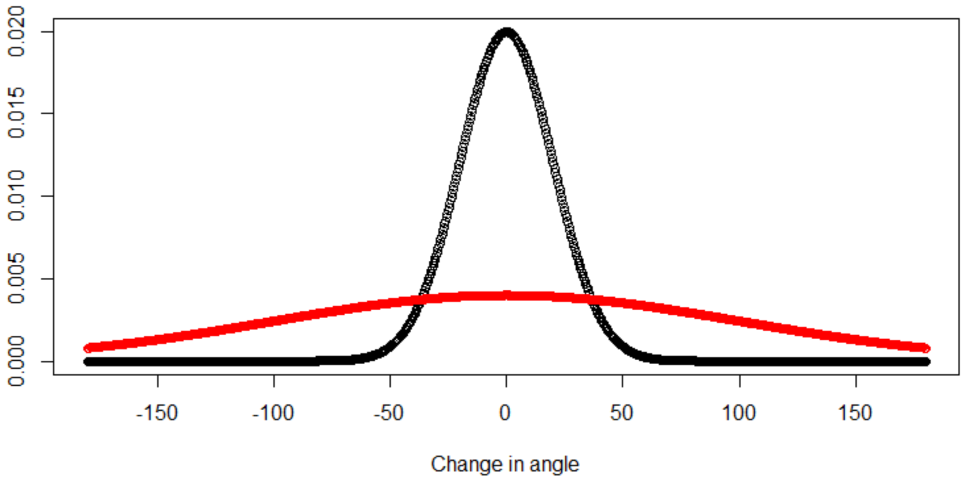


Figure 13. Graphical representation of distribution of changes in movement angles [degrees] depending on *sigK*. Red line shows changes for large (> 0.7) and black for small *sigK* (< 0.3).

For parameter selection, we therefore, choose values of *sigK* which influence 'wiggliness' of *m*seals' movement in the entire range of HSI: (0.3 < *sigK* < 1). b is allowed to take values between -1 and 1, and imp_{dist} from 0 to 1.

We use Latin hypercube sampling (McKay et al. 1979) with R package lhs (Carnell 2018) to define 60 combinations of the above three parameters (Figure 14,

Table 8).

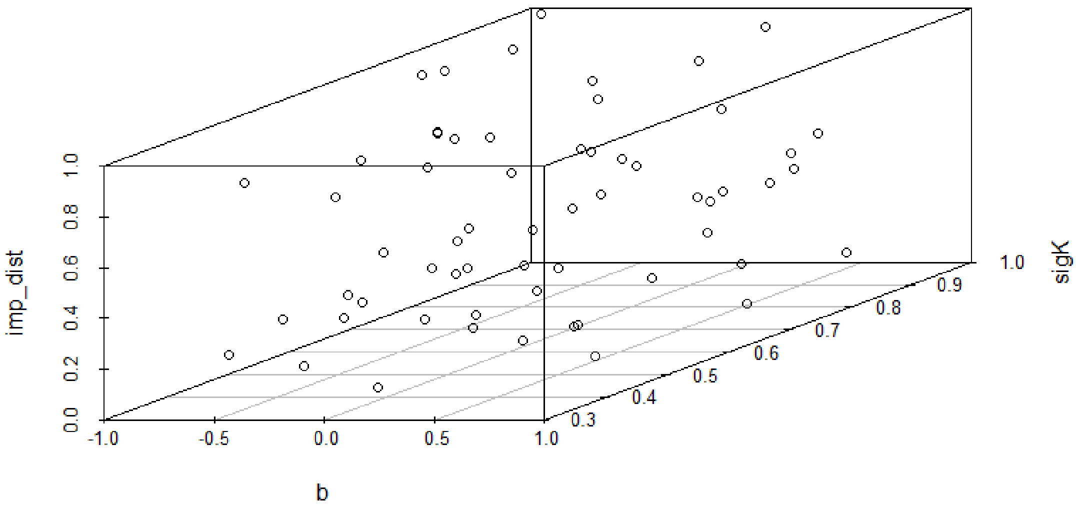


Figure 14. Graphical description of combination of parameters used in calibration of fine-scale movement. *b* 'wiggliness' coefficient; *sigK* variance parameter controlling the strength

of the relationship with HSI*; imp_dist* and parameter defining changes in strength of bias in relation to distance to target.

Table 8. List of parameter combinations used in parameterisation of fine-scale movement and the assigned index number. Parameter combination for index #2 (highlighted) is used in the final model.

index #	*b*	*sigK*	*imp_dist*	index #	*b*	*sigK*	*imp_dist*
0	0.581515	0.944333	0.089439	*30*	0.526619	0.620513	0.713959
1	0.255844	0.306151	0.654612	*31*	0.674758	0.499858	0.072034
2	**-0.70362**	**0.520879**	**0.015244**	*32*	-0.60511	0.954967	0.475018
3	0.026169	0.352705	0.41837	*33*	0.632957	0.314947	0.350423
4	0.796067	0.338396	0.279738	*34*	0.545178	0.794958	0.019815
5	-0.29869	0.592238	0.868994	*35*	0.414722	0.366689	0.516942
6	-0.39148	0.880297	0.822215	*36*	0.837147	0.768219	0.572813
7	-0.01137	0.752122	0.861139	*37*	-0.2468	0.999314	0.256561
8	0.906414	0.380799	0.75862	*38*	0.876193	0.405715	0.97557
9	-0.30727	0.587148	0.342479	*39*	-0.54323	0.554627	0.795538
10	-0.80898	0.789058	0.942483	*40*	0.125839	0.868243	0.907463
11	0.483547	0.577685	0.643827	*41*	-0.76608	0.445803	0.80567
12	-0.33411	0.726635	0.594545	*42*	-0.57796	0.5268	0.67521
13	-0.03675	0.401096	0.039919	*43*	0.226484	0.454042	0.616631
14	-0.99628	0.818811	0.89596	*44*	0.729527	0.420848	0.488849
15	-0.88757	0.832927	0.631795	*45*	-0.79377	0.893817	0.929927
16	-0.43359	0.388413	0.318656	*46*	0.048288	0.913337	0.314969
17	0.661391	0.471285	0.21464	*47*	0.352396	0.854852	0.122507
18	-0.16276	0.705802	0.147601	*48*	0.968696	0.759629	0.722114
19	0.452209	0.900769	0.516083	*49*	0.739127	0.687419	0.55757
20	0.32431	0.432119	0.296862	*50*	-0.48683	0.644961	0.686155
21	-0.40296	0.933459	0.463078	*51*	-0.52139	0.330802	0.229808
22	0.943403	0.496929	0.385454	*52*	-0.85796	0.844043	0.114344
23	-0.10472	0.608617	0.836584	*53*	0.392163	0.809019	0.774475
24	0.167913	0.655908	0.057829	*54*	-0.1981	0.535348	0.189071
25	-0.95564	0.683704	0.152013	*55*	-0.23235	0.710695	0.243956
26	-0.08553	0.672026	0.415702	*56*	0.088391	0.486439	0.536381
27	-0.64034	0.562733	0.170159	*57*	0.294347	0.923218	0.380746
28	0.160258	0.965786	0.958395	*58*	-0.9084	0.983291	0.990932
29	0.806092	0.637669	0.435496	*59*	-0.68787	0.734208	0.749921

We run one simulation for each parameter combination for 500 time-steps for 50 *m*seals. Two movement state variables: speed and turning angles, as well as HSI of patches visited by seals and distance to target is outputted at each time step for each individual.

Two emergent patterns are used to parameterise the BCRW: frequency distribution of turning angles and correlation of turning angle between current and previous time step (patterns 1.1-1.4 in Table 1). Because step length was directly drawn from the observed distribution and because we assumed no relationship between step length at time t and t-1, only turning angles were considered as POM patterns. Some of the graphs refer to step length (speed) but this is only for illustrative reason.

The observed values for the above listed statistics and data processing is given in section 1.4.10 (see also Table 1).

To compare the frequency distribution of modelled and observed values, we first calculate the proportion of observed and modelled turning angles for a range of bins: turning angles are divided into 10 degrees bins between -180 and 180. We then calculate the standardised absolute error (SAE) between mean for all 50 *m*seals' (x_{mod}) and mean for all 62 observed seals' (x_{obs}) proportions for each bin and sum it over *n* bins as follows for each parameter combination:

$$SAE = \frac{1}{n}\sum_{i=1}^{n} \left| \frac{x_{mod_i} - x_{obs_i}}{x_{obs_i}} \right| \qquad \text{Eq. 17}$$

Calculating standardised squared errors (SSE), instead of SAE, is frequently used in POM (e.g Frank and Baret 2013). Both measurements express average model prediction error in units of the variable of interest. Since the errors are squared before they are averaged, the SSE gives a relatively high weight to large errors. This means the SSE should be more useful when large errors are particularly undesirable. SSE has, on the other hand, a tendency to be increasingly larger than SAE as the sample size increases. This can be problematic when comparing SSE results calculated on different sized test samples, which is the case in our model. According to (Willmott and Matsuura 2005) SAE is a more natural measure of average error, and (unlike SSE) is unambiguous, and we, therefore use SAE in our analysis. Throughout the text 'best 15%' refers to parameters combination resulting in 15% lowest SAE (best fit).

Besides SAE, we also check if the modelled means for each bin fall between observed minimum and maximum for each bin. Tagged seals represent a subset of harbour seal population and the model should be able to reproduce values within the observed ranges and not only values close to mean of all observed animals.

The observed data show significant correlations between speed turning angle at time t and t-1 (Pearson's correlation, df=527672, $p<0.01$, $r^2=0.16$). We calculate the same correlation for the modelled results (all individuals combined) using linear regression.

2.2.3 Parameter selection – pattern-oriented modelling

Final parameter selection, identifying the parameter combination best matching the observed patterns, is based on i) the parameter set which had lowest SAE for patterns 1.1 – 1.2 and are within the observed range for these patterns and ii) show significant correlation in turning angles.

Figure 15 depicts SAE for all 60 indices for two movement state variables: speed and turning angle for the four patterns (1.1 – 1.4 in Table 3). All parameter combinations result in model predictions comparable to the observed frequency distribution of speed (pattern 1.1) (results for all 60 parameter combinations are available on demand). Only three parameter combinations (indices 2, 5 and 13) result in frequency distribution of modelled turning angles matching the observed and having at least 75% of bins falling within the observed values. Out of these three, parameter combination corresponding to index 2 had lower SAE than the others. The remaining parameter combinations result in a more uniform distribution of turning angles without the distinct observed peak around 0 degrees (Figure 16). All parameter combinations result in significant correlation in speed and turning angles at time t and t-1 (results for 60 combinations available on demand), but the correlation strength for two movement state variables is closer to observed for index 2 than 5 and 13. This parameter combination is therefore used in the final model simulation. The distribution and correlation of speed and turning angles for the final parameter set (*b*=-0.70, *sigK*= 0.52, imp_{dist}= 0.02; index 2 in

Table 8) is shown on Figure 16.

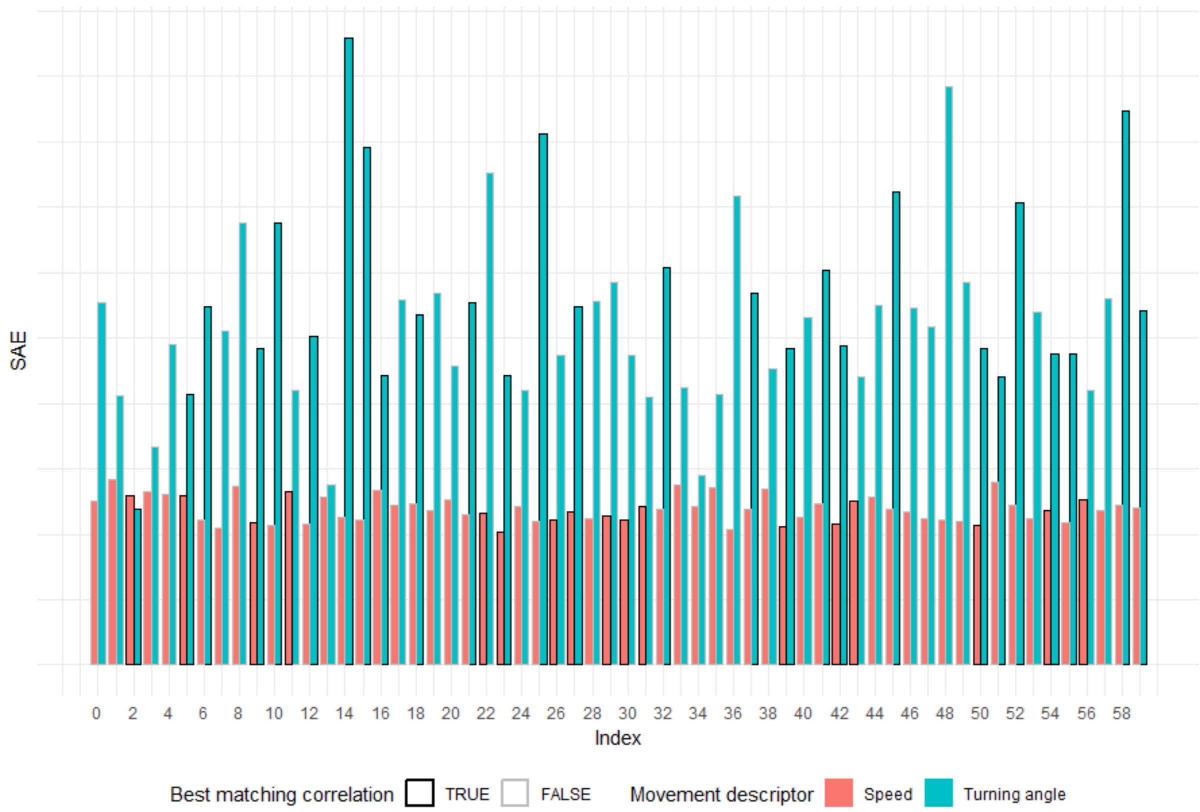


Figure 15. Standardised absolute errors (SAE) for 60 combinations (indices) of parameters used in the parameter selection for fine-scale movement for distribution of two movement state variables: speed and turning angles. Colour of the frame of the bars indicates indices

for which the strength of correlation is closest to observed. SAE for the movement state variables are not directly comparable as the value of SAE depends on the input data.

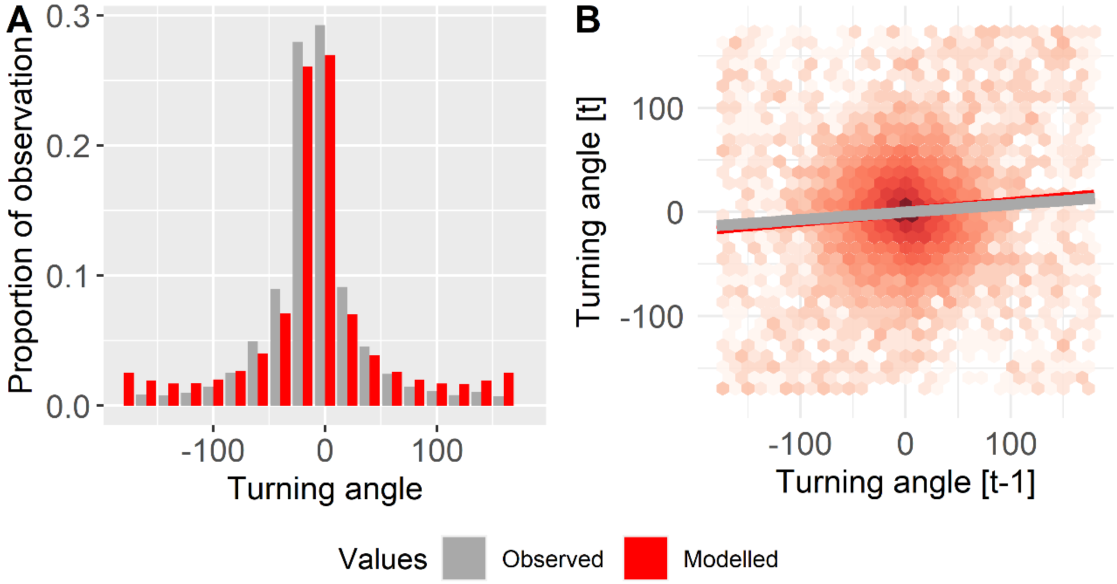


Figure 16. Observed (black) and modelled (red) distribution of speed (top left), turning angles (top right), correlation between speed at time t and t-1 (lower left), and correlation between turning angle at time t and t-1 (lower right) for index with best fitting parameter combinations (index #2, Table 8). The observed and modelled correlations in turning angles are significant (R^2=0.07, p<0.01, $t_{1,276040}$=39.2 for turning angles of the observed values and R^2=0.09, p=0.01, $t_{1,34137}$=2.5 for the modelled values).

2.3 Parameters and data related to general movement, physiology and behaviour

2.3.1 Description of parameters

There are eleven parameters related to general movement, physiology and behaviour of *m*seals (Table 9): three related to memory-based movement of *m*seals (**REMEMBER PATCHES** and **REMEMBER HAUL-OUT SITES**), four related to energy intake, one related to energy expenditure and three related to decisions about resting and hauling-out (Table 9). Most parameters related to memory and resting had to be calibrated, as there are no values of these parameters measured for seals. We also calibrate two parameters related to energy intake. Duration of haul-out is parameterised based on values reported in the literature (see details below)

Table 9. Model parameters related general movement, physiology and behaviour. The 'code names' are the names used in the NetLogo code in the current version of the model.

Parameters and state variables[14]	**Values and unit**[15]	**Description**	**Source**	**Reference**
CALCULATE NET ENERGY: Energy expenditure				
BMR multiplier for each activity	-		Observed	Table 6
FORAGE: Remember patches				
ref-mem-decay-rate (r)	0.009	Memory decay rate	Calibrated	Eq. 5
FORAGE: Remember haul-out sites				
haul-out_detection_distance (HO_{dist})	2.07 km	Distance at which *m*seals remember passed by haul-out sites	Calibrated	Section 1.7.1.4
mem_level_passedBy_ho	0.5	Memory level of haul-out sites which is memorised by passing by	Calibrated but see section 2.3.2	Section 1.7.1.4
FORAGE: Intake energy				
#Fish_hsi_multiplier, ($N_{HSI=1}$)	#/m^2	Initial number of fish per m^2 of a patch with HSI=1	Calibrated	Eq. 6, Initialisation
search_rate (sr)	13.12 m^2/time step	Average search rate which *m*seals can 'scan' during one time step (15min)	Calibrated	Eq. 6
mean_g_per_fish	48 g	Mean mass of fish	Observed	Table 5
mean_kJ_per_gOffish	4.7 kJ/g	Mean energy value of fish	Observed, Sensitivity analysis	Table 5
TIME TO REST? and TIME TO HAUL-OUT?				
b_prob	0.343	Coefficients of logistic regressions defining probability of hauling-out	Calibrated	Section 1.7.2,Eq. 10
HAUL-OUT				
mean_durHO (HO_{dur}), sd_durHO	7.37, 3.6 h	Duration of haul-out event, drawn from a log normal distribution around mean and sd	Parameterised	Section 1.7.5

Net energy intake of *m*seals is calculated based on standard energy balance: intake – expenditure. Parameters related to energy expenditures, expressed as multipliers of BMR for various activities, are relatively well documented for *m*seals for their main activities (such as

[14] Names of the parameters as used in the code, names used in the text, if different than in the code, are given in ()

[15] Values used in the final model simulation

swimming, resting, diving), and are mainly based on pool experiments (Sparling 2004, Sparling et al. 2006, 2007). Energy expenditure of seals varies seasonally (e.g. Rosen and Renouf 1998). Most studies present either daily energy expenditure of seals based on annual expenditure or expenditure during a period of high energy demand such as moulting or breeding. There are few studies from outside these periods and the reported values range between 14.3 and 21.43 MJ/day (Markussen et al. 1990, Härkönen and Heide-Jørgensen 1991, Renouf and Noseworthy 1991, Rosen and Renouf 1998, Sparling 2003, Kastelein et al. 2005). These values are either based on studies of harbour seals or a similar species like grey seals for which energy expenditure is reported per 1 kg of body mass. Digestion is an energetically costly activity and seals postpone digestion until they haul-out or rest (Sparling et al., 2007; Table 5). In order for the *m*seals to show energy expenditure within the observed values, *m*seals spent energy for digestion during each long-digestion break regardless if it is at sea or during haul-out (see section 1.7.2).

2.3.2 Parameter selection: parameterisation and calibration – procedure

Memory decay, *r* is varied between 0.003 and 0.01. This allows us to test range of options from when *m*seals remember most of the patches within the entire 1-month model situation (r = 0.003) to having complete memory loss after a week (Figure 17).

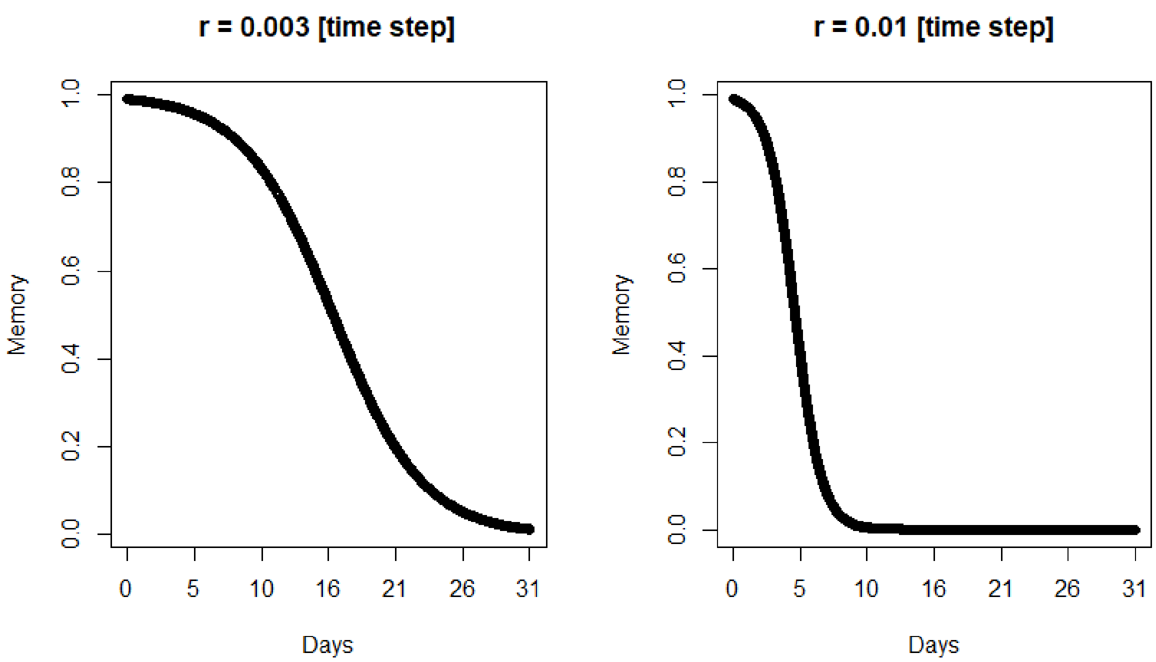


Figure 17. Memory decay with time using two extreme values of decay rate (r) used in the parameter selection.

haul-out_detection_distance is varied between 1 and 5 km. Although parameter *mem_level_passedBy_ho* cannot be directly measured and it should, therefore, be calibrated, we set this value to 0.5 as it had very little effect on the model results (data not presented here but available on demand) to minimise number of combinations of the calibrated/parameterised parameters.

In the model, the amount of fish caught by *m*seals per one dive bout (= duration of time step) is dependent on search rate (*sr*, [m^2/time step]) and density of fish available in a given food patch (*N*, [fish/m^2]). Both parameters are difficult to measure in nature, especially since *sr* is not the actual area *m*seals can 'scan' over a time but a value averaged over a dive bout and therefore including time spend on ascent and descent, inter-dive intervals and handling time when fish are not actually searched.

We test various values of N based on ICES transformed catchability data [kg/km^2] (Moriarty and Greenstreet 2017, Walker et al. 2017). The maximum value observed for ICES within the study area squares for the species occurring in seals' diet for the study site = 26386.09 kg/km^2 (details on calculation of this number are not presented here but are available on demand). If one fish = weighted mean [g] based on seal diet from the study area (48 g; Table 5), $N_{HSI=1}$ = 0.5. However, as we have very little knowledge on actual fish abundance and seal search behaviour, as well as not all fish species from seals' diet are monitored by ICES, we varied $N_{HSI=1}$ as integer number between 0.5 and 2 fish/m^2 and *sr* between 1 and 60 m^2/time step (15 min).

b_prob is varied between -0.45 and -0.10 resulting in probability of hauling-out with time, blubber % and distance to haul-out site as shown on Figure 18*; a_prob* is kept constant for all simulations but adjusted by parameter '*mult'* to test situations when all of the three probabilities are low for the entire range of variable of interest (time, blubber % and distance to haul-out site) (see lowest panels of Figure 18).

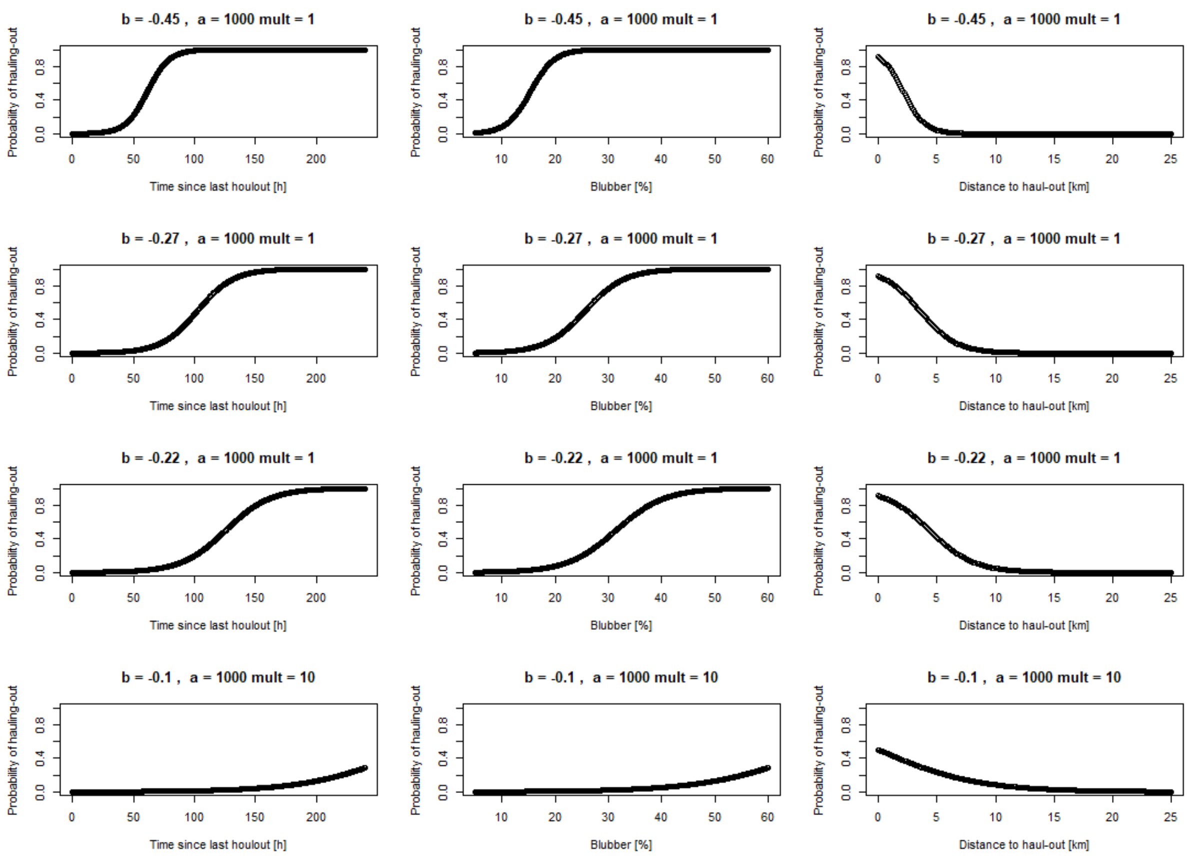


Figure 18. Probability of hauling-out with time, blubber % and distance to haul-out site using range of coefficient *b_prob* (Eq. 10) used in parameter selection. *a_prob* is kept constant for all simulations but adjusted it by parameter '*mult*'.

There is large variation in reported duration of haul-out of harbour seals outside moulting and breeding season (Thompson and Miller 1990, Cunningham et al. 2009, Ramasco et al. 2014). Also, as stated in section 1.4, harbour seals are known to spend time resting in very shallow waters nearby haul-out sites (resting very close to shore).

Data from 14 adult harbour seals tagged by SMRU for which we have data for time outside moulting and breeding (September-April) for the East Coast of Scotland around Firth of Forth area, showed that the distribution of haul-out durations is right-skewed between 0.25 and 10.5 h and mean = 2.3h (Figure 19) but there is no information on time seals spend resting close to shore. Currently, haul-out statistics are usually collected by a dry/wet sensor placed on telemetry devices, which can stay dry even if seals are resting very close to shore. It is, therefore, hard to evaluate whether reported haul-out duration includes resting close to shore or only time when seals are on land. We, therefore, used data from additional 12 individuals GPS[16] tagged in Moray Firth and transmitting in October-December 2014

[16] This is a subset of 58 seals tagged in Moray Firth as described in section 1.4.10. The above described analysis of 12 individuals is part of another project looking at characteristic of foraging trips and hence only 12 used.

(University of Aberdeen, Lighthouse Field Station) and estimated what is the distribution of duration of inshore resting (onshore haul-out and resting very close to shore). To do so, we select >6h trips and calculated the time from the end of each trip to the start of the next trip. For reasoning behind choosing trips >6h see 'Patterns 2.6: Frequency distribution of trip duration and 2.7: trip extent' in section 2.2.3. The results also show right skewed distribution ranging from 0.2 to 35 h and mean = 4.8 h (Figure 19).

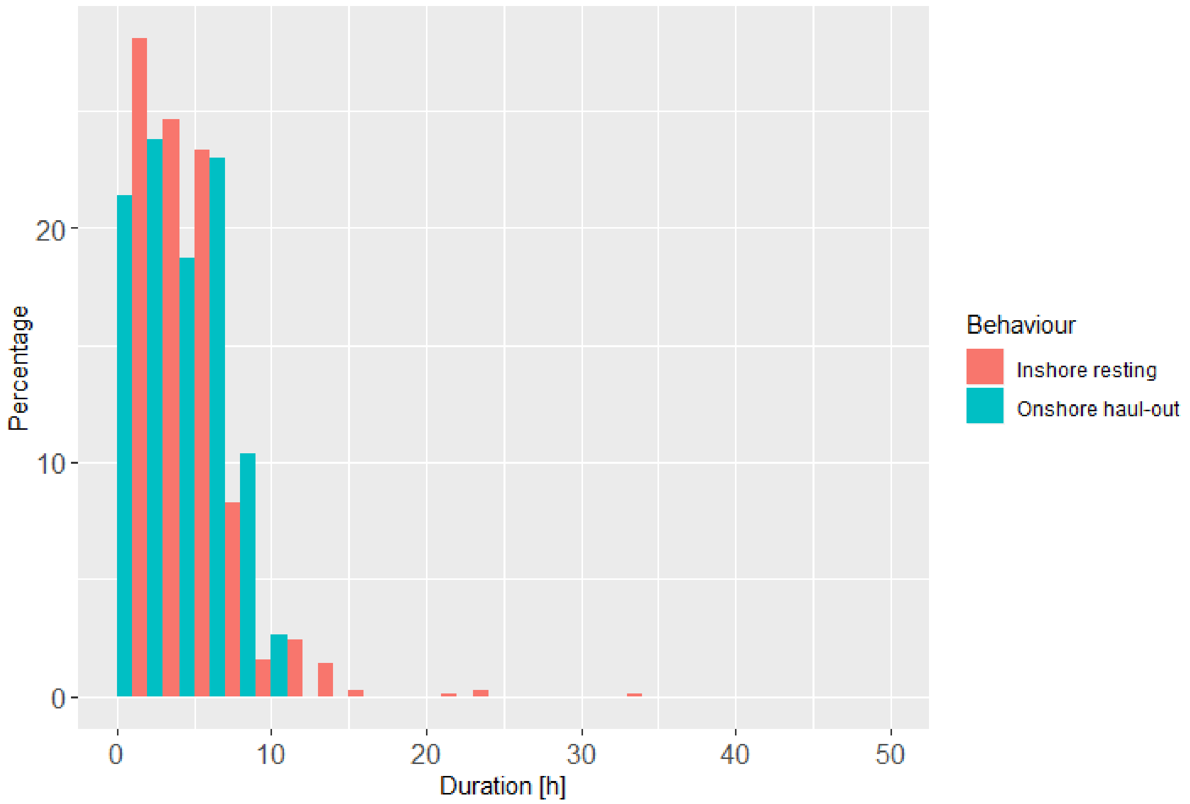


Figure 19. Observed distribution of onshore and inshore (onshore plus resting close to shore) haul-out time based on GPS tagged seals along the East Coast of Scotland and Moray Firth.

Due to large variation of reported haul-out durations and difference between duration of inshore and onshore haul-out as described above, we parameterise haul-out duration taking it from range of distributions with mean between 2.3 h (value from 14 seals tagged at the study area) and 12h (max reported in literature (Thompson and Miller 1990, Cunningham et al. 2009)) as shown by 'minimum' and 'maximum' on Figure 20. Modelled duration of haul-out is drawn from log-normal distribution and then back transformed.

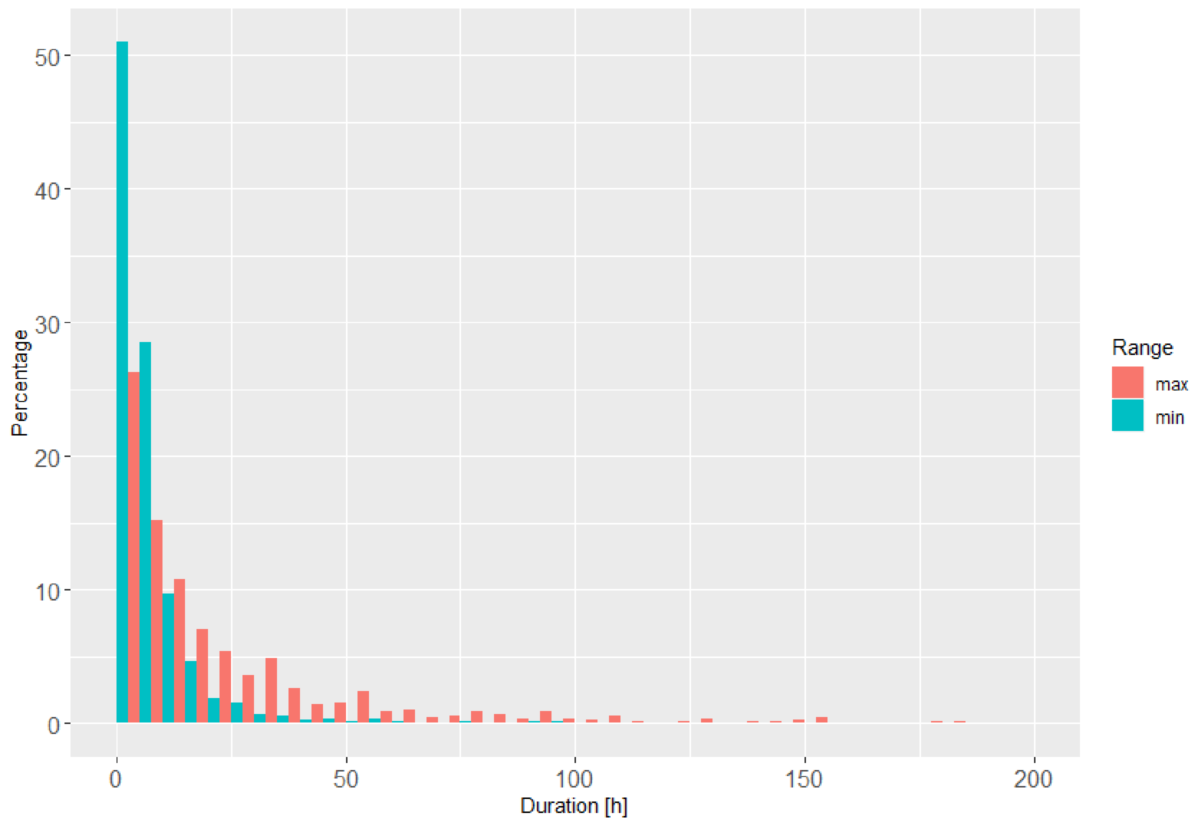


Figure 20. Modelled ‘minimum’ and ‘maximum’ distribution of haul-out duration used during parameter selection.

Similarly to parameter selection of fine-scale movement, we use Latin hypercube sampling (McKay et al. 1979) with R package lhs (Carnell 2018) to define 150 combinations of the six parameters in the parameterisation/calibration process (Table 10, Figure 21).

Table 10. Parameter combinations used in parameter selection related to memory-based movement and processes influencing resting and haul-out behaviour. Highlighted index shows the parameter combination used in the final simulations.

index	*N*	*sr*	*r*	HO_{dist}	HO_{dur}	*b_prob*	index	*N*	*sr*	*r*	HO_{dist}	HO_{dur}	*b_prob*
0	0.5	27.67	0.004	2.66	6.14	-0.449	*75*	3	9.78	0.005	3.23	3.84	-0.168
1	4.5	56.65	0.003	4.32	9.10	-0.195	*76*	3.5	1.27	0.004	1.35	6.95	-0.186
2	2	4.16	0.004	2.84	8.62	-0.268	*77*	5	47.09	0.008	3.93	7.95	-0.391
3	3.5	54.76	0.005	4.85	6.47	-0.304	*78*	3.5	41.92	0.009	1.34	6.81	-0.426
4	1.5	52.39	0.009	1.83	8.19	-0.333	*79*	3.5	38.48	0.009	4.35	6.84	-0.188
5	4	31.95	0.010	1.96	11.01	-0.326	*80*	5.5	11.85	0.007	1.69	11.66	-0.131
6	0.5	12.68	0.007	4.03	3.28	-0.120	*81*	1	5.23	0.008	3.89	9.70	-0.247
7	1	31.61	0.008	2.50	10.22	-0.242	*82*	5	44.33	0.004	1.22	11.17	-0.247
8	3	21.76	0.009	3.30	10.50	-0.285	*83*	4	32.72	0.008	2.26	7.65	-0.418
9	2	41.16	0.005	2.98	7.04	-0.405	*84*	4	48.31	0.005	1.95	8.34	-0.159
10	5	30.50	0.006	1.42	4.91	-0.433	*85*	1.5	23.47	0.004	1.46	7.61	-0.260
11	0.5	58.28	0.006	3.35	10.30	-0.207	*86*	0.5	16.91	0.006	2.70	8.48	-0.376
12	0.5	48.81	0.008	4.53	9.21	-0.155	*87*	5	29.28	0.010	4.17	2.57	-0.109
13	5.5	43.29	0.004	2.29	7.41	-0.204	*88*	3.5	56.86	0.004	2.95	8.79	-0.198

14	3.5	15.93	0.007	2.58	10.13	-0.193	*89*	3	33.78	0.009	3.99	4.85	-0.402
15	4	18.76	0.007	1.45	9.39	-0.167	*90*	4.5	22.64	0.004	2.06	9.74	-0.212
16	2	34.11	0.006	1.01	10.86	-0.396	*91*	4.5	53.51	0.009	4.21	7.85	-0.153
17	3.5	37.06	0.004	4.65	10.84	-0.353	*92*	4	59.18	0.005	4.59	2.56	-0.134
18	5	29.44	0.007	3.11	5.36	-0.274	*93*	1	25.53	0.007	4.72	7.53	-0.311
19	5	21.24	0.004	3.70	4.22	-0.398	*94*	1	55.95	0.005	3.79	5.52	-0.368
20	3	45.27	0.006	3.51	7.11	-0.408	*95*	6	48.07	0.007	1.59	8.40	-0.230
21	3	3.01	0.006	1.77	4.28	-0.107	*96*	1	39.22	0.009	2.45	10.95	-0.436
22	1	20.48	0.005	1.87	5.91	-0.227	*97*	4.5	2.04	0.009	2.47	5.99	-0.375
23	4.5	46.91	0.007	1.83	11.97	-0.224	*98*	3.5	34.95	0.006	1.03	7.92	-0.114
24	4	46.20	0.003	1.90	10.03	-0.177	*99*	2.5	56.20	0.006	1.10	6.49	-0.320
25	1	51.59	0.009	4.13	8.90	-0.173	*100*	3.5	37.42	0.005	3.82	3.14	-0.150
26	6	44.22	0.007	2.92	5.79	-0.317	*101*	5.5	25.91	0.006	4.23	2.74	-0.394
27	4.5	14.21	0.008	1.07	8.87	-0.306	*102*	3.5	44.98	0.009	3.08	11.70	-0.370
28	6	28.90	0.004	3.63	7.45	-0.416	*103*	3.5	6.49	0.003	3.57	6.34	-0.141
29	4	5.48	0.007	3.04	11.18	-0.385	*104*	0.5	17.88	0.004	2.79	3.68	-0.126
30	3.5	33.32	0.005	2.44	5.43	-0.348	*105*	5.5	27.90	0.007	2.75	4.48	-0.148
31	3	20.26	0.003	4.88	5.28	-0.385	*106*	3	14.58	0.008	2.35	6.07	-0.164
32	3	24.06	0.007	1.13	11.88	-0.411	*107*	4	49.46	0.004	2.12	3.82	-0.299
33	1.5	59.54	0.006	1.92	5.07	-0.446	*108*	1	41.88	0.007	3.42	10.70	-0.301
34	4.5	7.60	0.010	3.09	8.68	-0.209	*109*	3.5	8.94	0.005	4.48	2.83	-0.360
35	2.5	36.45	0.006	2.72	10.80	-0.182	*110*	3.5	57.87	0.009	4.66	11.78	-0.435
36	5.5	2.64	0.004	1.78	3.42	-0.315	*111*	3	47.76	0.009	1.54	11.36	-0.251
37	2.5	58.78	0.004	3.01	5.15	-0.413	*112*	1	28.37	0.010	1.32	5.56	-0.356
38	1.5	59.90	0.007	1.17	4.42	-0.163	*113*	5	40.04	0.010	3.43	8.05	-0.341
39	3.5	35.43	0.008	2.32	11.45	-0.181	*114*	4	13.84	0.007	4.55	10.38	-0.263
40	5.5	46.47	0.006	2.38	2.79	-0.277	*115*	4.5	54.90	0.007	1.49	3.94	-0.145
41	2	12.31	0.009	4.90	2.92	-0.336	*116*	5.5	39.13	0.004	2.14	4.39	-0.216
42	4	36.10	0.009	2.77	2.68	-0.444	*117*	2.5	3.63	0.003	3.54	7.14	-0.171
43	3	7.91	0.005	1.64	4.98	-0.256	*118*	4.5	51.29	0.010	1.28	5.84	-0.101
44	5.5	14.90	0.008	4.70	4.78	-0.379	*119*	2.5	10.05	0.005	4.74	9.90	-0.292
45	4	49.80	0.008	4.29	7.31	-0.409	*120*	5	11.06	0.009	2.02	10.27	-0.421
46	5.5	1.55	0.004	4.42	7.71	-0.431	*121*	3	20.92	0.005	4.45	3.53	-0.272
47	0.5	18.47	0.008	1.26	6.28	-0.283	*122*	4	25.23	0.010	2.53	9.56	-0.290
48	2	35.67	0.005	2.88	7.25	-0.136	*123*	4.5	23.20	0.009	3.77	6.18	-0.323
49	1	5.91	0.008	3.64	10.44	-0.313	*124*	4	27.28	0.006	1.74	3.46	-0.442
50	4	10.47	0.004	2.41	11.26	-0.335	*125*	2.5	49.30	0.005	1.63	8.27	-0.400
51	0.5	16.73	0.008	1.19	11.60	-0.308	*126*	5.5	53.81	0.006	2.56	3.20	-0.242
52	3.5	19.12	0.009	2.61	3.06	-0.223	***127***	4	**13.18**	**0.009**	**2.07**	**7.37**	**-0.343**
53	1.5	19.70	0.006	1.13	4.64	-0.327	*128*	5.5	15.32	0.006	4.76	4.02	-0.351
54	4.5	57.40	0.006	1.67	9.25	-0.239	*129*	1	42.79	0.008	2.87	6.63	-0.219
55	3.5	6.88	0.005	4.84	9.30	-0.381	*130*	3.5	39.84	0.003	4.98	10.57	-0.387
56	1.5	50.31	0.008	2.25	10.07	-0.252	*131*	0.5	33.10	0.008	3.32	3.08	-0.339
57	6	26.35	0.008	3.21	4.80	-0.212	*132*	3	40.97	0.009	4.81	9.79	-0.112
58	3	52.08	0.003	3.15	9.59	-0.423	*133*	4.5	22.57	0.007	3.98	9.04	-0.121

59	4.5	13.45	0.004	3.52	7.79	-0.198	*134*	0.5	17.23	0.005	4.11	3.34	-0.129
60	6	24.57	0.005	3.18	2.97	-0.104	*135*	5	52.68	0.005	4.50	6.69	-0.177
61	2.5	55.32	0.010	4.04	9.45	-0.280	*136*	4.5	50.67	0.003	1.38	5.21	-0.347
62	5	4.75	0.004	3.84	6.58	-0.371	*137*	4	29.75	0.006	4.07	4.57	-0.142
63	6	42.31	0.005	2.18	4.09	-0.219	*138*	4.5	45.76	0.007	4.62	5.33	-0.296
64	2.5	18.24	0.003	3.67	4.67	-0.270	*139*	5	11.56	0.006	2.65	5.72	-0.236
65	3.5	8.76	0.004	3.95	5.65	-0.108	*140*	2	37.90	0.008	4.41	8.24	-0.257
66	3.5	32.34	0.007	1.99	9.02	-0.234	*141*	4.5	38.17	0.008	3.75	11.84	-0.117
67	1.5	6.94	0.005	3.25	10.62	-0.138	*142*	4	8.17	0.005	3.87	8.10	-0.365
68	5	43.54	0.008	2.91	3.71	-0.232	*143*	1.5	2.30	0.004	1.58	8.74	-0.278
69	4	9.54	0.007	3.39	11.39	-0.330	*144*	5.5	54.27	0.006	4.28	8.55	-0.190
70	4	31.18	0.003	2.21	4.18	-0.357	*145*	2.5	3.97	0.010	4.96	9.49	-0.428
71	1.5	26.86	0.007	3.28	4.07	-0.158	*146*	6	53.25	0.009	4.39	9.92	-0.265
72	2	34.49	0.008	3.60	11.55	-0.287	*147*	2.5	16.21	0.010	1.53	3.61	-0.203
73	2	24.99	0.009	3.46	11.10	-0.439	*148*	5	30.25	0.006	2.17	6.87	-0.296
74	3	22.14	0.008	4.18	5.98	-0.124	*149*	2	40.43	0.009	4.94	6.42	-0.362

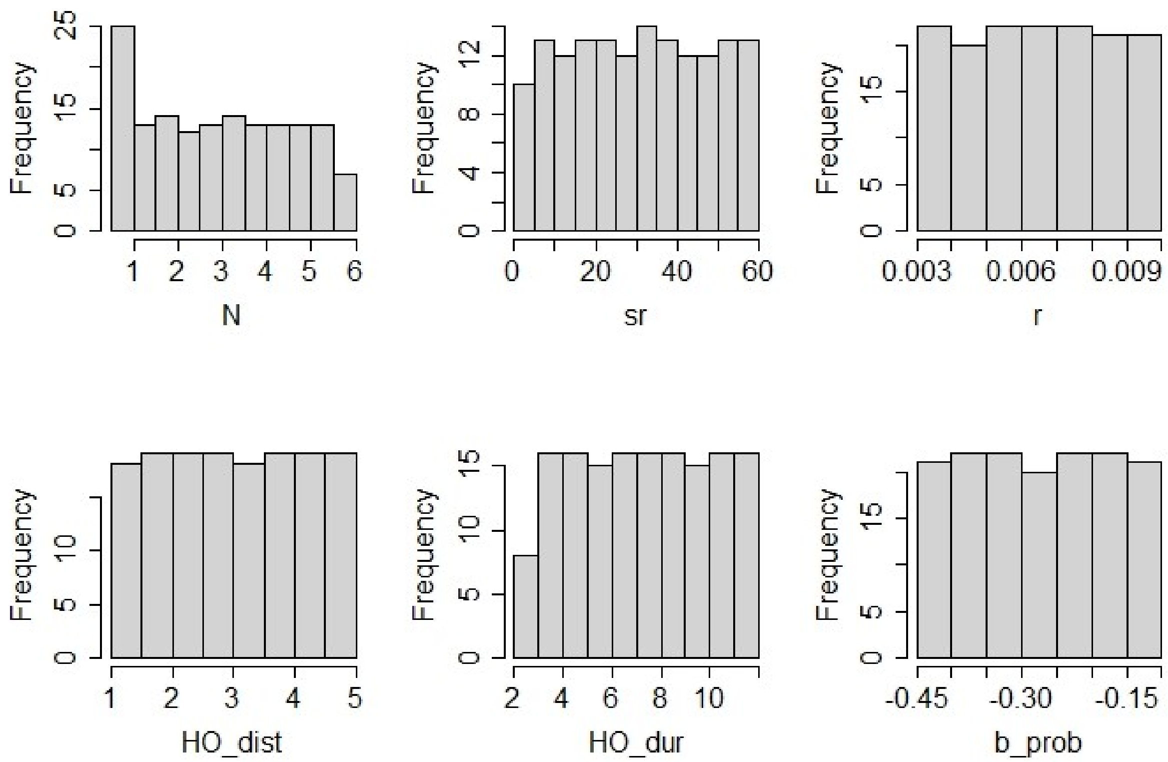


Figure 21. Frequency of six calibrated/parametrised parameters used in model parameter selection.

2.3.3 Parameter selection – pattern-oriented modelling

We run one simulation for 350 individuals for one month for each parameter combination and test it against nine observed patterns (patterns 2.1-2.9 in Table 1): 2.1) daily consumption of fish; 2.2) daily energy expenditure; 2.3) changes in proportion of blubbers over model duration; 2.4) daily proportion of time spent resting and hauling-out; 2.5) frequency distribution of number of individually visited haul-out sites; frequency distribution of 2.6) trip duration and 2.7) extent; 2.8) frequency distribution of at-sea positions with distance from the departure haul-out site; and 2.9) overlap of kernel densities.

We first calculate the fit between observed and modelled results for all nine patterns for each parameter combination using various method depending on the pattern (see below). Parameter combination (index) which had best fit for largest number of patterns is used in the final model simulations. We first present how and whether the chosen parameter combinations reproduced the observed patterns, and then described the process behind choosing the final parameter combination.

Pattern 2.1: Daily consumption of fish

Observed values show that adult harbour seals consume about 3.8 – 4.8 kg of fish per day (Härkönen and Heide-Jørgensen 1991, Kastelein et al. 2005, Sharples et al. 2009, Wilson and Hammond 2016). We retain parameter combinations which resulted in mean daily consumption within this range (Figure 22).

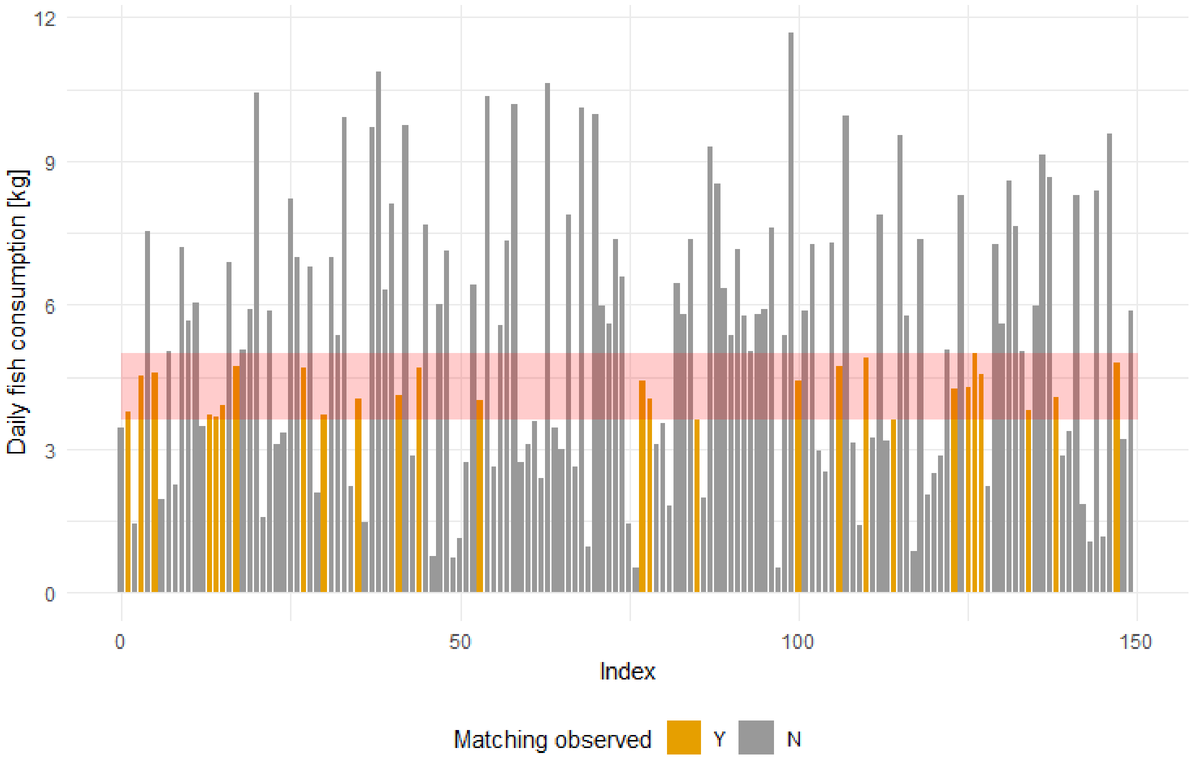


Figure 22. Daily fish consumption for 150 parameter combinations. Red horizontal polygon indicates observed range and bars are colour coded depending if they fall within this range.

Highest fish consumptions are associated with larger number of available fishes (*N*) and search rate (*sr*) (

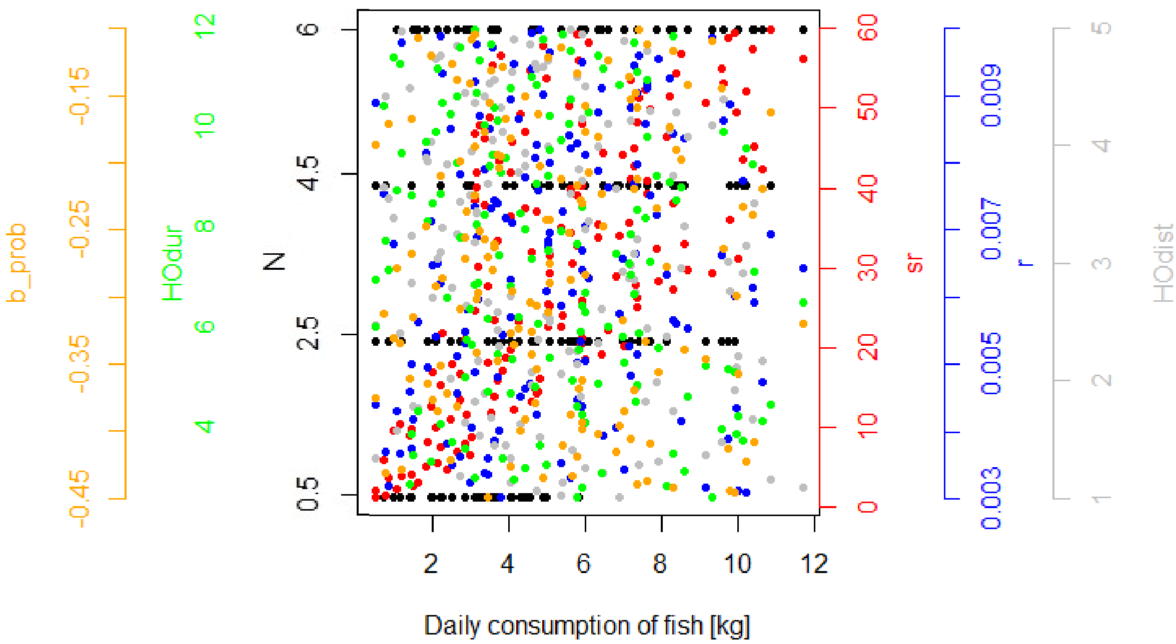


Figure 23).

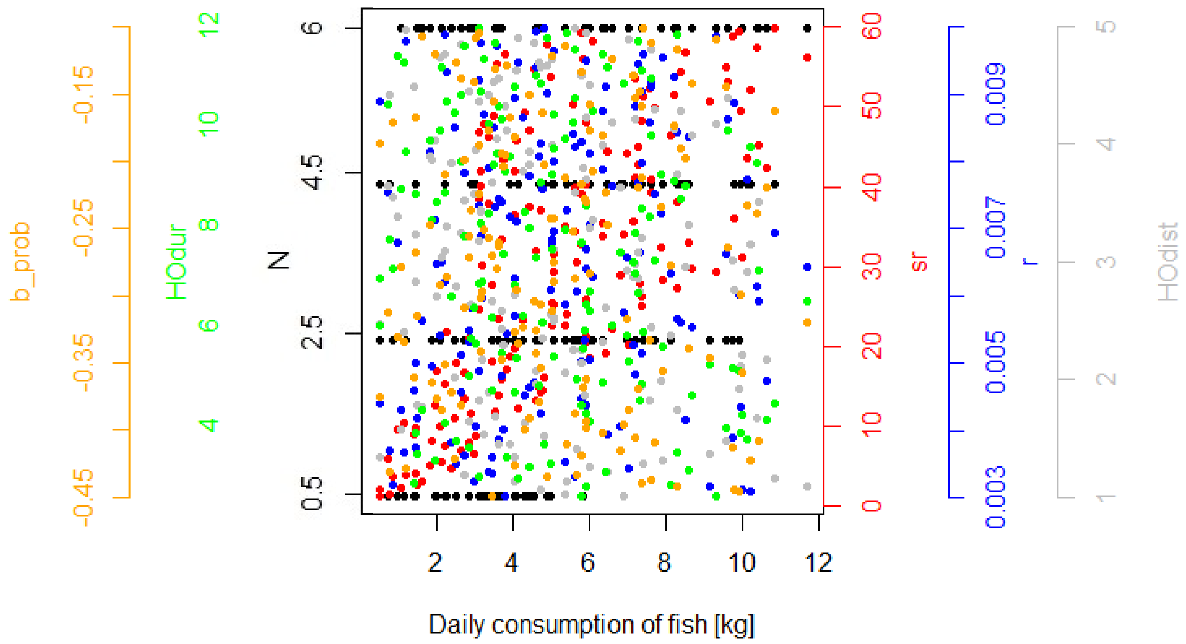


Figure 23. Parameter space for 150 parameter combinations for six parameterised parameters for daily fish consumption pattern.

Pattern 2.2: Daily energy expenditure

Daily energy expenditure is calculated as the cumulative energy expenditure at the end of the day (**CALCULATE NET ENERGY**). Indices with mean (for all *m*seals) daily values falling between observed range (14.3 - 21.43 MJ/day) are retained.

Almost all indices reproduce the observed daily energy expenditure and the five indices which don’t are very close to the lower observed value (Figure 24).

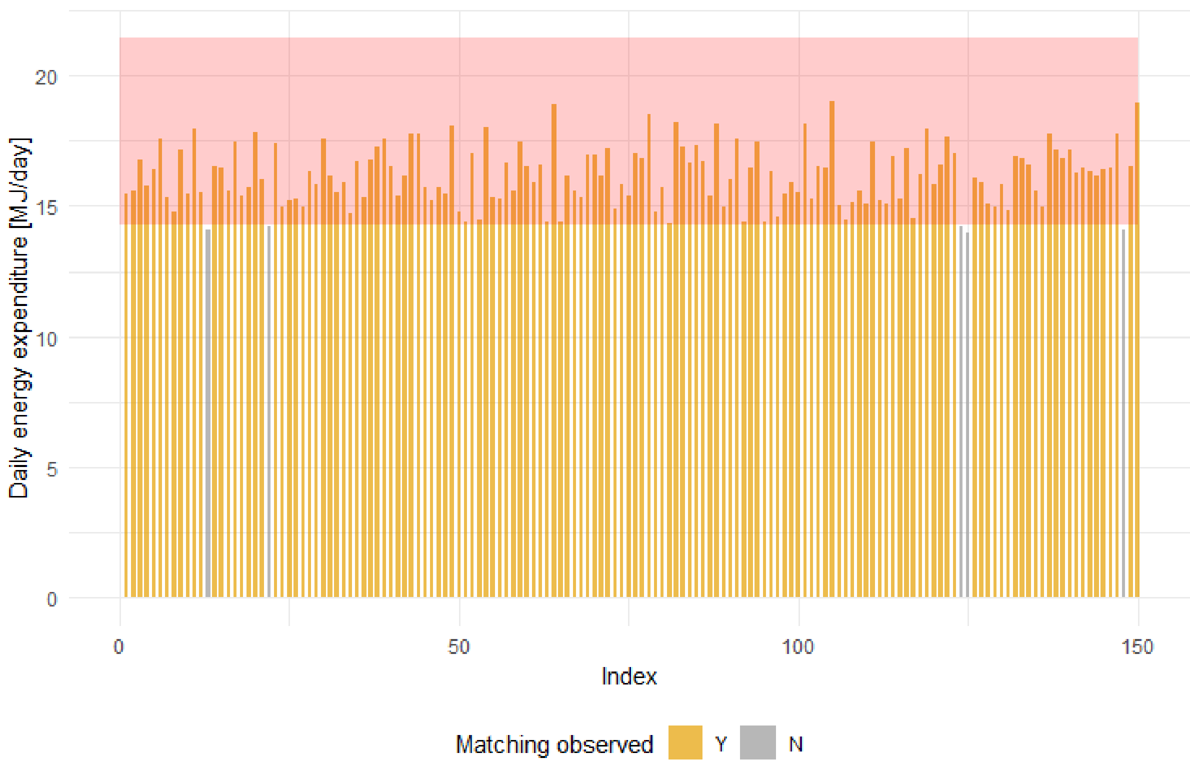


Figure 24. Daily energy expenditure [MJ/day] for 150 parameter combinations ('Index'). Red horizontal polygon shows range of observed values and colour of the bars indicates whether the model results fit within these values.

Pattern 2.3: Changes in proportion of blubber over model duration

Similarly to energy expenditure proportion of stored blubber vary seasonally for harbour seals (e.g. Renouf and Noseworthy 1991). Very few studies describe changes in blubber mass or thickness of harbour seals outside moulting and breeding season. (Renouf and Noseworthy 1991) reports that in September – October total body mass of seals remains stable or slightly increase towards the end of this season. Data from East coast of Scotland (SMRU) and the Wadden Sea (NIOZ) from harbour seals, show slight increase in total body mass during autumn, however there is a large variability in the data (

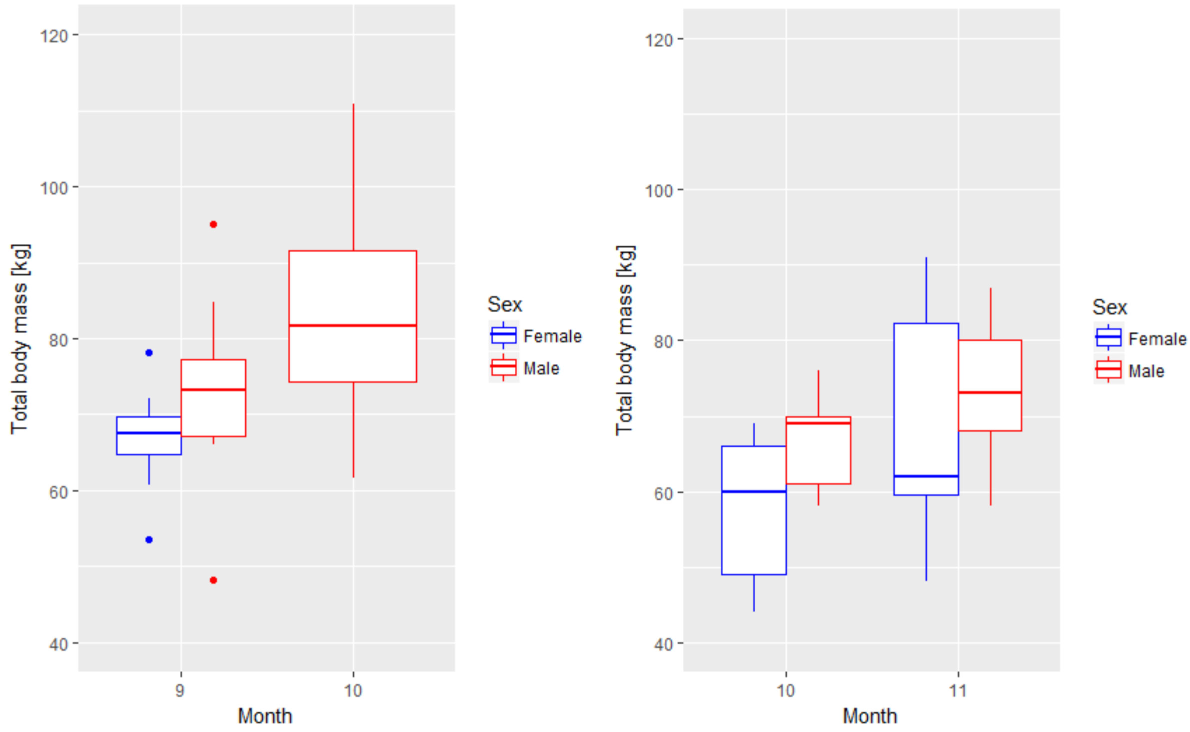


Figure 25). We, therefore, test output of the model against stable body mass/blubber content by visual comparison and by retaining results which had no more than 5% change in blubber % between the beginning and at the end of model simulation. We also calculate maximum blubber proportion. Simulations with mean values over 45% for all *m*seals are considered unrealistic (Beck et al. 2000, 2003).

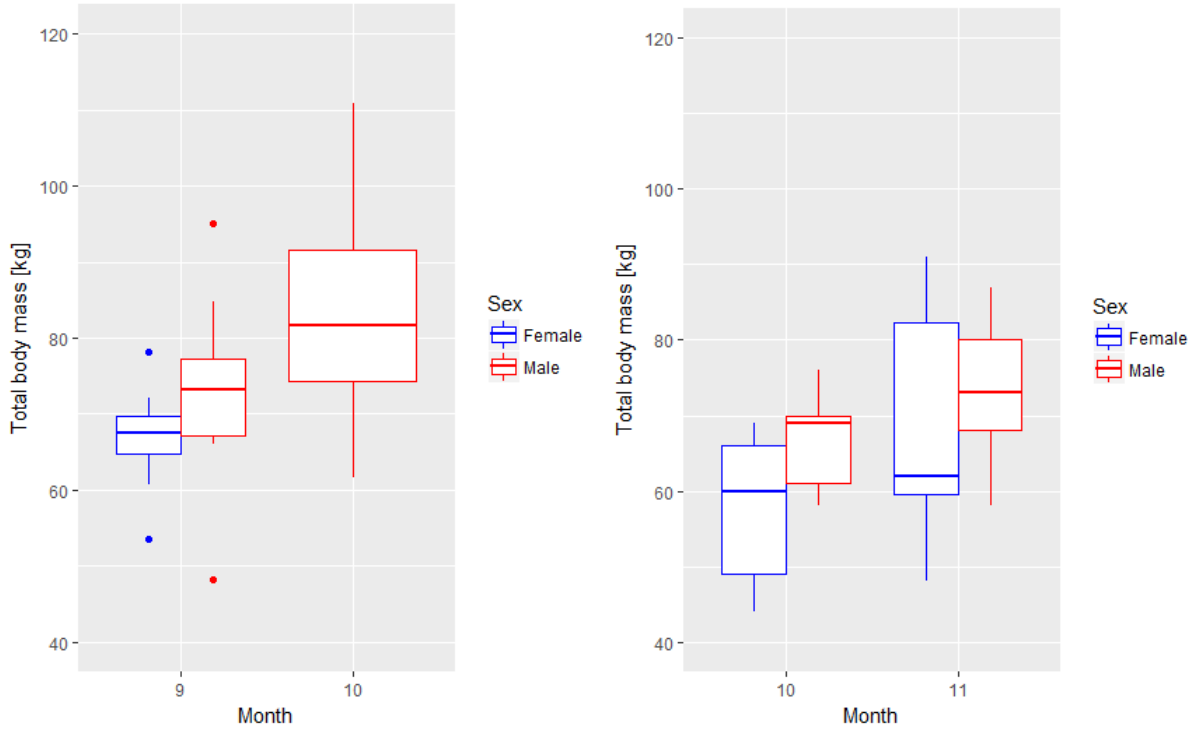


Figure 25. Changes in total body mass of adult males and females harbour seals in the autumn (October-December) from Scotland (SMRU, left panel) and the Wadden Sea (right panel).

Seventy-nine indices result in changes in blubber % between start and end of model duration within 5% (Figure 26). Parameter combination showing no changes over time, as observed, largest decrease and largest increase as shown on Figure 28.

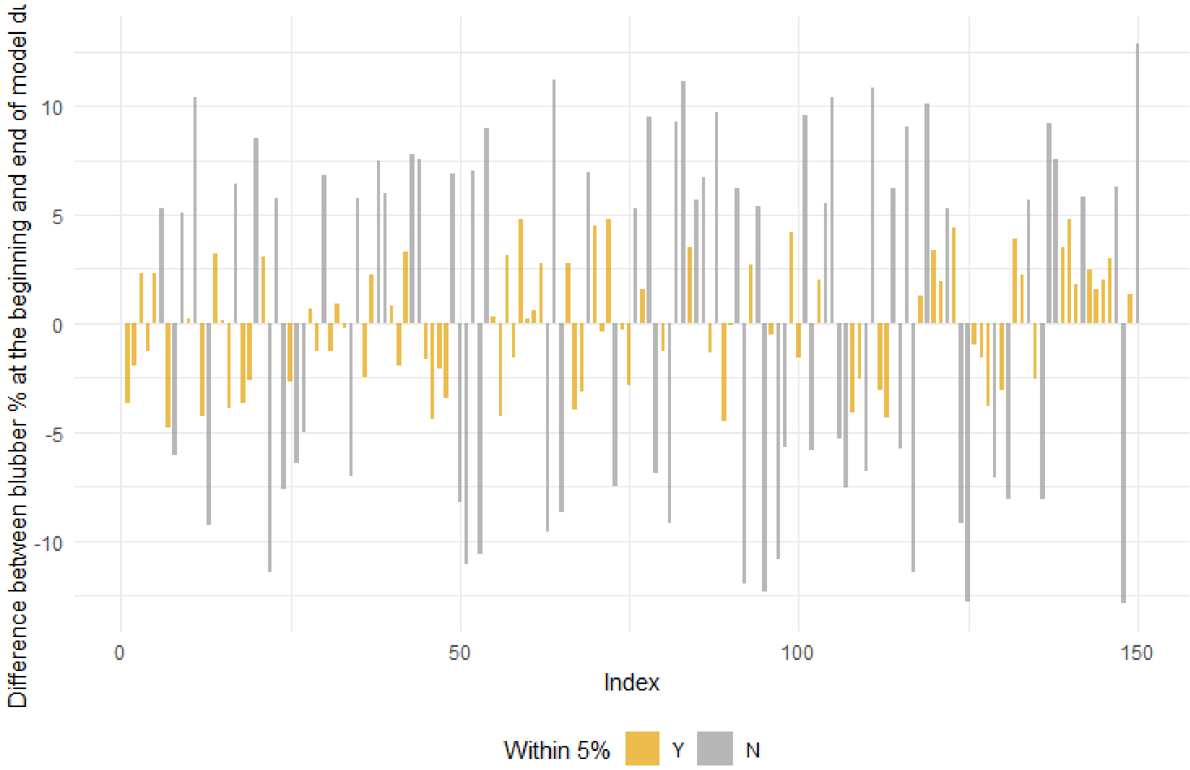


Figure 26. Difference in blubber % between start and end of model simulations for 150 combinations of parameters ('Index). Values within 5% are considered matching the observed values (colours of bars).

Search rate (*sr*) and number of available fishes per m^2 (*N*) have largest effect on changes in blubber %. Simultaneous increase in these two values results in largest increase in blubber % at the end of model duration (

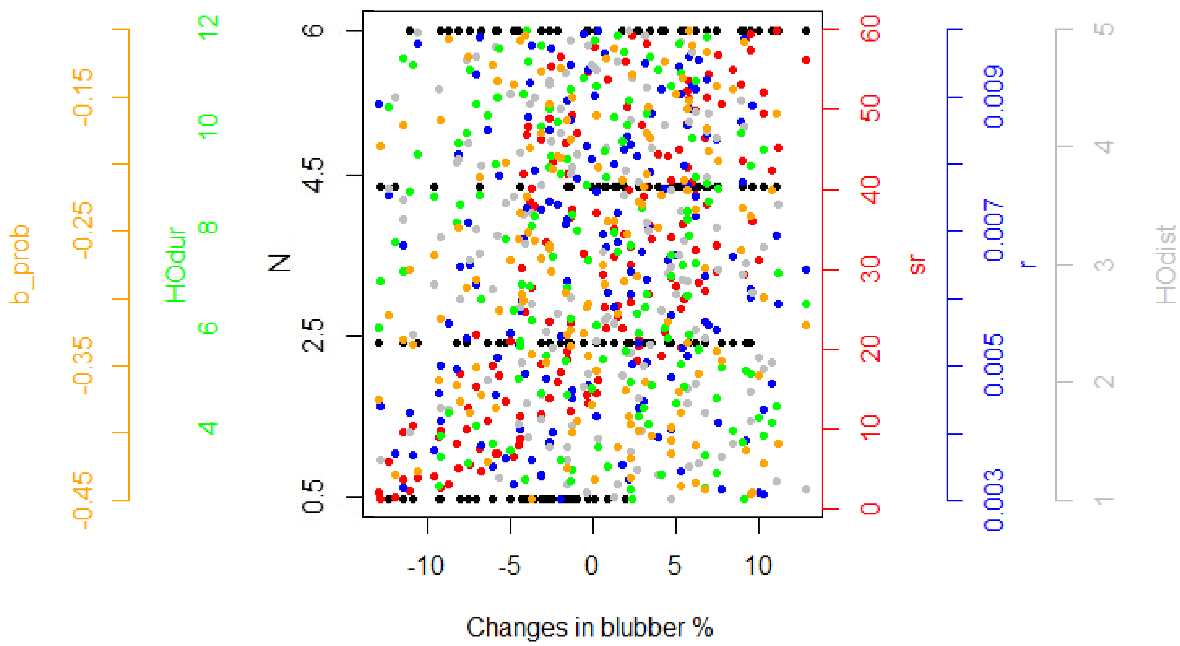


Figure 27).

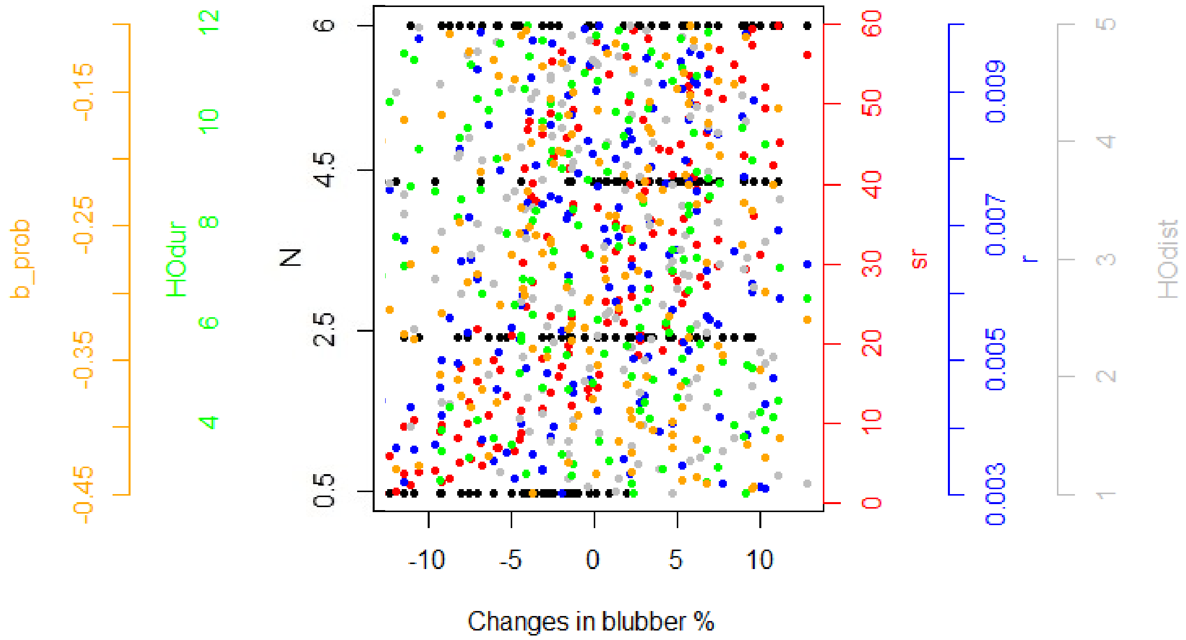


Figure 27. Parameter space for 150 parameter combinations for six parameterised parameters for changes in proportion of blubber pattern.

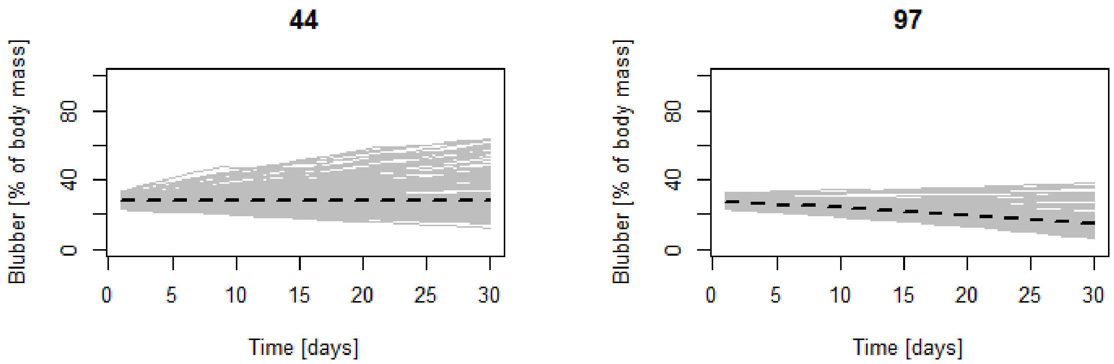
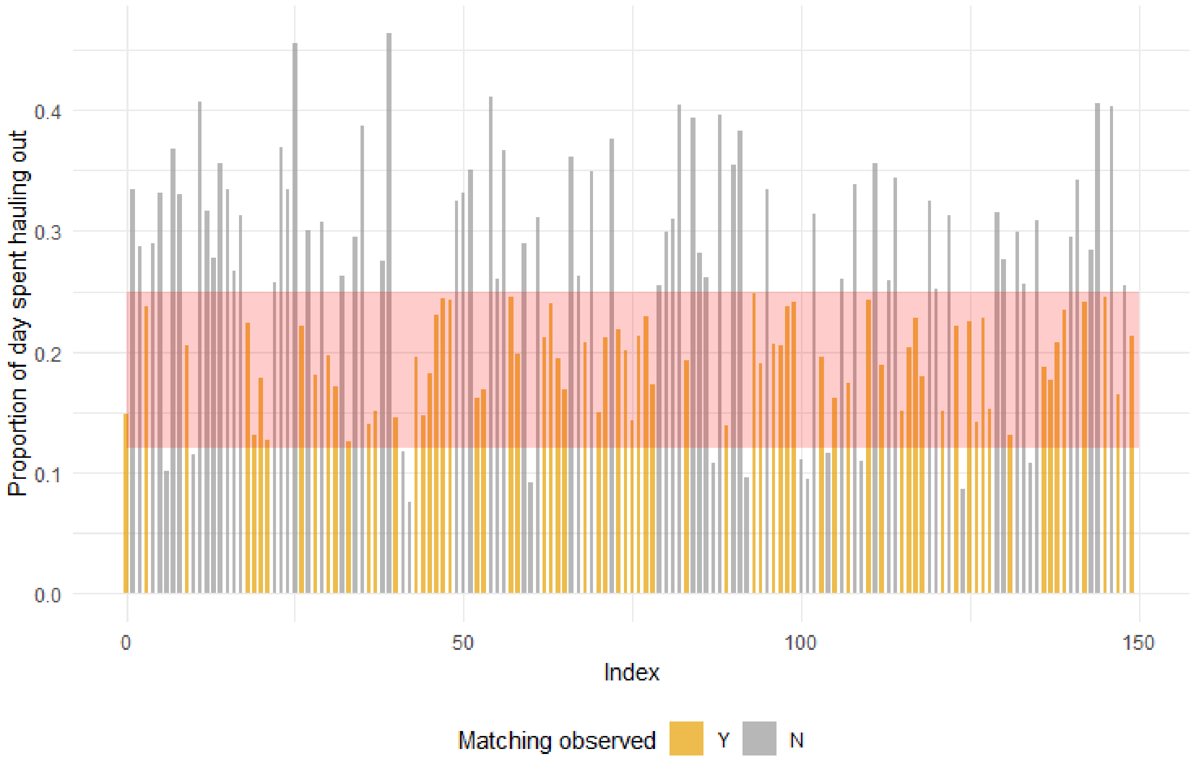


Figure 28. Changes in blubber % (y-axis) over model duration (x-axis [Days]). Dashed black line shows mean value for 350 *m*seals and grey lines depict individual changes. Parameter combination showing no changes over time, as observed (left panel), and largest decrease (right panel) examples. Numbers over each panel refer to index number – parameter combination (Table 10).

Pattern 2.4: Daily proportion of time spent resting at sea and hauling-out

We analyse the daily proportion of time *m*seals spend hauling-out and compare it to 12 – 20% reported in the literature (Cunningham et al. 2009, Ramasco et al. 2014, Russell et al. 2015). We only consider studies which report this proportion for harbour seals outside breeding and moulting season. We also compare the proportion of time *m*seals spent resting at sea and compare it to 6-28% reported in the literature (McConnell et al. 1999, Vincent et al. 2010, Mcclintock et al. 2013, Ramasco et al. 2014, Mikkelsen et al. 2019). We retain parameter combinations which fulfil these two criteria.

Seventy and eighty-eight parameter combinations result in proportion of time spent hauling-out and resting at sea within the observed values respectively (Figure 29). Forty indices resulted in simultaneous fit for these two activities.



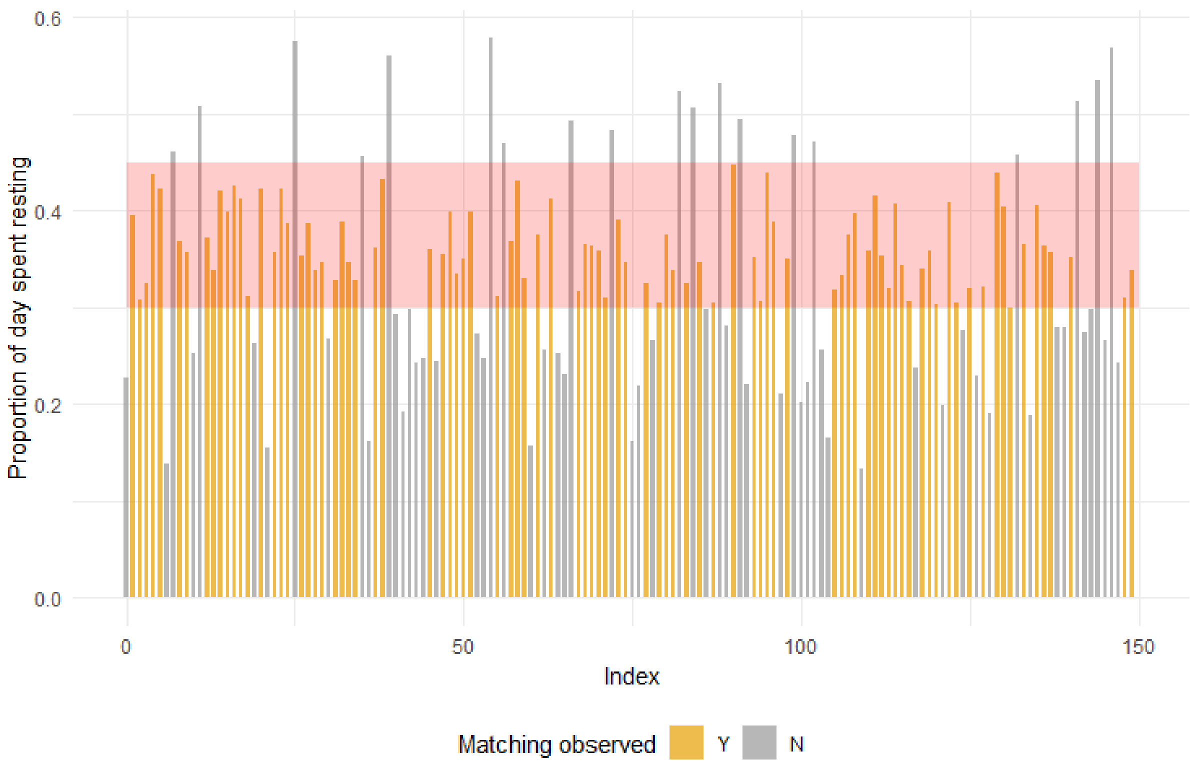
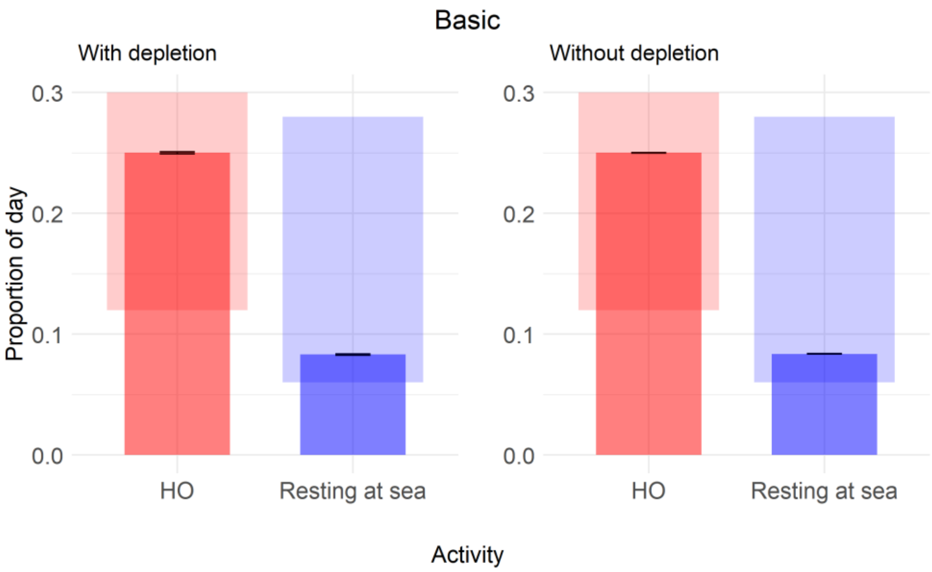


Figure 29. Proportion of day spent hauling-out (upper panel) and resting (haul-out + resting at sea) (lower panel) for 150 parameter combinations (‘index’). Red horizontal polygons show the range of observed values for these two activities. The colour of bars shows whether a given index reproduces the observed values.

The proportion of day spent hauling out is, not surprisingly, dependent on mean haul-out duration parameter (HO_{dur}), whereas proportion of day spent resting at sea is additionally affected by search rate (*sr*). High proportion of day spent hauling-out and resting is also never associated with low *b* parameter (Figure 31, Figure 18). The smaller *b*, parameter which defined probability of hauling-out with the three parameters (time since last haul-out, blubber % and distance to haul-out site, Figure 18) the shorter haul-out duration and the longer resting at sea (Figure 30).


Basic
With depletion
Without depletion
Proportion of day
0.0
0.1
0.2
0.3
HO
Resting at sea
Activity

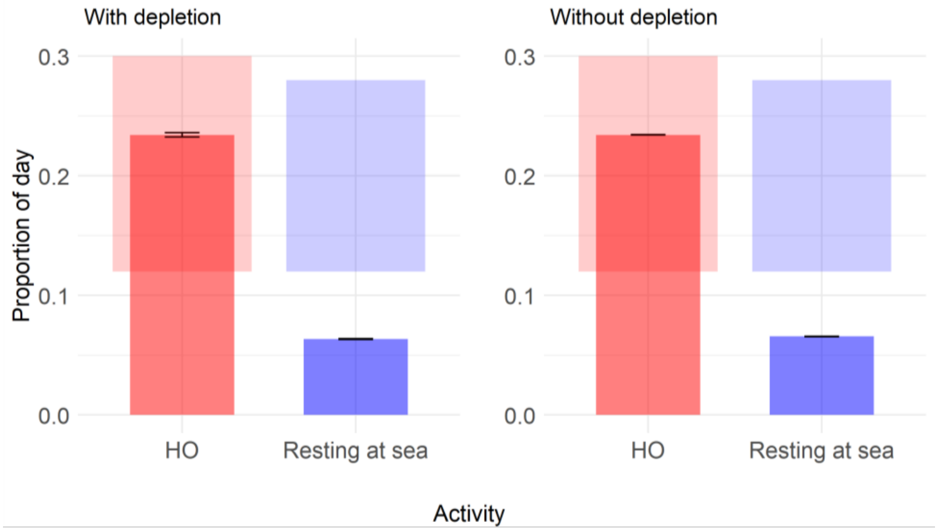

With depletion
Without depletion
Proportion of day
0.0
0.1
0.2
0.3
HO
Resting at sea
Activity

Figure 30. Comparison between daily activity budget of seals with b= - 0.10 (upper) and b = - 0.34 (lower) and the remaining parameters as in the final model.

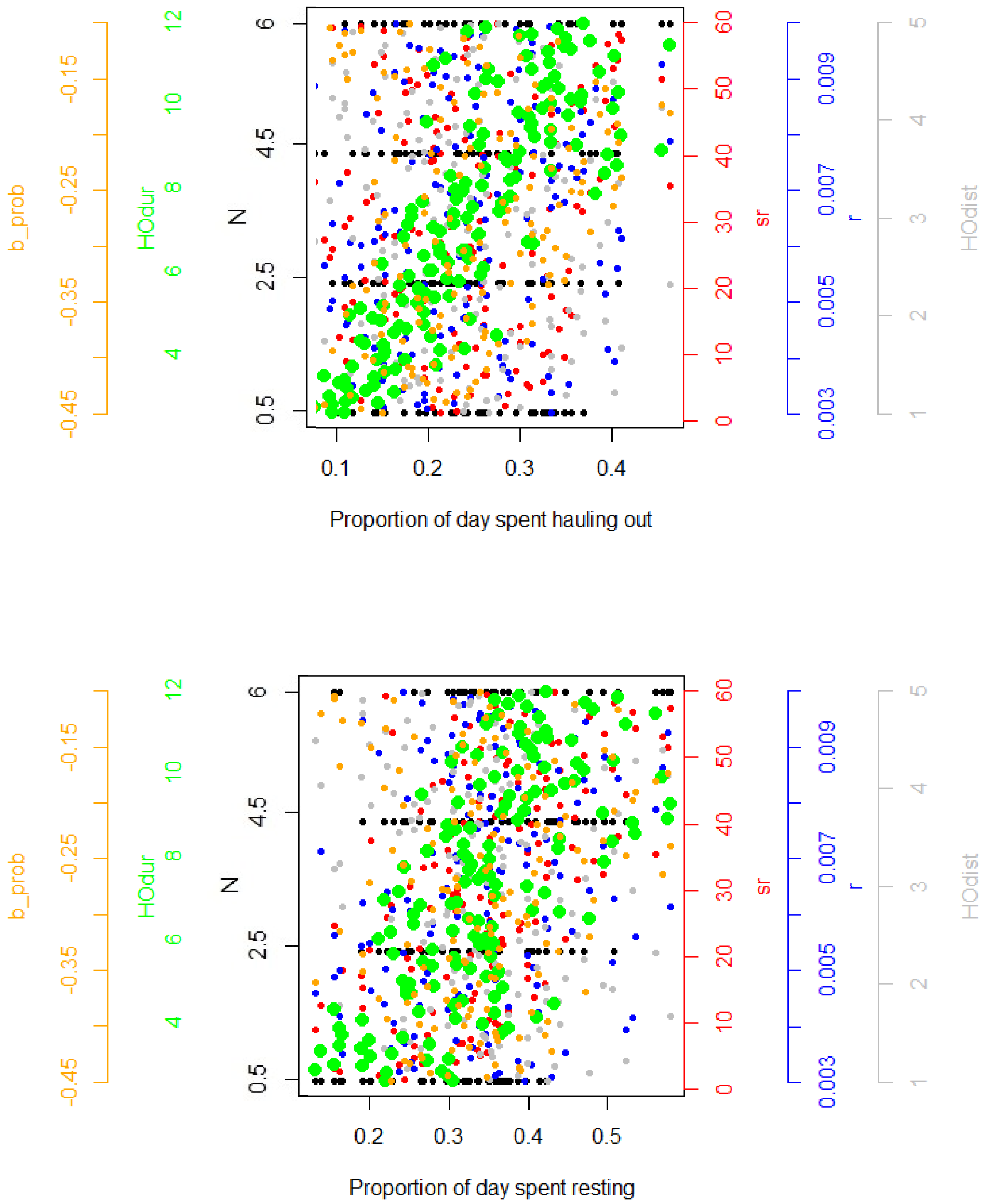


Figure 31. Parameter space for 150 parameter combinations for proportion of day spend hauling-out (upper panel) and resting (lower panel). Enlarged green points highlight the results discussed in the above paragraph.

Non-digestive reasons are the main reasons behind hauling-out for majority of parameter combinations (

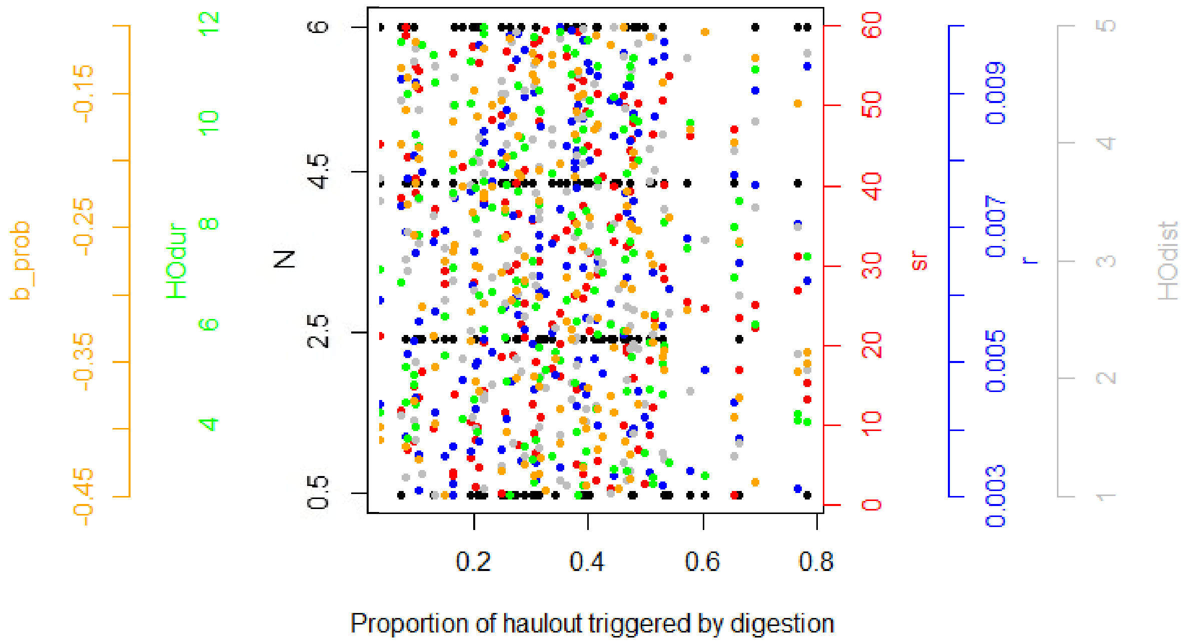
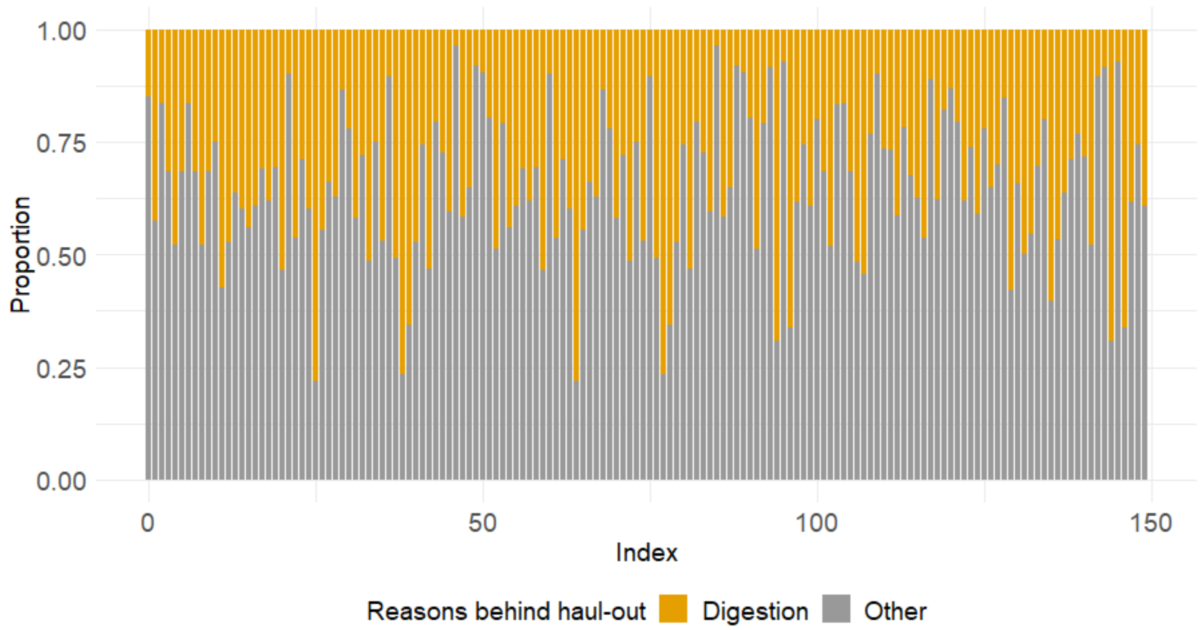


Figure 32). There is no clear pattern in parameter space which would define the reasons behind hauling-out (Figure 33).



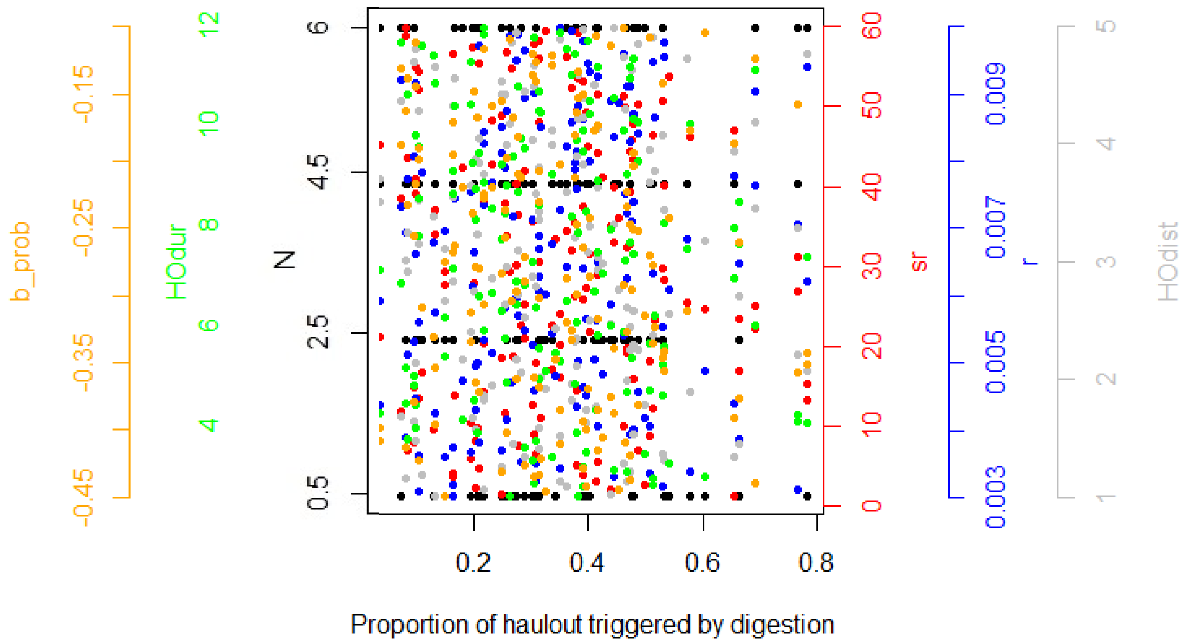


Figure 32. Proportion of ‘reasons’ behind haul-out for each parameter combination (index). ‘Other’ refers to non-digestive reasons.

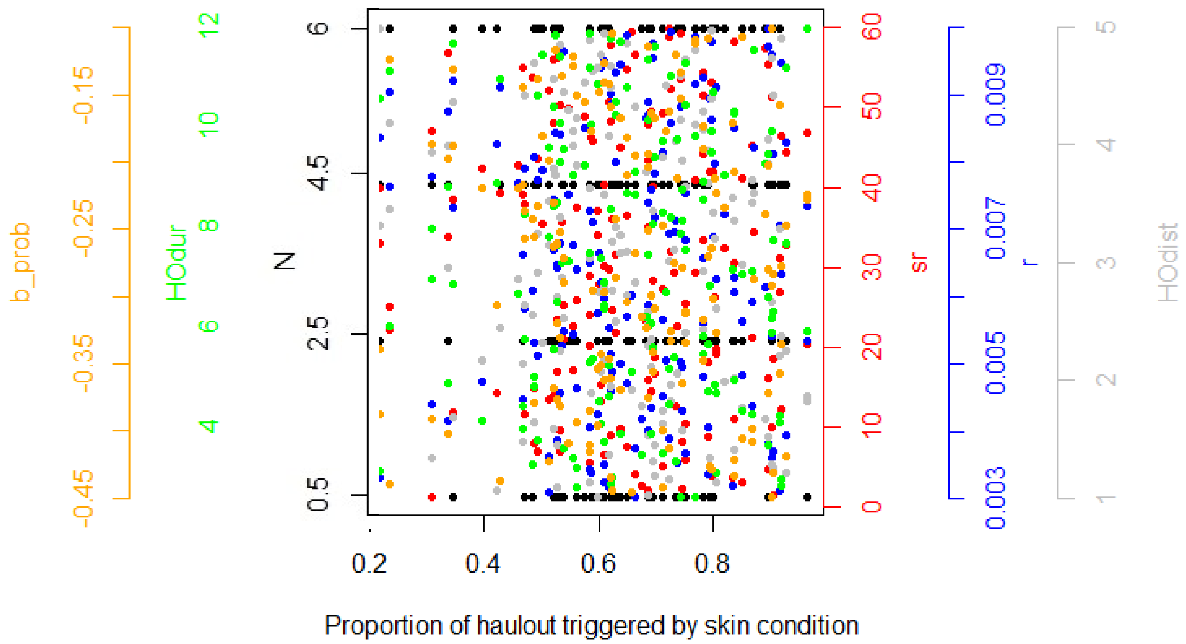


Figure 33. Parameter space for 150 parameter combinations for six parameters used in parameter selection for proportion of haul-out events triggered by digestion (upper panel) and non-digestive reasons (lower panel).

Pattern 2.5: Frequency distribution of number of individually visited haul-out sites

The frequency of the observed number of individually visited haul-out sites clustered within 5x5 km squares (as the modelled sites) is based on data from 14 individuals tagged at the modelled site (East Coast of Scotland, Table 1) between 2008-2018. To compare distribution of modelled and observed values, we first calculate proportion of observed and modelled individually visited sites in bins of 2. We then calculate sum of SAE for each bin and then identify best 15% (see section 2.2.2, Eq. 17).

Most parameter combinations result in low number (<= 2) of haul-out sites visited by *m*seals, as also observed, and 23 combinations are categorised as best 15% (Figure 34).

Figure 35 shows frequency distribution of number of haul-out sites for the parameter combinations with lowest (best match) and highest SAE (worse match). The 'worse match' represents only one case (index 93), all the remaining parameter combination resulted in low number of visited sites as also observed. Number of haul-out sites is, therefore, not considered as a strong pattern (see section 0 for further discussion) in the parameter selection, as all parameter combinations result in a good match.

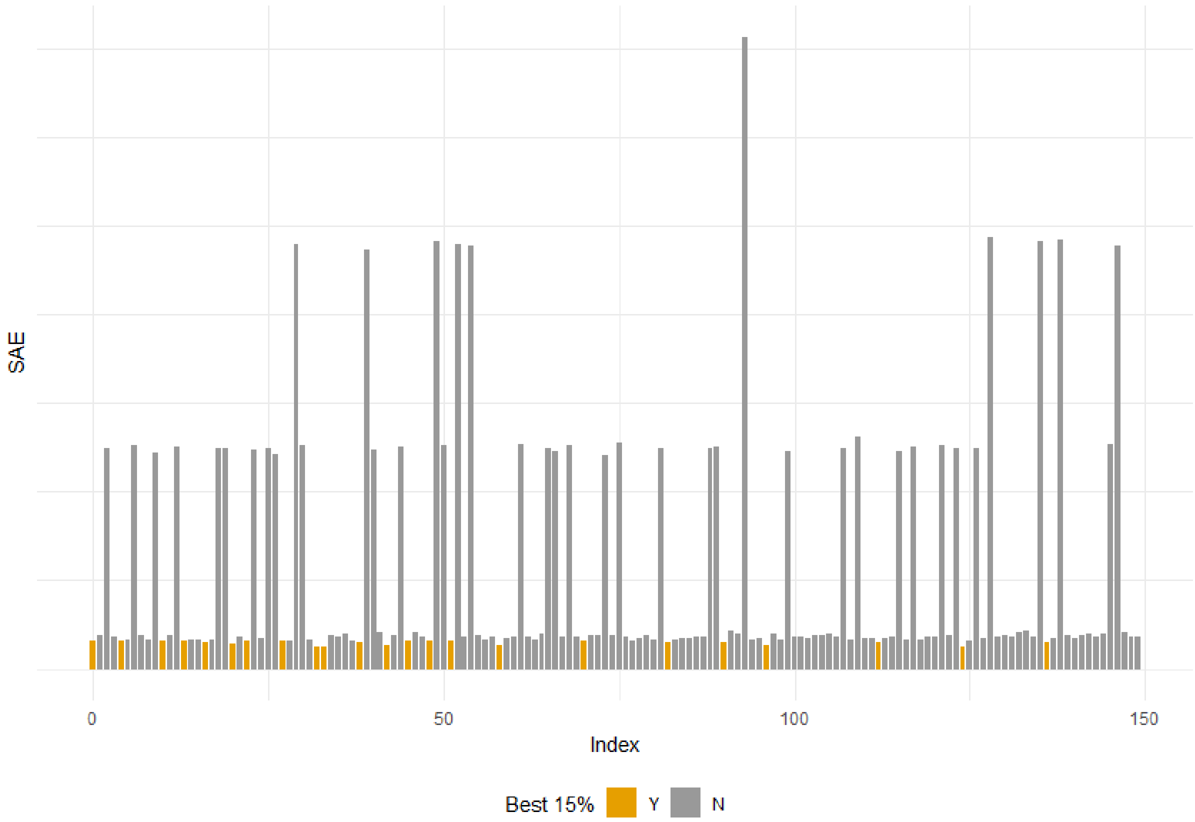


Figure 34. Standardised absolute error (SAE) of 150 combinations of parameters (index) for frequency distribution of number of individually visited haul-out sites. Values of SAEs strongly depend on the unit of the values for which the error was calculated and has no meaning, hence no values indicated on y-axis.

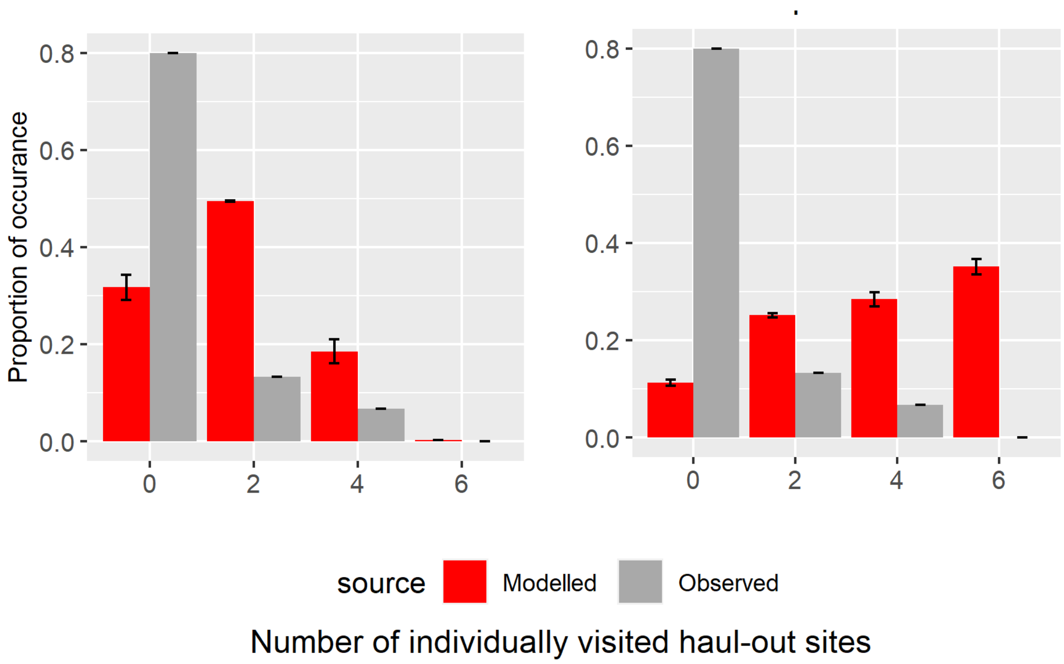


Figure 35. Distribution of individually visited haul-out sites for modelled (red) and observed (grey) seals. The pattern for parameter combination with lowest (best match, left panel, index 32) and highest (worse match, right panel, index 93) SAE. Vertical line show means for each data set. Numbers over each panel refer to index number (Table 10).

No clear pattern in the relationship between parameter space and SAE of number of observed haul-out sites is observed (Figure 35, Figure 36).

Figure 36

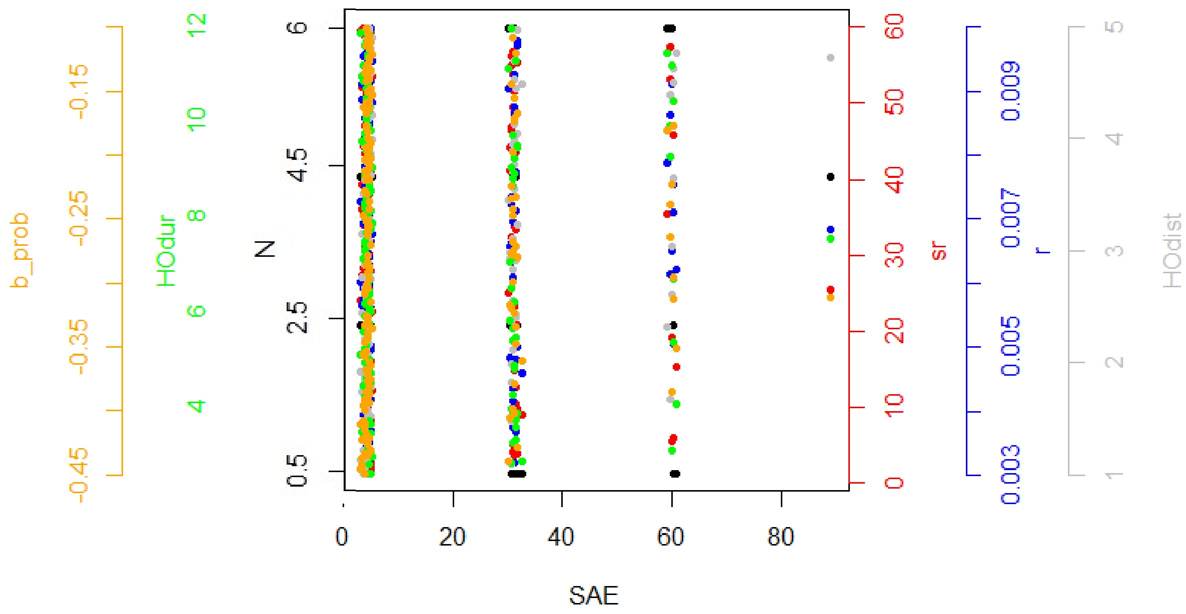


Figure 36. Parameter space for 150 parameter combinations for six parameterised parameters for frequency distribution of number of visited haul-out sites pattern.

Patterns 2.6: Frequency distribution of trip duration and 2.7: trip extent

The observed extent and duration of foraging trips differs between sexes, season and region. For harbour seals in Scotland, most trips are below 12 h (Thompson and Miller 1990, Cunningham et al. 2009), with mean duration around 30 – 60 h (Thompson et al. 1998, Cunningham et al. 2009, Sharples et al. 2012) and maximum duration of 12 days (Thompson et al. 1998), although the study does not indicate if this particular trip was during breeding season, which might have influenced its length.

However, the definition of a foraging trip differs between studies; some studies define trips as movement between two consecutives on-shore haul-out events, and others define them as trips over a threshold duration to exclude near-shore resting periods. We define a foraging trip as *m*seals' movement between two consecutive haul-out events over a period exceeding 6h following the definition by (Sharples et al. 2012). Plotting all observed trips (not only > 6h, based on tracking data of 62 individuals (see details in section 2.2 and Table 1), trip duration against their extent reveals that trips < 6h are always very close to the departure haul-out site, and are most likely resting close to shore. The average trip duration for the observed seals based on the same telemetry dataset is 28h (sd = 35h), with majority of trips < 20h. Haul-out duration is not included in the trip duration. Accessibility of haul-out sites along Scottish coastline is often influenced by tides. In approximate terms, we assume that a haul-out is usually inaccessible in the interval between mid-flood and mid-ebb tides (approximately 6h). Ignoring the actual complexity of local tidal profiles, we choose a 6h threshold that reflects the time that longer haul-outs would be interrupted by tide-driven inaccessibility. We thus use this value to exclude short ‘trips’ that were forced through tidal inaccessibility in the observed data.

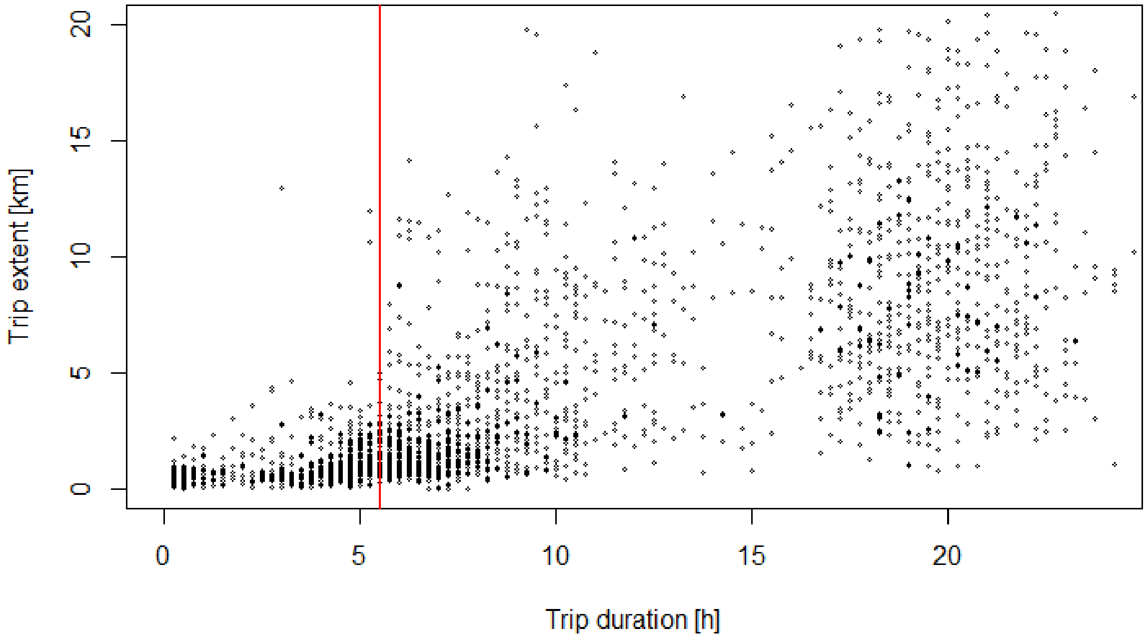
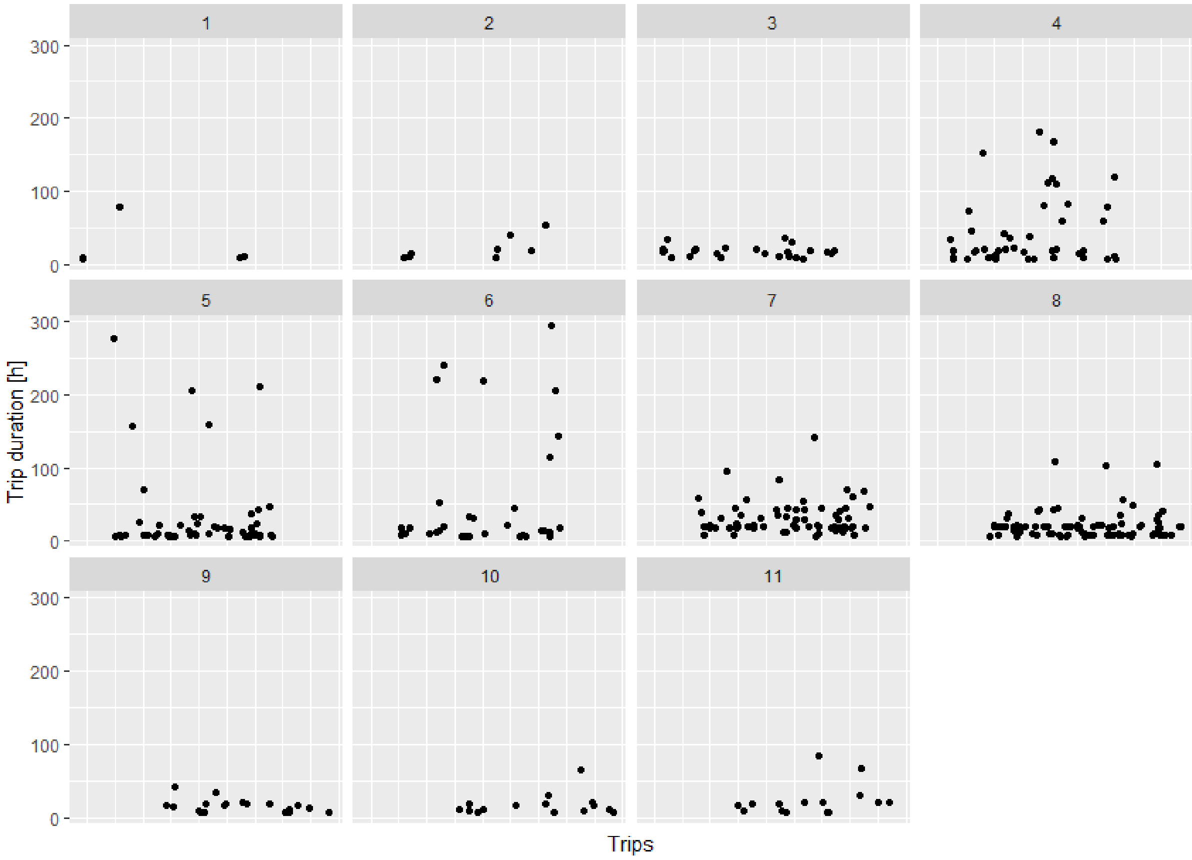


Figure 37. Observed relationship between trip durations and their extent based on telemetry data from 62 seals off East coast of Scotland and Moray Firth. Vertical red line indicates a 6h threshold defining foraging trip.

Harbour seals are coastal phocids and their trip extent is usually within 40 km of the coast (Thompson et al. 1998, Cunningham et al. 2009, Sharples et al. 2012).

The study by (Sharples et al. 2012) shows that there are large inter-region variations in trip duration and extent along the Scottish coastline. We therefore, compared the results of model simulations to data from seals tagged at the modelled study site and another east coast site in Moray Firth using the same individuals as for calculation of frequency of trip durations. Trip extent is calculated as maximum Euclidean distance (in straight line) from the departure haul-out site and *m*seals’ positions during this trip. We only calculated trip extent of trips > 6h.

The individuals observed at the study site, seals tagged around Firth of Forth area and St Andrews (Table 1, Figure 2) show multiple short foraging trips, interchanged by longer and further away trips (



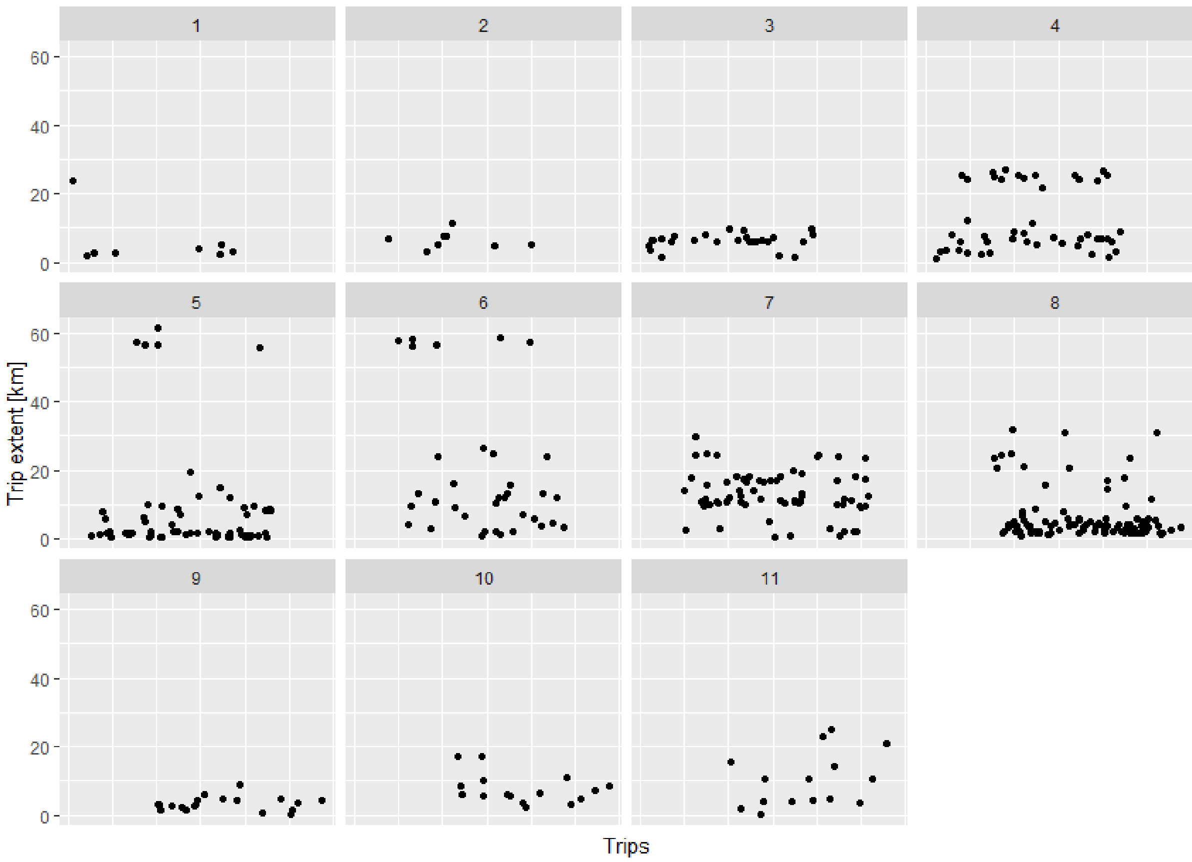
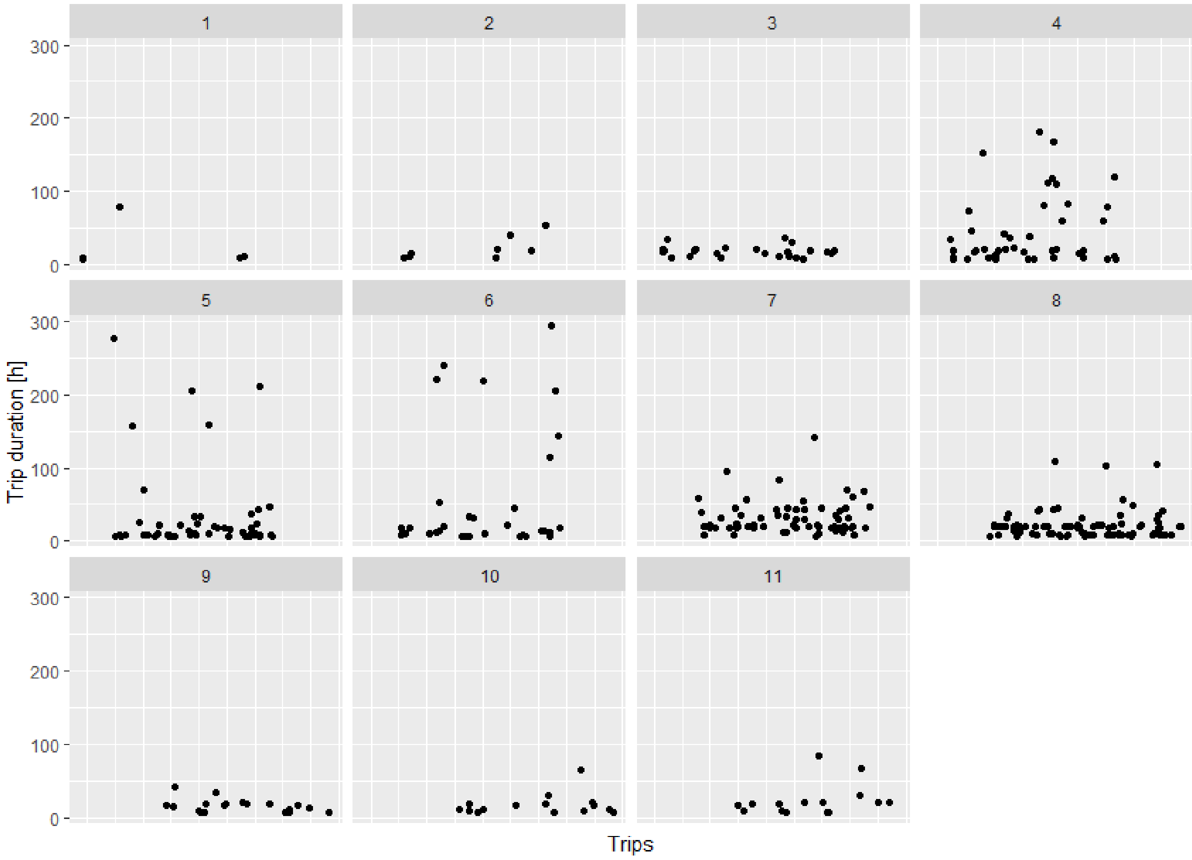


Figure 38), and we, therefore, compare frequency distribution of trip duration and extent and not just mean and/or range. We follow the same method to compare observed and modelled patterns as for ‘Number of individually visited haul-out sites’.



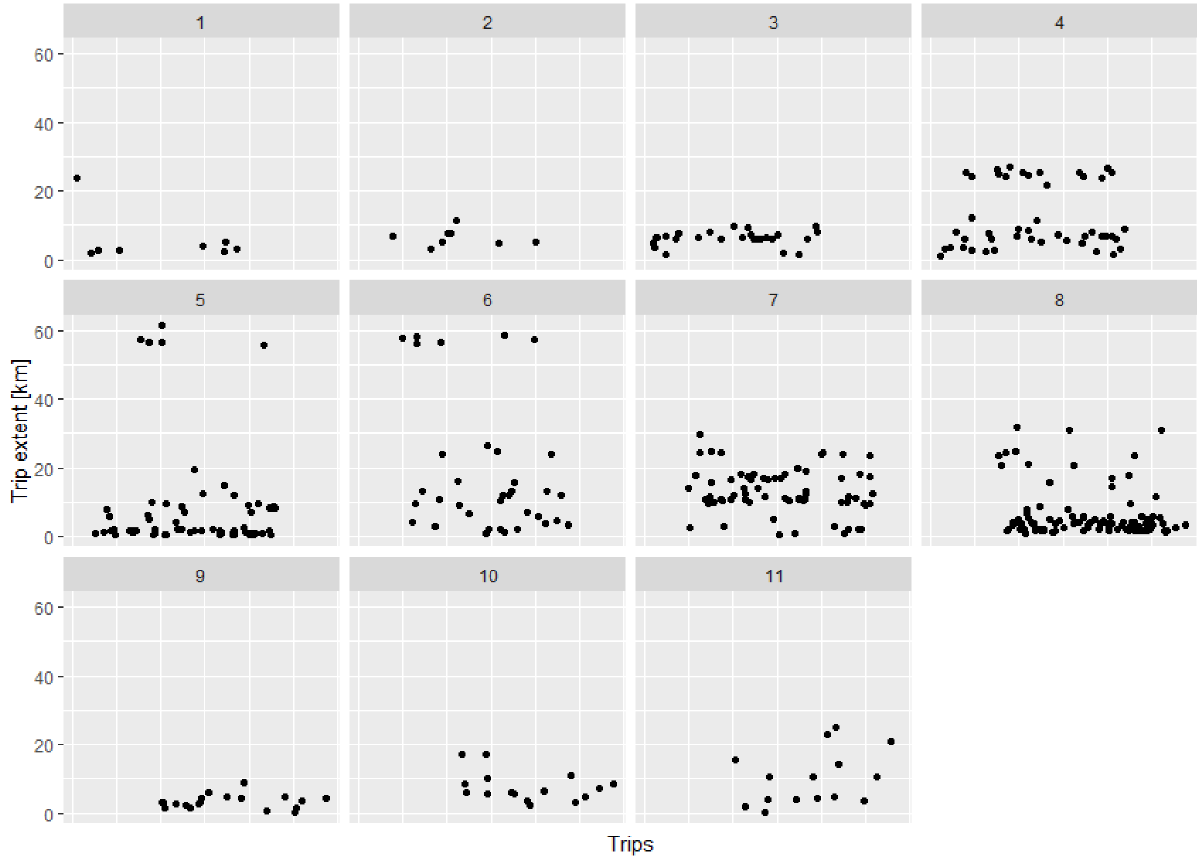


Figure 38. Trip duration (top) and extent (bottom) of consecutive trips for 11 individuals tagged off the East Coast of Scotland (Firth of Forth area).

None of the parameter combinations reproduce the same distribution of trip duration as observed: all combinations underestimate number of short trips. To test whether this mismatch is related to our definition of foraging trips as >6h, we present the results for modelled trips >6h and all trips (>0h). The mismatch remains the same regardless whether modelled trips are >6h (

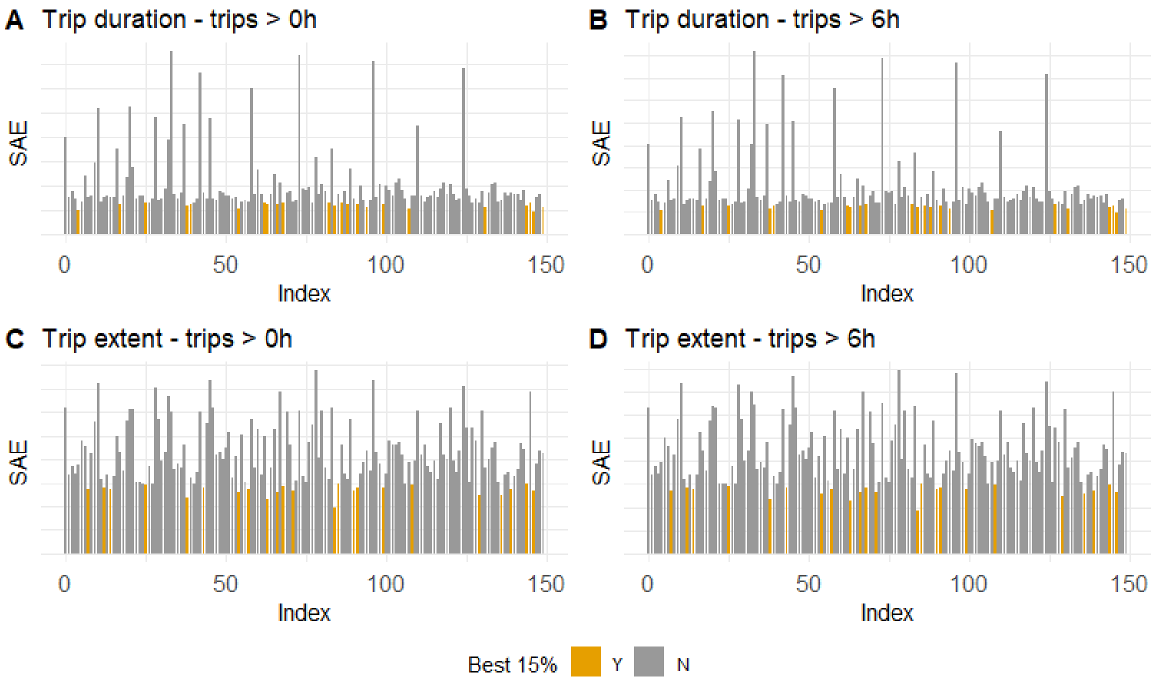


Figure 39,

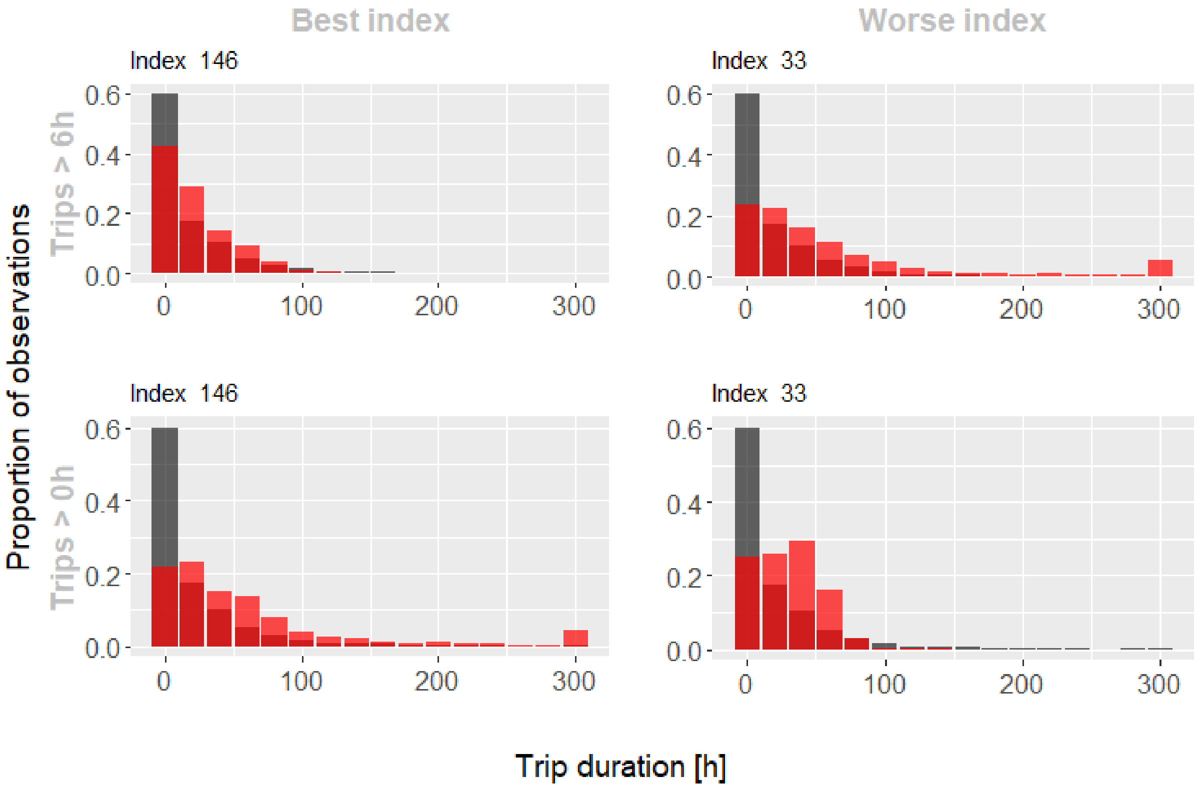


Figure 40). However, both best and worse match reproduce the frequency within the observed range, although below the observed mean.

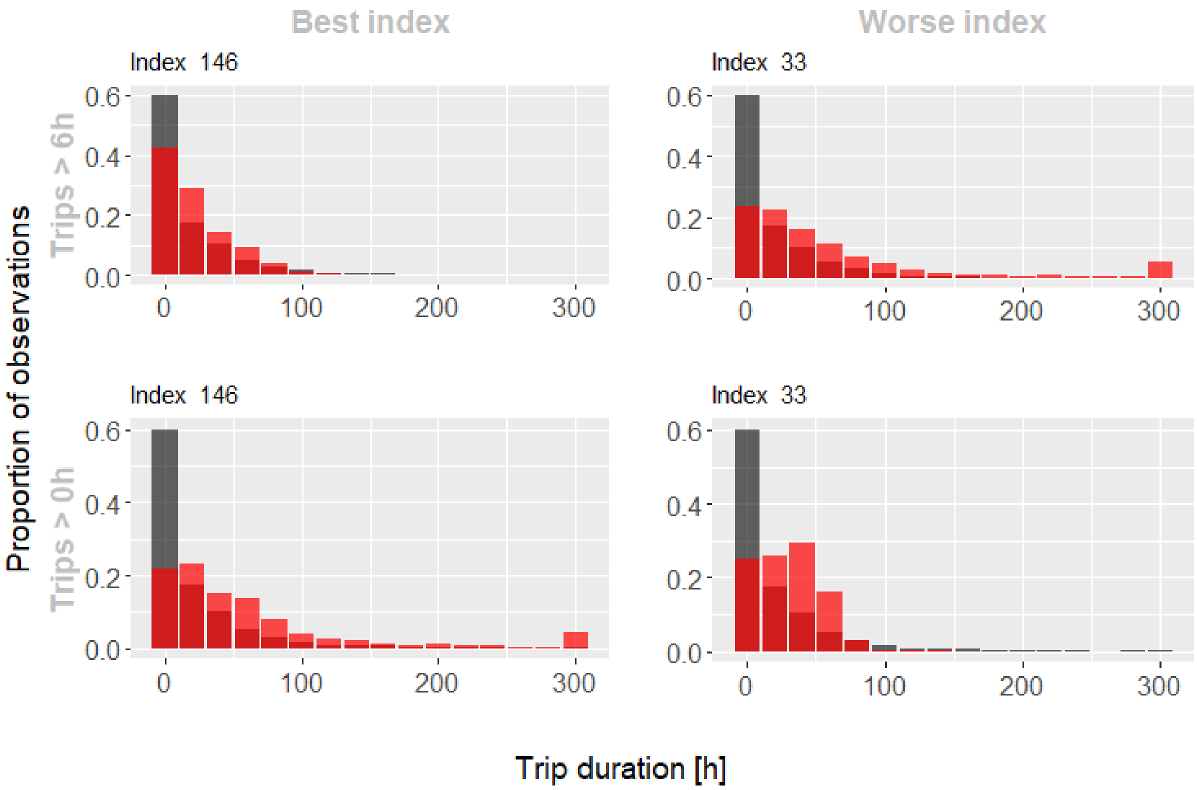


Figure 40 shows parameter combinations with lowest (best fit) and highest (worse fit) SAE.

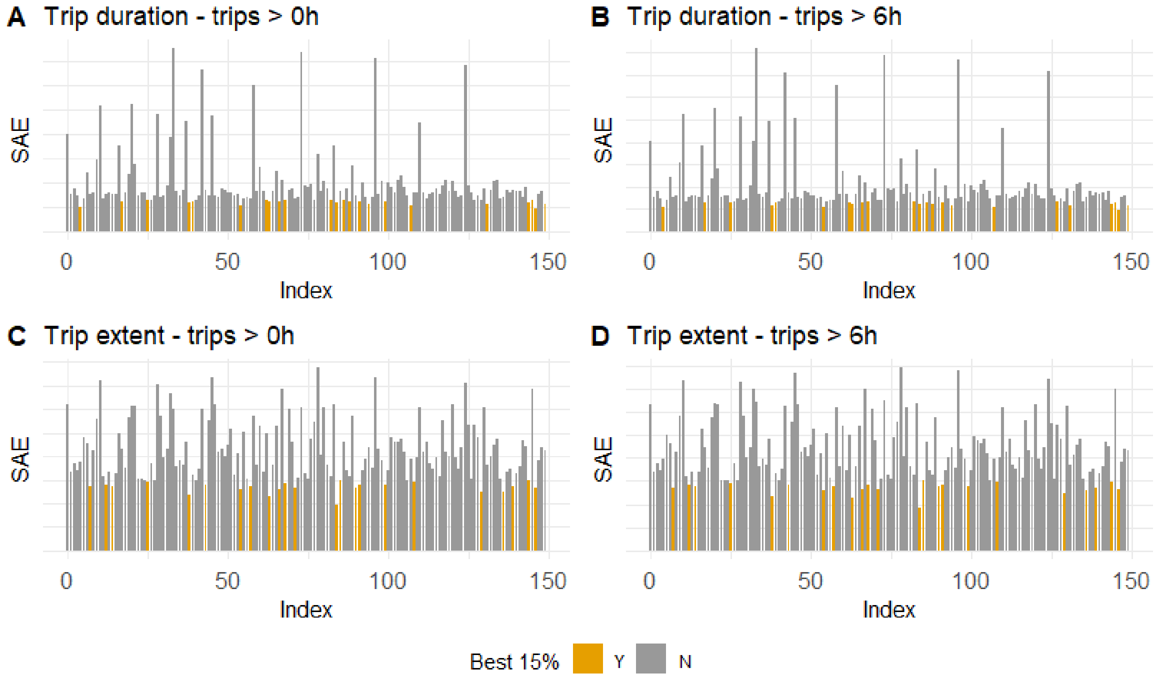


Figure 39. Standardised absolute error (SAE) of 150 combinations of parameters (index) for trip duration (A-B, upper panel) and extent (C-D, lower panel) with 15% of best matches marked in yellow. Left panels (A, C) show the comparison based on all modelled trips (>0h) and observed trips >6h and right panels (B, D) show the comparison based on both observed and modelled trips >6h. Values of SAEs strongly depend on the unit of the values for which the error was calculated and has no meaning, hence values indicated on y-axis.

Figure 40. Frequency distribution of trip duration for modelled (red) and observed (grey) pattern for indices with best (lowest SAE, left panel) and worse (highest SAE, right panel)

match. Upper panels show the comparison based on modelled and observed trips >6h and lower panels show the comparison based on observed trips >6h and all modelled trips considered (trips > 0h). Numbers over each panel refer to index number (parameter combinations) (Table 10).Most parameter combinations show comparable distribution of trip extents as observed (

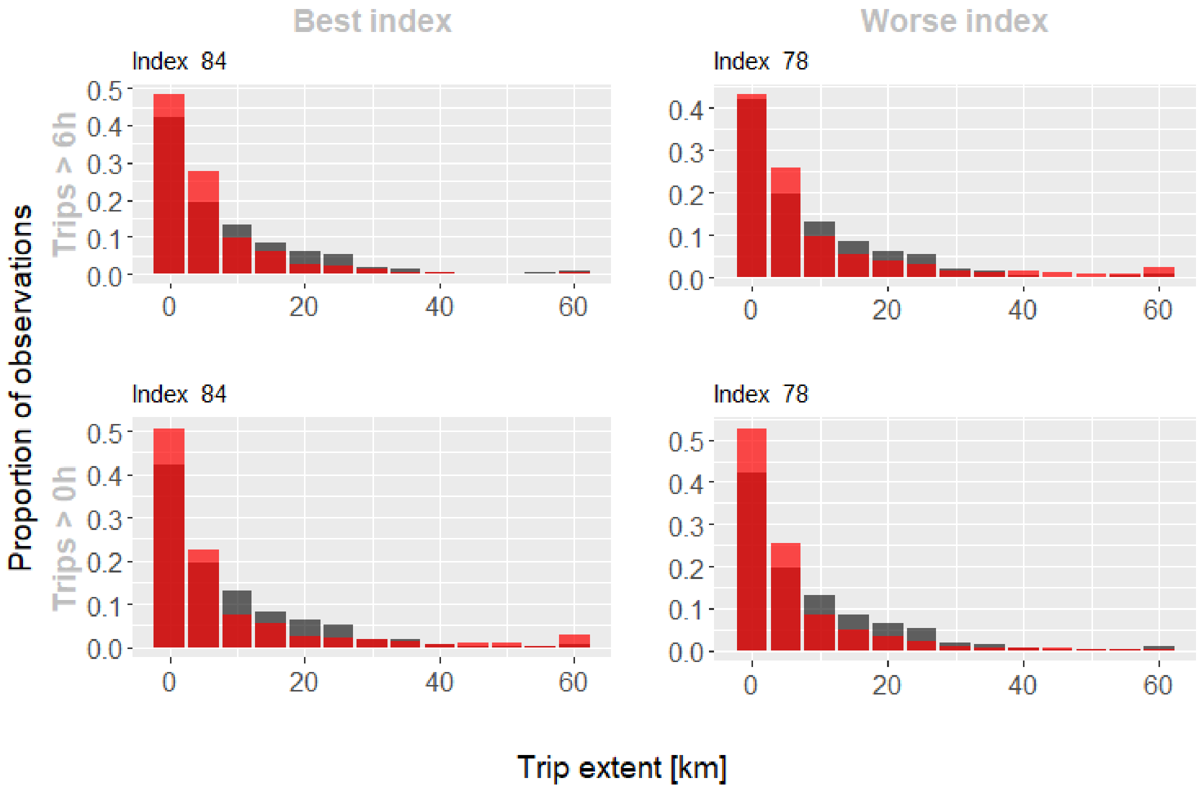


Figure 41), and this pattern, similarly to number of individually visited haul-out sites, is not considered as 'strong' pattern (see section 0).

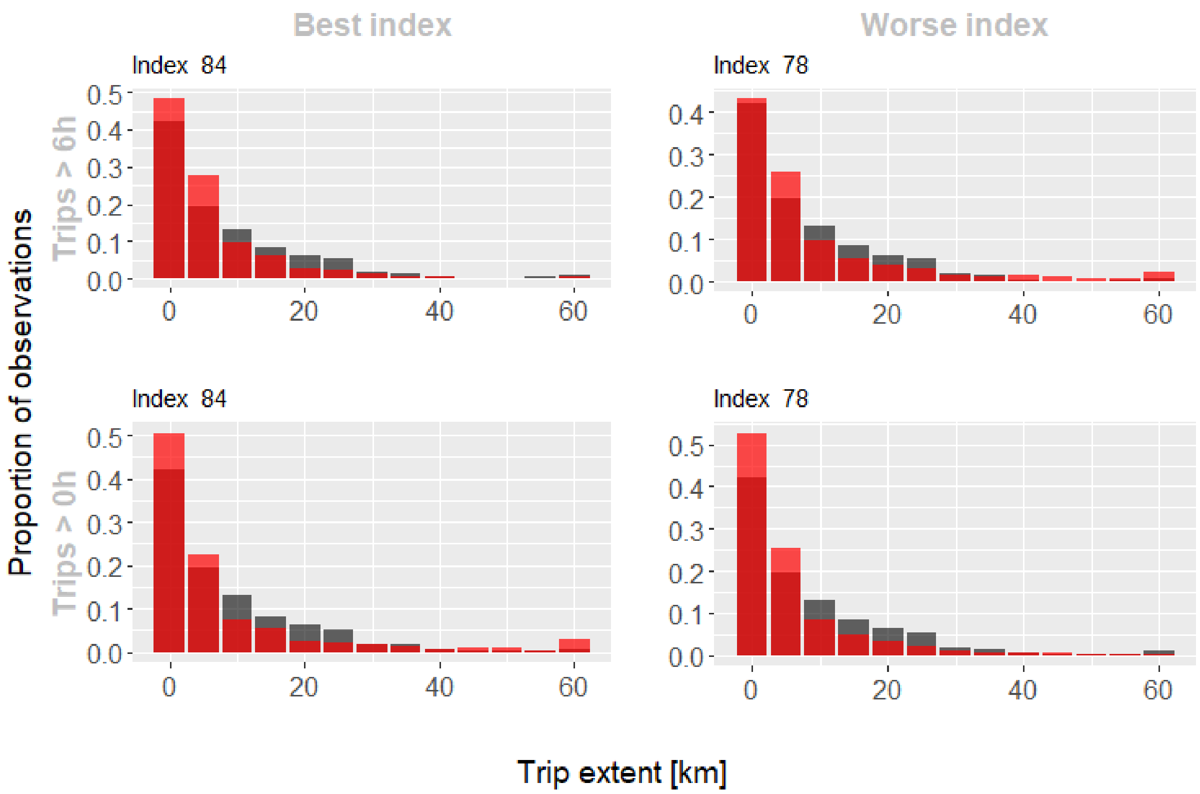
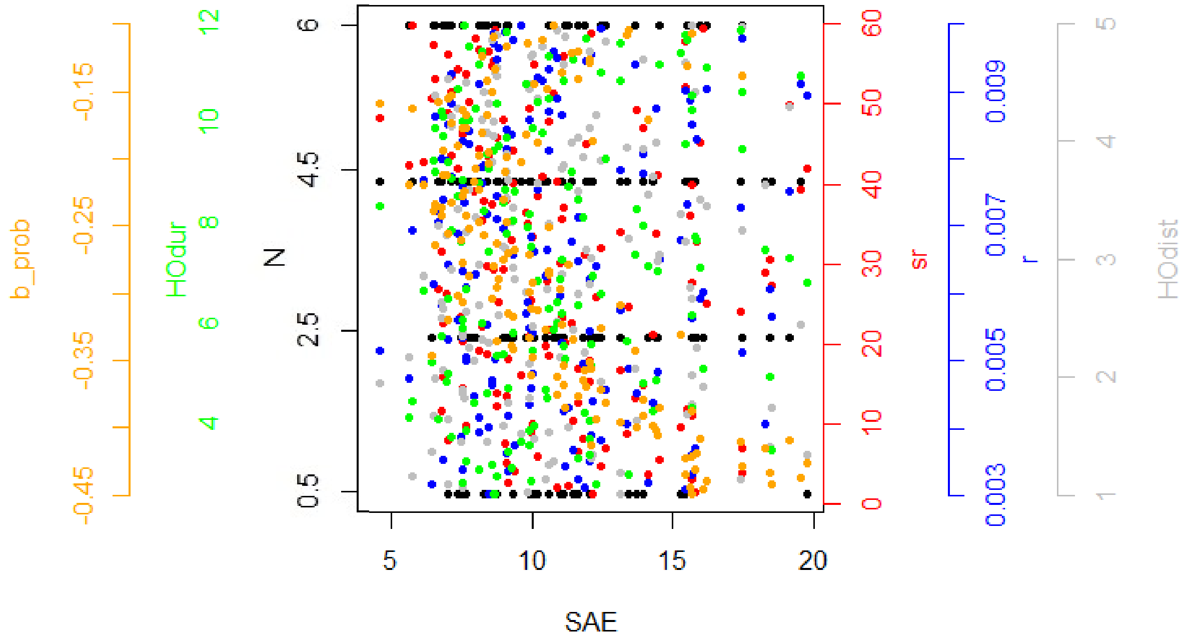


Figure 41. Frequency distribution of trip extent for modelled (red) and observed (grey) pattern for indices with best (lowest SAE, left panel) and worse (highest SAE, right panel) match. Numbers over each panel refer to index number (parameter combinations) (Table 10). Top panels show the comparison based on modelled and observed trips >6h and lower panels show the comparison based on observed trips >6h and all modelled trips considered (trips > 0h).

Most of the indices with high SAE for frequency distribution of trip duration pattern are associated with low *b* value (Figure 42, Figure 18). No clear relationship between parameter space and SAE of trip extent is evident (Figure 42).


b_prob
HOdur
N
sr
r
HOdist
SAE

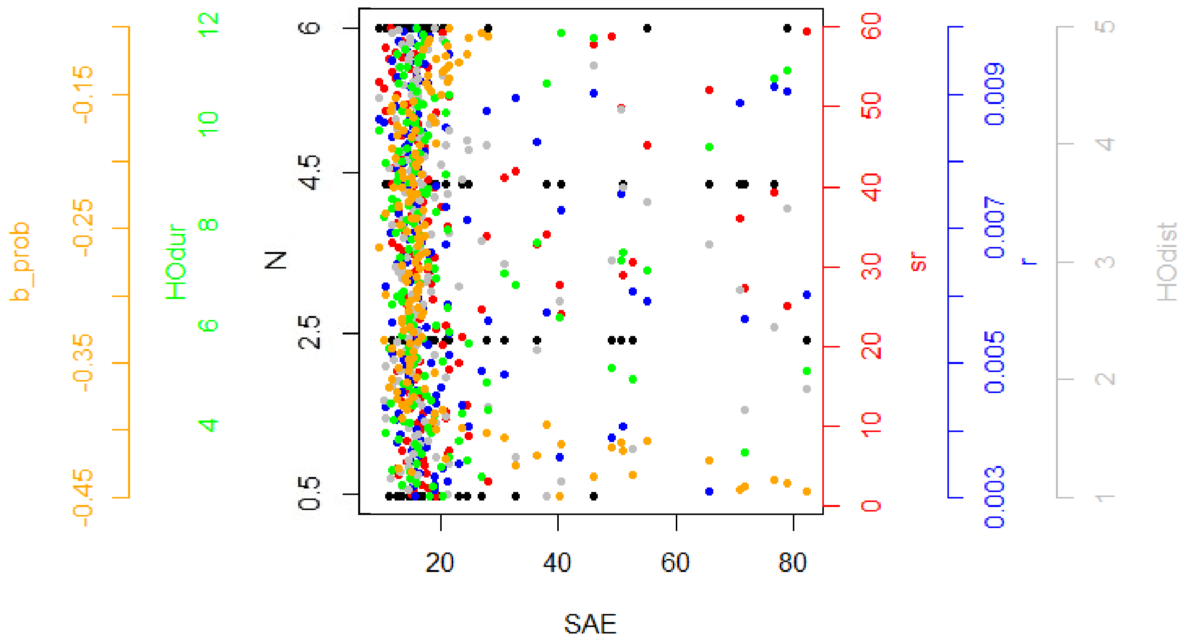

b_prob
HOdur
N
sr
r
HOdist
SAE

Figure 42. Parameter space for 150 parameter combinations for six parameterised parameters for frequency distribution of trip duration (upper panel) and extent (lower panel) pattern.

Pattern 2.8: Frequency distribution of at-sea positions with distance from the departure haul-out site

The observed maximum trip extent values are based on the same telemetry dataset as in case of patterns 2.6-2.7 (Table 1). Distance is calculated as Euclidean distance in straight line between each location and *m*seals' last visited haul-out site.

All parameter combinations reproduce highest frequency distribution of locations very close to shore, as observed. All parameter combination, however, underestimate proportion of location at 15-25 km away from the haul-out sites, however within the observed range (

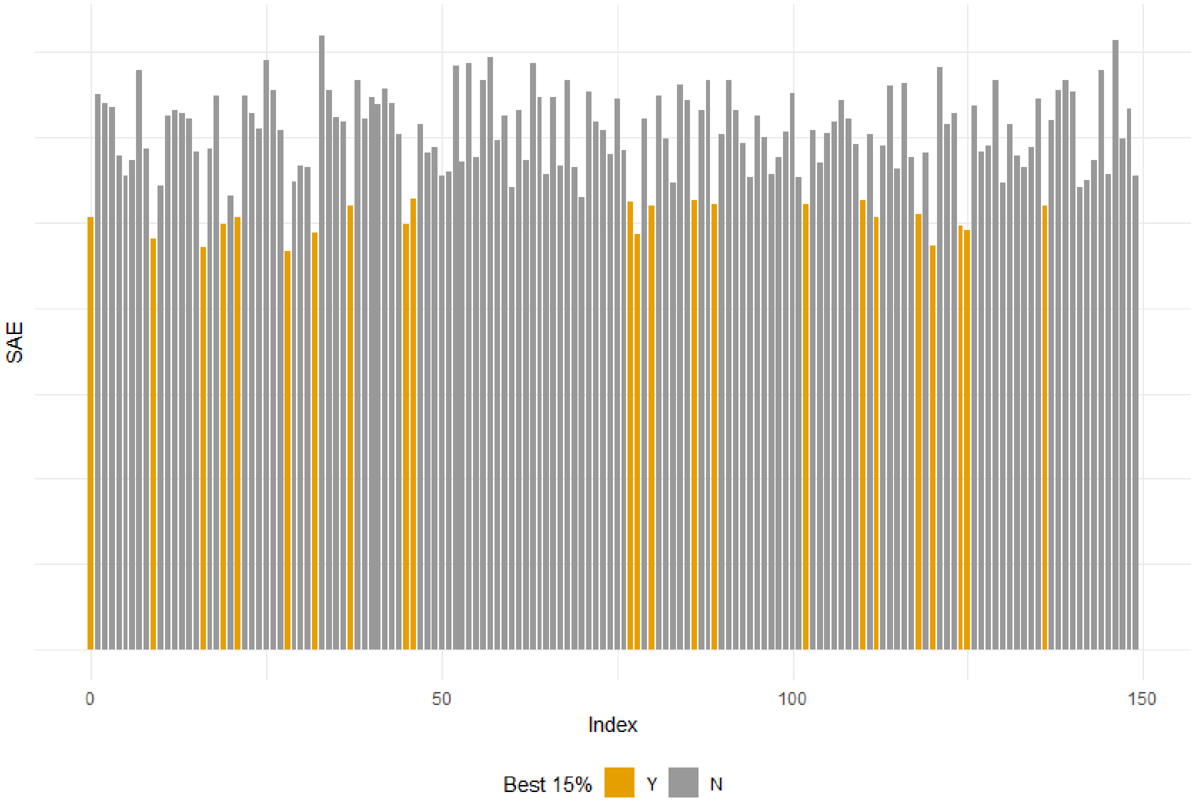


Figure 43,

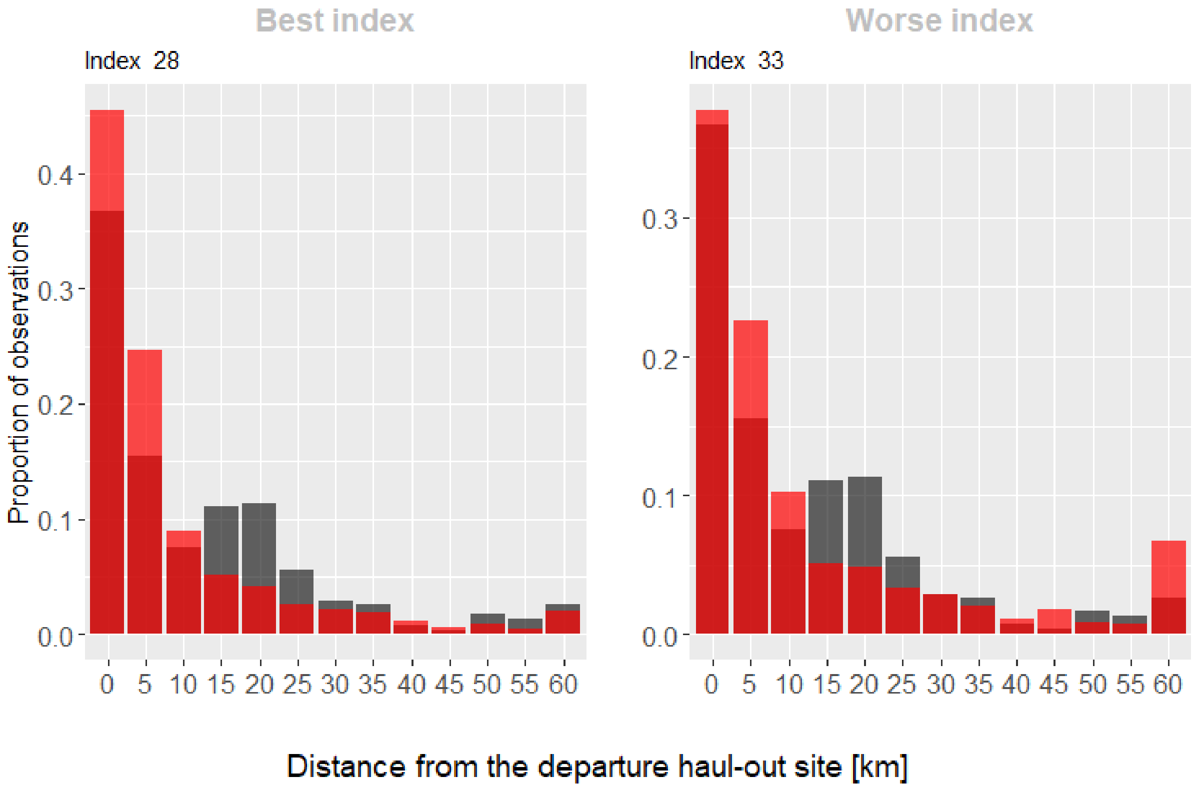


Figure 44).There is no clear pattern between the range of used parameter combinations and SAE (Figure 45).

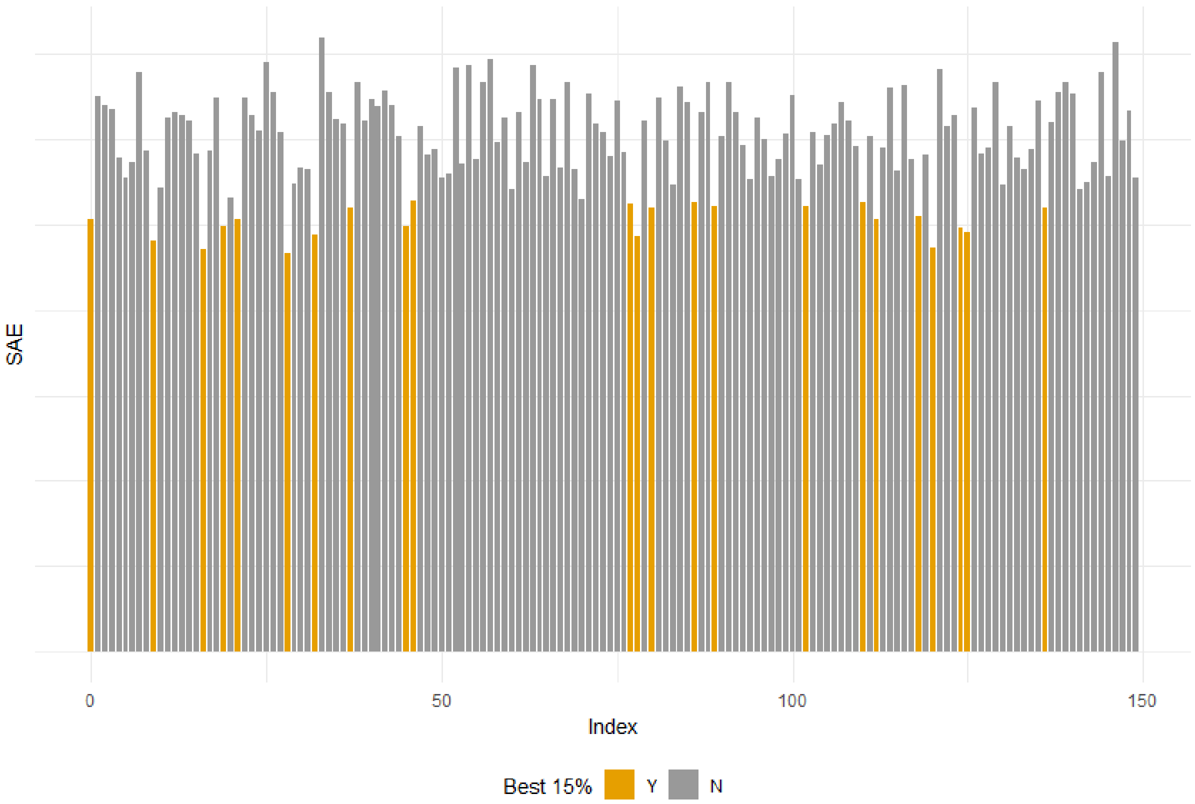


Figure 43. Standardised absolute error (SAE) of 150 of parameter combinations (index) for frequency distribution of at-sea locations with distance from the departure haul-out site

with 15% of best matches marked in yellow. Values of SAEs strongly depend on the unit of the values for which the error was calculated and has no meaning, hence values indicated on y-axis.

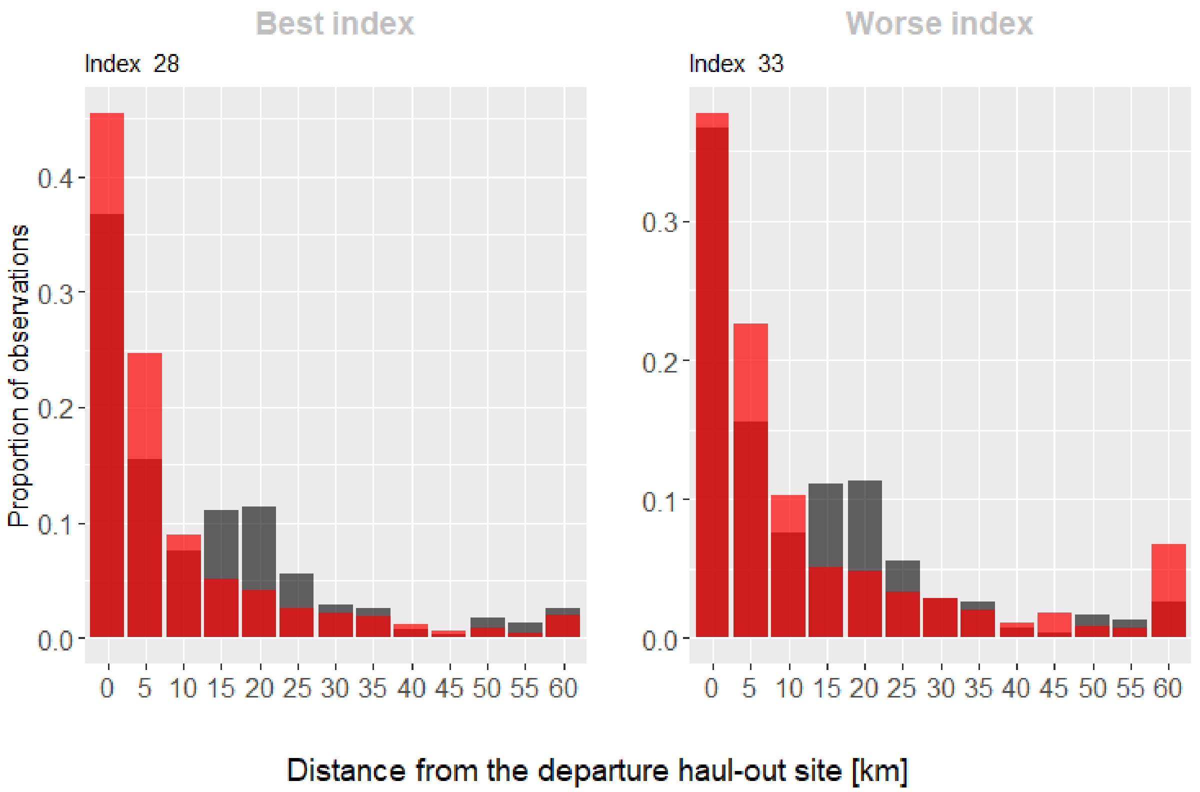
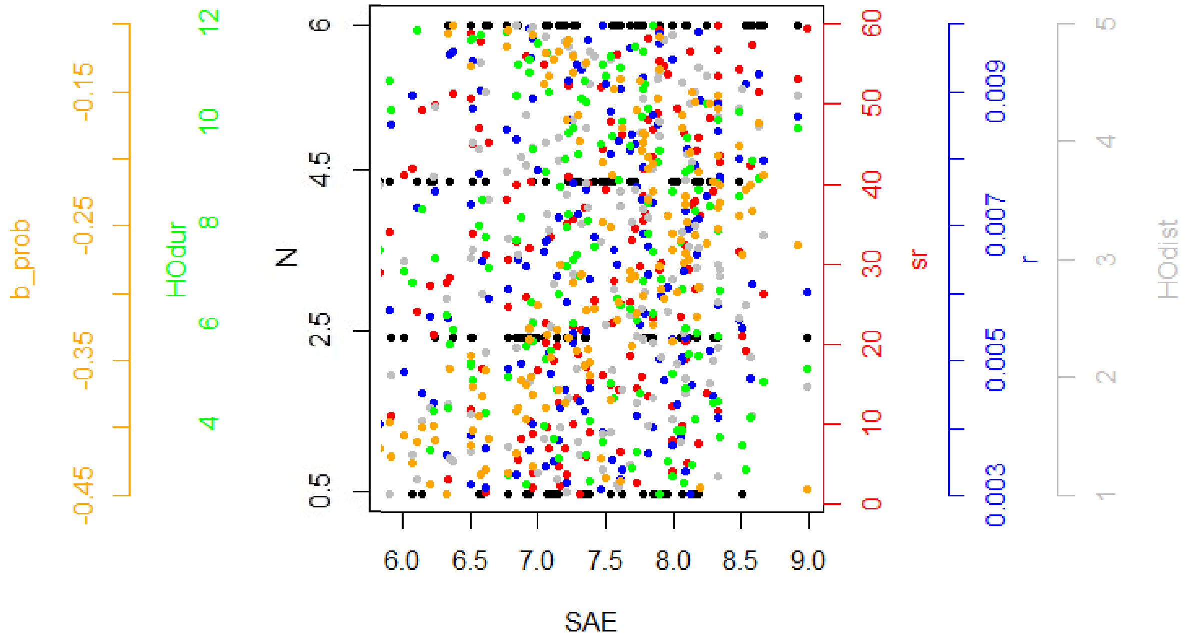


Figure 44. Frequency distribution of at-sea locations of *m*seals with various distances from the departure haul-out sites for modelled (red) and observed (grey) pattern for parameter combinations (index) with best (lowest SAE, upper panel) and worse (highest SAE, lower panel) match. Numbers over each panel refer to parameter



combination index number (Table 10).

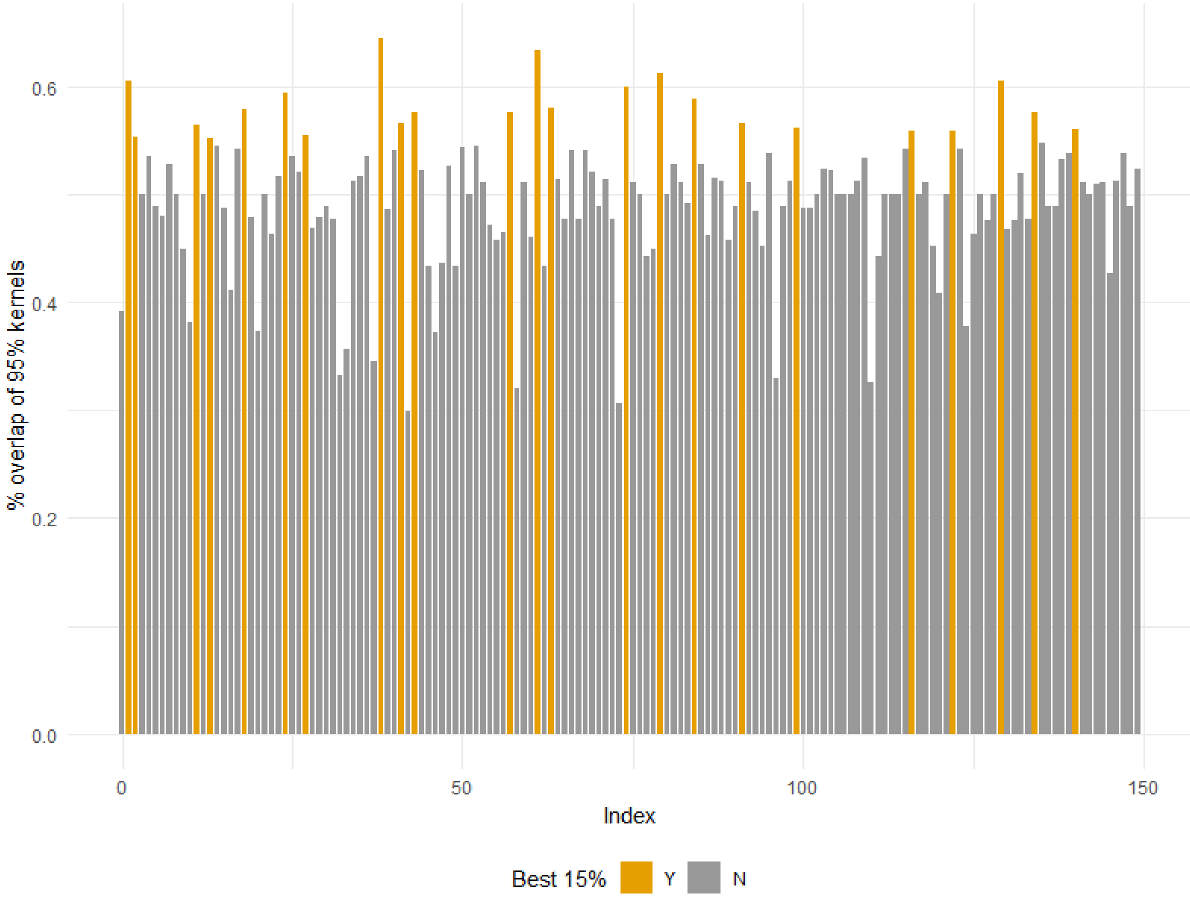
Figure 45. Parameter space for 150 parameter combinations for six parameterised parameters for frequency distribution of at-sea positions with distance from the departure haul-out site pattern.

Pattern 2.9: Overlap of kernel densities

Comparison between observed and modelled distribution of *m*seals is based on overlap of kernel utility distribution (KUD): proportion of the home range of *m*seals covered by the home range of observed ones and vice versa.

The observed data come from 14 adult individuals of harbour seals tagged at the modelled site (East Coast) between 2007-2018 and transmitting in autumn-spring. Both modelled and observed data are based on seals' location at sea – positions when animals are hauling-out are, therefore, removed (see section 1.4.10 and Table 3). Cumulative number of *m*seals' presence for each modelled patch (1 x 1km) at the end of each model simulation is used to calculate the above-mentioned spatial statistics. KUD is calculated using the *kernelUD* function of the adehabitatHR package (Calenge 2006) with *h* adjusted for each index with '*href*' smoothing method, but for a given index h for modelled and observed is the same. We do not consider presence of land in calculations of KUD. Ninety-five % contours where calculated and the % of their overlap is estimated using *kerneloverlaphr* function. As overlap between observed and modelled is more informative than between modelled and observed (see below), we retain indices with highest overlap between observed and modelled 95 % contours (Best 15%)

Percentage overlap between modelled and observed and between observed and modelled is given on Figure 46.



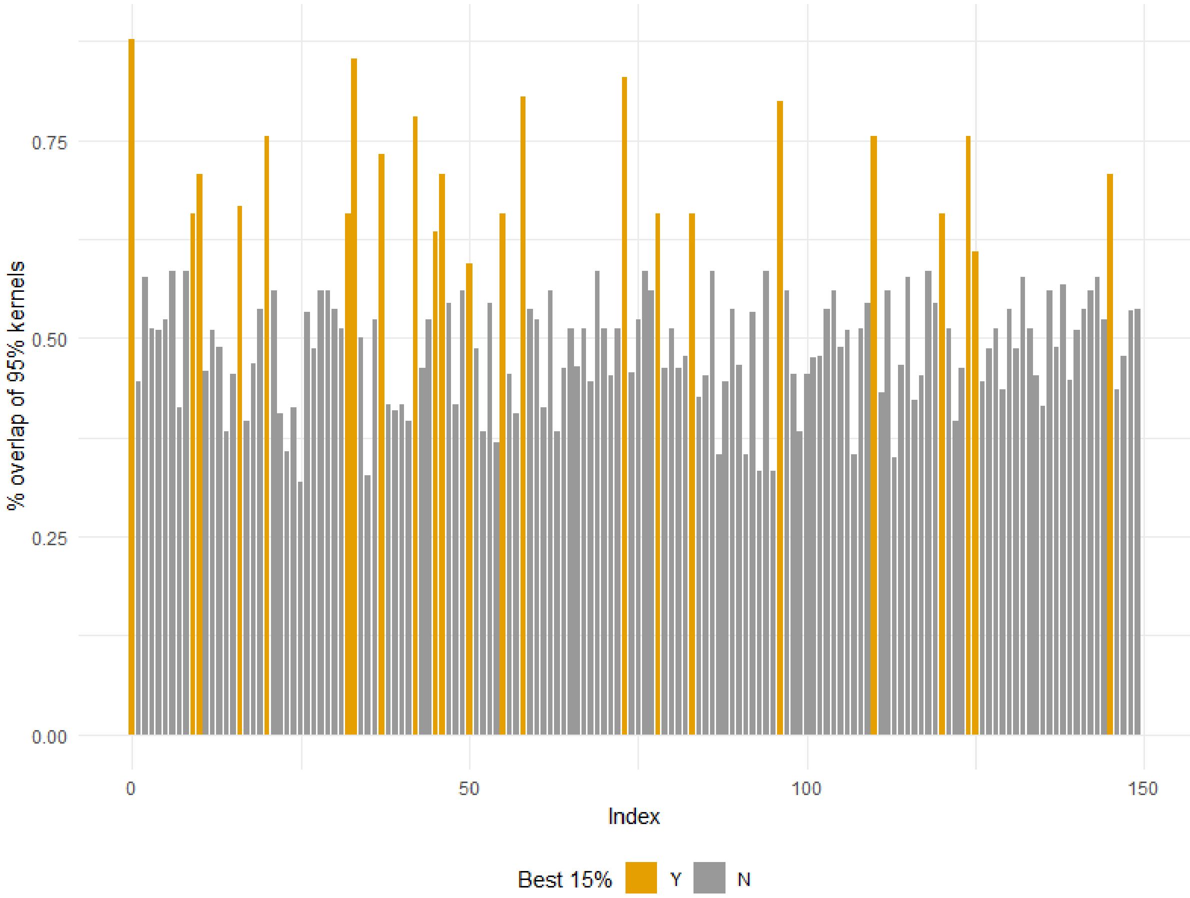


Figure 46. Standardised absolute error (SAE) of 150 combinations of parameters (index) for overlap in 95% kernel contours of home ranges. Top panel refers to proportion of modelled kernels overlapping with observed and lower panel: proportion of observed kernels overlapped by modelled home ranges. Colour of bars show indices with 15% best fit between modelled and observed.

Most indices with best 15% describing the percentage of kernels of *m*seals overlapping with observed ranges result in a poor match when compared visually. Percentage of observed kernels overlapping with modelled happened to be a better descriptor (

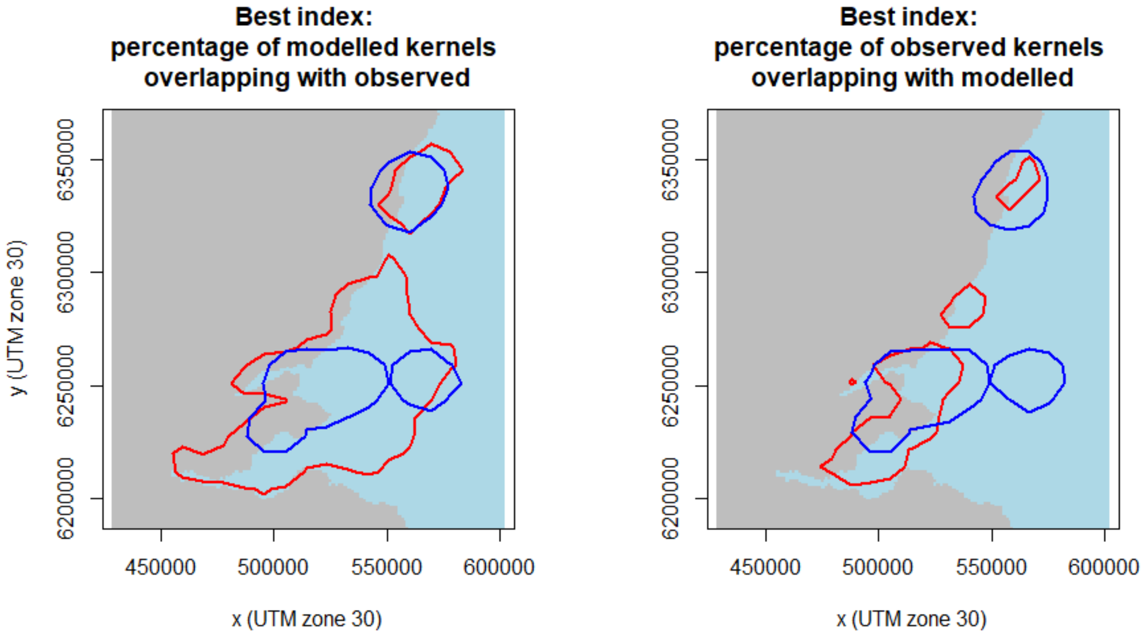


Figure 47), and this descriptor is used in the below parameter selection.

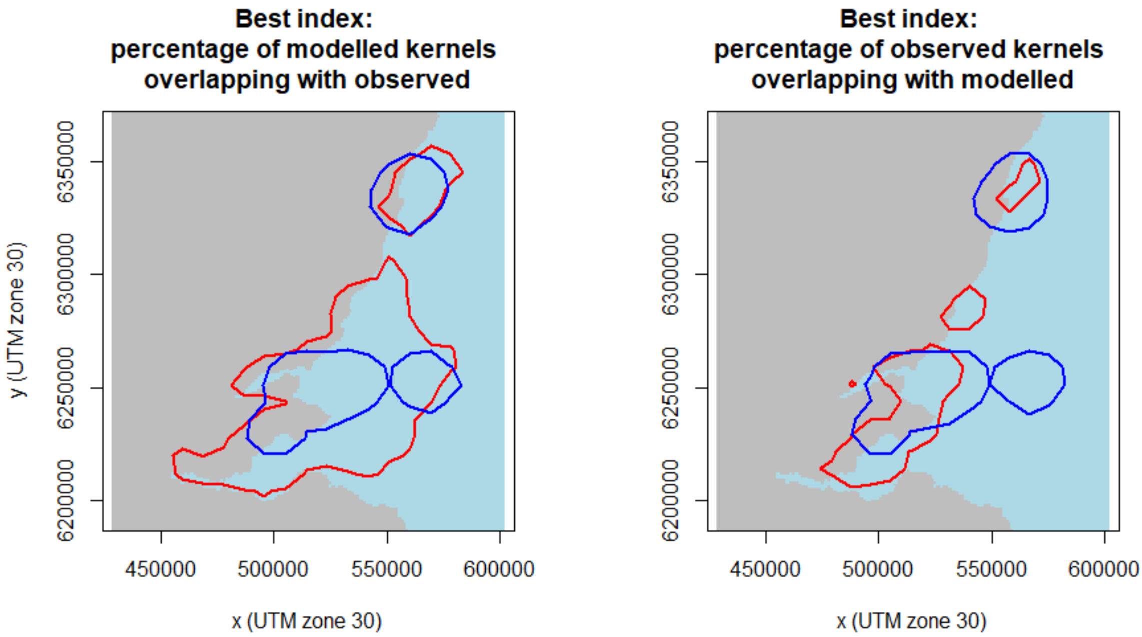


Figure 47. Comparison between observed (blue) and modelled (grey) 95% kernel contours for parameter combination which belonged to best 15% of indices describing percentage of modelled kernels overlapping with observed ranges (left panel) and percentage of observed kernels overlapping with modelled ranges (right panel).

There is no clear pattern between parameter combination and percentage of observed kernels overlapping with modelled (Figure 48).

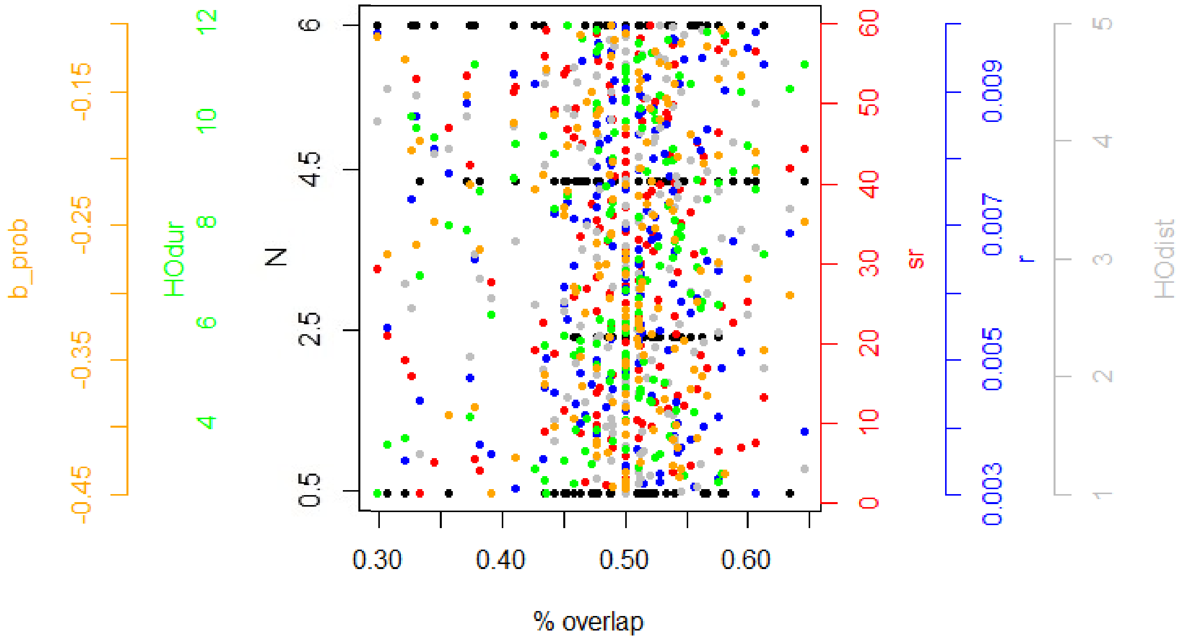


Figure 48. Parameter space for 150 parameter combinations for six parameterised parameters for overlap of kernel densities pattern (% of observed kernels overlapping with modelled).Parameter selection – final parameter combination

There is no single parameter combination which would reproduce all nine patterns according to reproducibility criteria (Table 11). We, therefore, divide patterns into weak and strong. A strong pattern is defined as pattern which is well documented in the literature, and well identified in the observed data. A strong pattern is also this one which emerges from the model only with the use of narrow set of parameter combinations, and therefore acts as a good ‘filter’ in parameter selection. A weak pattern is a pattern which emerges from the model and matches the observed pattern regardless parameter combinations or is not reproduced at all by any parameter combination and is, therefore, not very informative in parameter selection (Table 11).

Parameter combination indices 3, 77, 123, 125 and 127 are common to all strong patterns. Out of these five indices, 127 had the lowest SAE for the frequency distribution of trip duration pattern, pattern which is poorly reproduced by the model, and this parameter combination corresponding to this index will be used in the final model evaluation (Table 10).

Interestingly, index 127 corresponds to number of available fish of 2 fish/m^2 in HSI=1 and search rate of 13.2 m^2/time step. With this search rate and fish density, if *m*seals forage in patches with HSI=1, and number of caught fish is drawn from a Poisson distribution (Eq. 9) there is a small probability that *m*seals can catch > 40 fishes, as the number of caught fish is drawn from a passion distribution with mean = 26. Although there are very few studies showing number of prey-catch attempts and their success for seals, Aart and Thompson (pers com.)reported, based on accelerometery data, up to 30 attempts per dive. Most of the areas at the modelled study site, had HSI<0.1 (Figure 4) and therefore N = 0.8 fish/m^2. This would result with average number of caught fish between 5 and 15. Study by Vance (pers. com.) show average number of prey-catch attempts per dive bout (~ 4 dives) to be 8-12. Although final parameter combination may not necessary reflect the true numbers/processes observed in nature, but are arbitrary numbers, they result in realistic biological processes.

Table 11. Summary of patterns used in parameter selection of general movement and behaviour of *m*seals, their type and criteria used to compare observed and modelled. 'Type' describes whether a pattern is considered 'strong': pattern which is well documented in the literature, and well identified in the observed data, A strong pattern is also this which emerges from the model only with the use of narrow set of parameters combination, and therefore acts as a good 'filter' in parameter selection. A 'weak' pattern is a pattern which emerges from the model and matches the observed pattern regardless parameter combinations or is not reproduced at all by any parameter combination and is, therefore, not very informative in parameter selection. SAE refers to standardised absolute error, best 15% - parameters combination resulting in 15% lowest SAE (best fit). Patterns are numbered as in Table 3 for consistency.

Pattern	**Type**	**Methods of comparison between modelled and observed**
2.1 Daily consumption of fish	Strong	Falling within the observed range
2.2 Daily energy expenditure	Weak	Falling within the observed range
2.3 Changes in proportion of blubber over model duration	Strong	Falling with +/- 5% change between start and end of model duration
2.4 Daily proportion of time spent resting and hauling-out	Strong	Falling within the observed range
2.5 Frequency distribution of number of individually visited haul-out sites	Weak	SAE, best 15%
2.6 Frequency distribution of trip duration	Weak	SAE, best 15%
2.7 Frequency distribution of trip extent	Weak	SAE, best 15%
2.8 Frequency distribution of at-sea positions with distance from the departure haul-out site	Weak	SAE, best 15%
2.9 Overlap of kernel densities	Strong	% overlap, visual

3. Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both regarding empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design is not ad hoc but based on carefully scrutinised considerations.

Summary:

We discuss the simplifying assumptions underlying the submodels that control *m*seals movement, energetics and behaviour in the Objectives part of the ODD (1.4).

4. Implementation verification

This TRACE element provides supporting information on: whether the computer code for implementing the model has been thoroughly tested for programming errors

Summary:

The computer code is continually tested during model development to ensure that each consecutive step in development is only initiated after the model had passed a wide range of visual and statistical tests. Visual inspection of movement tracks is carried out using NetLogo 6.0.4 and R 3.5.2. Below we present only selection of checks.

4.1 AVOID LAND

Implementation was tested by writing an output file from the model run to check that when close to land a *mseal* would choose a direction towards where there was less land ahead. (An example of the output is given in Table 12).

Table 12. Example of testing and debugging land avoidance procedure by checking whether *m*seals move towards the areas with less land ahead. If an *m*seal is avoiding land (avoid? = TRUE), it ‘counts’ number of land patches ahead of it (count-right and count-left). It then moves towards the area which ‘has less’ land ahead. As illustrated in line 2 of this table for *m*seal with ID=1, this *m*seal has 4 patches in the right direction and 0 in the left. It turns left to move along the coast (avoidance-mode-left) as tis direction has less land ahead (left<right = TRUE (1)).

Tick	*m*seal ID	avoid?	count-right	count-left	avoidance-mode-right	avoidance-mode-left	left<right	left>right	Check 1_left	Check 2_left	Check 3_right	Check 4_right
1	0	FALSE	0	0	FALSE	FALSE	0	0	0	1	0	1
1	1	TRUE	4	0	FALSE	TRUE	1	0	1	1	0	1
1	2	FALSE	0	0	FALSE	FALSE	0	0	0	1	0	1
1	3	TRUE	5	4	FALSE	TRUE	1	0	1	1	0	1
1	4	FALSE	0	0	FALSE	FALSE	0	0	0	1	0	1
1	5	TRUE	0	1	TRUE	FALSE	0	1	0	1	1	1
1	6	TRUE	1	0	FALSE	TRUE	1	0	1	1	0	1
1	7	TRUE	4	5	TRUE	FALSE	0	1	0	1	1	1
1	8	TRUE	2	4	TRUE	FALSE	0	1	0	1	1	1
1	9	TRUE	0	1	TRUE	FALSE	0	1	0	1	1	1
1	10	FALSE	0	0	FALSE	FALSE	0	0	0	1	0	1

4.2 BIASED CORRELATED RANDOM WALK

We evaluate the 'bias' part of CRW (Figure 5, Eq. 3) by testing relationship between distance to target (haul-out site or patch) and turning angle (

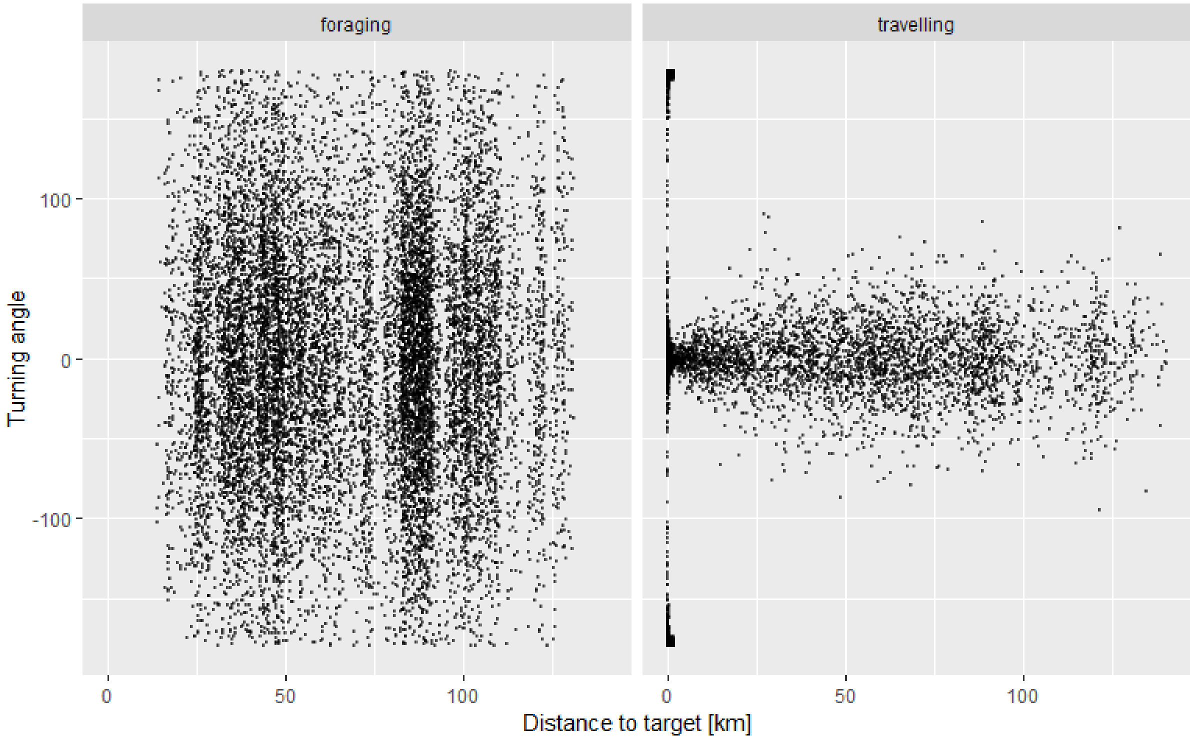


Figure 49).

In order to achieve this, we divide the data into 'foraging' and 'travelling' by assuming that *m*seals' movement in HSI<=0.4 ('bad' habitat, corresponding to low fish availability) refers to 'travelling' and HSI>=0.7 ('good' habitat with higher fish availability) to 'foraging'. Here, the term 'foraging' has this specific definition, as compared to the default definition used elsewhere in this document, where foraging is defined as any at-sea movement of *m*seals. The choice of these two above HSI thresholds is only for visual/analysis purpose and it is not based on any observed data. Bias towards target is much more pronounced when *m*seals are travelling (low HSI) compared with when it was foraging (high HSI): the range of turning angles (difference in angle between previous and current turn) is much larger in areas with higher HSI ('foraging') when movement of seals is more tortuous like in area restricted search type movement. In the areas of low HSI ('travelling') *m*seals have more directional movement (turning angles close to 0) towards the target (

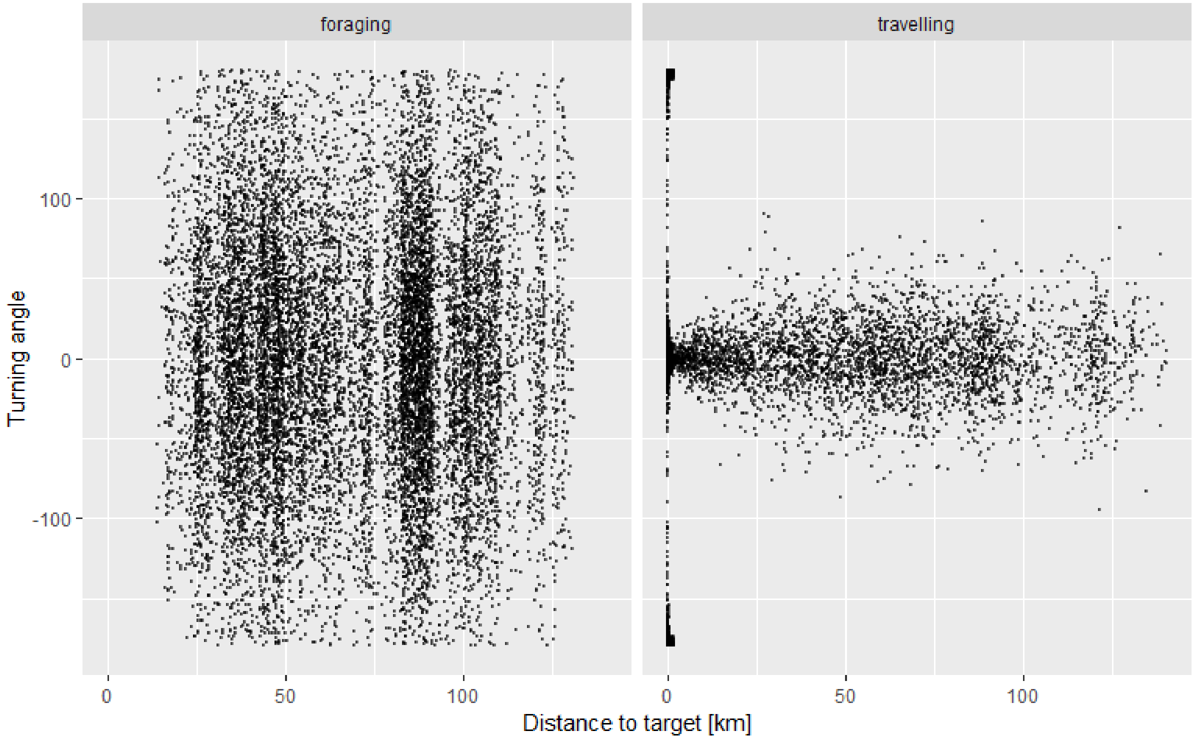


Figure 49).

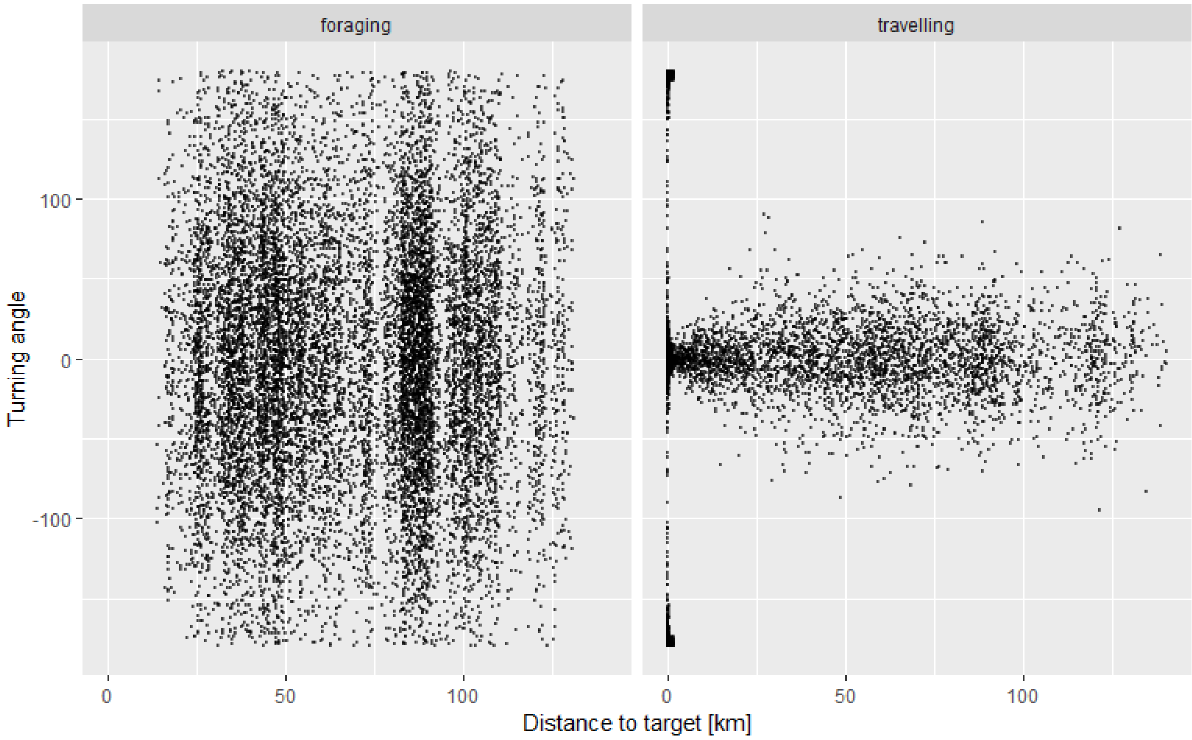


Figure 49. Relationship between *mseal* turning angles and distance to target for two behavioural states.

4.3 TIME TO REST? and TIME TO HAUL-OUT?

The debugging of **TIME TO HAUL-OUT?** ensures that all possible combination of the three reasons behind hauling-out are represented properly in the code. Table 13 summarises all possibilities and colour-match each of them with colours in if else statement (see section 1.7.2 and below).

Table 13. List of combinations of all triggers behind *m*seals’ resting and the resulting behaviour

NEED TO DIGEST?	**NEED TO HAUL-OUT FOR NON-DIGESTIVE REASONS?**	**GENERAL CONDITION GOOD?**	**IF ELSE LEVEL – RESULTING BEHAVIOUR**
TRUE	TRUE	TRUE	REST
FALSE	FALSE	FALSE	FORAGE
TRUE	FALSE	FALSE	REST
FALSE	TRUE	TRUE	FORAGE
TRUE	FALSE	TRUE	REST
FALSE	FALSE	TRUE	REST
TRUE	TRUE	FALSE	REST
FALSE	TRUE	FALSE	FORAGE

```
If NEED TO DIGEST TRUE
[rest]
else
        [
        if NEED TO HAUL-OUT FOR NON-DIGESTIVE REASONS FALSE
        {
                If GENERAL CONDITION GOOD TRUE
                [rest]
                else
                [forage]
        }
                        else
                        [forage]
        ]
```

We also plot distances to the target (next) haul-out at the time *m*seals ‘decide‘ to haul-out for long-digestion in order to see whether it is more likely to happen closer to this haul-out, as intended, and it does (lower left panel in Figure 9, Figure 50).

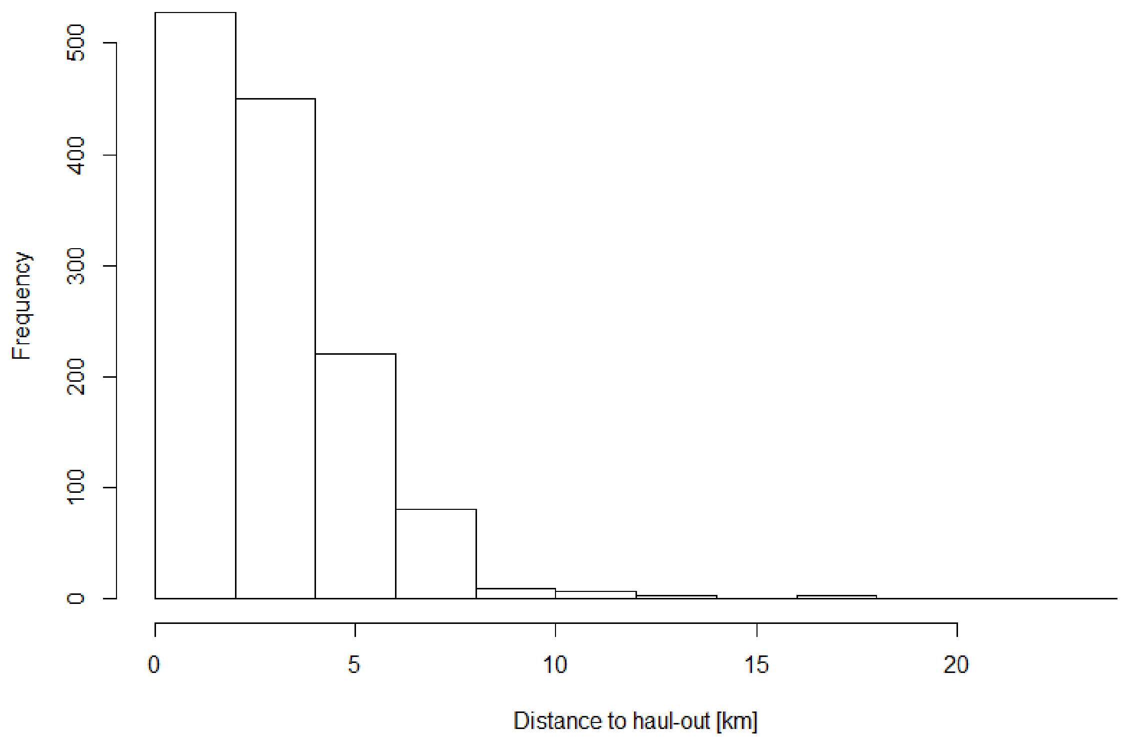


Figure 50. Frequency distribution of distances to the next, target haul-out site at the time *m*seals' 'decide' to haul-out for long-digestion.

4.4 CHOOSE NEXT TARGET PATCH, CHOOSE NEXT TARGET HAUL-OUT SITE, REMEMBER PATCHES, REMEMBER HAUL-OUT SITES

See Figure 6 for an example of visual inspection of these procedures.

5. Model output verification

This TRACE element provides supporting information on: how well model output matches observations

Summary:

The model can reproduce a range of patterns observed at population and individual levels such as energetic patterns: daily energy expenditure, food consumption and changes in proportion of stored blubber; movement and other behavioural patterns: number of visited haul-out sites, trip extent and utility distribution and daily activity budget. However, the model currently fails to reproduce very short trips of *m*seals. The model is also able to capture individualistic behaviour of seals such as site fidelity towards haul-out and foraging sites. Thus, it generally succeeds in reproducing, as an emergent property of the model, central-place foraging of seals driven by physiological (such as need of digestion) and cognitive (memory-driven movement) processes.

The mean daily food consumption of *m*seals (pattern 2.1, Table 1) was 4.16 kg ± 1.3 kg (mean ± sd throughout the result section), which is within the observed values ranging 3.8 – 4.8 kg (Härkönen and Heide-Jørgensen 1991, Kastelein et al. 2005, Sharples et al. 2009, Wilson and Hammond 2016).

Mean daily energy expenditure of *m*seals (pattern 2.2, Table 1) is 16.2 +/- 4.1 MJ/day (sd around 50 means = 0.14 MJ/day based on 50 simulations). This fits within the range of observed values which are between 14.3 and 21.43 MJ/day. The model reproduced no changes in blubber proportion (pattern 2.3, Table 1) over three-month simulation as observed (Figure 51B). Majority of individuals did not exceed their blubber proportion over 40% of total body mass. During 50 simulations none of the *m*seals reduced its blubber content to <5% of total body mass and died (Figure 51C) .

*M*seals spent a similar mean proportion of time hauled-out and resting at sea (Figure 51A, pattern 2.4, Table 1) as observed (hauling-out: observed (range reported in literature): 12-25% (Cunningham et al. 2009, Vincent et al. 2010, Ramasco et al. 2014, Russell et al. 2015), modelled: 21.4 ± 0.2%; resting at sea: observed: 6-28% (McConnell et al. 1999, Vincent et al. 2010, Mcclintock et al. 2013, Ramasco et al. 2014), modelled: 9.2 ± 0.4% (Figure 51A). The majority of haul-out events (71%, see

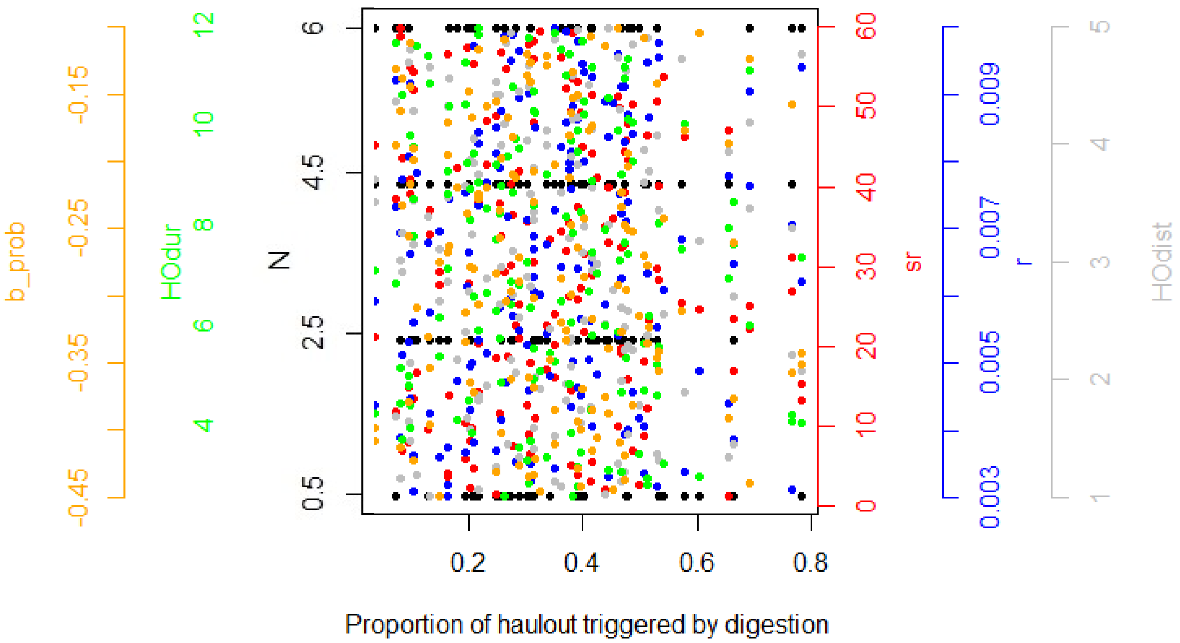


Figure 32) are triggered by non-digestive reason, the remaining 29% by digestion.

Each *m*seal visits very few haul-out sites, consistent with the observations (Figure 52A, pattern 2.5, Table 1). *M*seals perform longer (in time) foraging trips (pattern 2.6, Table 1) than observed, and the model underestimates the number of very short foraging trips (Figure 52B and see also parameterisation in section 2.3). The model is able to reproduce comparable frequency distribution of extent of foraging trips (pattern 2.7, Table 1) as observed (Figure 52C). Also the frequency distribution of *m*seals' at-sea positions with distance from the departure haul-out site (pattern 2.8, Table 1) is comparable to observed although the model overestimates the number of positions very close to the haul-out sites and underestimates number of positions 15 – 25 km from the sites (Figure 52D). The model is able to reproduce the same core areas of *m*seals' geographical distribution (pattern 2.9, Table 1) as observed (Figure 51D). The size of the kernels depends not only on number of observed seals but also the tagging place. We only have information on harbour seals tagged off St Andrews and Aberdeen and have very few tracks from Firth of Forth area (for place names see Figure 2). *M*seals did not use the area east of St Andrews (the 'Wee Bankie', Figure 2) as intensely as the observed seals. There are, however, only two observed seals frequently visiting the bank in the original data set. We, therefore, consider the model to be able to capture the overall spatial distribution of seals.

There is very little variation between model results between 50 replicates for all POM patterns (Figure 51, Figure 52).

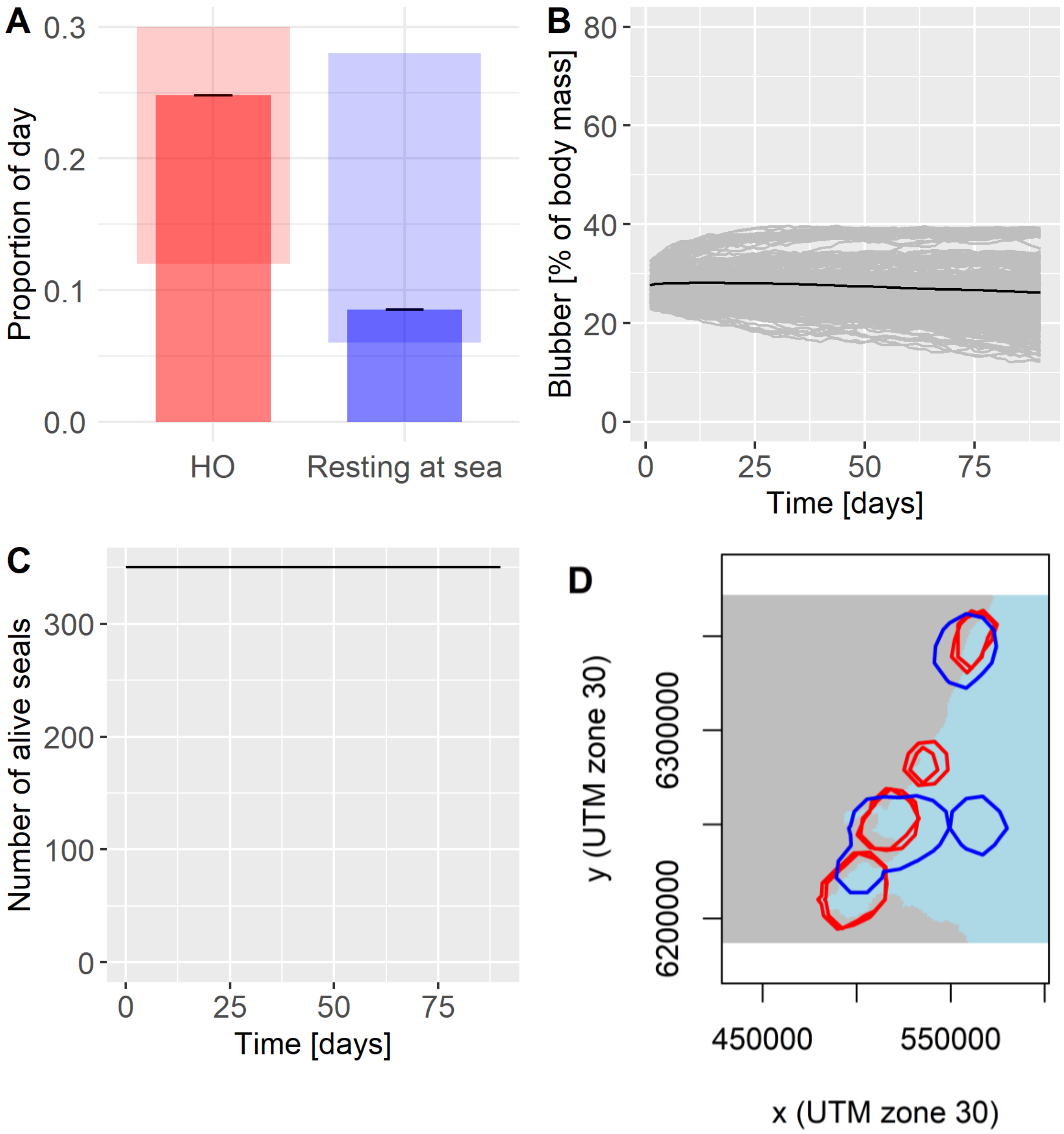


Figure 51. (A) Modelled (bars) and observed (horizontal polygons) proportion of time seals spent hauling-out (HO) and resting at sea; (B) Changes in blubber proportion over model duration. Black line shows overall mean. Grey lines show 350 *m*seals from a random replicate. The observed data show no change in blubber proportion in the autumn; (C) Number of alive *m*seals over three months simulations; (D) 95% kernel density contours for observed (blue) and modelled (red) seals.

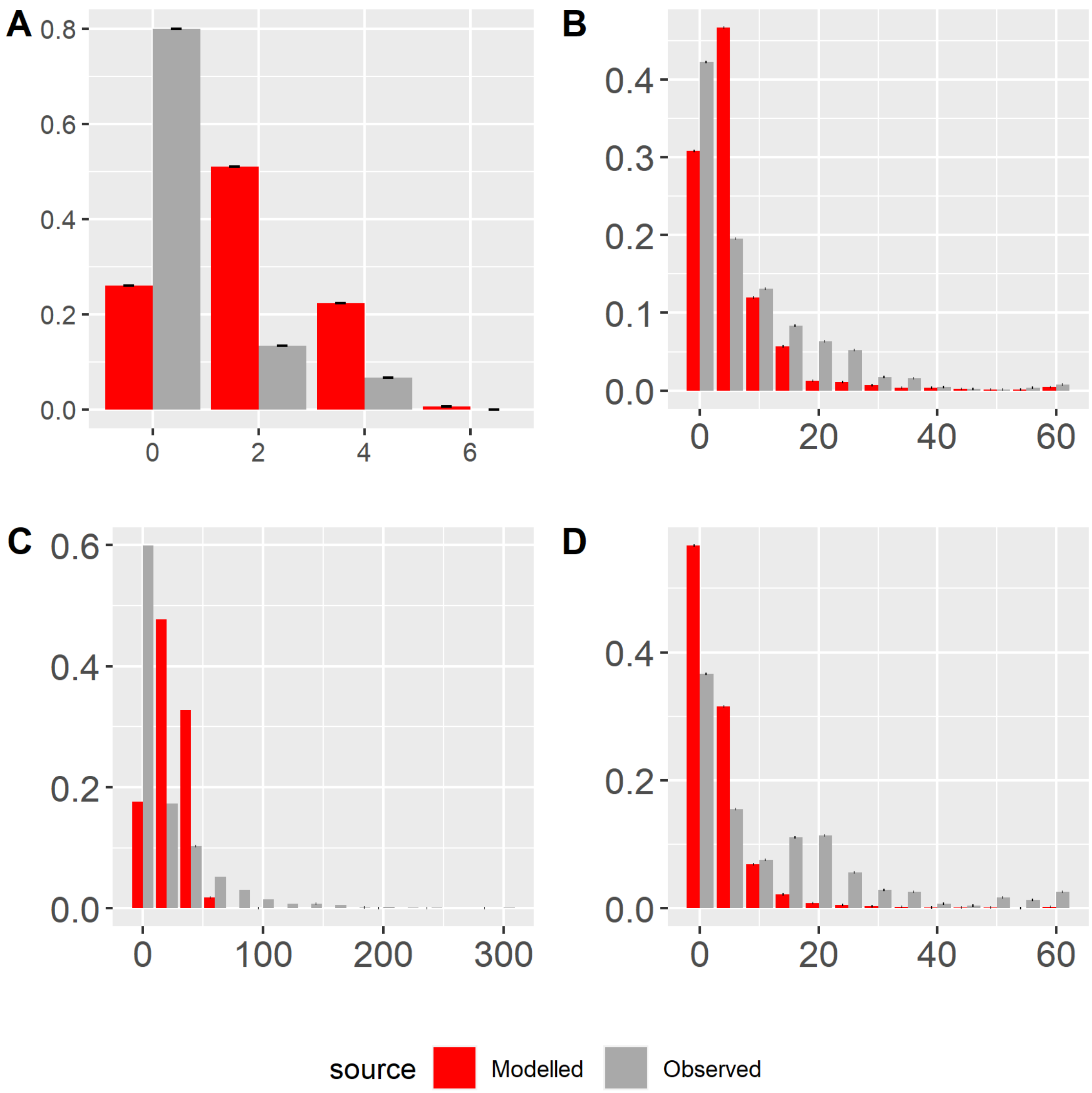


Figure 52. Modelled (*m*seals, red) and observed (grey) (A) frequency distribution of number of individually visited haul-out sites; frequency distribution of: (B) trip extent; (C) trip duration; and (D) distribution of at-sea positions with distance from the departure haul-out site. Error bars show +/- standard deviation around means resulting from 50 replicates of the model or SD between observed seals.

Food depletion (pattern 3.1, Table 1) is calculated as percentage changes in HSI of each patch at the beginning and at the end of model simulation (three months). Below we present the mean results of 50 simulations. Maximum decrease of HSI value due to depletion is

17.4%. The highest depletion occurs along the coast and close to popular haul-out sites (Figure 51, Figure 53).

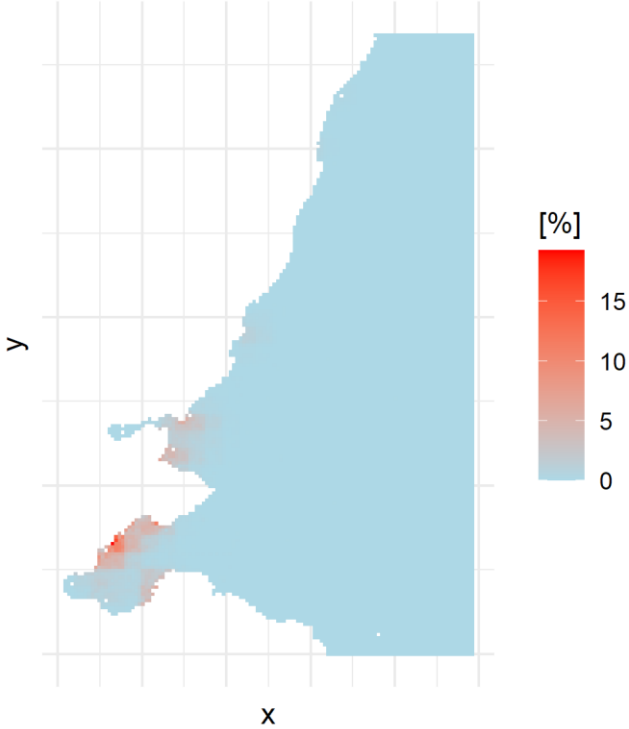


Figure 53. Food depletion depicted as decrease [%] in values of habitat suitability index (HSI) between beginning and end of model simulation (mean of 50 replicates).

We plot foraging trips of five randomly chosen harbour seals for which we have telemetry data during the study period. We then visually compare it to five, randomly chosen *m*seals from one simulation, which visited the same haul-out sites as the observed seals. The observed tracks show high inter-individual variation and this is also demonstrated by the mseals. Some *m*seals go further offshore, some are more stationary and some repeatedly follow the coats, as also observed (

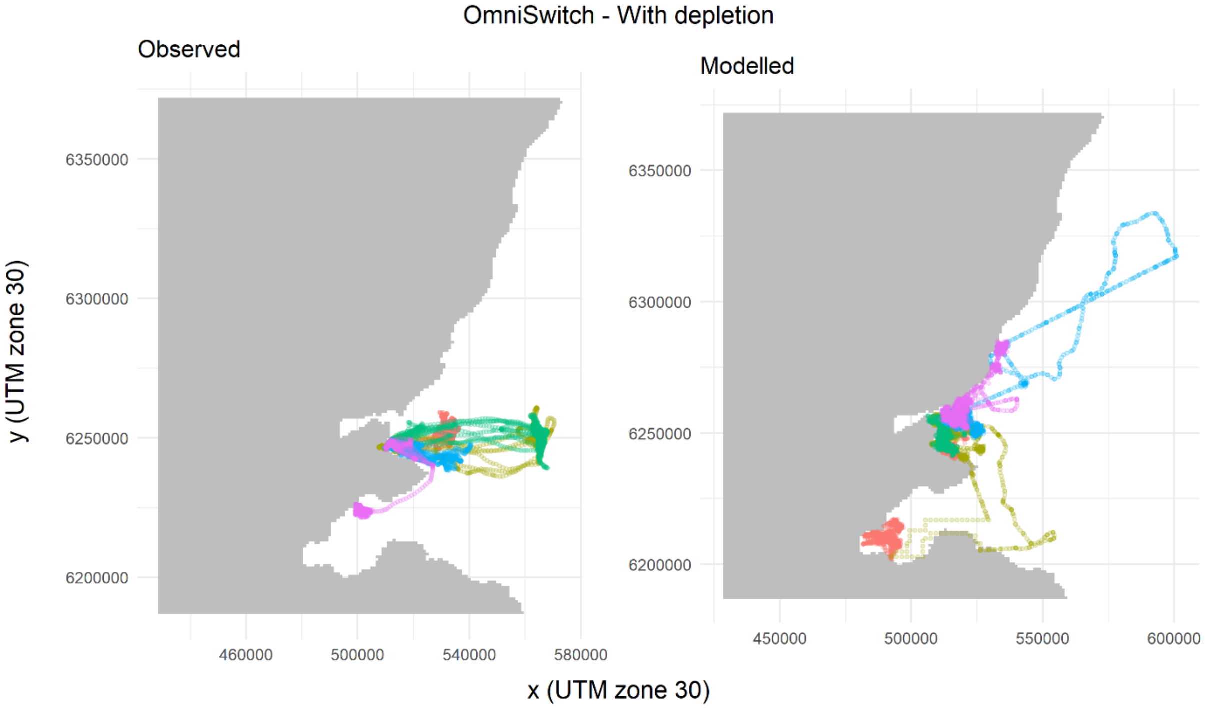


Figure 54). Two of the observed seals are repeatedly visiting so-called ‘Wee Bankie’ – a sandy area east offshore from St Andrews (Figures 2 and

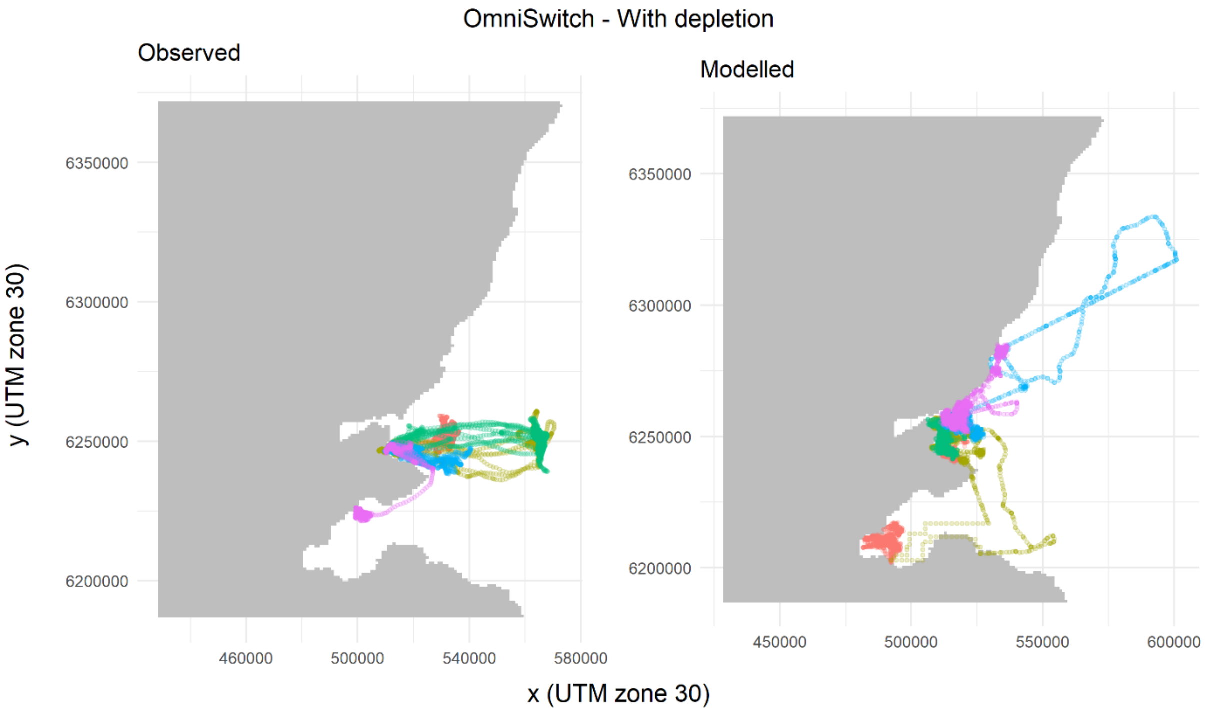


Figure 54). However, none of the *m*seals from the randomly chosen individuals visit this area.

To picture at-sea site fidelity of *m*seals and observed seals (pattern 3.3,Table 1), we quantified the extent to which the consecutive foraging trips of each of the randomly chosen seals, as above (*m*seals and observed), overlapped. To do it we divided the study are into 5x5 and 25x25 km squares (Figure 3) and calculated how many of these squares overlapped between the consecutive trips of each seal. The model was able to reproduce a general observed site fidelity trend with most seals having large overlap between consecutive trips (Figure 55). There was however large variation between seals from different simulations.

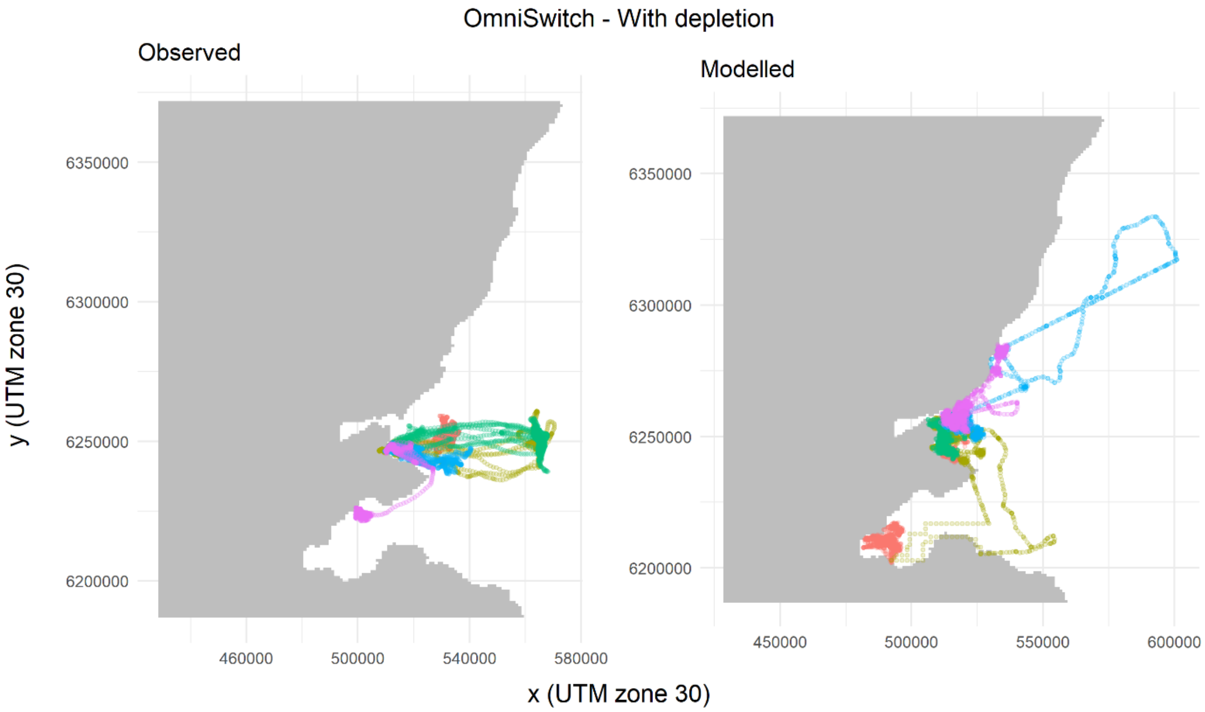


Figure 54. Foraging trips for five random observed (left panel) and five modelled (*m*seals, right panel) seals represented by points.

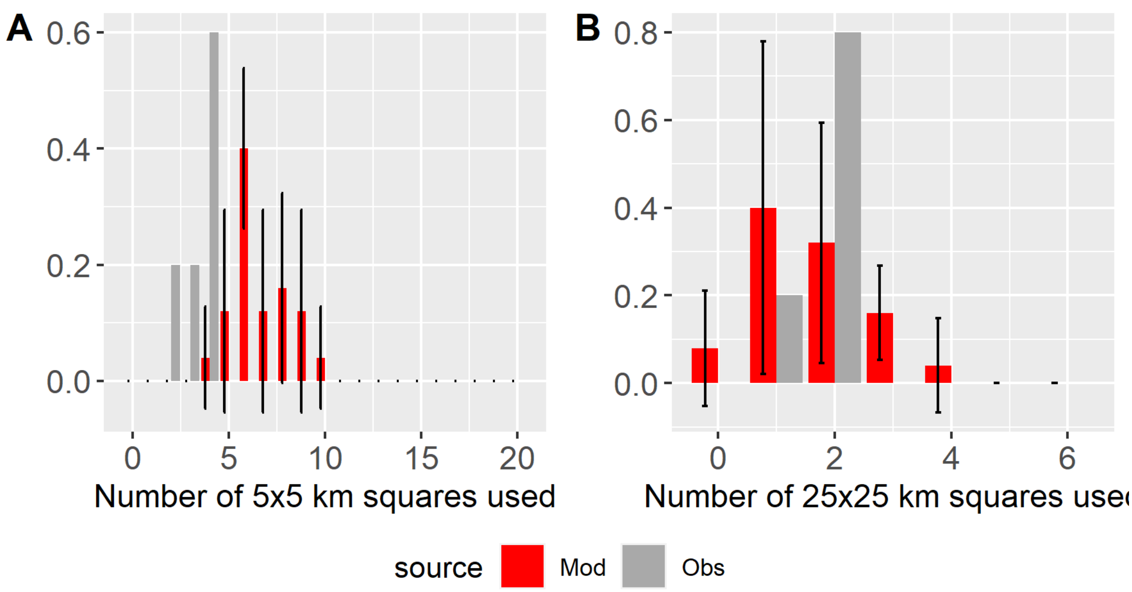


Figure 55. Frequency distribution of the number of squares (5x5 and 25x25 km) which overlapped between consecutive foraging trips for five random observed (grey) and five

random modelled (*m*seals, red) seals whose tracks are shown in Figure 8. The error bars show variation between simulations.

6. Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

The first part of this section presents the results of global sensitivity analysis (SA) which explores how variation of four parameters affects the results of the four strong patterns (Table 11). The results of SA show little variation of the results with changes in parameter values. The largest changes are driven by parameters related to digestive physiology of *m*seals: stomach capacity and the length of short digestive breaks.

The second part of this section presents the results of robustness analysis which explores how the results of the main model change when certain processes are removed, or certain analytical modifications of the model are done. We test model performance when

i) food depletion does not take place,

ii) *m*seals' movement is not driven by memorised foraging patches and *m*seals' movement at sea is, therefore, only driven by correlated random walk,

iii) the underlying habitat suitability index (HSI) differs: a) the habitat is more patchy, b) prey is distributed uniformly over the study site,

Removing food depletion has no effect on the model results. The 350 modelled individuals do not deplete the habitat to the magnitude which affects their behaviour and performance. Depletion may however play a role in defining seal behaviour and physiology over longer model duration and/or for larger seal colonies.

Removing memory results in *m*seals going further away from the shore than observed and not showing any site-fidelity to at-sea patches. However, the daily fish consumption and changes in proportion of blubber remain similar to the results of the final model. The observed spatial distribution of *m*seals is, therefore, strongly influenced by memory driven movement both further out at sea and near the haul-out sites. This finding is in accord with by other studies (e.g. Nabe-Nielsen et al. 2013)**.**

Applying the random habitat suitability map reveals, that even if potential patches with high prey abundance may be present further off-shore, *m*seals stay relatively close to shore. Whether this behaviour is related to the fact that near-shore habitat is already 'good enough' for *m*seals to maintain good body condition, or *m*seals are not able to find these spots, is unknown, and would require further model analysis and modification. However, considering much higher fish consumption, in comparison to final model, we suggest that the first argument is quite likely. This higher fish consumption results in

unrealistic increase in blubber proportion, an increase in time spend on digestion (resting) and a higher than observed and larger food depletion than in the main model. Simulations on new habitat result in better match between modelled and observed frequency distribution of trip duration than the final model but still underestimating number of very short trips. Simulations on uniformly distributed prey habitat resulted in lower fish consumption than observed and, therefore, decrease in proportion of blubber but not below mortality threshold. Distribution of *m*seals and characteristics of their trips (extent and duration) was comparable to the results of the final simulations

6. 1 Sensitivity analysis

The aim of the sensitivity analysis (SA) is to explore the influence of varying parameters outside the range used in the final model simulation on the outputs of the model. We run global SA of parameters which values are uncertain or are not measurable (Marino et al. 2008). We test the effect of varying stomach capacity, distance at which shortest path network is established, time of short resting at sea and calorific value of fish (Table 14).

Table 14. List of parameters, their description, value used in the final model simulation and variation range used in the global sensitivity analysis.

Name of parameter/ state variable	Description	Value used in the final model simulation	Variation range in the sensitivity analysis	Reference to the section of this document
StomachCap	Volume of stomach defining how much fish *m*seals can eat before taking a short digestive break	Proportional to total body mass	-25 and + 25%	Section 1.7.2, Table 4
Short digestion (durationOfResting)	Duration of at-sea digestion break needed to empty the stomach	45-60 min	-30 and + 30 min	Sections 1.7.2, 1.7.3, Table 4
Shortest path	Distance from the shore at which network of shortest paths is established	7 km	-3 and + 3 km	Section 1.7.4.3, Table 4
Mean_kJ_per_gOfFish	Calorific value of 1g of fish	4.7 kJ	-25 and + 25%	Table 5

We analyse the effect of varying one parameter at a time but also the interaction effect between them by varying parameters simultaneously. We follow the Design of Experiment methodology first formulated by (Lorscheid et al. 2012) and applied in ABMs by (Thiele et al. 2014). We use full factorial design of the extreme values of each of the parameters (Table 14) leading to 16 combinations and we run one simulation over one month for each of these combinations. We then analyse the results with the use of FrF2 (Groemping 2011) and DoE.base (Groemping 2013) packages in R, following the description by (Thiele et al. 2014). We do not run stepwise fitting of a linear regression model to the data of SA, as suggested by Thiele et al., 2014, but we base our conclusions on visual analysis of the plots (Figure 56, Figure 57), as discussed below. The results of regression models can be strongly influenced by the sample size, and not necessarily reflect the actual effect of different parameters (White et al. 2014).

We use only strong POM patterns (Table 11) as output: pattern 2.1 Daily consumption of fish (‘Fish_cons)’; 2.3 Changes in proportion of blubber over model duration (‘Blubber’); 2.4 Daily proportion of time spent resting (‘All_resting’) and hauling-out (‘Hau’out'); and 2.9 Overlap of kernel densities (‘Kernel_overlap’) . We analyse the results of each parameter combination as a percentage change between simulation with varying parameter(s) and the results of a given pattern in the final model simulation.

Most of the patterns only vary by few percent when the chosen parameters are varied at their maximum range. Increase in fish consumption up to 4% in comparison to final model simulations is the lasrgest variation out of all patterns. Variation in duration of short digestion and stomach capacity has less effect on the five POM patterns than shortest path and fish calorific value. Interestingly, blubber pattern is not affected by combination of parameters (Figure 56).

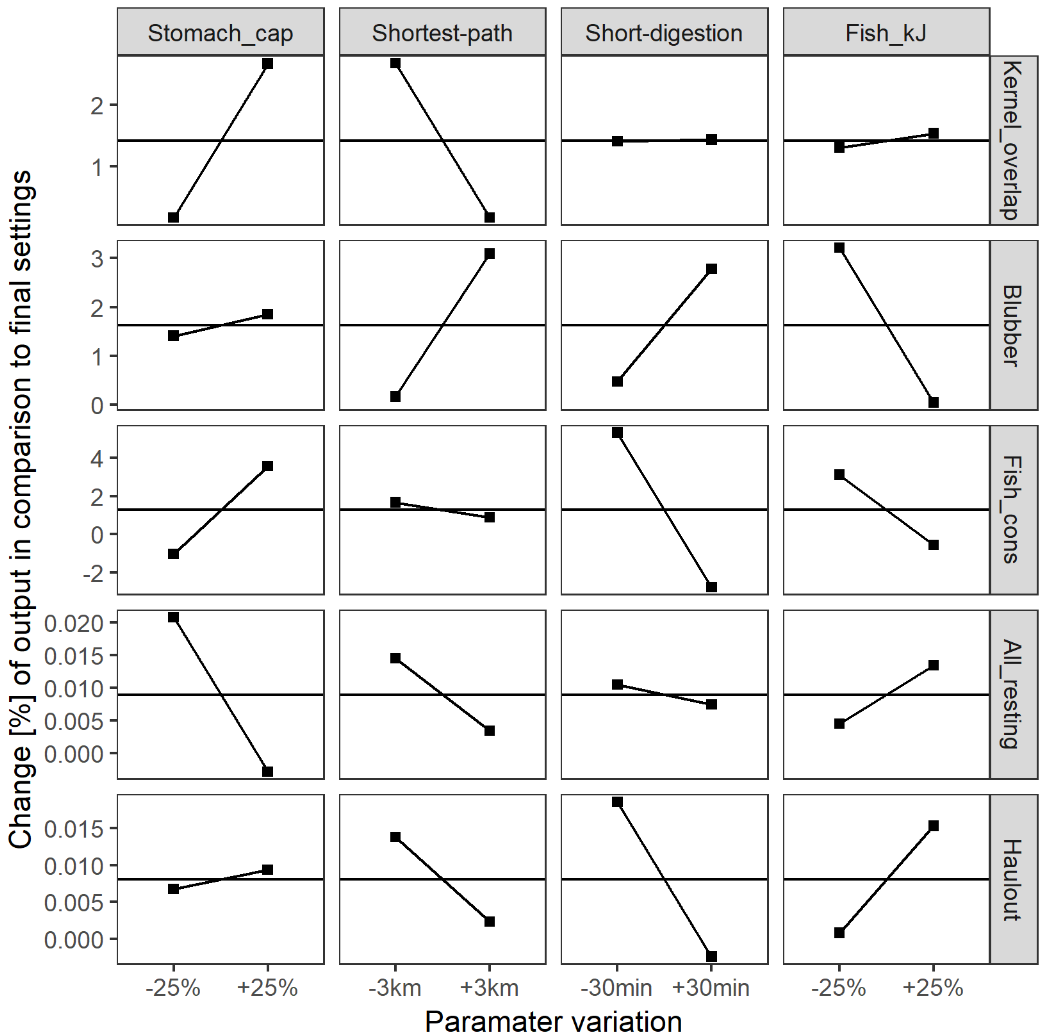


Figure 56. Main effect plots. Parameters in columns and outputs (patterns) in rows. Horizontal lines (without rectangles) in rows visualise mean values. Right rectangle higher than left rectangle indicates a main effect with a positive sign and vice versa. Rectangles on the same output value (y-axis) indicate no main effect.

Changes in kernel overlap are mostly affected by interaction between shortest path/stomach capacity and stomach capacity/fish calorific value. Resting and fish consumption are, not surprisingly, mostly affected by combination of parameters defining length of short digestion (including stomach capacity) and fish calorific value (Figure 57).

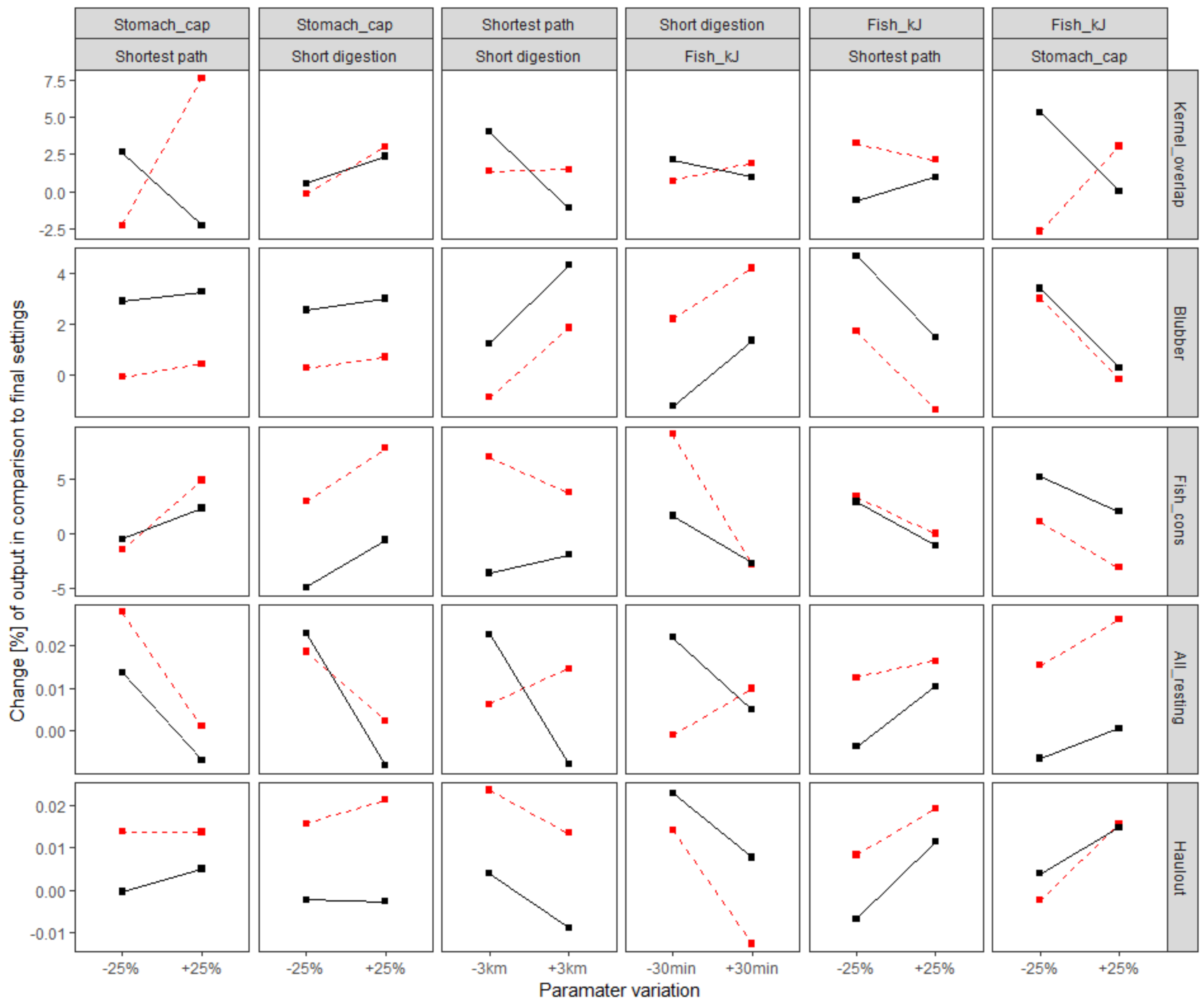


Figure 57. Interaction effect plots. The two-way interaction effect plots indicate interaction effects if the lines for a factor combination are not parallel. The less parallel the lines are, the higher is the expected interaction effect.

6.2 Robustness analysis

6.2.1 Design of robustness analysis

The aim of the robustness analysis is to analyse to the extent to which different decisions about the model processes influence model dynamics and how robust is the explanation provided by the model to major changes in its structure (Levins 1966, Railsback and Grimm 2012, Thiele and Grimm 2015, Grimm and Berger 2016). We, therefore, perform structural and analytical modifications of the model to understand which processes are essential to the model and when and why our model does not work, i.e., when the model mechanisms that explain a certain phenomenon break down. For the robustness analysis we choose processes which are difficult to measure and understand in nature, and therefore hard to justify their need in the model.

We run the following model modifications:

I. ‘No food depletion’: the number of available fish per each patch does not change over model duration. The aim of this step is to test whether depletion is an important driver of seal movement and behaviour. This modification is run over three months as the main model

II. 'No memory': at-sea movement of *m*seals is only driven by CRW. *M*seals do not memorise the visited patches and do not move towards a specific target patch after leaving haul-out sites but move, instead, according to CRW. The CRW is still biased toward the haul-out sites once *m*seals move towards a haul-out site. This modification aims at understanding whether the POM patterns (especially movement patterns) of the model emerge as the results of returning to previously visited patches, the need of seals to return to haul-out sites, or the combination of both. This modification is run over one month

III. 'Modified HSI'. In order to investigate the influence of the specific HSI map used here on model output, we also run the model using an artificial habitat suitability map produced by drawing a distribution of 'hot spots' at random and map with uniformly distributed prey(Figure 58). The initial HSI assigned to each square was 0.04 which translates to 0.08 fish/m^2. These two modifications are run over three months.

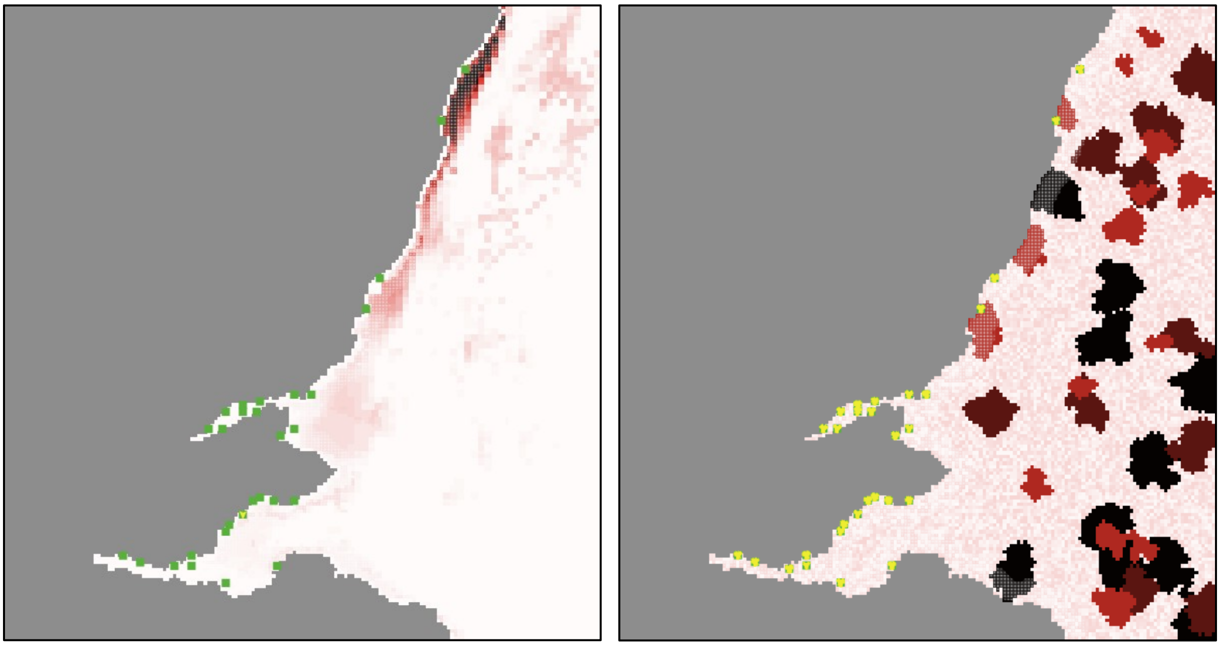


Figure 58. Model domain with the habitat suitability index used in the final model simulations (left) and simulated (right) for the robustness analysis. HSI is represented by red colour pallete with patches with high index being darker. Green squares represent haul-out sites. For uniform distribution, each 1x1 km square has assigned the same number of fish

We test the results of 10 repetitions over three-months time period of each of the structural modification against nine patterns (2.1 – 2.9 and 3.1, Table 1). For 'Simulation over three months' model we run only one simulation. The values of the parameters were kept constant (they were set to the final model simulation values) for all modifications. We use visual comparison between modified and main model to evaluate the ability of the models to reproduce the observed patterns and to compare how model results change between the final and the modified simulations.

6.2.2 Results

I. No depletion

Removing food depletion from the model has no effect on all nine patterns. The model performed similarly to the final model simulations. The modified model shows similar daily fish consumption and daily energy expenditure as the main model (

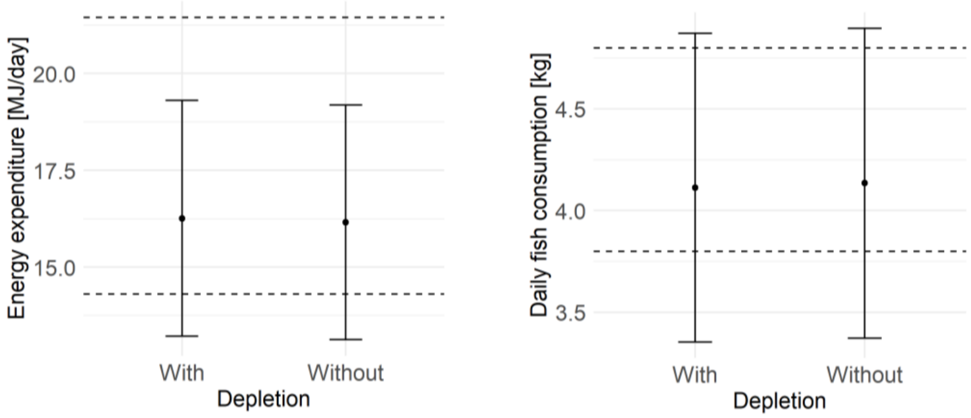


Figure 59). All characteristics of foraging trips: extent, duration and distance from the departure haul out sites as well as number of uniquely visited sites remains comparable between main model and model without food depletion (Figure 60). Also activity budget, changes in proportion of blubber, number of alive seals over model duration and spatial distribution of seals is comparable between models with and without depletion (Figure 60).

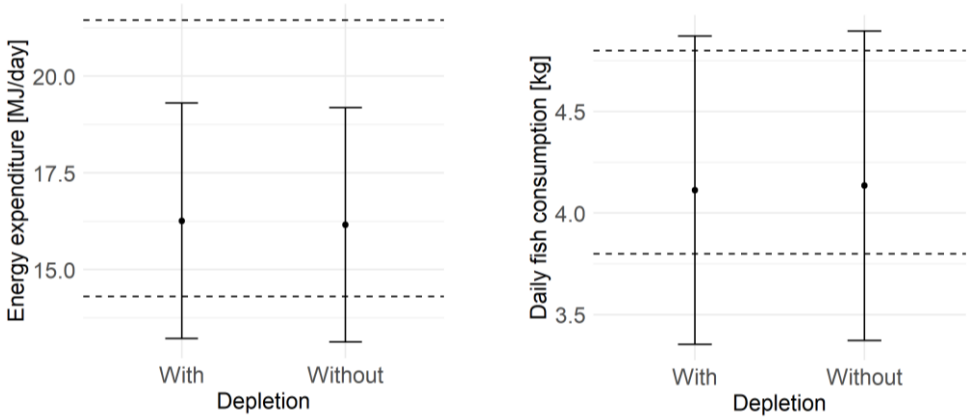
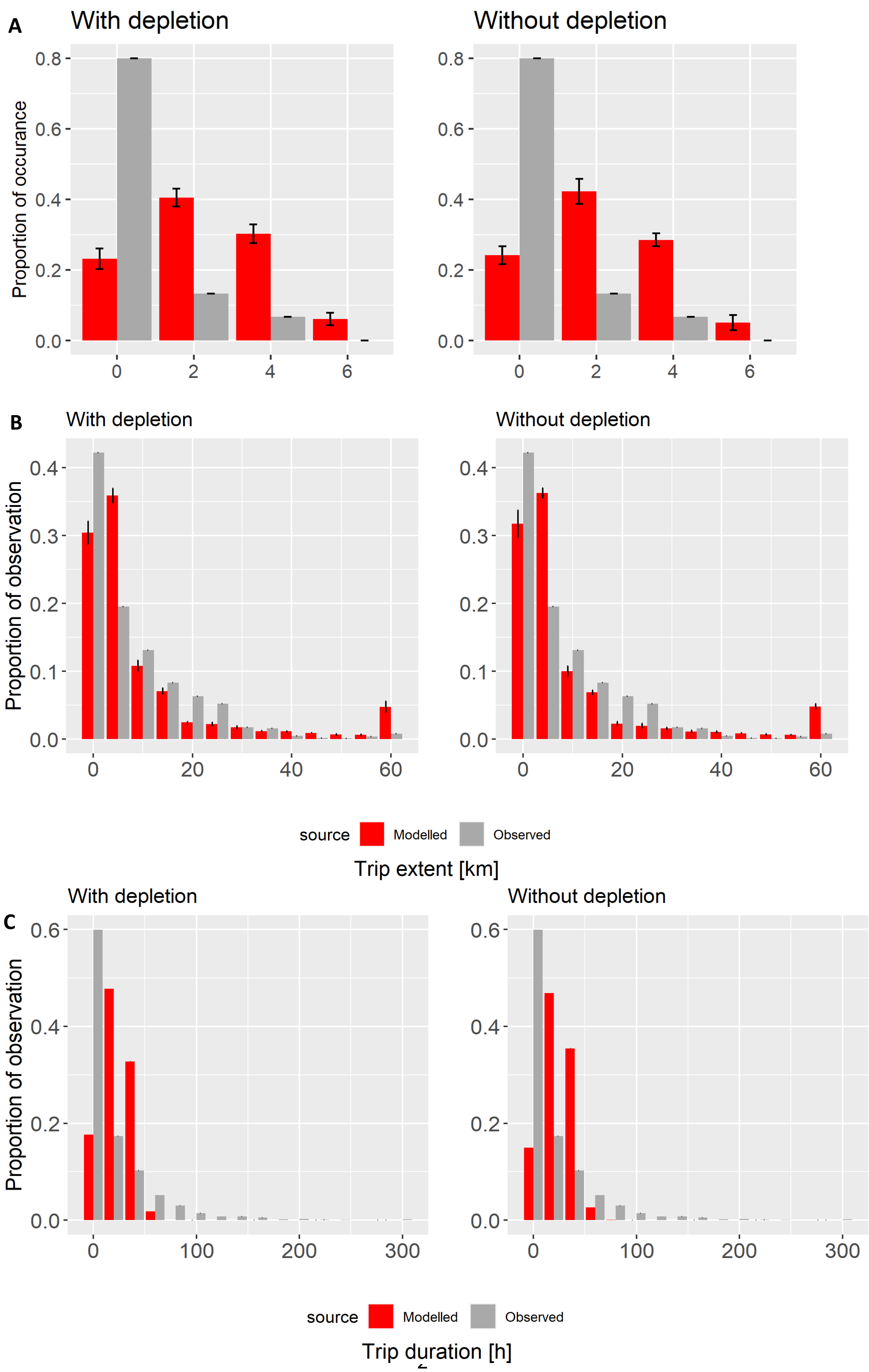


Figure 59. Comparison between daily energy expenditure (left panel) and daily fish consumption (right panel) between simulation including and excluding depletion. Dashed horizontal lines show range of observed values. SD are based on 10 simulations.


A
With depletion
Without depletion
Proportion of occurance
0.0
0.2
0.4
0.6
0.8
0
2
4
6
B
With depletion
Without depletion
Proportion of observation
0.0
0.1
0.2
0.3
0.4
0
20
40
60
source
Modelled
Observed
Trip extent [km]
C
With depletion
Without depletion
Proportion of observation
0.0
0.2
0.4
0.6
0
100
200
300
source
Modelled
Observed
Trip duration [h]

1722

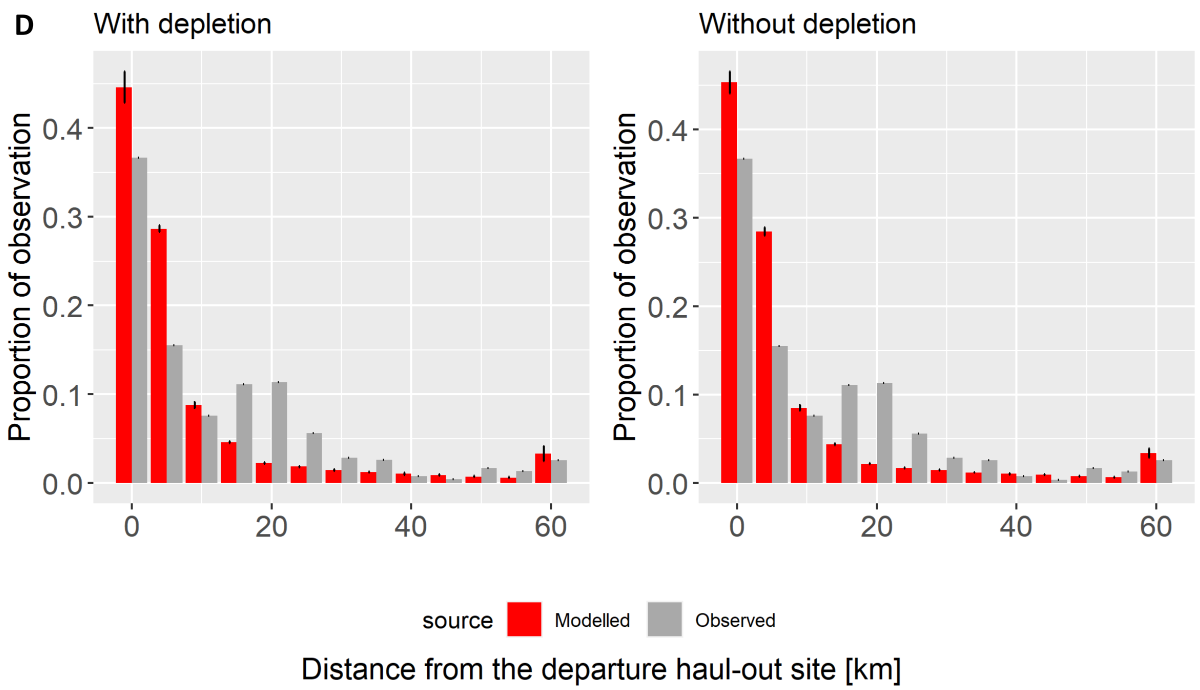
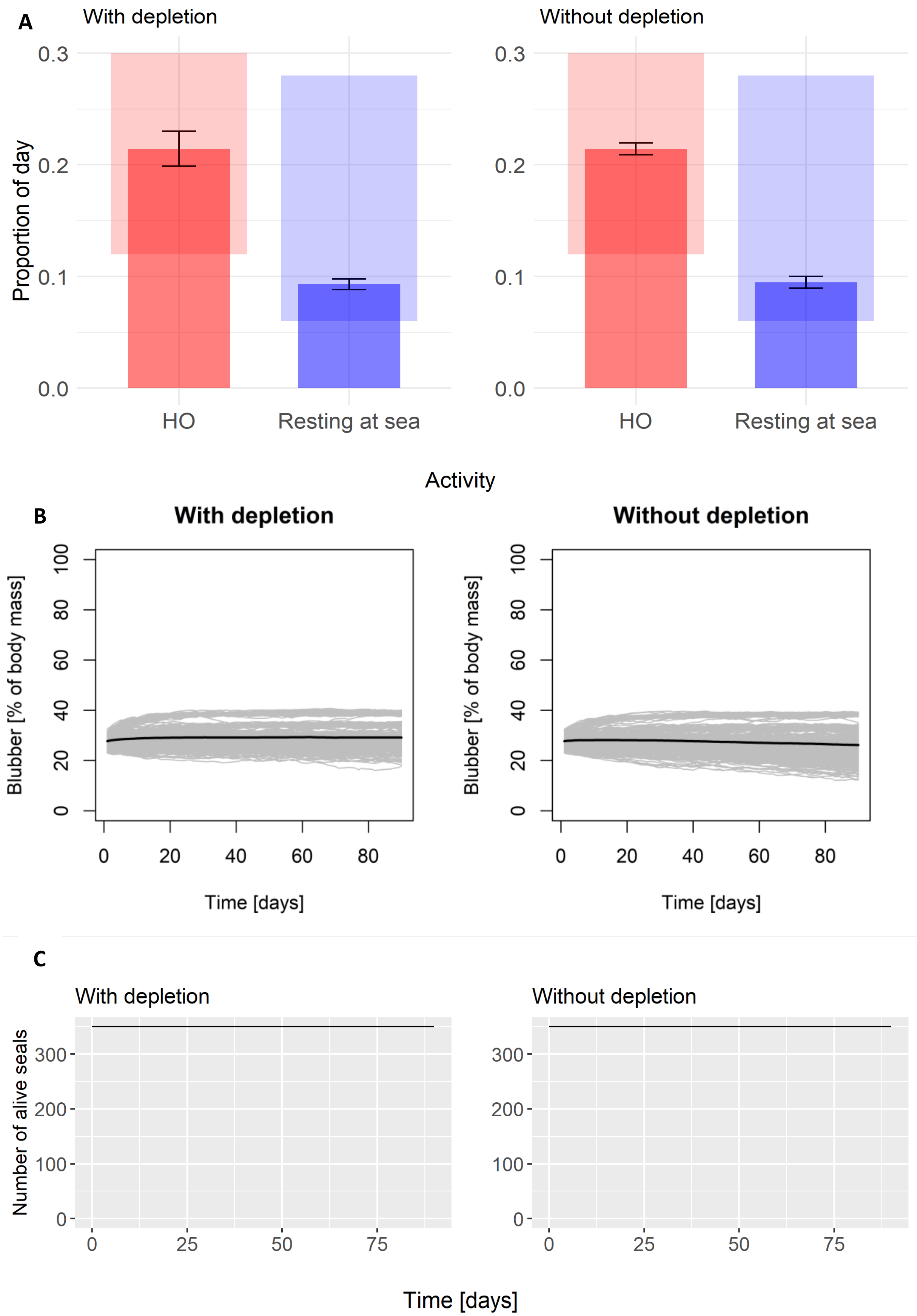


Figure 60. Modelled (red) and observed (grey) number of individually visited haul-out sites (A), frequency distribution of: trip extent (B), trip duration (C) and locations with distance the departure haul-out site (D) for the model with and without food depletion. Error bars show +/- standard deviation around means resulting from 10 replicates of the model


A
With depletion
Without depletion
Proportion of day
0.3
0.2
0.1
0.0
HO
Resting at sea
Activity
B
With depletion
Without depletion
Blubber [% of body mass]
0
20
40
60
80
100
Time [days]
C
With depletion
Without depletion
Number of alive seals
300
200
100
0
25
50
75
Time [days]

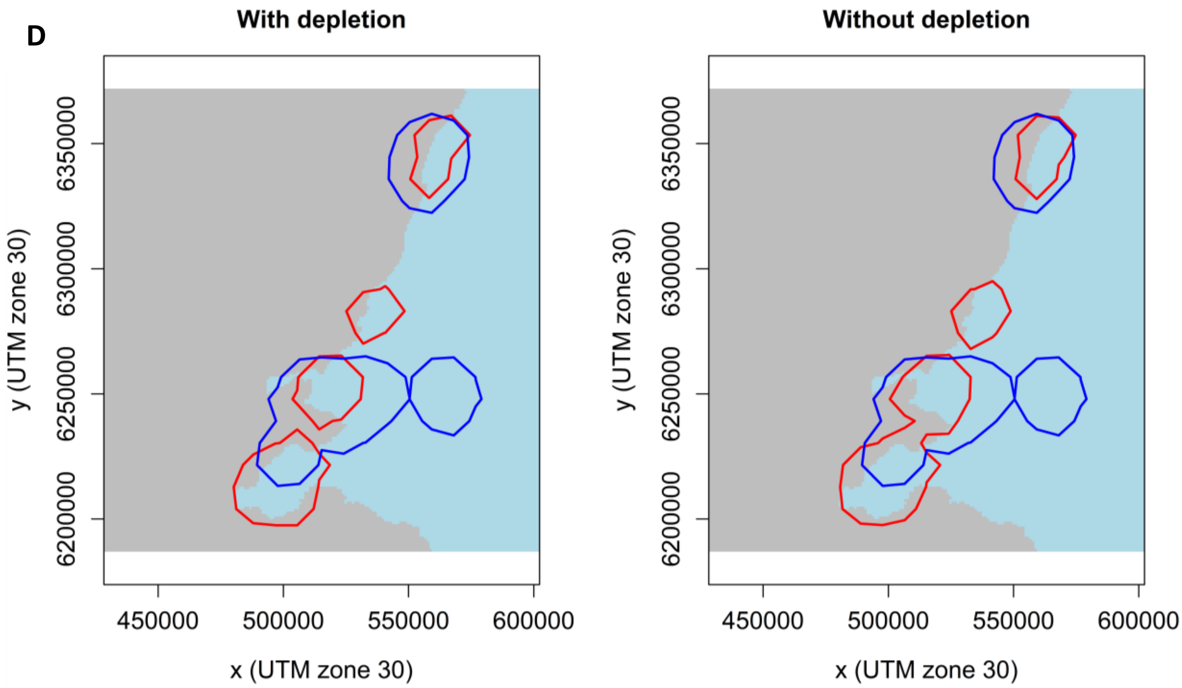
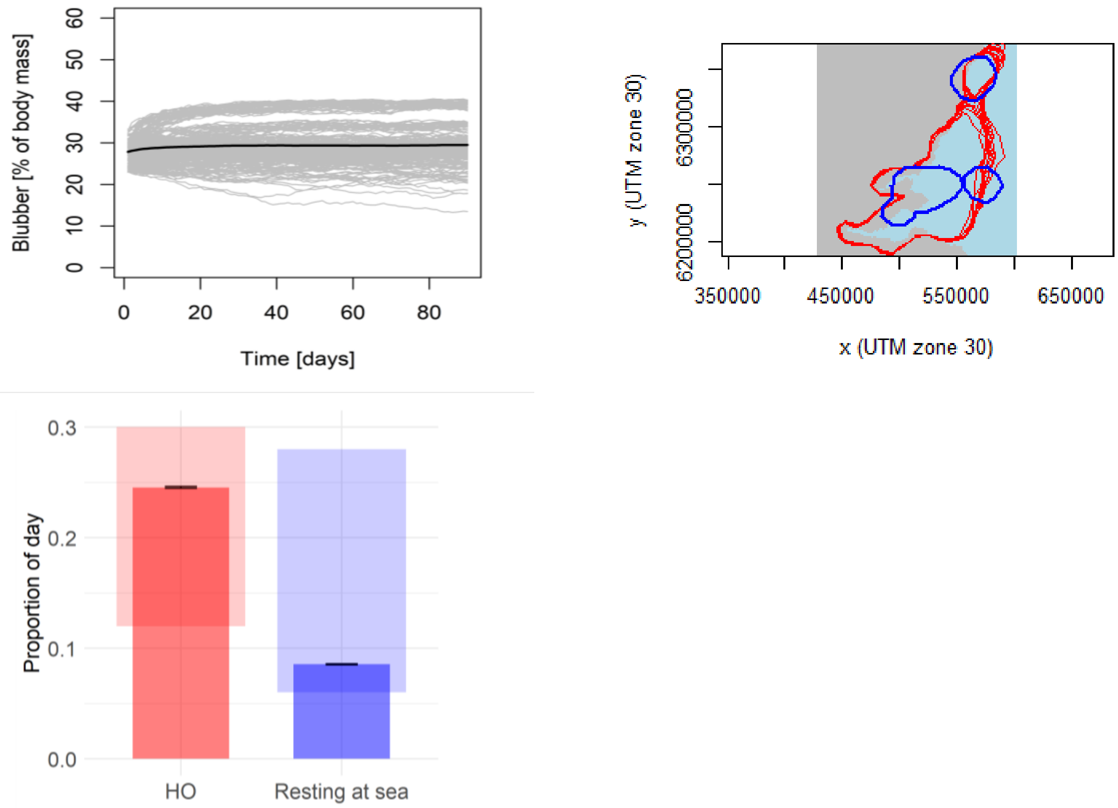


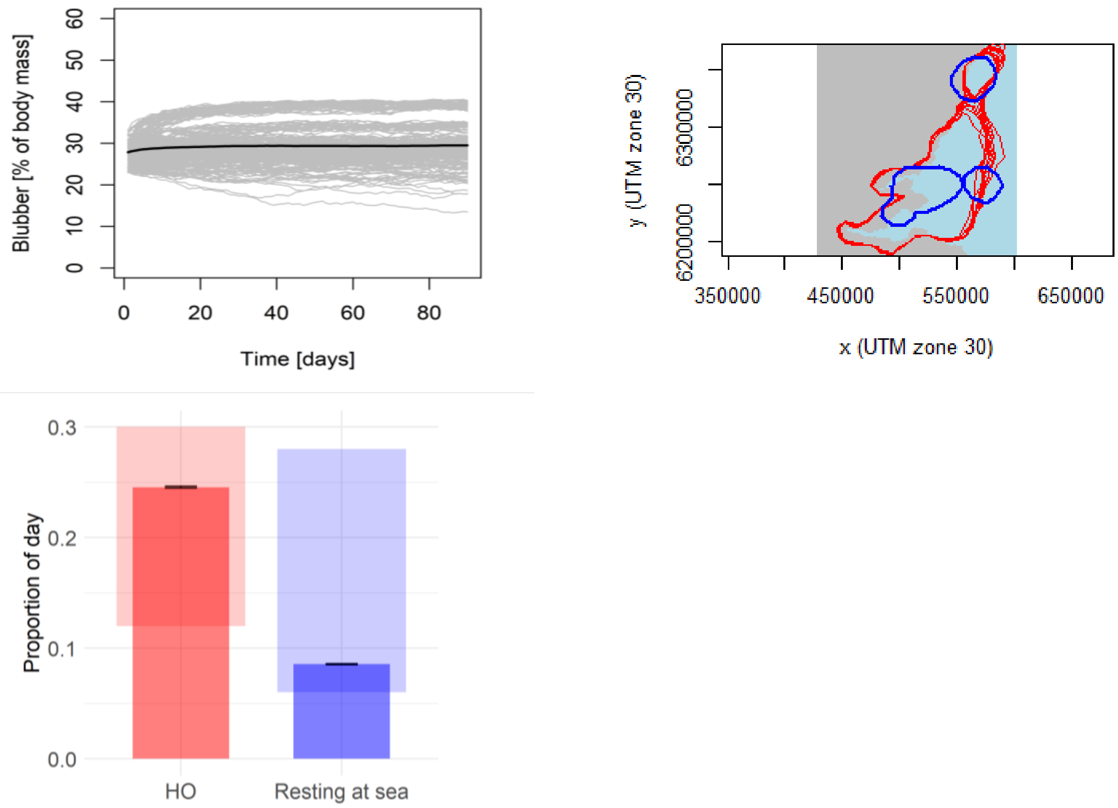
Figure 61. Comparison between the results of the modified model which had no food depletion and the main simulations (A): modelled (vertical bars) and observed (horizontal bars) mean proportion of daily time seals spend hauling-out (HO) and resting bat sea; (B) changes in blubber proportion over model duration. Black line shows overall mean. Grey lines show 350 *m*seals from a random replicate. The observed data show no change in blubber proportion in the autumn.; (C) Number of alive seals over model duration; (D) 95% kernel density contours for observed (blue) and *m*seals (red, mean for 10 replicates).

II. No memory

Removing memory driven patch choice from the model results in *m*seals travelling further away from the shore and haul-out sites. This is reflected in longer trip extents, the distribution of positions being further from the departure haul-out sites (



) and larger size and extent of 95% kernels compared to observed and emerging from the final model (Figure 63). The frequency distribution of trip durations and number of individually visited haul-out sites (



), changes in proportion of blubber and proportion of day spend resting and hauling-out (Figure 63) remain the same as the results of the main model simulations. The same tendency applies to daily fish consumption (4.4 ± 0.3 kg) and daily energy expenditure (16.0 ± 0.12 MJ). All *m*seals survive till the end of simulations.

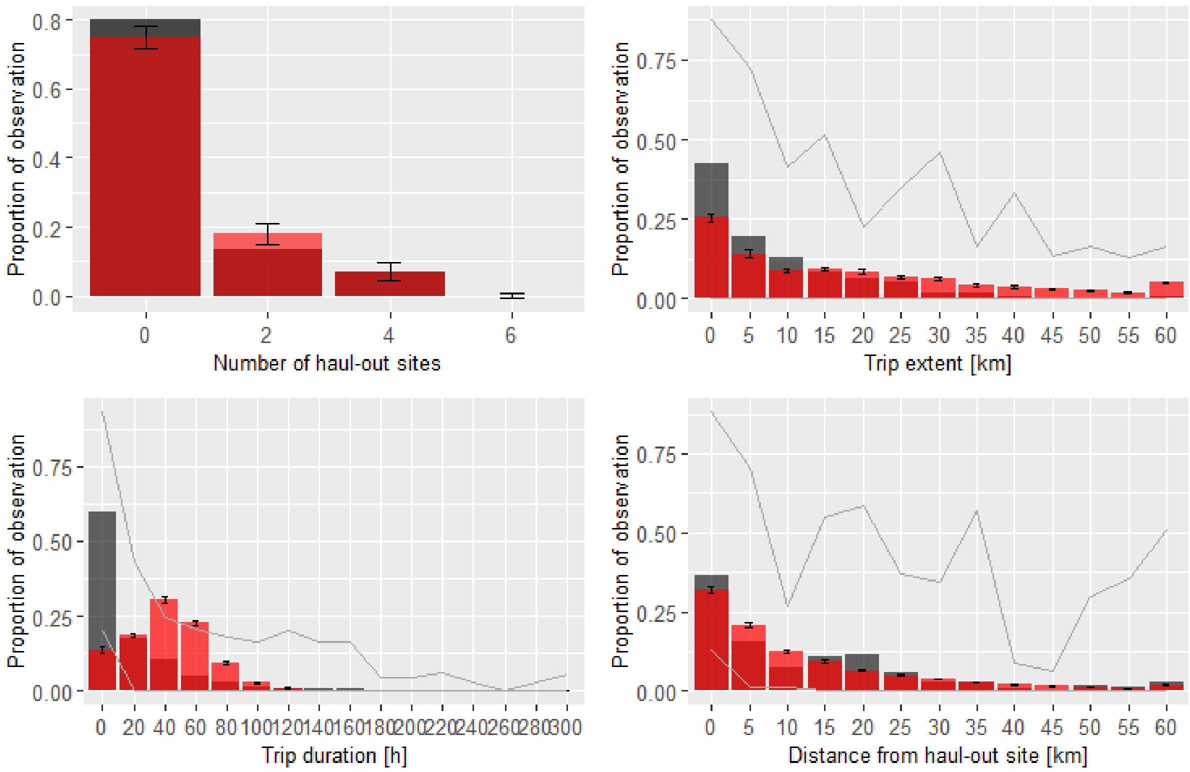


Figure 62. Modelled (red) and observed (grey) number of individually visited haul-out sites (upper left panel), frequency distribution of: trip extent (upper right panel), trip duration (lower left panel) and locations with distance the departure haul-out sites (lower right panel) for the model without memory-driven patch choice. Error bars show +/- standard deviation around means resulting from 10 replicates of the model. Grey lines show the range of

observed values. As the maximum observed values may come from different observed individuals, the sum may be different than 1.

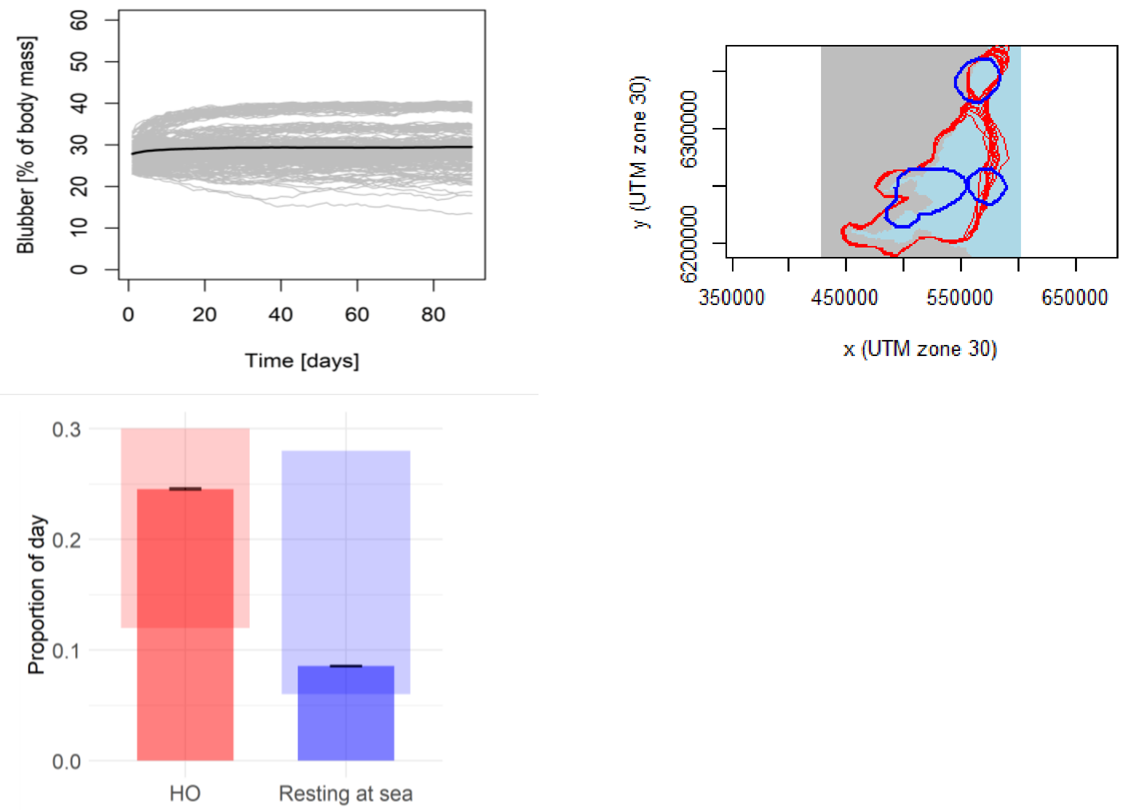


Figure 63. Results of the modified model without memory driven patch choice. Upper panel: changes in blubber proportion over model duration. Black line shows overall mean and dashed lines variation between 10 replicates. Grey lines show 350 *m*seals from a random replicate. The observed data show no change in blubber proportion in the autumn. Lower left panel: modelled (bars) and observed (horizontal polygons) proportion of time seals spend hauling-out (HO) and resting at sea; upper right panel: 95% kernel density contours for observed (blue) and *m*seals (red). Modelled kernels are shown separately for 10 replicates of the model.

III. Modified HSI

a) Randomly distributed hot spots

Changing underlying habitat suitability map does not affect frequency distribution of trip duration and number of visited haul-out sites in comparison to the results of the main model. It does, however, showed higher proportion of very short trips in comparison to the final model (Figure 64, Figure 52). The spatial distribution expressed by 95% kernels shows similar 'core' distribution but much larger offshore extent in comparison to the results of observed seals and final simulations. This larger extent is, however, driven by few individuals which explored some of the 'hot spots'. The majority of *m*seals stay, however, close to the shore (

Figure 65). The modification of the habitat results in larger proportion of time *m*seals spent hauling-out and less resting at sea in comparison to the final model, slightly increase in proportion of blubber by the end model duration (7.8 ± 0.5 %) (

Figure 65) resulting from larger fish consumption (7.0 ± 0.4 kg), and increased daily energy expenditure (18.2 ±0.6 MJ/day) due to increased time spent digesting. *M*seals depleted up to 8% of the resources, (Figure 66). All *m*seals survive till the end of simulations (Figure 65D).

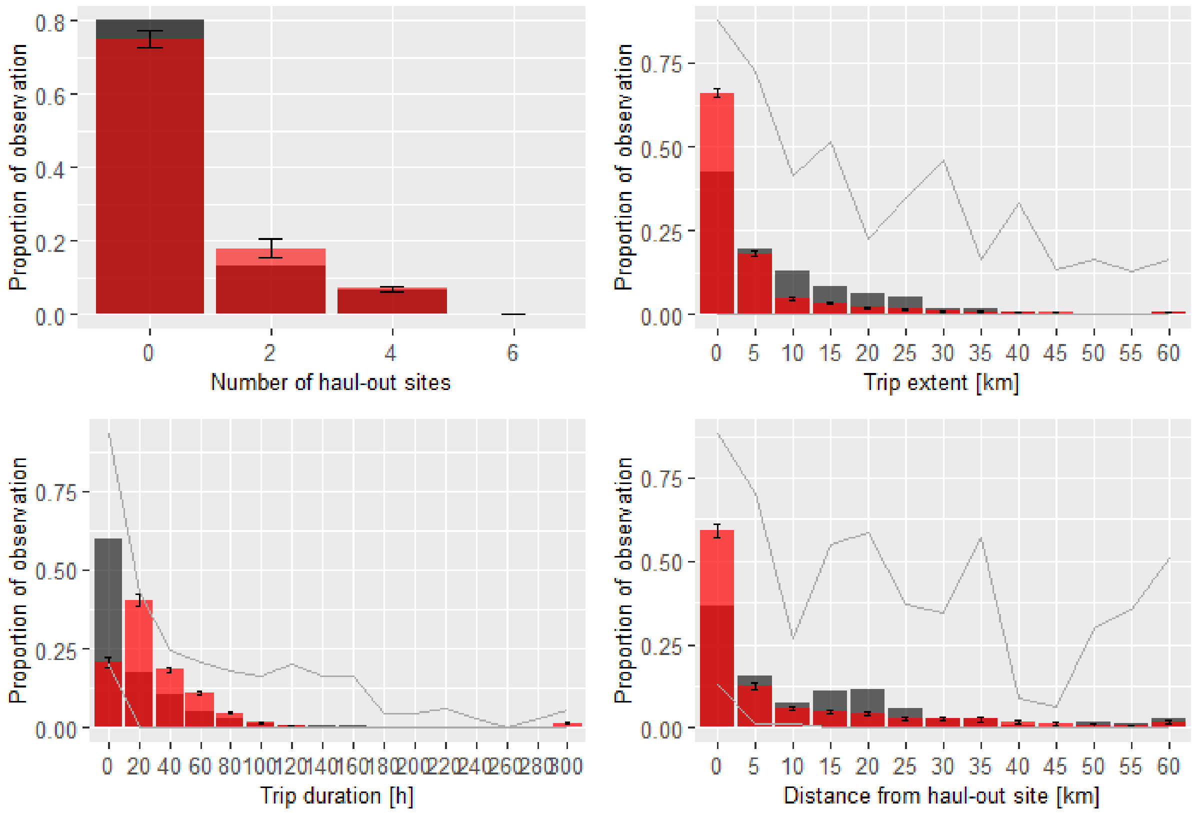


Figure 64. Modelled (red) and observed (grey) number of individually visited haul-out sites (upper left panel), frequency distribution of: trip extent (upper right panel), trip duration (lower left panel) and locations with distance from the departure haul-out site (lower right panel) for the model with modified habitat suitability. Error bars show +/- standard deviation around means resulting from 10 replicates of the model. Grey lines show the range of observed values. As the maximum observed values may come from different observed individuals, the sum may be different than 1.

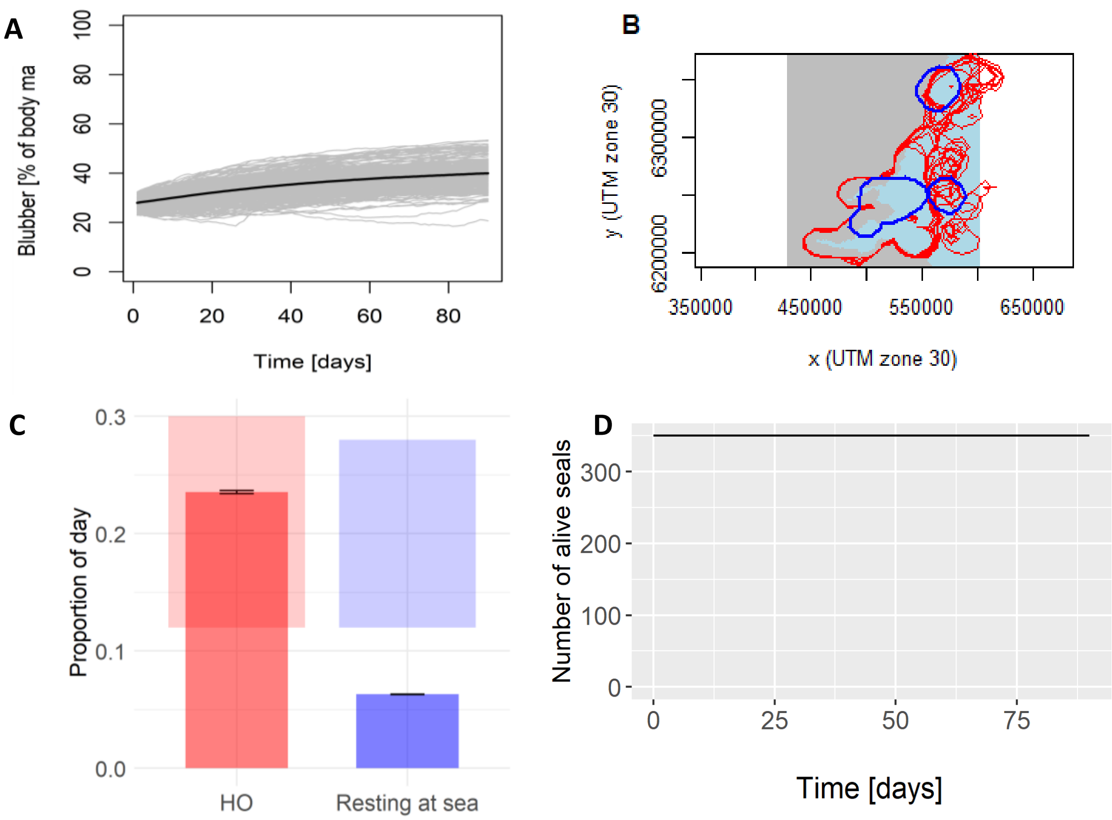


Figure 65. Results of the model with modified habitat suitability. A: changes in blubber proportion over model duration. Black line shows overall mean and dashed lines variation between 10 replicates (variations are very small). Grey lines show 350 *m*seals from a random replicate. The observed data show no change in blubber proportion in the autumn; B: 95% kernel density contours for observed (blue) and *m*seals (red). Modelled kernels are shown separately for 10 replicates of the model; C: modelled (bars) and observed (horizontal

polygons) proportion of time seals spend hauling-out (HO) and resting at sea; D: number of alive seals over model duration.

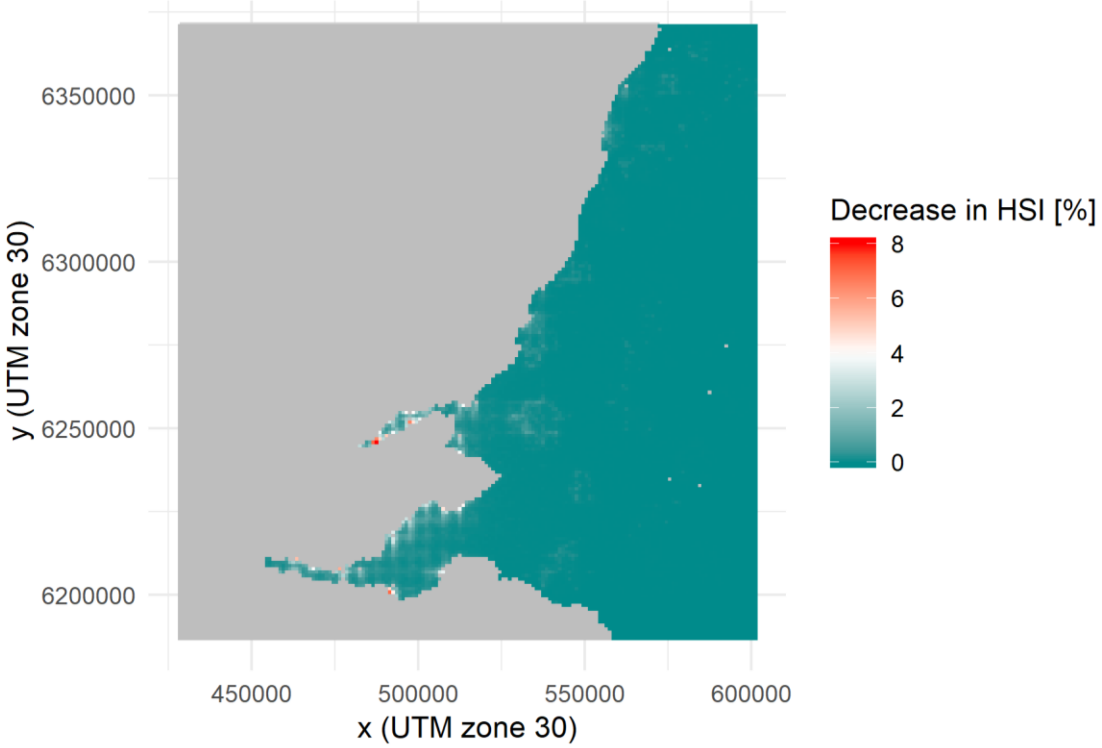


Figure 66. Food depletion expressed at percentage change of habitat suitability index between beginning and end of the model simulation for the model with modified habitat suitability index.

b) Uniformly distributed prey

*M*seals moving over uniformly distributed habitat consumed similar amount of fish as observed and as in the final model simulation (mean 4.1 kg/day in modified model). Similarly, to the final simulation, none of the *m*seals died (Figure 68A and D). All modelled individuals showed similar decrease in blubber and there was no division between *m*seals which would remain fat over the entire model duration and skinny seals. Distribution of seals was comparable to the final simulation (Figure 68B) which is also reflected in similar time spent hauling-out and resting at sea as (Figure 68A) and trip characteristics as in the main model (Figure 67B-D, Figure 69). The site fidelity of *m*seals was also comparable (Figure 70). Number of visited haul-out sites did not differ between this model modification and the main model (Figure 67A).

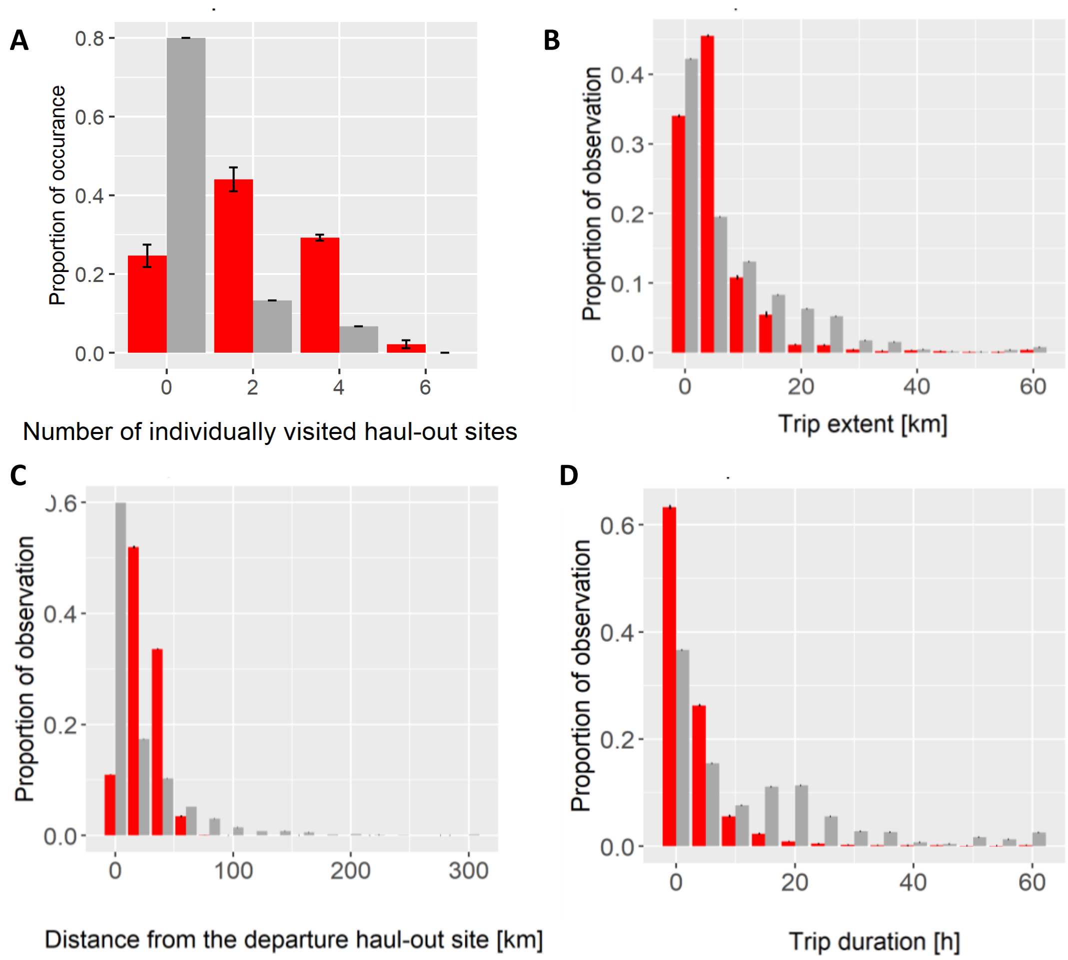


Figure 67. Modelled (*m*seals, red) and observed (grey) (A) frequency distribution of number of individually visited haul-out sites; frequency distribution of: (B) trip extent; (C) trip

duration; and (D) distribution of at-sea positions with distance from the departure haul-out site for seal foraging over habitat with uniformly distributed prey.

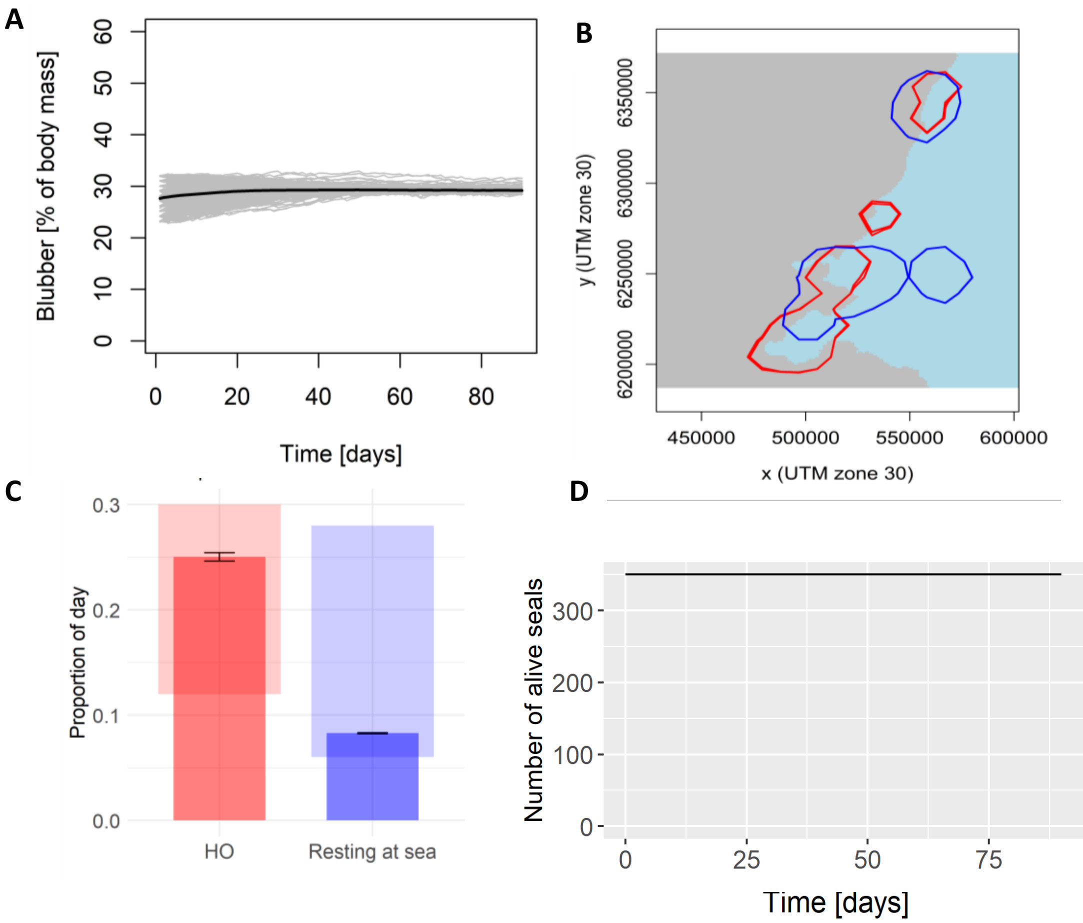


Figure 68. (A) Changes in blubber proportion over model duration. Black line shows overall mean. Grey lines show 350 *m*seals from a random replicate. The observed data show no change in blubber proportion in the autumn; (B) 95% kernel density contours for observed (blue) and modelled (red) seals; (C) Modelled (bars) and observed (horizontal polygons) proportion of time seals spent hauling-out (HO) and resting at sea; (D) Number of alive

*m*seals over three months simulations for seal foraging over habitat with uniformly distributed prey.

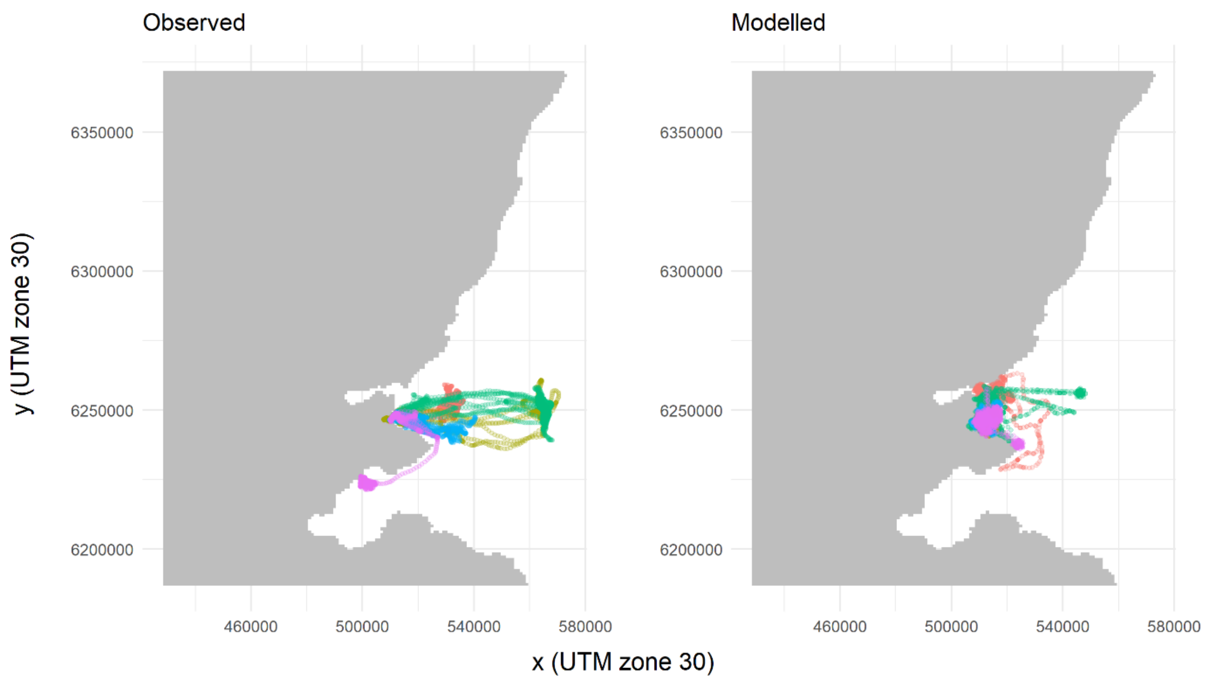


Figure 69. Foraging trips for five random observed (left panel) and five modelled (*m*seals, right panel) seals represented by point for seal foraging over habitat with uniformly distributed prey.

Figure 70. Frequency distribution of number of squares (5x5 and 25x25 km) which overlapped between consecutive foraging trips for five random observed (grey) and five random modelled (*m*seals, red) seals whose tracks are shown in Figure 70 for seal foraging over habitat with uniformly distributed prey

7. Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that are not used, and preferably not even known, while the model is developed, parameterised, and verified. By documenting model output corroboration, model users learn about evidence, which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

Testing the model on independent data - data coming from a different region and population, is a subject of separate projects. Results of these projects will be presented in a different publication. The model will be applied to harbour seals off the Dutch coast and from inner Danish waters (Kattegat). It is very likely that the model would have to be re-parameterised in order to reproduce patterns observed in other areas.

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9. Model code

Model code and all input files necessary to run the model, as well as, instruction how to run the model can be found in online repository https://github.com/MagdaChu/AgentSeal.