Marine Mammal Scientific Support Research Programme MMSS/001/11

MR 5.1:

Report

At-sea usage and activity

Sea Mammal Research Unit
Report to
Scottish Government

July 2015 [version F2]

The citation information is provided separately for each sub-task on page 2

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Editorial Trail			
Main Author	**Comments**	**Version**	**Date**
B. McConnell	collation of individual sub-task reports	V1	25/01/2015
B. McConnell, D. Thompson	addition of information to original report	V2	11/03/2015
Marine Scotland	comments	V3	22/04/2015
P. Irving, J. Williamson	review	V4	27/04/2015
B. McConnell	review	V5	16/06/2015
B. McConnell	review	VF1	29/07/2015
O. Racu	final editing	VF2	15/08/2015

<ins>Citation information for each sub task</ins>

Jones, E. L., McConnell, B. J., Sparling, C. & Matthiopoulos, J. (2015) Produce, publish and maintain seal usage maps with confidence intervals. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 6pp.

Jones, E. L, Smout, S., Morris, C. D. & McConnell, B. J. (2015) Determine data sparse regions. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 12pp.

Jones, E. L., Smout, S. & McConnell, B. J. (2015) Review the extent of how new survey data affect usage estimates. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 2pp.

Russell, D. J. F. (2015) Classify activity between foraging and travelling usage using a state-space model approach. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 5pp.

Russell, D. J. F. (2015) Determine environmental covariates of preference for all activity, and foraging activity. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 7pp.

Jones, E. L., Smout, S. & McConnell, B.J. (2015) Determine environmental covariates for usage preference around the UK. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MR 5.1, St Andrews, 18pp.

Contents

1 Introduction 5
1.1 Explanation of mapping usage and habitat preference 5
2 MR5.1.1 Produce, publish and maintain seal usage maps with confidence intervals 6
2.1 Executive summary 6
2.2 Results 6
2.3 References 6
3 MR5.1.2 Determine data sparse regions 7
3.1 Executive summary 7
3.2 Introduction 7
3.3 Methods 7
3.4 Results 9
3.4.1 Grey seals 9
3.4.2 Harbour seals 9
3.5 Recommendations 15
3.5.1 Grey seals 15
3.5.2 Harbour seals 16
3.6 Discussion 16
3.7 References 17
3.8 Acknowledgements 18
3.9 Appendix 19
4 MR5.1.3 Review the extent of how new survey data affect usage estimates 21
4.1 Executive summary 21
4.2 Introduction 21
4.3 Methods 21
4.4 Results 21
4.5 Discussion 21
5 MR5.1.4 Classify activity between foraging and travelling usage using a state-space model approach 23
5.1 Executive summary 23
5.2 Introduction 23
5.3 Methods 24
5.3.1 Data 24
5.3.2 State space modelling approach 24
5.4 Results 25
5.5 Discussion 27
5.6 References 28
6 MR5.1.5 Determine environmental covariates of preference for all activity, and foraging activity 29
6.1 Executive summary 29

6.2 Introduction 29
6.3 Methods 30
6.3.1 Environmental data 30
6.3.2 Modelling 30
6.4 Results 31
6.4.1 Grey seals 31
6.4.2 Harbour seals 33
6.5 Discussion 34
6.6 References 36
7 MR5.1.6 Determine environmental covariates for usage preference around the UK 37
7.1 Executive summary 37
7.2 Introduction 37
7.3 Methods 37
7.3.1 Movement data 37
7.3.2 Environmental data 38
7.3.3 Modelling 39
7.4 Results 40
7.4.1 Grey seals 40
7.4.2 Harbour seals 43
7.5 Conclusions 44
7.6 References 45
7.7 Appendix 47

1 Introduction

Within this task there were six subtasks:

- MR5.1.1 Produce, publish and maintain seal usage maps with confidence intervals.
- MR5.1.2 Determine data sparse regions.
- MR5.1.3 Review the extent of how new survey data affect usage estimates.
- MR5.1.4 Classify activity between foraging and travelling usage using a state-space model approach.
- MR5.1.5 Determine environmental covariates of preference for all activity, and foraging activity.
- MR5.1.6 Determine environmental covariates for usage preference around the UK.

1.1 Explanation of mapping usage and habitat preference

Three different approaches have been used to predict the distribution of seals around the UK.

Usage maps based on kernel-smoothing existing telemetry data. These map the intensity of space use based directly on locations observed from tagged animals. The full usage maps also use a simple spatial model (a ‘null model’), so that areas where telemetry data are absent can be included. The null model is based on available telemetry and represents a fitted relationship between the intensity of usage and the distance from shore/haul-out site. The model predicts a simple smooth decay in the intensity of usage with distance, and so cannot capture the complexity of usage patterns seen in data-rich areas. Usage maps are scaled according to the size of local populations inferred from counts at onshore haul-out sites, so that the total over the whole predicted surface should be equal to the total seal population summed over the entire UK.

Usage maps based on habitat preference. Habitat preference models were developed in which observed telemetry data were associated with explanatory variables such as sea bottom temperature, depth and thermal stratification (these may represent processes such as biological production in the marine environment). The models take into account the fact that the marine environment changes regionally, and uses these relationships to predict usage in areas where telemetry data cannot be obtained but environmental data are available at an appropriate resolution. The models can then predict intensity of use at sea given an underlying map of these habitat variables. Predictions of at-sea usage take into account the number of seals that are observed locally, onshore. The total over the whole predicted surface should be equal to the total seal population of the UK.

Activity-specific preference in the North Sea. To investigate whether seal habitat preference differs with regard to activity (e.g. foraging) foraging and overall habitat preference for the North Sea were compared using a subset of variables. For harbour seals there were only marginal differences between overall and foraging preference whereas in grey seals the difference was more marked. The predictions based on foraging preference can be used to highlight important areas for these seals foraging in the North Sea. Because they are based on foraging, these preference maps are not analogous to usage but represent the percentage of foraging seals predicted to be in each cell at any one time. The total over the whole predicted surface sums to 100%.

2 MR5.1.1 Produce, publish and maintain seal usage maps with confidence intervals

Jones, E. L., McConnell, B. J., Sparling, C. & Matthiopoulos, J.

2.1 Executive summary

Grey and harbour seal usage maps have been published updated to incorporate data up to 2013.

2.2 Results

Seal usage maps were developed to characterise the spatial distribution of grey and harbour seals around the UK. Subsequently, these maps were updated in 2013 to reflect additional telemetry and survey data, and incorporate software developments GIS layers and a detailed report can be downloaded from Marine Scotland Interactive:

http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/Themes/usage.

A manuscript based on this work is currently in review: (Jones, E.L. *et al.*, in press).

2.3 References

Jones, E. L., McConnell, B. J., Smout, S., Hammond, P. S., Duck, C. D., Morris, C. D., Thompson, D., Russell, D. J. F., Vincent, C., Cronin, M., Sharples, R. & Matthiopoulos, J. (in press) Patterns of space use in sympatric marine colonial predators reveals scales of spatial partitioning. *Marine Ecology Progress Series*.

3 MR5.1.2 Determine data sparse regions

Jones, E. L, Smout, S., Morris, C. D. & McConnell, B. J.

3.1 Executive summary

The deployment of telemetry tags on UK seals is patchy both in space and time. The data-sparse regions around the UK were identified. This will allow future targeted regional deployments of telemetry tags to improve in the synoptic usage maps produced under MR5.1.1.

The criteria for classifying regions as *data sparse* were defined as:

- No telemetry data have been collected; or
- The underlying population of seals are known to have recently increased significantly, and although telemetry data exist, there is a strong possibility that at-sea distribution may have changed.
- Existing telemetry data is over 10 years old and sample size of telemetry data is unrepresentative of the seal population in an area.

Based on these criteria, recommendations were made about where future tagging effort should be directed.

3.2 Introduction

The deployment of telemetry tags on seals around the UK is patchy both in space and time. The objective of this report is to identify data-sparse regions around the UK.

Telemetry deployments on grey seals have been carried out using SMRU tags since 1985 (McConnell *et al.*, 1992a). Although many hundreds of grey and harbour seals have been tagged over the past 30 years, there are regions around the UK where little or no telemetry data exist. In addition, there have been temporal changes in the underlying populations of both species (Thomas 2013; Lonergan *et al.*, 2007; Duck *et al.*, 2013), and the way that seals use geographical space may alter over time. Populations of animals in some areas are known to have increased considerably since the most recent tag deployments. In these areas it is important that additional deployments are considered so that a representative sample of the population can be tagged to capture the spatial behaviour of enough individuals that population-level inferences can be drawn. The analysis below is based on identifying regions where:

- No telemetry data have been collected; or
- The underlying population of seals are known to have recently increased significantly, and although telemetry data exist, there is a strong possibility that at-sea distribution may have changed.
- Existing telemetry data is over 10 years old and sample size of telemetry data is unrepresentative of the seal population in an area.

To make the strongest possible inference, the entire UK and Irish telemetry datasets were analysed.

3.3 Methods

Movement data: Telemetry data from grey and harbour seals were from two types of logging device: Satellite Relay Data Logger (SRDL) tags that use the Argos satellite system for data transmission and GPS phone tags that use the GSM mobile phone network with a hybrid Fastloc protocol (Argos User's Manual 2011; McConnell *et al.*, 2004). Telemetry data were processed through a set of data-cleansing protocols to remove null and missing values, and duplicated records from the analysis. Positional error, varying from 50m to over 2.5km affects SRDL telemetry points. Errors were assigned by the Argos system to six location quality classes. A Kalman filter was developed to obtain position estimates accounting for observation error (Royer & Lutcavage, 2008). SRDL data were first speed-filtered at 2ms^{-1} to eliminate outlying locations that would require an unrealistic travel speed (McConnell *et al.*, 1992b). Observation model parameters were provided by the location quality class errors (Vincent *et al.*, 2002) and process model parameters were derived by species from the average speeds of all GPS tags. GPS tags are generally more accurate than SRDL tags and 75% of locations have an expected error of less than or equal to 55m (Dujon *et al.*, 2014). However, occasional outliers were excluded using thresholds of residual error and number of satellites. Movement SRDL data were interpolated to 2-hour intervals using output from the Kalman filter and merged with linearly interpolated GPS data that had been regularised to 2-hour intervals. Data from 259 grey seal tags (Appendix Table 1) and 277 harbour seal tags were used (Appendix Table 2). Tag deployment occurred outside each species' moulting seasons, and tag deployment lasted on average for 4.1 months for grey seals and 3.3 months for harbour seals. Telemetry data were primarily collected between June and December for grey seals, and between January and June for harbour seals.

Terrestrial count data: Grey and harbour seals are surveyed during August when harbour seals are moulting and haul-out on land for an extended period. During standard aerial surveys all seals along a specified coastline are counted and coordinates are recorded to an accuracy of up to 50m. Surveys take place within two hours of low tide when low tide is between 12:00 and 18:00 hours. (Lonergan *et al.,* 2011; Thompson *et al.,* 2005). Ground and boat count data collected by other organisations were also used in the analysis, and all sources of data collection are summarised in Appendix Table 3.

Offshore marine renewables: Polygons of wind farms (operational, under construction, consented, in planning, pre-planning, and search areas), tidal turbines, wind power installations, and export cable agreements were obtained as GIS files from The Crown Estate (2014).

Analysis: Data-sparse areas were identified in three separate analyses as: (1) areas where animals had been observed during terrestrial count surveys but where no tagged animals had hauled-out; (2) areas where telemetry data had previously been collected but where significant increases in the underlying population may have caused redistribution of animals at-sea; and (3) the only available telemetry data were over 10 years old and the number of telemetry trips per terrestrial count was less than 0.1. These were arbitrary thresholds, chosen so that a visual assessment of the data was possible and a reasonable number of discrete areas could be chosen.

The analysis was conducted using R 3.1.2 (R Development Team, 2014) and maps were produced using Manifold 8.0.28.0 (Manifold Software Ltd, 2013). Using the seal usage map software described in Jones *et al.,* (2013), 5x5km^2 haul-out sites were identified from terrestrial counts:

- A haul-out was termed as a 'null haul-out' if no tagged animals had visited that site, according to the telemetry data.
- Haul-outs that had been visited by tagged animals were termed as 'telemetry haul-outs'. Seals move between different haul-out sites. If an animal had never been to a haul-out with associated terrestrial data during the time it was tagged, count information was assigned from the nearest haul-out based on Euclidean distance. Individual animal's movements at-sea were divided into trips, defined as the sequence of locations between defined haul-out events and each location in a trip was assigned to a haul-out site. The number of trips associated with each telemetry haul-out was calculated, and 'trips per seal' was derived by dividing the number of trips by the most recent terrestrial count.

Once specific data-sparse areas were identified for future tag deployments, a recommended number of tags was calculated for each area. This was based on the numbers of surveyed animals, tagged animals and trips in areas where data were considered adequate to estimate usage robustly. The estimated minimum number of trips needed per seal observed during surveys was set at 0.1 trips per seal.

3.4 Results

3.4.1 Grey seals

Figure 3.1 shows 259 grey seal tracks from telemetry deployments between 1991 and 2013. Many terrestrial count locations have surveys from multiple years associated with them and so only the most recent count is shown. Although telemetry deployment locations are localised, there is good at-sea coverage of telemetry data around the UK due to individual grey seals travelling large distances.

- Data-sparse areas were selected visually where there were (a) greater than around 100 animals associated with the null haul-out(s), and (b) few telemetry data in the vicinity of the null haul-outs(s) (Figure 3.1):
  - West Shetland (Papa Stour), which is around 40km from the Aegir wave power installation currently in development.
  - South-west coast of Orkney (Scapa Flow and Pentland Skerries in the Pentland Firth), an area where there are a number of wave and tidal development being built or at planning phase.
  - Inner Moray Firth, east Scotland, that is close to consented offshore wind farm developments.
  - Ards Peninsula and Strangford Lough, Northern Ireland, which are close to the Strangford Lough tidal development, and the planned Mull of Galloway tidal array. This is an area where few telemetry data have been collected.

- Donna Nook and Blakeney Point, East Anglia, had telemetry deployments in 2005. However, the grey seal population in this area has increased dramatically in recent times (pup production increased 15% from 2,566 in 2010 to 3,359 in 2012 (SCOS, 2013)), and they are in close proximity to many planned and operational offshore wind farms (Figure 3.2).

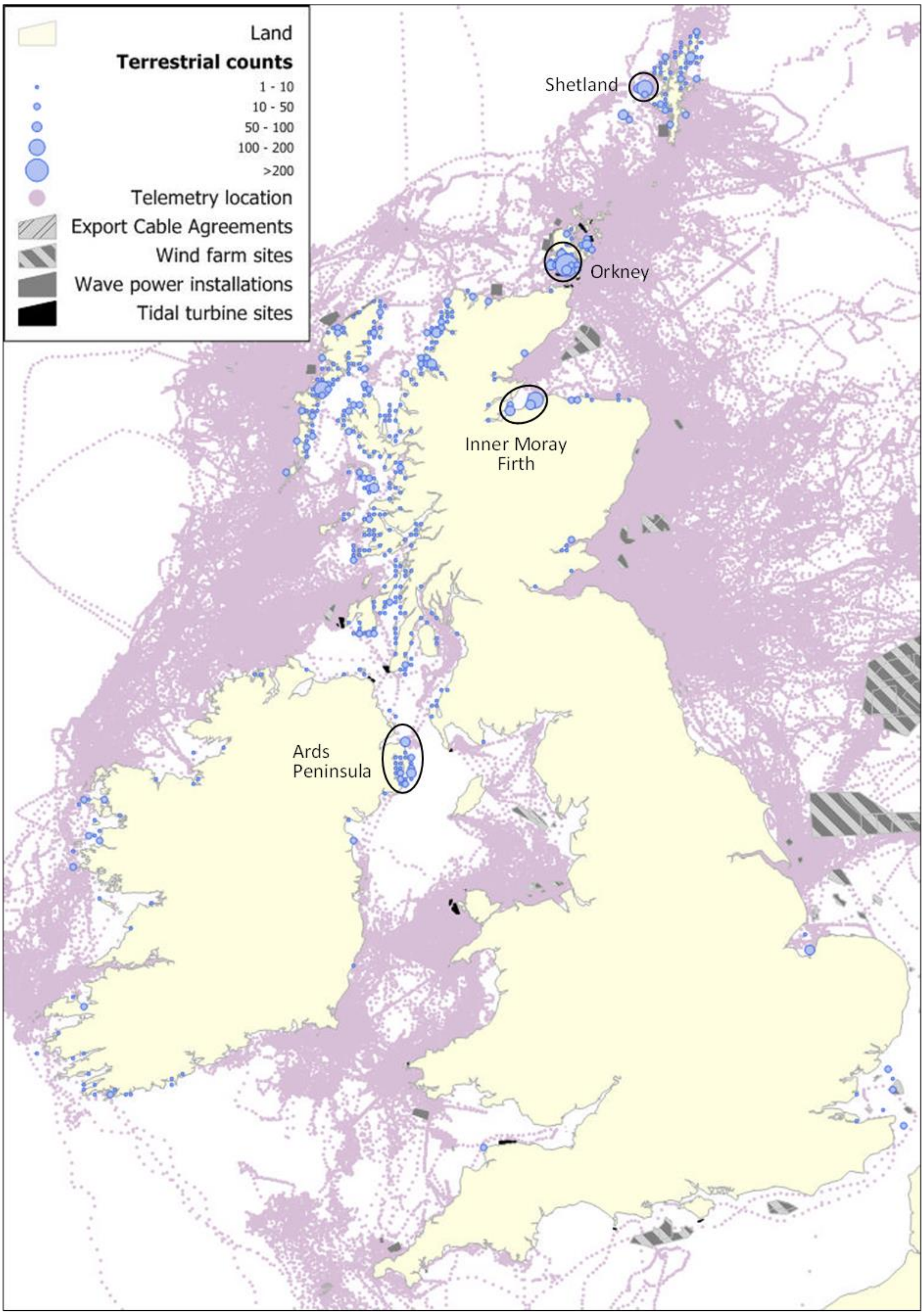
- Only 30% (77 of 259 animals) of telemetry deployments have occurred since 2006, so additional data-sparse regions were selected where (a) all telemetry data in the area were more than 10 years old, and (b) there were less than 0.1 trips per seal (Figure 3.2):
  - Moray Firth, east Scotland (Brora to Lossiemouth) is close to four consented offshore wind farm developments (Beatrice, Z1 Stevenson, Z1 Telford, Z1 MacColl) and Beatrice demonstrator site.
  - East Ireland (Lambay Island). The nearest offshore renewable developments are around 100km from this area.
  - Scroby Sands, East Anglia is in direct proximity to the operational Scroby Sands offshore wind farm, and is also close to many other planned offshore wind farms.

3.4.2 Harbour seals

Figure 3.3 shows 277 harbour seal tracks from deployments between 2003 and 2013. Although a comparable number of tags have been deployed on both species, there are many more ‘null haul-outs’ for harbour seals because their at-sea and on-land spatial distributions are different from grey seals: they primarily stay within 50km of their haul-out sites (Jones *et al.*, in press), and haul-out in less aggregated groups.

- Data-sparse regions identified for harbour seals are:
  - Central mainland Shetland (east and west coasts), where there are few telemetry data, particularly on the west coast and the area is close to the Aegir wave power installation currently in development.
  - South-west Orkney (Scapa Flow), an area where a number of wave and tidal developments are being built or at planning phase.
  - Summer Isles, north-west Scotland where there are few telemetry data within 50km of the area. However there are no planned offshore marine renewable developments within 100km.

    - South Uist, Outer Hebrides, West Scotland and Inner Hebrides (from southern Skye to Isle of Mull), and Donegal Bay and Carlingford Lough, Ireland, where there are few telemetry data available. However, there are no offshore marine renewables planned in the vicinity.
    - No areas where there have been large increases in the population that may result in at-sea redistribution (and where contemporary tags are not available) were identified.
- For harbour seals, over 70% of telemetry data have been collected since 2006 (Figure 3.4). The only data-sparse region where tags were deployed more than 10 years ago (2003) is Shetland and there were less than 0.1 trips per seal, which shows that a small sample of the population were tagged. However, since that time the harbour seal count has declined by 38% from 4,883 during the 2000-2005 census to 3,039 during the 2007-2012 census (Duck *et al.*, 2013).



(1)

Figure 3.1. Grey seal tracks showing: existing historical telemetry locations (purple), terrestrial moult counts of null haul-out sites (blue), and offshore marine renewable installations (grey and black). Recommended areas for future telemetry deployments are shown outlined in black.

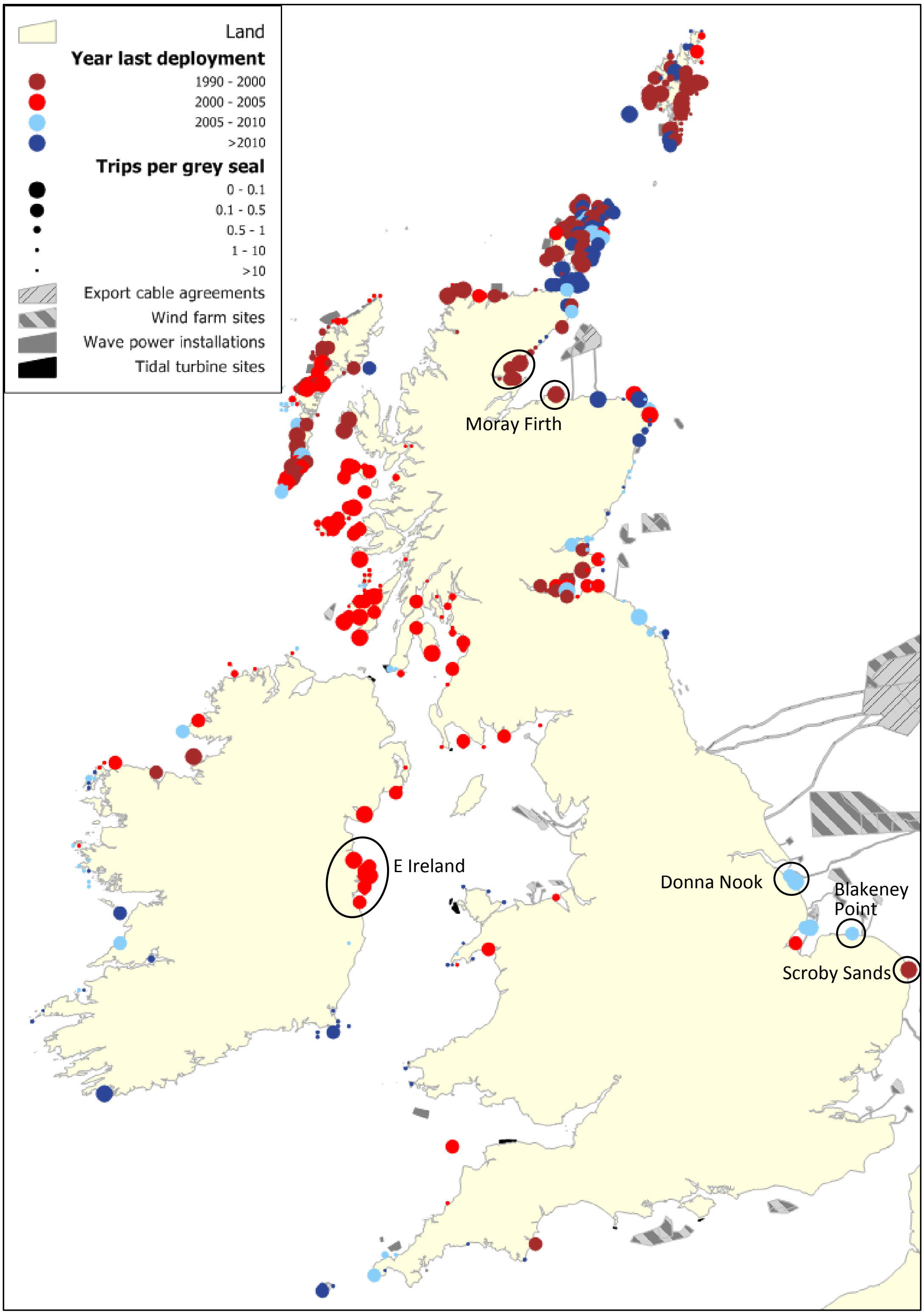


Figure 3.2. Recommendations for future tagging effort for grey seals (black outlines) based on the age of most recent telemetry deployment (red = >10 years), and trips per seal (<0.1), and few or no more recent telemetry data are present in the area. In addition, Donna Nook and Blakeney Point have been identified as areas where future telemetry tagging effort should be concentrated due to the recent increases in population at these sites. Recommended areas for future telemetry deployments are shown outlined in black.

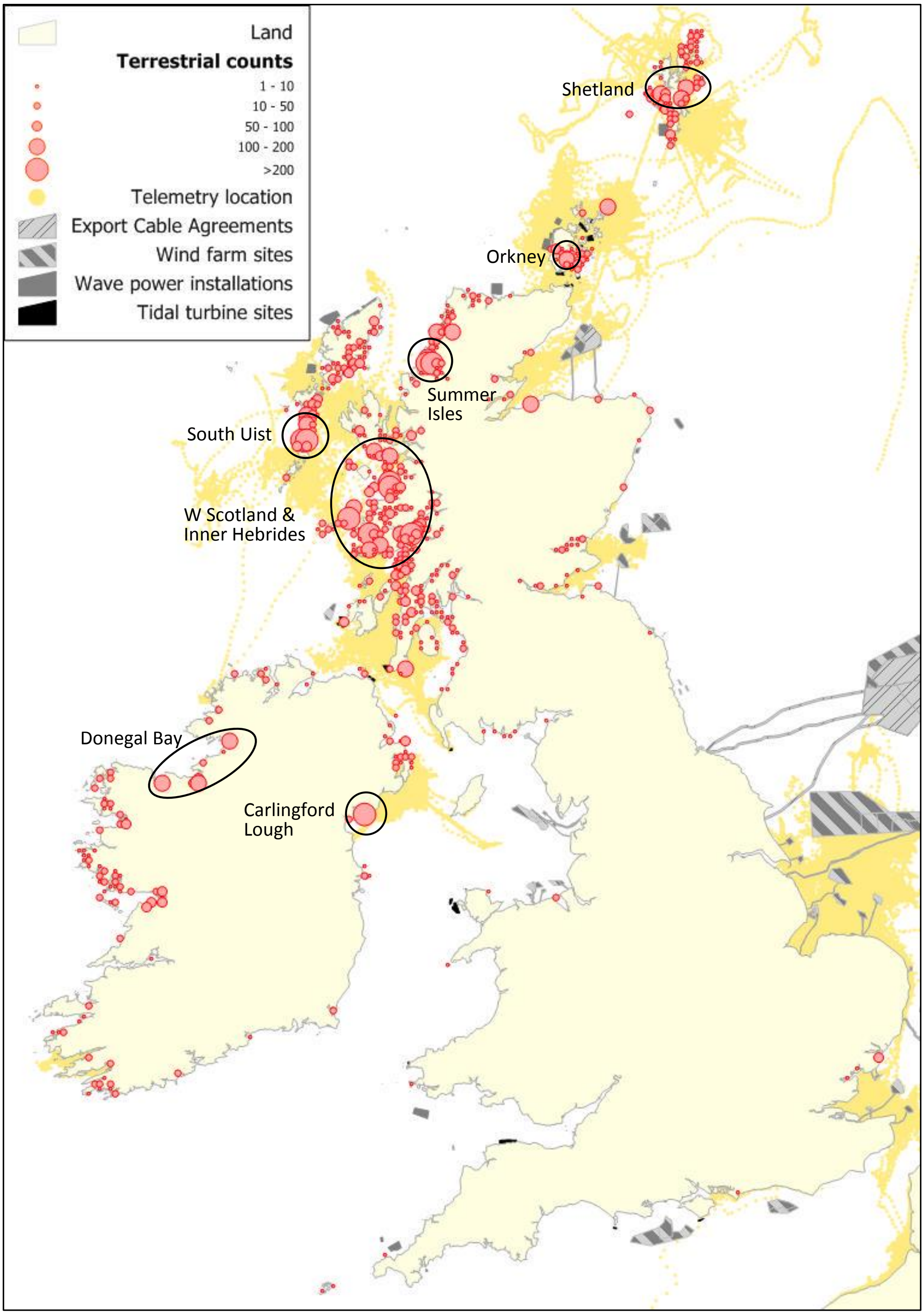


Figure 3.3. Harbour seal tracks showing: existing historical telemetry locations (yellow), terrestrial moult counts of null haul-out sites (red), and offshore marine renewable installations (grey and black). Recommended areas for future telemetry deployments are shown outlined in black.

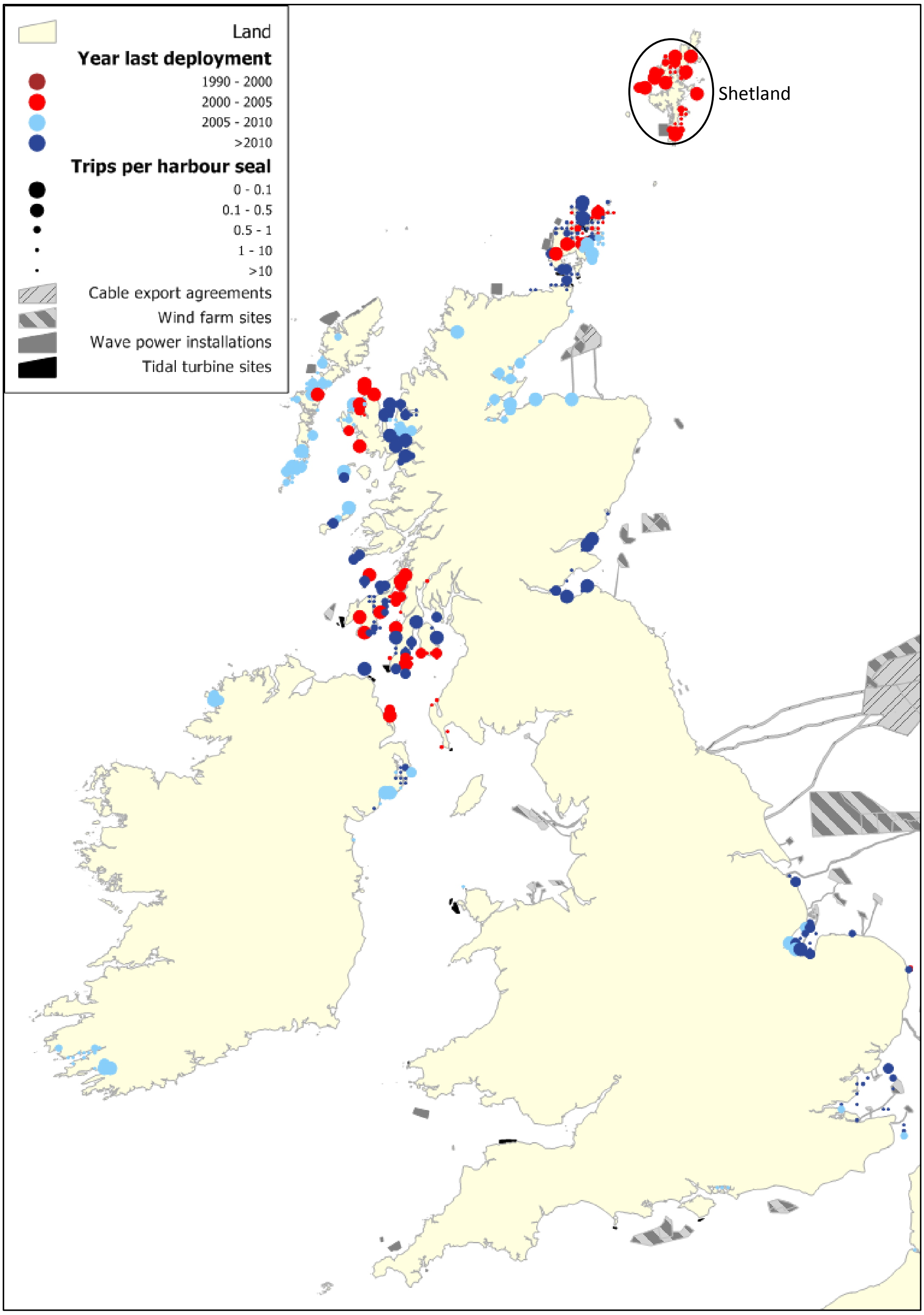


Figure 3.4. Recommendations for future tagging effort for harbour seals (black outlines) based on the age of most recent telemetry deployment (red = >10 years), and trips per seal (<0.1), and few or no more recent telemetry data are present in the area.

3.5 Recommendations

Specific areas that could benefit from additional telemetry tagging are prioritised below (Tables 3.1 and 3.2). A recommended minimum number of tags was estimated by calculating the average number of trips per individual seal by species (based on telemetry locations from 259 grey seals and 277 harbour seals). Terrestrial counts were aggregated for each area of interest, using the most recent count available for each haul-out. The aggregated terrestrial count was then divided by the average number of trips per seal to give a recommended estimate of the minimum number of tags required.

3.5.1 Grey seals

Table 3.1. Summary of recommended tagging areas for grey seals.

Area	Site description	Reason for selection			Proximity to renewable developments	Minimum # recommended tags
		Data sparseness	Population increase	Non-contemporary data		
West Shetland	Papa Stour	✓			✓	4
South-west Orkney	Scapa Flow & Pentland Skerries in the Pentland Firth	✓			✓	10
East Scotland	Inner Moray Firth	✓			✓	5
	Moray Firth (Brora to Lossiemouth)			✓	✓	8
East Anglia	Donna Nook & Blakeney Point		✓		✓	39
	Scroby Sands			✓	✓	4
Northern and East Ireland	Ards Peninsula & Strangford Lough	✓			✓	4
	Lambay Island			✓	×	3

3.5.2 Harbour seals

Table 3.2. Summary of recommended tagging areas for harbour seals.

Area	Site description	Reason for selection			Proximity to renewable developments	Minimum number of recommended tags
		Data sparseness	Population increase	Non-contemporary data		
East and west Shetland		✓		✓	✓	14
South-west Orkney	Scapa Flow	✓			✓	6
North-west Scotland	Summer Isles	✓			✓	10
Outer Hebrides	South Uist	✓			×	15
West Scotland and Inner Hebrides	Southern Skye to Isle of Mull	✓			×	58
East &west Ireland	Donegal Bay	✓			×	8
	Carlingford Lough	✓			×	4

3.6 Discussion

A total of eight sites for grey seals and seven sites for harbour seals were identified as data sparse regions where future tagging effort should be focussed. Recommendations for the number of tags required are provided.

The assumptions made for this analysis include:

- The telemetry data are representative of the population, specifically in terms of sex and age.
- Animals stay where they are tagged and make multiple return trips to the area.

The recommended numbers of new tag deployments were based on attaining a 0.1 ratio of telemetry trips to counts. In some cases this led to high numbers, which may not be practicable. However these numbers do provide assistance in prioritizing areas for future data collection.

3.7 References

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3.8 Acknowledgements

We would like to thank the following people and institutions for telemetry, terrestrial data and/or survey funding that contributed to this analysis: Dr Cecile Vincent, University of La Rochelle; Dr Michelle Cronin, Coastal & Marine Research Centre, University College Cork; Professor Paul Thompson, University of Aberdeen; Dr Carol Sparling, SMRU Marine; Ed Rowsell and Barry Collins, Chichester Harbour Conservancy; Jolyon Chesworth, Langstone Harbour Authority; Marine Current Turbines Ltd; Northern Ireland Environment Agency; Department of Arts, Heritage, Gaeltacht and the Islands; Countryside Council for Wales; Welsh Assembly Government; Scottish Natural Heritage; National Environmental Research Council; Lisa Morgan, RSPB; Kate Lock and the Skomer Island wardens, Natural Resources Wales.

3.9 Appendix

Table 1. Summary of grey seal telemetry deployments by year (taken from Jones *et al*., in press).

Year	Tag type	Number of tags	Sex ratio (m:f)	Age (adult:pup) (NA = excluded)	Mean tag lifespan (days)
1991	SRDL	5	4 :1	5 : 0	106
1992	SRDL	12	8 :4	12 : 0	107
1993	SRDL	3	1 :2	0 : 3	59
1994	SRDL	4	2 :2	0 : 4	59
1995	SRDL	21	15 :6	15 : 6	92
1996	SRDL	20	8 :12	20 : 0	59
1998	SRDL	14	10 :4	14 : 0	119
1999	SRDL	6	4 :2	0 : 11	75
2001	SRDL	11	7 :4	10 : 10	140
2002	SRDL	20	11 :9	24 : 0	110
2003	SRDL	24	14 :10	31 : 0	120
2004	SRDL	31	14 :17	11 : 0	146
2005	SRDL	11	5 :6	2 : 0	155
2006	SRDL	2	1 :1	19 : 0	66
2008	SRDL / GPS	10 / 9	9 :10	7 : 5	186
2009	GPS	12	2 :10	4 : 26	180
2010	GPS	30	13 :17	3 : 0	128
2011	GPS	3	3 : 0	3 : 1	109
2013	GPS	11	10 :1	3 : 3	164
TOTAL		**Mean=259**	**141 : 118**	**183 : 69**	**Mean=12**

Table 2. Summary of harbour seal telemetry deployments by year (taken from Jones *et al.*, in press).

Year	Tag type	Number of tags	Sex ratio (m:f)	Age (adult:pup) (NA = excluded)	Mean tag lifespan (days)
2003	SRDL	26	11 :15	26 : 0	161
2004	SRDL	29	15 :14	29 : 0	116
2005	SRDL	21	12 :9	21 : 0	94
2006	SRDL / GPS	25 / 30	36 :19	51 : 0	90
2007	SRDL / GPS	1 / 8	5 :4	6 : 0	108
2008	GPS	15	14 :1	0 : 0	129
2009	GPS	10	3 :7	10 : 0	84
2010	GPS	10	8 :2	10 : 0	92
2011	GPS	31	22 :9	31 : 0	96
2012	GPS	68	40 :28	68 : 0	77
2013	GPS	3	2 :1	3 : 0	56
TOTAL		**Mean=277**	**101:81**	**255 : 0**	**Mean=99**

Table 3. Summary of grey and harbour seal terrestrial surveys. Unless specified otherwise in the description, all surveys took place during August (taken from Jones *et al.*, in press). *SMRU aerial surveys were completed in 2011 in Northern Ireland and 2011 and 2012 in the Republic of Ireland. These were not incorporated in this analysis.

Area surveyed	Method	Description	Data used
Scotland	Aerial survey (helicopter)	Both species surveyed approx. every 1-5 years using SMRU protocol	1996-2013
Moray Firth, Firth of Tay, Donna Nook, The Wash in East Anglia, and Thames estuary	Aerial survey (fixed-wing)	Both species surveyed annually using SMRU protocol	1996-2013
Chichester and Langstone harbour	Ground counts through Chichester Harbour Authority	Harbour seals surveyed annually	1999-2012
Cornwall and Isles of Scilly, south-west England	Boat survey (Leeney *et al.*, 2010)	Grey seals surveyed in April	2007
Isles of Scilly	Ground counts (Sayer, Hockley & Witt, 2012)	Grey seals	2010
North Wales	Ground counts (Westcott & Stringell, 2003)	Grey seals counts extended over 12 months	2002, 2003
Skomer Island, West Wales	Ground counts	Adult grey seals	2013
Ramsey Island, West Wales	Ground counts	Grey seals	2007-2011
Northern Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol.	2002*
Strangford Lough, Northern Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol.	2006, 2007, 2008 and 2010*
Republic of Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol.	2003*
Northern France	Ground counts with extrapolation (Hassani *et al.*, 2010)	Harbour seals surveyed annually.	1996-2008

4 MR5.1.3 Review the extent of how new survey data affect usage estimates.

Jones, E. L., Smout, S. & McConnell, B. J.

4.1 Executive summary

Currently (in the MR5.1.1 task) survey count data are averaged over the historical duration of data collection within each 5km cell. Thus recent survey counts in regions that have been frequently surveyed will have lesser influence on the usage maps than recent counts in areas where surveys have not been frequent.

This situation could be improved by modelling recent regional trends in counts, such that predicted maps of usage can be produced at all sites for current or recent years.

4.2 Introduction

Terrestrial surveys of grey and harbour seals are carried out in August, approximately every 1-5 years in areas where the majority of grey and harbour seals haul out (i.e. Scotland and east England). At a broad-scale (i.e. UK-wide), the spatial distribution changes little when new data are incorporated because historical counts are currently averaged to produce the usage maps. This method captures only long-term changes in the size of local populations and is not sensitive to rapid local change.

4.3 Methods

If greater sensitivity to changes in terrestrial counts is required, then the time-series count data for each haul-out could be used to estimate current population size according to the following protocol: dependent on the amount of count data at each haul-out, trend models could be implemented to predict the current (2014) population at data-rich sites (where many years of data were available). Population averaging could still be used at data-poor sites that were surveyed infrequently. This robust method would allow recent terrestrial counts to have a greater weighting when estimating population sizes at data-rich sites. Therefore, changes in the population over a relatively short time (e.g. 2-3 years) would become apparent.

4.4 Results

Figure 3.1 shows the effect of the updated methodology on the existing grey and harbour seal maps. When the maps are used to delineate smaller areas of interest (e.g. by offshore renewable developers), there can be notable changes in the predicted population sizes in those areas. For example, around Orkney the harbour seal population estimate will decrease and the grey seal population estimate would increase using the updated methodology versus the current one.

4.5 Discussion

For long-term management, it may be preferable to smooth 'noisy' population data over time and space in order to obtain robust estimates (current methodology). However it may also be useful to implement the alternative trend-based methodology explored here, which is more sensitive to short term change, in order to highlight changes in at-sea usage associated with areas of rapid ongoing population change that follows a consistent trend, such as the growth in the grey seal population at Donna Nook.

Figure 4.1. Areas where grey or harbour population estimates and standard deviation will increase (blue) and decrease (red) as a result of changing the population estimation methodology in the usage maps from historical averaging to contemporary population estimates.

5 MR5.1.4 Classify activity between foraging and travelling usage using a state-space model approach

Russell, D. J. F.

This work, co-funded by DECC, is published in *Ecology* (McClintock *et al.*, 2013) and is in press in *Oikos* (Russell *et al.*, 2015). The work is summarised below, in part using extracts from these papers. For more information please refer to these papers.

5.1 Executive summary

From telemetry tags deployed on 63 grey seals and 126 harbour seals behavioural and movement data were used within a Bayesian state-space model (SSM), to define population-level activity budgets around Britain. How time spent in four states (resting on land (hauled out), resting at sea, foraging and travelling) was influenced by seasonal, intrinsic and extrinsic covariates was examined. It was found that a substantial proportion of time was spent resting at sea, when underlying habitat may be of little importance or unrelated to foraging, highlighting the potential problem of using all location data to define habitat preference in seals.

There are two key limitations to this approach. First, it was found that for 20% of the harbour seals, only one diving state was defined. This is likely to be because harbour seals exhibit shorter trips than grey seals, and segments of travelling and foraging are likely to last under 6 hours, which was the interval considered here to allow the lower resolution Argos data to be included. The second issue is that tidal currents may lead to unreliable movement-based classification of foraging and travelling. Due to the potential magnitude of this problem in areas of high tidal energy, all tags on individuals that spent the majority of time in an area of high tidal energy (e.g. Pentland Firth) were excluded. In task MR5.1.5 (in this Report) two improvements to deal with the above defined limitations were implemented.

5.2 Introduction

Outwith the pupping and moulting seasons, both grey and harbour seals make foraging trips to sea interspersed with haul-outs on land. Their foraging trips are typically characterised by travel to, from and between localised areas in which area restricted search, and presumably foraging, take place (Thompson *et al.*, 1991, 1998). Seals dive to both forage and travel, and spend extended periods of time on the surface (hereafter referred to as resting at sea) in inshore waters when intertidal haul-out sites are unavailable (Thompson *et al.*, 1991). In previous studies on grey seals (Breed *et al.*, 2009; 2011) , movement data within state-space models were used to divide foraging trips into foraging and travelling sections, where directed movements were associated with travelling behaviour and tortuous slow movements were associated with foraging behaviour. They excluded all activity within 2-5 km of land to avoid misclassifying inshore resting behaviour as foraging. Such boundaries may result in an underestimate of inshore foraging (Thompson *et al.*, 1991), which is especially important for harbour seals that have a coastal distribution, with some individuals staying exclusively within 10 km of the coast (Sharples *et al.*, 2012). Furthermore, investigation of the SMRU telemetry data revealed that individuals of both species spend prolonged periods of time stationary on the surface of the water offshore. Using only movement data, such behaviour would be misclassified as foraging behaviour. Thus a framework was developed in which both behavioural and movement data could be used to classify complete activity budgets encompassing four hierarchical states: (1) resting, or (2) diving and then within each of these categories as (1a) resting on land (hauled out), (1b) resting at sea (non-diving), (2a) area-restricted search behaviour which was defined as foraging, and (2b) faster movements with lower turning angles defined as travelling (McClintock *et al.*, 2013; Russell *et al.*, 2015) .

5.3 Methods

5.3.1 Data

Data from telemetry transmitters deployed on grey and harbour seals in Britain between 1991 and 2008 (Matthiopoulos *et al.*, 2004), and between 2001 and 2011 (Sharples *et al.*, 2012), respectively, were used. The tags used included both Sea Mammal Research Unit (SMRU) Argos SRDL (Satellite Relay Data Logger) tags and GPS/GSM phone tags that used Fastloc GPS (Wildtrack Telemetry Systems Ltd). As well as locational data, the tags also transmitted both detailed and summarised behavioural data based on patterns of submergence as determined by wet/dry and pressure sensors. Depending on the tag settings either two or six hour summary records were available, providing the proportion of time spent engaged in one of three mutually exclusive behaviours. These behaviours were determined on-board the tag using sensor information and were classified as "hauled out", "diving", and "at-surface". A haul-out event occurred when the tag had been dry for 10 minutes and ended when the tag had been wet for 40 seconds (the start and end times were then adjusted accordingly). Dives started when the tag was below a specified depth threshold (1.5, 2, 4 or 6 m) for a specified period (6-16 seconds) that both depended on tag settings. Dives ended when the animal moved shallower than the depth threshold. The remaining time (not hauled out or diving) was categorised as at-surface.

To allow inclusion of all tags, all summary data were aggregated into six hour intervals, resulting in four intervals in each day, beginning at midnight (GMT). Intervals were flagged as inestimable if there was a gap of > 12 hours between the observed locations surrounding the interpolated location, or if there were no summary data for the 6 hour interval. Tag deployments were excluded from the study if >50% of intervals were inestimable or if there were <10 days of data. Following these procedures, data remained for 65 grey seals and 126 harbour seals; tag durations were between 17 and 256 days (median 178) for grey seals, and between 26 and 245 days (median 115) for harbour seals.

5.3.2 State space modelling approach

First, resting and diving were defined based on behavioural thresholds. Time diving was then allocated into foraging and travelling using movement data within a state space model (McClintock *et al.*, 2013). Through this process, three latent states were (z_t) for time intervals $t = 1,...N$: resting ($z_t = R$) , foraging ($z_t = F$), and travelling ($z_t = T$). The behavioural data used to classify resting were the combined proportion of a time interval t spent hauled out and at the surface ($\omega_{r,t}$) vs diving ($\omega_{d,t}$). It is assumed state $z_t = R$ when $\omega_{r,t} > T_r$. In other words the assumption is $z_t \in \{F,T\}$ when $\omega_{d,t} > T_d$, where T_d is $1-T_r$.
A value of 50% could not be used as the threshold because the activity of diving must include a surface breathing overhead but in the summary data this overhead is included in at-surface behaviour. To obtain a threshold, data were extracted on the proportion of time spent diving in summary intervals from GPS tags from which most summary intervals were transmitted. There was little individual variation in the maximum proportion of time spent diving with medians of 88.8% for both grey and harbour seals, thus the surface overhead (minimum time above the depth threshold) associated with diving was estimated as 11.2%. Based on a majority rule, the threshold for an interval to be assigned to diving was half of the maximum that could be spent under the depth threshold and thus $T_d = 0.444$ and $T_r = 0.556$. Diving states were assigned to foraging or travelling based on step distance (the distance travelled during the 6 hour interval; s_t) and bearing (φ). The distribution of step length and bearing for resting states was defined. The movement and behavioural data therefore relate to the latent states as shown in Figure 5.1.

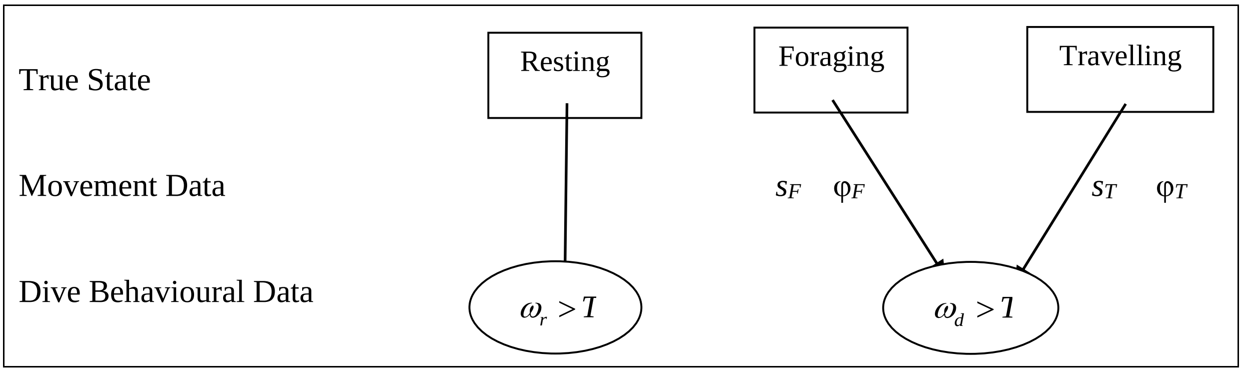

Figure 5.1. Structure of how the data are used to estimate whether an interval is resting, foraging or travelling.

Following McClintock *et al.*, (2013), it was assumed that step distance (s) would be longest when travelling and a Weibull distribution was used where the state-specific scale parameter was constrained $a_{i,T} > a_{i,F}$ For the bearing (φ) a wrapped Cauchy distribution was assumed. Time steps with $\omega_{d,t} > T_d$ were assumed to be equally likely to have been travelling or foraging states, and incorporated “memory" into the state transition probabilities (ψ) as a first-order Markov process. For any flagged intervals, due to missing activity data or unreliable location data, state assignments were based entirely on the Markov property of the state transition probabilities and were excluded from further analysis.

Adopting a Bayesian perspective, the state-space model was fitted using a Markov chain Monte Carlo (MCMC) algorithm written in C (adapted from McClintock *et al.*, 2013). Data from each seal were run individually with two chains starting at different initial values with a burn in of 50,000 iterations. Convergence was judged by visual inspection of the chains and using the Gelman-Rubin (gbr) statistic. Usually 50,000 iterations were used for the posterior distributions but 50,000 more iterations were run if the gbr statistic was not 1.0.

5.4 Results

All harbour seals deployments (n=126) were used to assign resting on land, resting at sea and diving but it was found that only one diving state was identified in 20% of individuals. Excluding this 20% when examining travelling and foraging in harbour seals may have resulted in bias in describing the population level behaviour. Thus, only foraging and travelling separately in one region (south eastern Scotland) were considered, where there are defined foraging patches (Figure 5.2) and 28 of 30 individuals demonstrated both foraging and travelling states. Two diving states were identified in 63 of 65 grey seals. Given that exclusion of two individuals should result in minimal bias, full activity budgets for 63 grey seals were examined. Example graphical results are shown for a grey and harbour seal (Figure 5.2).

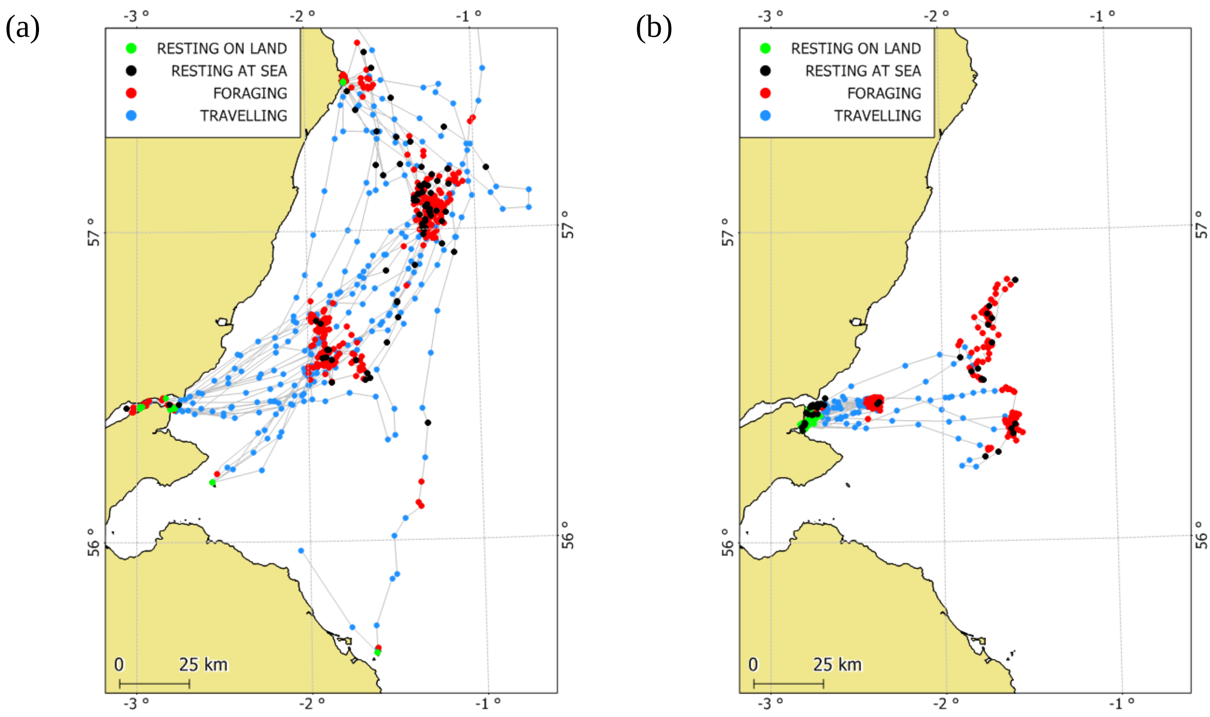

Figure 5.2. An example of a track characterised into foraging, travelling, resting on land and at sea for a grey (a) and harbour seal (b).

Activity budgets were also examined with regard to covariates: day of year (DOY), sex, age, time of day (TOD: four 6 hour intervals), region, and tag dive depth threshold. These were all input as factors with the exception of DOY which was included as a continuous covariate. It was found that all considered covariates significantly influenced activity budgets of both species. The time spent foraging and travelling varied with time of year in both species (Figures 5.3 and 5.4).

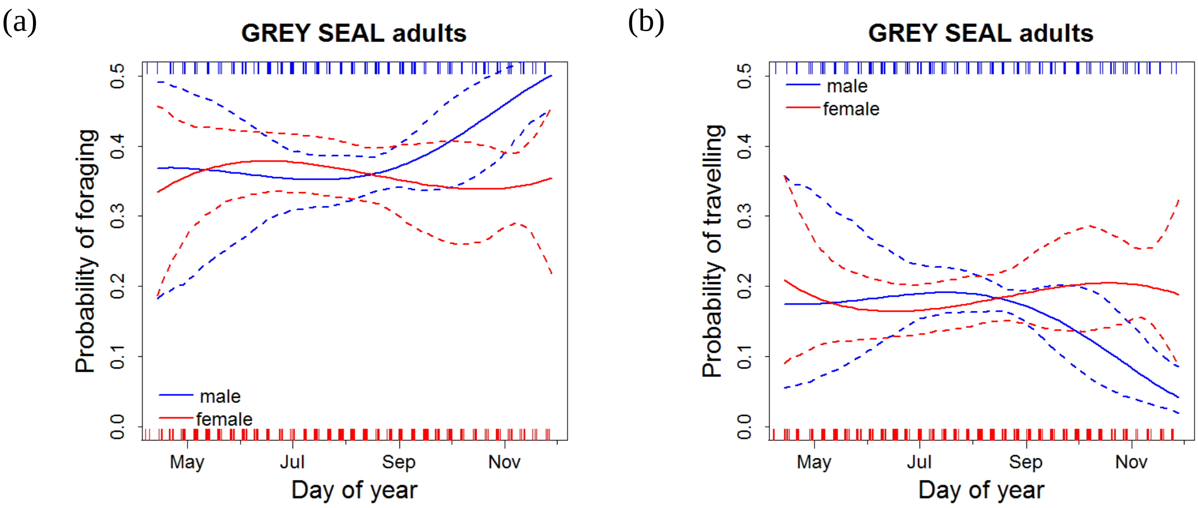

Figure 5.3. The predicted probability of foraging (a) and travelling (b) in adult grey seals with regard to time of year. The solid lines show the median predictions and the dotted lines, the 95% confidence intervals. The rug plots indicate the data coverage used to fit the models.

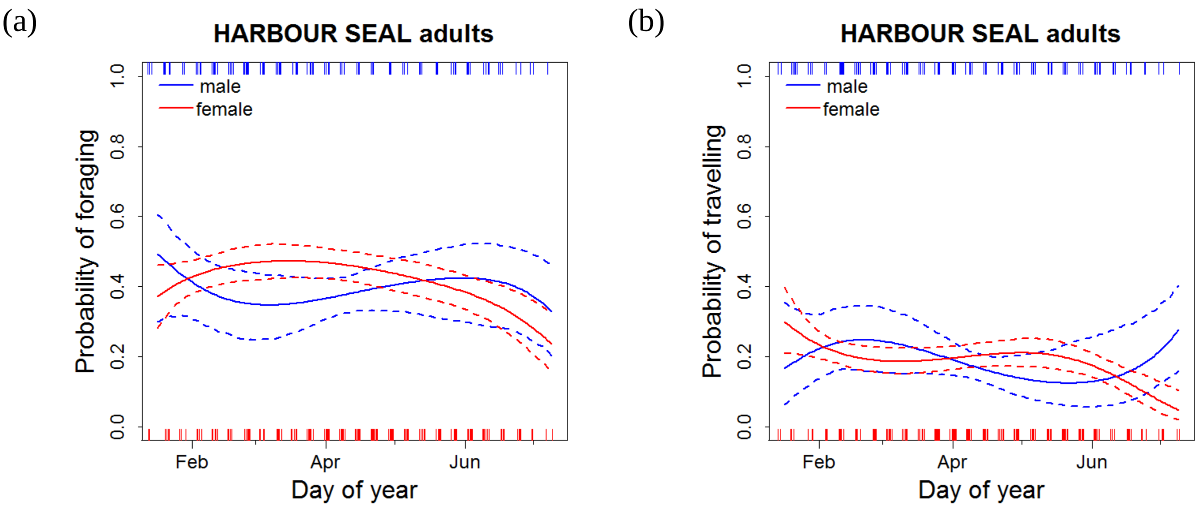

Figure 5.4. The predicted probability of foraging (a) and travelling (b) in adult harbour seals with regard to time of year. The solid lines show the median predictions and the dotted lines, the 95% confidence intervals. The rug plots indicate the data coverage used to fit the models.

5.5 Discussion

A model was successfully developed which allowed the quantification of the proportion of time spent resting on land, at sea, foraging and travelling. A substantial proportion of time was found to be spent resting at sea (>10%) and that, at least in some individuals, some of this time is spent offshore. This resting behaviour within trips highlights the importance of considering activity budgets to understand foraging effort. Indeed, regional patterns in traditional indicators of foraging effort (Sharples *et al.*, 2009) such as trip distance and duration did not align with the indicators (time spent diving) used in this study. Finally the substantial proportion of time resting at sea, when underlying habitat may be of little importance or unrelated to foraging, also highlights the potential problem of using all location data to define habitat preference in seals. In task MR5.1.5 (in this Report) this was examined by quantifying and comparing the habitat preference of grey and harbour seals defined using all locations and only foraging locations. This allowed key foraging areas to be predicted.

There were four major findings from analyses of these activity budgets: (1) there was no evidence that regional variation in foraging effort was linked to regional population trajectories in harbour seals; (2) grey seals demonstrated sex-specific seasonal differences in their activity budgets, independent from those related to reproductive costs; (3) in the two species there was evidence of temporal separation in time hauled out, but not in time foraging; and (4) in both species, time spent resting at sea was separated into inshore (associated with tidal haul-out availability) and offshore areas. Time spent resting at sea and on land was interchangeable to some extent, suggesting a degree of overlap in their functionality.

Further intensive behavioural studies are required to assess whether the findings regarding temporal haul-out segregation are a result of temporal segregation of a resource (haul-out site) or caused by differing drivers to haul out in these two species. In the former case, differing diurnal haul-out patterns for harbour seal populations hauling out at mixed and single species haul out sites would be expected. Such information is required in order to understand the drivers of haul-out behaviour in seals and to interpret dual species surveys used to monitor population trends; segregation of species at mixed haul-out sites would undermine scalars used to convert counts to population size.

There are two key limitations to this approach. First, it was found that for 20% of the harbour seals, only one diving state was defined. This is likely to be because harbour seals exhibit shorter trips than grey seals, and segments of travelling and foraging are likely to last under six hours which was the interval considered here to allow the lower resolution ARGOS data to be included. The second issue is that tidal currents may lead to unreliable movement-based classification of foraging and travelling

(Gaspar *et al.*, 2006). Due to the potential magnitude of this problem in areas of high tidal energy, all tags on individuals that spent the majority of time in an area of high tidal energy (e.g. Pentland Firth) were excluded. In Russell (2015), two improvements were implemented to deal with the above defined limitations. Using only the higher resolution GPS data, activity budgets were considered on a finer temporal resolution (two hours). The tidal vectors were also deleted from the track of each individual to get their active movements in the water and rerun the activity budget model allowing more accurate classification of foraying intervals and thus activity budgets.

5.6 References

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6 MR5.1.5 Determine environmental covariates of preference for all activity, and foraging activity

Russell, D. J. F.

6.1 Executive summary

Traditionally habitat preference analyses consider all available location data (MR5.1.6). However, habitat preference of seals may differ with activity, e.g. foraging versus travelling. This was investigated for harbour and grey seals in the North Sea, by quantifying habitat preference using (1) all at-sea locations and (2) only foraging locations (defined in task MR5.1.4 in this Report). The following covariates were considered: geodesic distance from haul-out site, depth, winter/spring sea surface temperature (SST) and sediment (percentage gravel, mud and sand); their influence was allowed to vary depending on the sex of the seal.

For grey seals, the covariates retained differed between the models including all locations (overall model) and only foraging locations (foraging model). In addition to geodesic distance, percentage gravel and SST, it was found that depth and percentage mud was also retained in the overall and foraging models, respectively. For harbour seals, all covariates (except percentage sand) were retained in both models. In general, for both species, the shape of the relationship between covariates and usage was similar in the overall and foraging models. Although the spatial predictions of overall and foraging usage were broadly similar in grey seals, there appeared to be more fine resolution variation in the predictions from the foraging model.

For harbour seals, the predictions from the foraging model showed a more restricted range of high coastal usage than from the overall model, especially in the Thames. When modelling habitat preference, considering all locations rather than only foraging locations, appears to be a trade-off because including all locations results in a higher sample size but may result in the masking of some relationships and the retention of covariates which may not actually drive species' distributions. For grey seals, there are some key differences between overall and foraging preference, probably as a result of their relatively long trips and thus spatially distinct travelling and foraging areas. Therefore, the most accurate quantification of foraging preference would result from using only foraging locations. In harbour seals which have much shorter trips and may switch more frequently between foraging and travelling, using overall preference may be more sensible as the higher sample size results in tighter confidence intervals.

6.2 Introduction

Habitat preference describes where an animal chooses to be, given its accessible environment. Using all locations in habitat preference modelling (e.g. Aarts *et al.*, 2008) assumes that preference is independent of activity state. If preference differs when, say, travelling and foraging, such clumping of activities risks multi-modal activity-specific preferences being masked and the resulting estimated "preference" may represent an environment not preferred when either foraging or travelling. Furthermore, as central-placed foragers, seals start and end foraging trips on land and the specific habitat which they travel through may not be important but may be correlated with certain environmental variables, such as distance to coast and depth. Using SMRU telemetry data, two analyses were conducted on both grey and harbour seals; first all at-sea locations (foraging, travelling and resting at sea) were used to determine their overall at-sea habitat preference (Aarts *et al.*, 2008) and second the foraging locations classified using a state-space model based on behavioural and locational data were used (Russell *et al.*, 2015). In this study there were two questions: (1) can non activity specific location data be used to represent foraging preference, (2) what spatial areas are predicted to be highly preferred and how is this affected by species and whether only foraging or all at-sea locations are considered.

6.3 Methods

The data used came from telemetry transmitters deployed on grey and harbour seals in the UK between 1991 and 2008 and between 2001 and 2011, respectively. For this study only seals hauling out in the North Sea as defined by the International Committee for the Exploration of our Seas (http://www.ices.dk/) were considered. This resulted in a sample size of 33 grey and 79 harbour seals. Behavioural and locational data were used to assign intervals of six hours to four states: resting on land, resting at sea, foraging and travelling (Russell *et al.*, 2015). For 12 of the harbour seals, diving could not be split into foraging and travelling states. It is likely that for these 12 individuals, foraging and travelling bouts often lasted less than six hours and thus foraging and travelling could not be differentiated at this resolution. It was assumed the diving intervals of these 12 animals either represent some exploratory foraging states or largely represent foraging. The period from the start of the breeding season and the end of the moulting season (September to mid-April for grey seals and June to September for harbour seals) were excluded for three reasons: (1) classification of states may be less reliable in the breeding season due to the presence of additional behaviours associated with breeding, such as displaying, which may be wrongly assigned to foraging and (2) habitat preference may differ during the breeding season and there was not sufficient data to look at seasonal changes, and (3) the tags fall off during the moult so few data are available.

A grid at a resolution of 5 by 5 km was generated and the locations used in the analyses (the interpolated mid-point of each six hour interval) were assigned to a grid cell. Due to the importance of accessibility it was only possible to include at-sea intervals if their originating and destination haul-out site was known. The greatest geodesic, around land, distance between a haul-out site and an at-sea location was calculated for each species: 348 km in grey seals and 328 km in harbour seals. This distance was assumed to represent the maximum accessible distance from a haul-out site and was used to generate buffers of accessibility around each haul-out site. Telemetry data are by nature presence-only data; thus to quantify the area available to the study seals pseudo-absences were generated (Aarts *et al.,* 2008). Ten pseudo-absences for each presence within the accessible area were generated. These absence data can be thought of as representative sample of points from the area that is accessible to the animals, and therefore as a means of communicating to a model the contrast between the environment actually used by the animals and the environment that is broadly available to them. Distribution was modelled as a binomial process (0 as pseudo-absence and 1 as presence) as a function of environmental covariates.

6.3.1 Environmental data

Six environmental covariates (Table 6.1) known to affect the distribution of seals or their prey were considered (Wright, Jensen & Tuck 2000; Aarts *et al.*, 2008): geodesic distance, depth, sediment (% gravel, mud, sand), winter/spring sea surface temperature. All environmental data were gridded at the resolution at which they were available and the presence/pseudo absence locations were overlaid onto this grid allowing environmental data to be assigned to each location. Winter/spring sea surface temperature affects recruitment of a key prey species of seals (sandeels; Arnott & Ruxton 2002) and subsequently the breeding success of top predators (Frederiksen *et al.*, 2005). The mean combined winter/spring sea surface temperature (SST) over a 15 year period (1990-2004) was used to reflect the spatial variation in SST.

6.3.2 Modelling

Generalised additive models (GAMs) were used to allow non-linear relationships between the covariates and the probability of presence. Ideally, to fit habitat preference models, a mixed effects model would be used to take into account the non-independence of data within individuals. However, telemetry data within individuals are often serially correlated whereas the accompanying pseudo-absence data are not; such a data structure is difficult to model within a mixed effect framework. Instead, 5-fold cross validation was used for model selection, which is robust to both the effects of individual and serial autocorrelation. In 5-fold cross validation the data are divided up (by individual) into five segments, and each combination of four segments are used to fit the model and the remaining segment of data is used to test the predictive ability of the model. Forward model selection was carried out based on the mean negative log likelihood across the 5-folds. Importantly, as well as for the covariates themselves, model selection was required to govern the flexibility (wiggliness) of the relationship between covariates and the probability of presence because over-fitting (too much wiggliness) could occur due to the artificially enlarged sample size as a result of non-independent data points. Increasing degrees of freedom in a smooth is associated with increased flexibility, the individual covariates were offered in the form of one (linear relationship), four or six degrees of freedom. If covariates were retained, interactions with sex were offered for the covariates as preference may differ between sexes. Sediment was made up of three components which summed to 100%. Percentage sand was highly correlated with the other two components and so although all three covariates were offered to each model, if either percentage mud or gravel was retained, percentage sand was no longer offered for inclusion in the model. To avoid issues of artificially tight intervals for the predictions due to the residual autocorrelation within individuals, the final model predictions were generated using non-parametric bootstrapping by individual (n=1000).

For each species this modelling was conducted (1) using all at-sea locations including resting, foraging and travelling, and (2) using only foraging locations, except for 12 harbour seals for which only one diving state was define so all diving intervals were included.

6.4 Results

Table 6.1 shows the covariates that were retained, their flexibility (degrees of freedom) and if an interaction with sex was retained in the model. The median deviance explained across the 5 folds is also shown for each model. Deviance explained was marginally higher in the foraging compared to overall models. The shapes of these relationships from the foraging model are shown in Figures 6.1 and 6.2. For grey seals, the covariates retained differed between the overall and foraging model. In addition to geodesic distance, percentage gravel and SST, it was found that depth and percentage mud were also retained in the overall and foraging models, respectively. For harbour seals, all covariates (except percentage sand) were retained. In general, for both species, the shape of the relationship between covariates and probability of presence was similar in the overall and foraging models.

Table 6.1. Retained covariates, their flexibility (degrees of freedom: dof) and whether they interacted with sex. For each model, the median deviance explained across the five folds of data is also shown in brackets. The order in which covariates were retained by model selection, a measure of their relative importance, is also shown with 1 being the first covariate retained.

Covariate	**Grey seal**						**Harbour seal**					
	At-sea (41%)			Foraging (42%)			At-sea (67%)			Foraging (68%)		
	Order	dof	Sex	Order	dof	Sex	Order	dof	Sex	Order	dof	Sex
Geodesic distance	1	6	-	1	6	-	1	6	yes	1	1	-
Depth	4	6	-	-	-	-	2	6	yes	2	6	yes
Winter/spring SST	3	4	-	3	4	-	4	1	yes	5	1	yes
Gravel (%)	2	4	-	2	4	-	5	6	yes	3	6	-
Mud (%)	-	-	-	4	6	-	3	4	-	4	6	-
Sand (%)	-	-	-	-	-	-	-	-	-	-	-	-

6.4.1 Grey seals

In the overall model, (Figure 6.1), depth was retained with preference for shallower depths. This result was expected since to go on foraging trips, seals have to depart from and return to land (depth=0). Furthermore, they spend prolonged periods of time resting in the shallows near tidal haul-out sites. Depth was not retained in the foraging model, probably because grey seals can dive to the seabed in most places in the North Sea so depth does not affect where they choose to forage. Another covariate, percentage mud, was only retained in the <u>foraging</u> model; foraging in areas of low percentage mud was preferred. The presence of mud may hinder seal foraging efficiency (Bowen *et al.*, 2002) and it is not the preferred habitat of their key sandeel prey (Wright, Jensen & Tuck 2000),

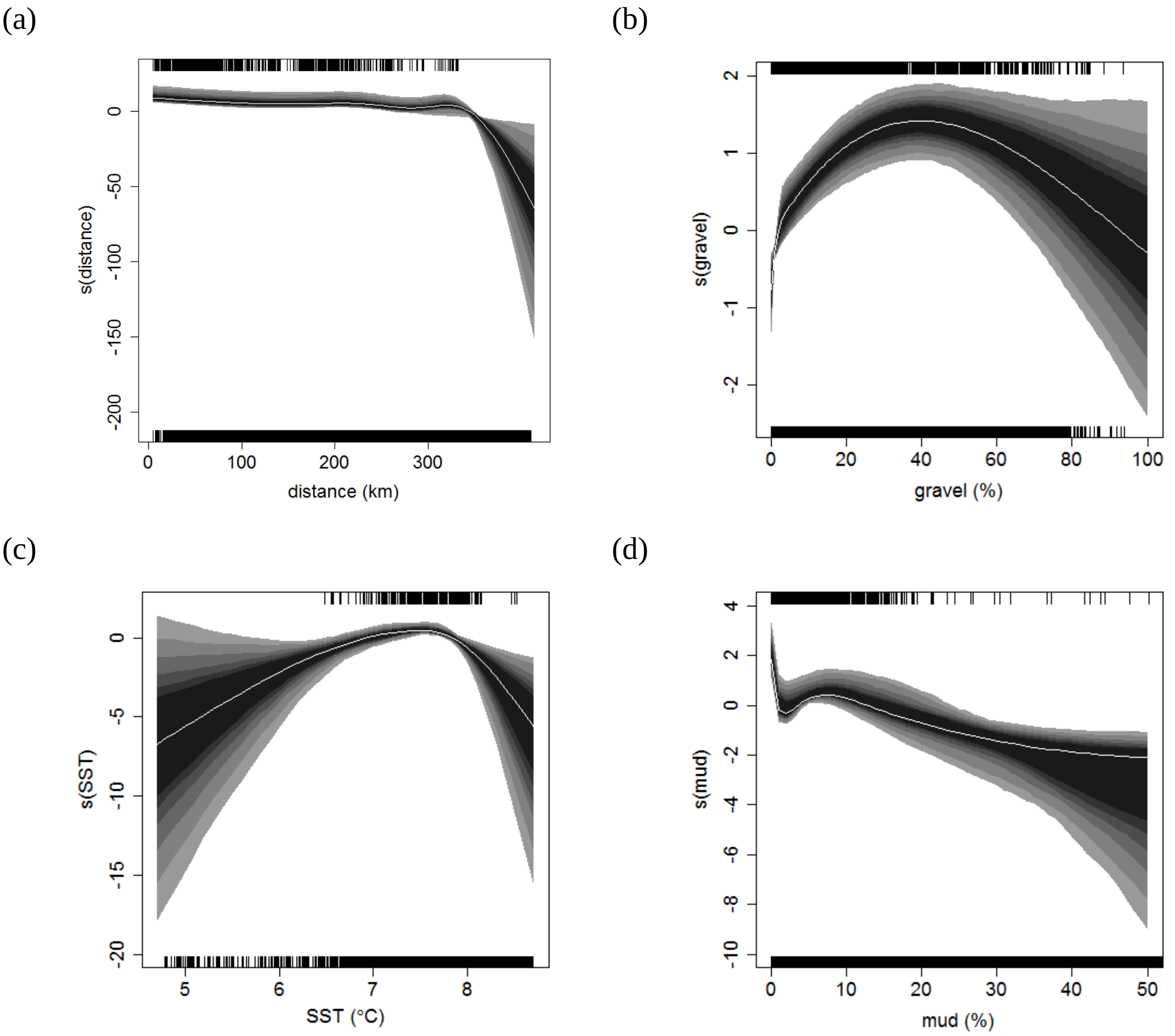


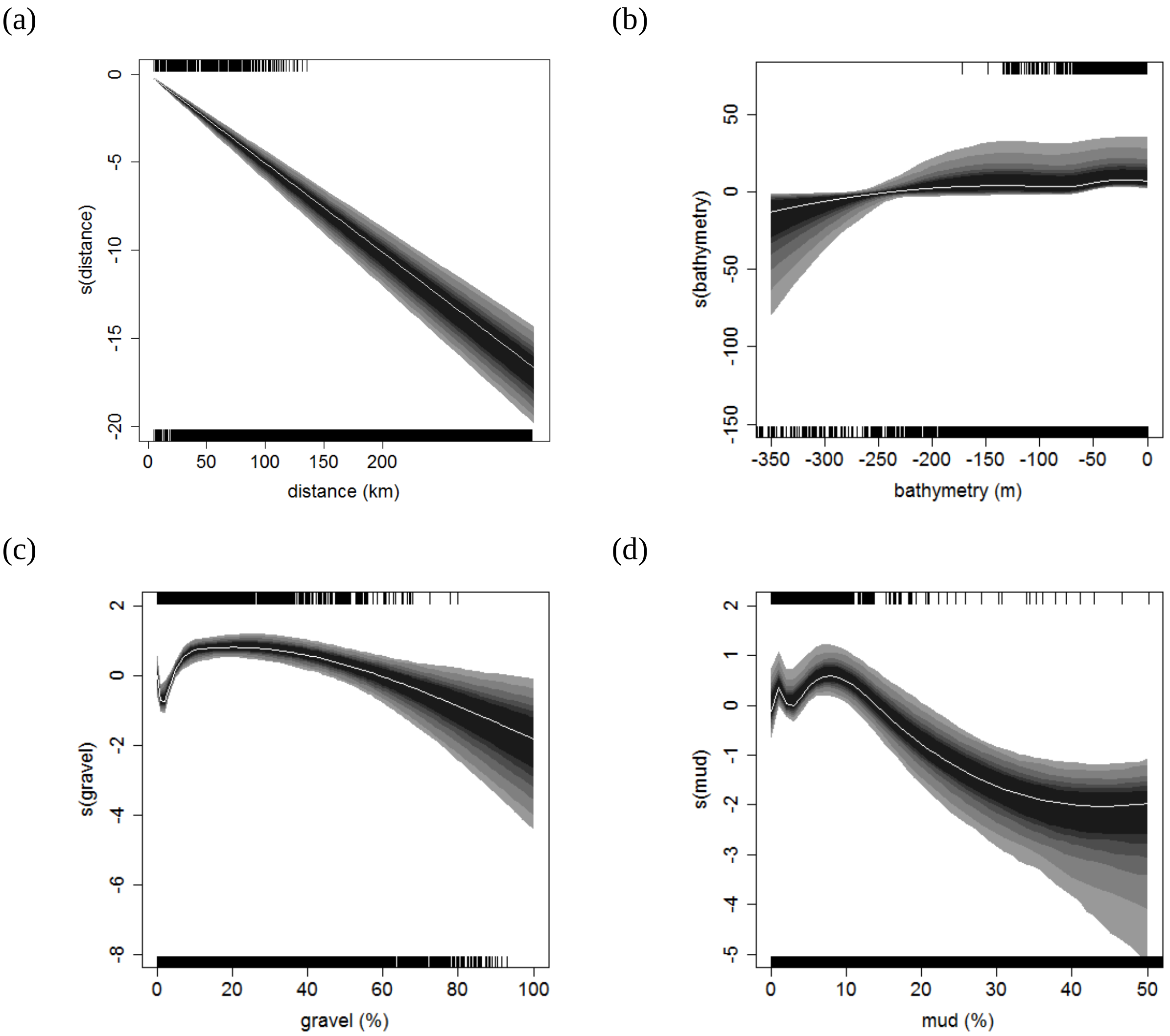
Figure 6.1. For grey seals, the marginal relationship between covariates and probability of foraging on the logit link scale.

whereas the presence of mud may not be important when travelling or resting at the surface. The relationship between the other covariates retained and preference was similar when considering all and only foraging locations. These similarities are likely to be a result of a lack of distinct preference associated with travelling or resting. The spatial, and thus environmental, proximity of travelling, foraging and resting locations will then result in a higher sample size and thus increased power when considering all locations (n=4665) compared to only foraging locations (n=2573).

Preference gradually decreased with increasing distance from a haul-out site, and then fell sharply after 350 km from the haul-out site. A previous study (Aarts *et al.*, 2008) found a positive linear relationship between percentage gravel and presence, probably a result of the associated habitat preference of their sandeel prey (Wright, Jensen & Tuck 2000). Here, with a higher sample size of individuals (n=79, compared to n=42), an increasing preference was found for high percentage gravel up to 40%, after which preference decreased but large confidence intervals surrounded this decrease. Preference peaked at a SST temperature of just under 8° Celsius, with the indication of decreased preference at higher temperatures. It is unlikely that this relationship is driven simply by the presence of sandeels because sandeel recruitment is negatively correlated with SST within the range considered here.

6.4.2 Harbour seals

All covariates (except percentage sand) were retained in both the overall and foraging models (Figure 6.2). However, in the overall model, sex interacted with the effect of all covariates except mud, whereas it only interacted with depth and SST in the foraging model. This difference may have been



(e)

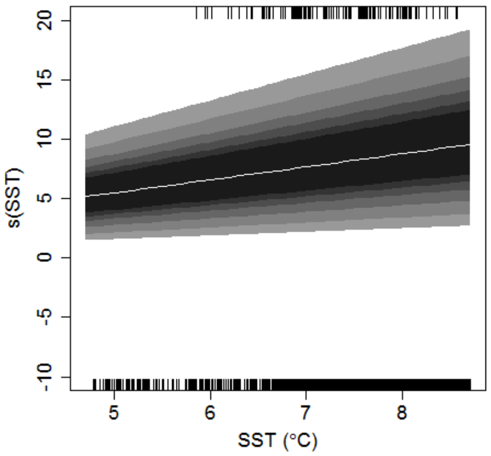


Figure 6.2. For harbour seals, the marginal relationship between covariates and probability of foraging on the logit link scale. If the effect of the covariate interacted with sex (b, e), only the relationship for females is shown.

due to a higher sample size when considering all (n=7690) compared to only foraging locations (n=4908). In general, the sex specific differences in overall and foraging habitat preference were of small magnitude. In the overall model, the probability of presence gradually decreased with distance until 200km, after which probability decreased sharply. In the foraging model, presence showed a gradual linear decrease with increasing distance from haul-out site. In reality, the magnitude of the difference in preference resulting from these differing shapes was small. Although SST was retained in both models, there was little preference for a particular SST; for females, there was indication of increased probability of presence and foraging with increasing SST. For the foraging model, the effect of percentage gravel was bimodal; seals preferred either no gravel or between 10 and 30% gravel, which may reflect habitat preferences of differing prey species. Preference was for a low percentage of mud; this was particularly evident in the foraging model.

6.5 Discussion

When modelling habitat preference, considering all locations rather than only foraging locations, appears to be a trade-off as including all locations results in a higher sample size but may result in the masking of some relationships and the retention of covariates which may not actually drive species' distributions. For grey seals, there are some key differences between overall and foraging preference, probably as a result of their relatively long trips and thus spatially distinct travelling and foraging areas. Thus the most accurate quantification of foraging preference would result from using only foraging locations. In harbour seals which have much shorter trips and may switch more frequently between foraging and travelling, examination of all locations may be more sensible as the higher sample size results in tighter confidence intervals. However, a larger difference between the foraging and overall preference would probably be observed if activity data at a finer temporal resolution (see Russell, 2015) were used within habitat preference modelling.

Spatial predictions for grey and harbour seals were generated using the relative moult counts from each haul-out site to give the percentage of the at-sea population in each 5 by 5 km cell (Figure 6.3 and 6.4 respectively). Although the predictions from the overall and foraging maps were broadly similar in grey seals, there appeared to be more fine resolution variation in the predictions from the foraging model. For harbour seals, the predictions from the foraging model showed a more restricted range of high coastal usage than from the overall model, especially in the Thames. Areas of high predicted usage varied between species; for harbour seals the areas of high usage were restricted to the coast. There were common areas of high predicted usage for both species, including the areas surrounding Orkney, Shetland and the Moray Firth. However, there were also key difference in south-east Scotland, and eastern England. These species specific differences are partly driven by differences in the spatial distribution of the two species on land and partly by differences in their preference; they show some dissimilarities in their preference for sediment, depth and SST.

The results of these models are useful in determining the preferred foraging habitat for seals, which will be, for the most part driven by the association between that habitat and their prey. The spatial predictions of the foraging habitat preference models are not analogous to the usage maps. They do not reflect usage because they do not consider preference and thus usage when travelling or resting at sea. The spatial predictions of foraging usage and their associated uncertainties can be used to delineate key foraging areas for seals.

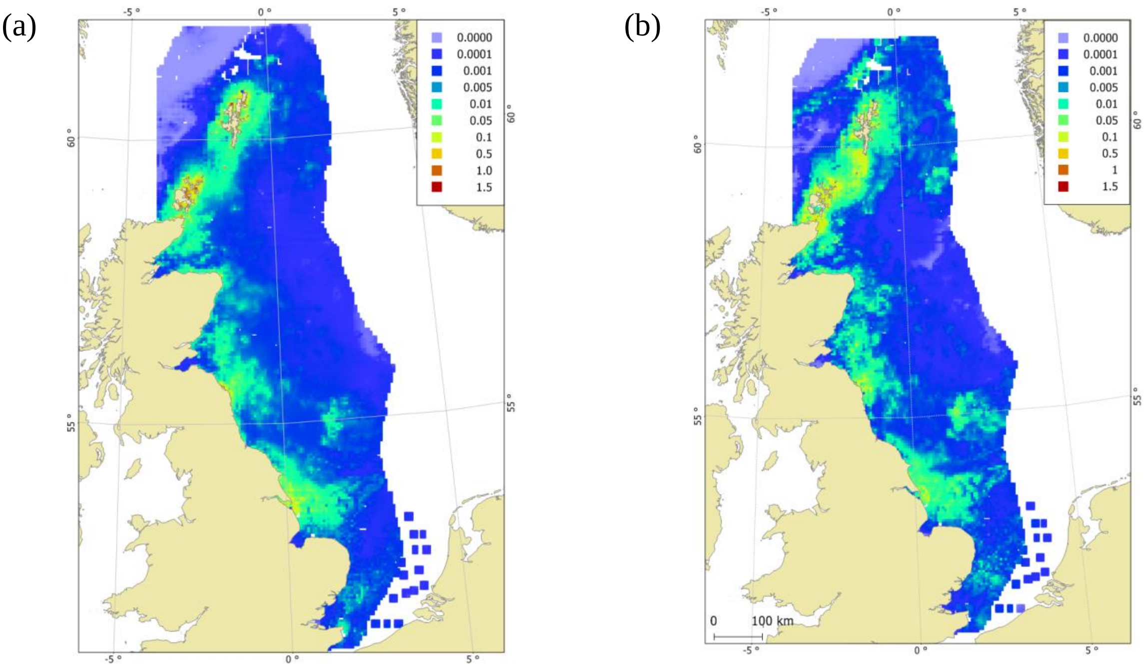


Figure 6.3. Predictions of the percentage of grey seals at sea in each 5 by 5km grid cell based on (a) the overall and (b) the foraging model.

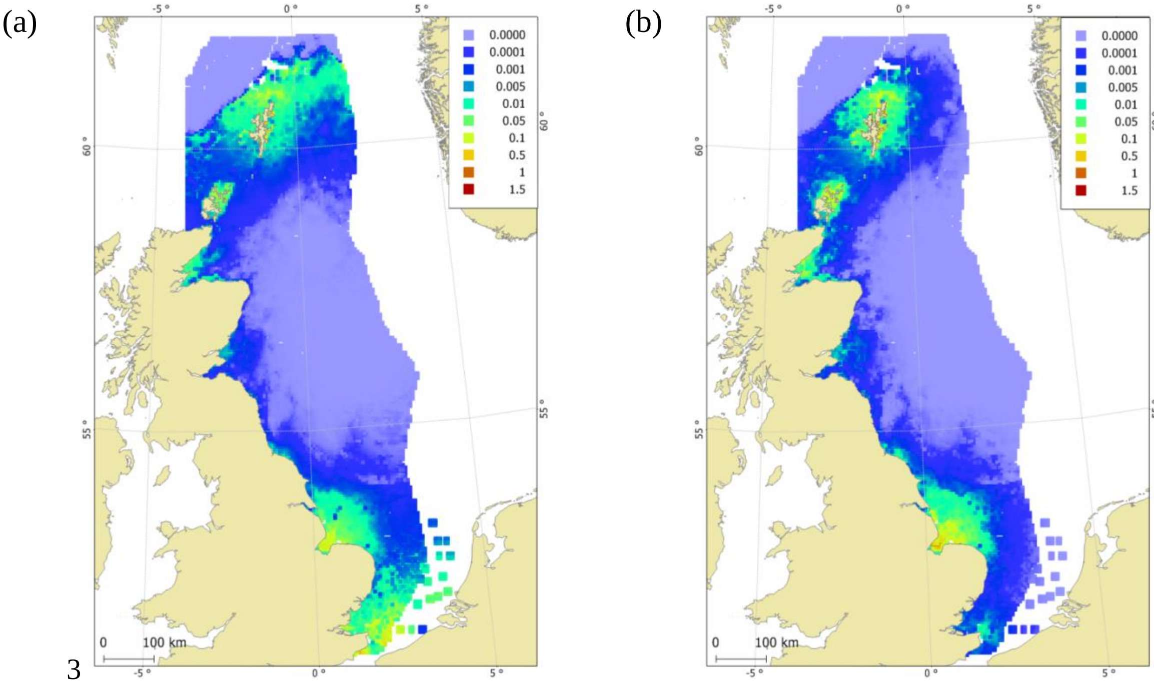


Figure 6.4. Predictions of the percentage of harbour seals at sea in each 5 by 5km grid cell based on (a) the overall and (b) the foraging model.

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Aarts, G., MacKenzie, M., McConnell, B.J., Fedak, M.A. & Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, **31**, 140–160.

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7 MR5.1.6 Determine environmental covariates for usage preference around the UK

Jones, E. L., Smout, S. & McConnell, B. J.

7.1 Executive summary

Habitat modelling for UK grey and harbour seals permitted construction of realistic distributions for areas where telemetry data were available, and to predict distributions for areas where direct observations were sparse or absent. Maps were produced for each species, showing habitat preference scaled to population size.

Both grey and harbour seals show a preference for shallower water (consistent with a central-place forager spending much of their time close to the coast). Grey seals prefer tidally stratified areas where the water column remains vertically well-mixed all year. They show preference for the potential between the surface and bottom temperature to be 3.6°C (with a near-bottom year-average temperature of 9.7°C, and show slight preference for substrate with increasing levels of sand (and subsequently decreasing levels of gravel). Harbour seals prefer areas with a near bottom salinity of 33.7 psu and increasing sea-floor slope. Harbour seals spend much of their time close to the coast, where mixing of the water column (that may influence prey distributions) is known to be primarily driven by salinity. Water column mixing, near bottom temperature and salinity, and sediment may all be associated with the distribution and concentration of prey that are utilised by grey or harbour seals.

The methodology will allow predictions based on the current models, e.g. for future scenarios including local seal population change, or changes in environmental variables such as sea temperature. The resulting maps can also be updated when new data become available, including seal telemetry or new environmental data.

7.2 Introduction

The potential impacts of marine renewable developments on marine mammals have been investigated with the objective of determining areas of core seal habitat for effective future management.

This study is designed to complement grey and harbour seal usage maps (see task MR5.1.1 in this Report), which use density estimation modelling to show spatial usage at a fine (5x5km^2) resolution over a broad range around the UK. This approach was necessary to capture the extensive spatial range of seal movement at-sea. Usage maps use simple regression models to predict usage in areas where there are few or no movement data available. The habitat preference study presented here takes a different approach to answer two more general ecological questions: (1) why do seals use certain areas at-sea?; and (2) can areas where movement data are unavailable be appropriately characterised?

To answer (1), a regression modelling approach was used to incorporate animal movement and population data, and environmental data to characterise seal habitat preference. This was combined with a modelling method known as 'Generalised Functional Responses' (GFRs) to answer question (2). The habitat preference maps were scaled to averaged population-levels (similar to the usage maps) to inform spatial planning.

7.3 Methods

7.3.1 Movement data

Telemetry data from grey and harbour seals were used as response variables to model habitat preference and terrestrial count data were used to scale these predictions to population level.

Terrestrial count data and movement data are defined in task MR5.1.1 in this report and at http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/Themes/usage.

A haul-out was defined on a 5x5km^2 grid square. Seal movements at-sea were divided into trips, defined as the sequences of locations between haul-out events. Data were retained when an animal was at-sea and on a return trip (departure and destination haul-out were the same). Geodesic distance was defined as the shortest distance between points taking into land into account. Thermal and salinity stratification data (see below) had the least spatial extent, so the telemetry data were clipped to produce a continuous prediction surface.

7.3.2 Environmental data

Habitat preference can be modelled as a function of environmental variables e.g. ocean depth for marine species. For central place foragers such as seals, which travel to remote areas, the accessibility of habitat is likely to be important (Matthiopoulos, 2003). Competition with conspecifics may also influence the distribution of animals (Wakefield *et al.*, 2011). Habitat preference models combine explanatory variables to describe why animals use geographic space in a certain way and can be used to predict how they will be distributed in areas for which direct observations are not available.

A summary of transformed covariates that are used as explanatory variables in this study of UK grey and harbour seals is provided in Table 7.1. Geodesic distance and bathymetry were chosen to represent geographic space used by seals and these covariates have previously shown to be important in characterising seal habitat preference (Aarts *et al.*, 2008). Sediment, sea water temperature and salinity were used as proxies for prey distributions. The difference between surface and bottom seawater temperature that produced a measure of water column mixing was chosen to represent primary biological production in the food web. Away from the coast and regions of fresh-water influence, the strength of water column stratification is primarily driven by “variations in solar-heating, wind-driven surface mixing, and tidally-driven bottom mixing” (Scott *et al.,* 2010). However, areas close to the coast are important to seals due to their proximity to haul-out sites, and in these areas density stratification in the water column is mainly due to differences in salinity. Four covariates were derived using temperature, salinity, tidal power, and depth to describe water column stratification in terms of thermal and density changes, and tidal stratification.

Geodesic distance was calculated for each haul-out to determine the distance between each seal location (presence/absence) and the corresponding haul-out. The median width of the 95% credibility limits for a subset of the SRDL positions were shown to be 4.4km (Bailey *et al.*, 2014). Therefore, geodesic distance was calculated on a 5x5km^2 grid to take account of this scale of uncertainty.

Gridded bathymetry data from SeaZone and produced by the UK Hydrographic Office S-57 were obtained from Edina Digimap. These had a resolution of 1 arcsec (~30m) near the coast and 6 arcsec (~180m) offshore and were based on the seabed depth at the Lowest Astronomical Tide (LAT). The data were then gridded to 3x3km^2 squares and mean depth (m), slope (°), and aspect (°) were derived. Aspect was then transformed into radians from degrees and the cosine and sine functions were applied to derive two covariates representing North-South (cosine) and East-West (sine) aspects.

Sediment type was derived from the British Geological Survey, which has core samples taken from locations spaced 5km apart on average. Data processing followed Aarts *et al.,* (2008): a simplified Folk classification system was applied to derive variables containing proportions of sand, gravel, and mud. Data were given as a percentage-by-weight of gravel (particles>2.0mm in diameter), sand (0.0625-2.0mm in diameter), and mud (particles< 0.0625mm in diameter). Spatial autocorrelation between the three covariates was calculated by randomly sub-sampling the cores to calculate the semi-variogram (Isaaks and Srivastava, 1990). The semi-variograms were used to independently krig each sediment covariate at a 1x1km^2 resolution, and resultant local estimates were normalised to 100%.

Fish recruitment and distributions may be affected by temperature and salinity (Arnott & Ruxton, 2002). Grey and harbour seals prey on benthic species such as sandeels (*Ammondites*) and therefore often forage at the sea floor (Photopoulou *et al.,* 2013; Pierce *et al.,* 1991). Near bottom (NBT) and sea surface temperature (SST) (°C), and near bottom (NBS) and sea surface salinity (SST) (psu) were produced by MyOcean using the European North West Shelf-Ocean Physics Non Assimilative Hindcast from the NERCPOL model. Monthly mean temperature or salinity was obtained from 1990 to 2004 at a 12x12km^2 resolution. Each variable was aggregated over the time-scale into monthly mean estimates.

Thermal stratification (°C) was derived by calculating the temperature potential between near bottom and sea surface temperatures (SST-NBT) on a temporally aggregated monthly basis.

Salinity stratification (psu) was similarly derived by calculating the salinity potential between near bottom and sea surface salinity (SSS-NBS) on a temporally aggregated monthly basis.

Spring and neap mean tidal stratification (m^{-2} s^{3}) were derived from total depth (h) and peak flow for a mean spring/neap tide (F_s) using $\log(h/F_s^3)$ (Simpson & Hunter 1974; Pingree & Griffiths 1978). Low values of tidal stratification indicate areas where the water column remains mixed all year, whereas high values indicate thermal stratification during summer. Thus higher values indicate stronger stratification (Scott *et al.*, 2010).

7.3.3 Modelling

Telemetry data are concentrated spatially and temporally resulting in patchy data that may be unrepresentative of the true distribution. GFRs address this problem by using data-rich regions to provide robust predictions for data-sparse and unobserved areas. This is achieved by including averages of covariates as covariates themselves, termed as 'availabilities'. Here, GFRs were used to identify determinants of core seal habitat and delineate them geographically around the UK.

Movement data were interpolated to two-hour intervals. Serial autocorrelation within-individual is implicit in telemetry data, and this was reduced by thinning individual animal data to 10% (chronologically selecting 1 in every 10 points). Telemetry data were presence-only and were modelled as a binomial process, generating pseudo-absences with a user-availability design (i.e. random selection). These pseudo-absences were termed as 'control' points (Aarts *et al.*, 2008). Although seals can swim large distances over a relatively short space of time (up to $2ms^{-1}$), it was important to ensure the selection of control points was biologically feasible. The farthest a seal travelled from the coast over the entire telemetry dataset was around 500km for both grey and harbour seals. Therefore, buffers of a radius of 500km were generated for each haul-out site extending away from the coastline. Each telemetry point at-sea was associated with a haul-out (i.e. the seal had departed from a specific haul-out site). Ten control points were generated randomly for each telemetry point within the buffer zone for the associated haul-out site.

Environmental covariates were overlaid onto the presence/pseudo-absence locations. NBT, NBS, THST, and SAST covariates varied in time and so were matched by month to each location. Geodesic distance was calculated for each location. Presences (and the corresponding pseudo-absences) were excluded from the analysis if any of the environmental covariates were missing, or if bathymetry showed the presence point was on land (<0m). Animals' responses to the environment change over geographic space and GFRs account for this implicitly. Therefore, availabilities should be diverse and capture as many environmental scenarios as possible. Environmental availabilities were calculated by taking the mean of each covariate from all control points for each haul-out site.

Multicollinearity between the covariates was tested using variation inflation factor analysis, with R package CAR (Fox & Weisberg, 2011). The threshold for high multicollinearity was taken to be 5. Neap tidal stratification and spring tidal stratification were highly correlated and so neap tidal stratification was removed from the analysis. The proportion of gravel and sand were also marginally collinear and so a principle components analysis was carried out for sediment (proportions of gravel, sand, and mud). All explanatory variables were centred and standardised (mean=0, sd=1) so all covariates were on the same scale, allowing the models the best chance of fitting. A principle components analysis was carried out on sediment, to eliminate multicollinearity from the proportions of gravel and sand (mud was a reciprocal). The first principle component score was used with the following loadings, explaining 63% of the cumulative variation in the data. This new explanatory variable was then centred and standardised.

SedimentPCA = (0.71 x % sand) + (-0.70 x % gravel) + (-0.04 x % mud)

Repeating the VIF analysis with sedimentPCA replacing % gravel and sand (and using scaled and centred variables) showed that multicollinearity between all variables was reduced below the threshold and ranged between 1.0 and 2.4.

Data from each animal was randomly sampled without replacement, with 70% used for model development and 30% for validation. Habitat preference modelling was carried out by fitting generalised linear mixed-effects models (GLMM) in the R-library LME4 (Bates *et al.*, 2014), implemented using GFRs. To account for individual animals contributing different amounts of telemetry data to the analysis (between-individual variation) due to varying tag lifespans, individual was used as an intercept-only random effect (Wakefield *et al.*, 2011). GFRs account for between haul-out site variability by using locally averaged covariates as fixed effects in the models, and allowing interactions with the other explanatory variables. Therefore, the models had flexibility to determine how preference changed regionally with respect to the average availability. One control point (0) was used for each telemetry location (1) and the data were modelled as a binomial process with a logit link function. Development samples for each species were used for model fitting and selection. A two-stage fitting process was implemented: firstly, forwards selection was used to determine which covariates should be included in the final models using Akaike's Information Criterion (AIC); and secondly, availabilities of retained covariates were added as interactions and all that had a p-value<0.01 were retained. The reason for splitting the selection process was that AIC should not be used with GFRs because it penalises against covariates that in some areas have very small coefficients but which in other areas a show strong preference/avoidance. Because the models deal with large spatial areas and extreme varying conditions, it is expected that certain covariates will be important in some areas and not others, but that regional importance needs to be retained in the model. To test that the underlying assumptions of the model had not been violated, model adequacy was checked graphically: partial residuals were used to check linearity, and QQ plots were produced to assess how well the error structure had been specified (Zuur *et al.*, 2009; Landwehr *et al.*, 1984). Spatial autocorrelation was assessed by calculating spline correlograms of Pearson's residuals using R package NCF (Bjornstad, 2013). Absolute goodness-of-fit for mixed models has been difficult to quantify until recently. A recently-published method to calculate R^2 was used to calculate the proportion of variation explained by the models (Nakagawa & Schielzeth, 2013). Temporal autocorrelation was examined using runs tests by individual animal using R library LAWSTAT (Gastwirth *et al.*, 2013). A prediction surface for each haul-out site was produced and normalised. This was then linked to the population estimate (see task MR5.1.1 in this Report for details) for that haul-out site, and these layers were aggregated to produce a continuous prediction surface for each species' at-sea sea usage.

7.4 Results

R^2 was 95% for the grey seal model and 96% for the harbour seal model. QQ-plots with simulated residuals plotted against fitted residuals with 95% confidence intervals showed linear relationships, suggesting that the error structure in the models had been correctly specified. There was almost no spatial autocorrelation evident in the model residuals. The mean p-value for the runs test for temporal autocorrelation for grey and harbour seals was 0.2 and 0.3 respectively, indicating that there was no evidence the data were not random. However, for grey seals 20 of the 120 animals and for harbour seals 5 of the 75 animals in the analysis had a p-value < 0.01, indicating that it could not be assumed the data were not temporally correlated. Validation data were fitted to the models and plotted along with the 95% confidence intervals derived using fixed and random effects variance (see Appendix Figure 1).

7.4.1 Grey seals

Covariates retained in the model were geodesic distance, spring tidal stratification, near bottom temperature, thermal stratification, and sediment. All availabilities were also retained, and first-order interactions were allowed between covariates and all of the averages. Near bottom temperature and thermal stratification were specified as quadratic covariates to allow some flexibility. Sixty-five percent of the deviance explained by the model was due to geodesic distance (35%), average geodesic distance (19%), and average spring tidal stratification (12%) (Table 7.1). A significant interaction between a covariate (e.g. geodesic distance) and its availability (average geodesic distance) shows that the incremental difference (δ) between the two is important, (i.e. it is important how different a covariate is from the regional average).

Table 7.1 Deviance explained in selected grey seal model

Covariate	Deviance explained
Intercept	19%
Geodesic distance	35%
Spring tidal stratification	3%
Near bottom temperature	3%
Thermal stratification	2%
Sediment	3%
Avg Geodesic distance	19%
Avg Spring tidal stratification	12%
Avg Near bottom temperature	1%
Avg Thermal stratification	1%
Avg Sediment	3%

Figure 7.1 shows that grey seals have preference for shallower water, which is expected of central-place foragers that spend much of their time close to haul-out sites (Aarts *et al.*, 2008). They prefer more tidally stratified areas where the water column remains vertically mixed all year (Scott *et al.*, 2010). They also display a preference for an optimal near bottom temperature of 9.7°C, which is high for sandeel habitat (Arnott & Ruxton, 2002) but near bottom temperature was calculated as a yearly average. Grey seals have a preference for well-mixed water columns, with the potential between the surface and bottom temperature ideally at 3.6°C. They also show a slight preference for substrate with increasing levels of sand (and subsequently decreasing levels of gravel), characterised by the sediment covariate.

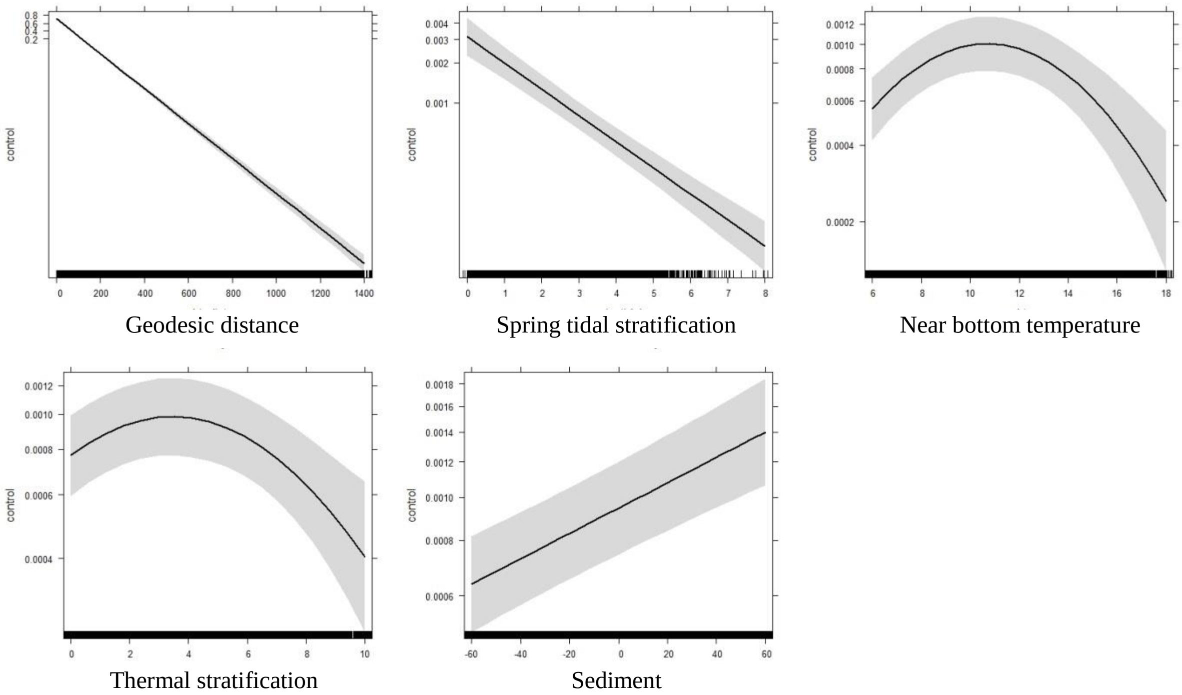

Figure 7.1. Marginal plots of grey seal probability of presence (0 to 1) for selected covariates with 95% confidence intervals.

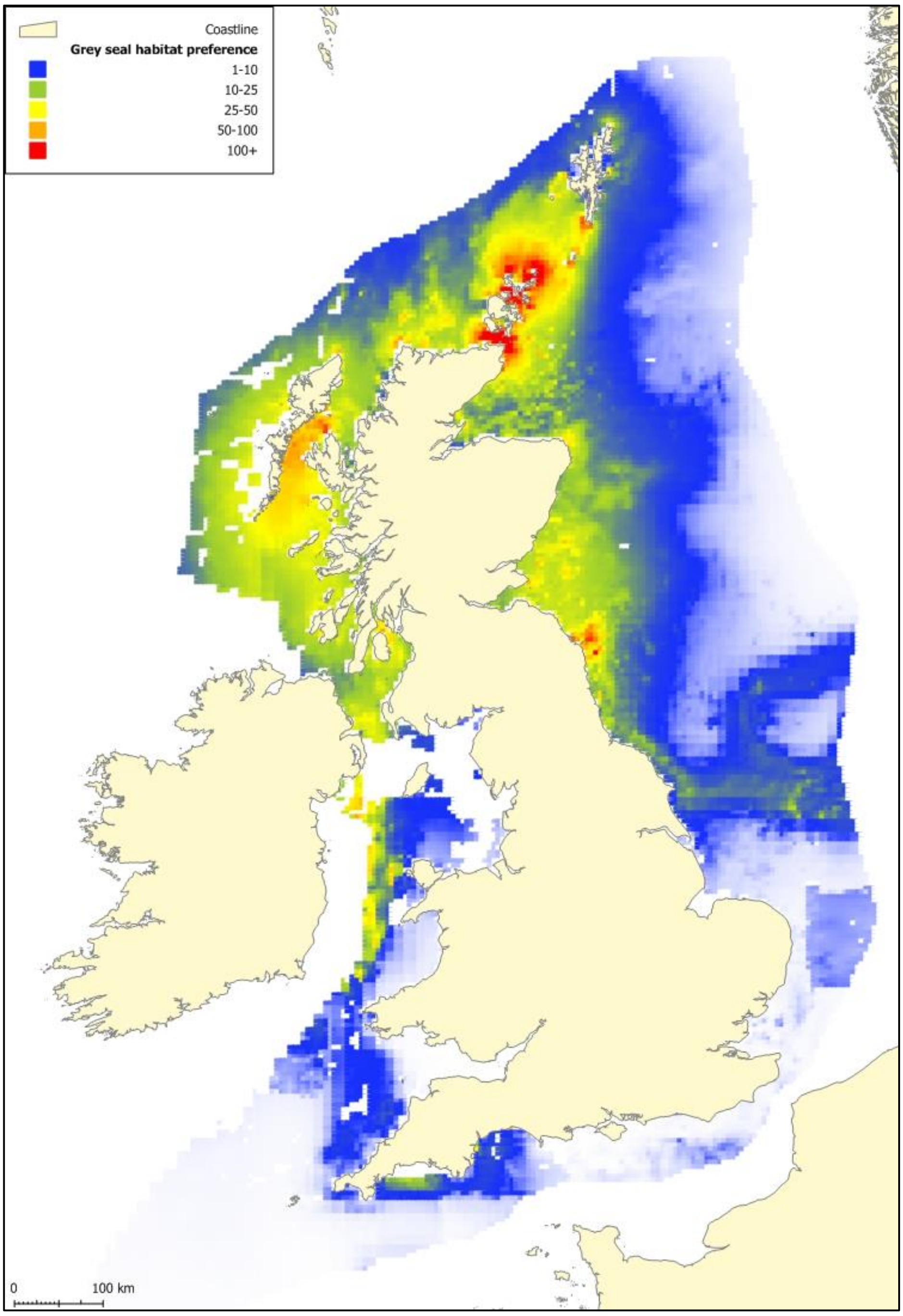

Figure 7.2. Grey seal habitat preference showing the predicted number of seals in each 5x5km^2 grid square. E.g. a yellow square denotes between 25 and 50 seals are within that grid square.

Figure 7.2 shows grey seal habitat preference, scaled to population-level. Areas of high usage are Orkney and Shetland, north Scotland; Isle of Harris, Outer Hebrides; and the Farne Islands, north-east England. Of particular interest are predictions in areas where no telemetry data are available around north-west Scotland and in the Moray Firth, showing that the model has the ability to make fine-scale predictions of usage where suitable environmental data are available at an appropriate resolution.

7.4.2 Harbour seals

Covariates retained in the model were geodesic distance, near bottom salinity, and slope. The selected model with availabilities as covariates gave unreasonable predictions, so the model with the lowest AIC but without availabilities was selected. Near bottom salinity was specified as a quadratic covariate. 87% of the deviance explained by the model was due to near bottom salinity (73%), geodesic distance (13%), and slope (1%) (Table 7.2).

Table 7.2. Deviance explained in selected harbour seal model.

Covariate	Deviance explained
Intercept	13%
Geodesic distance	13%
Near bottom salinity	73%
Slope	1%

Covariates selected by the model reflect the finding that harbour seals predominately stay within 50km of the coast (Jones *et al.*, in press). Figure 7.3 shows that harbour seals have preference for shallower water, a near bottom salinity of 33.7 psu (approximately the salinity of sea water, which is 34.7 psu), and for increasing sea-floor slope.

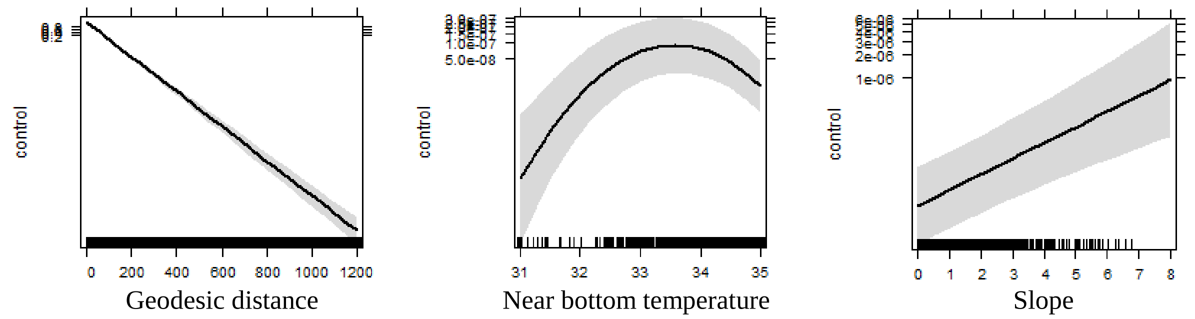

Figure 7.3. Marginal plots of harbour seal probability of presence (0 to 1) for covariates with 95% confidence intervals.

Figure 7.4 shows harbour seal habitat preference, scaled to population-level. With the exception of The Wash, east England, areas of very high usage are concentrated into small areas (5x5km^2 grid cells). Areas of high usage are mainly in Scotland (Shetland, Orkney, and west Scotland, Moray Firth, and (historically) Firth of Tay), and east England.

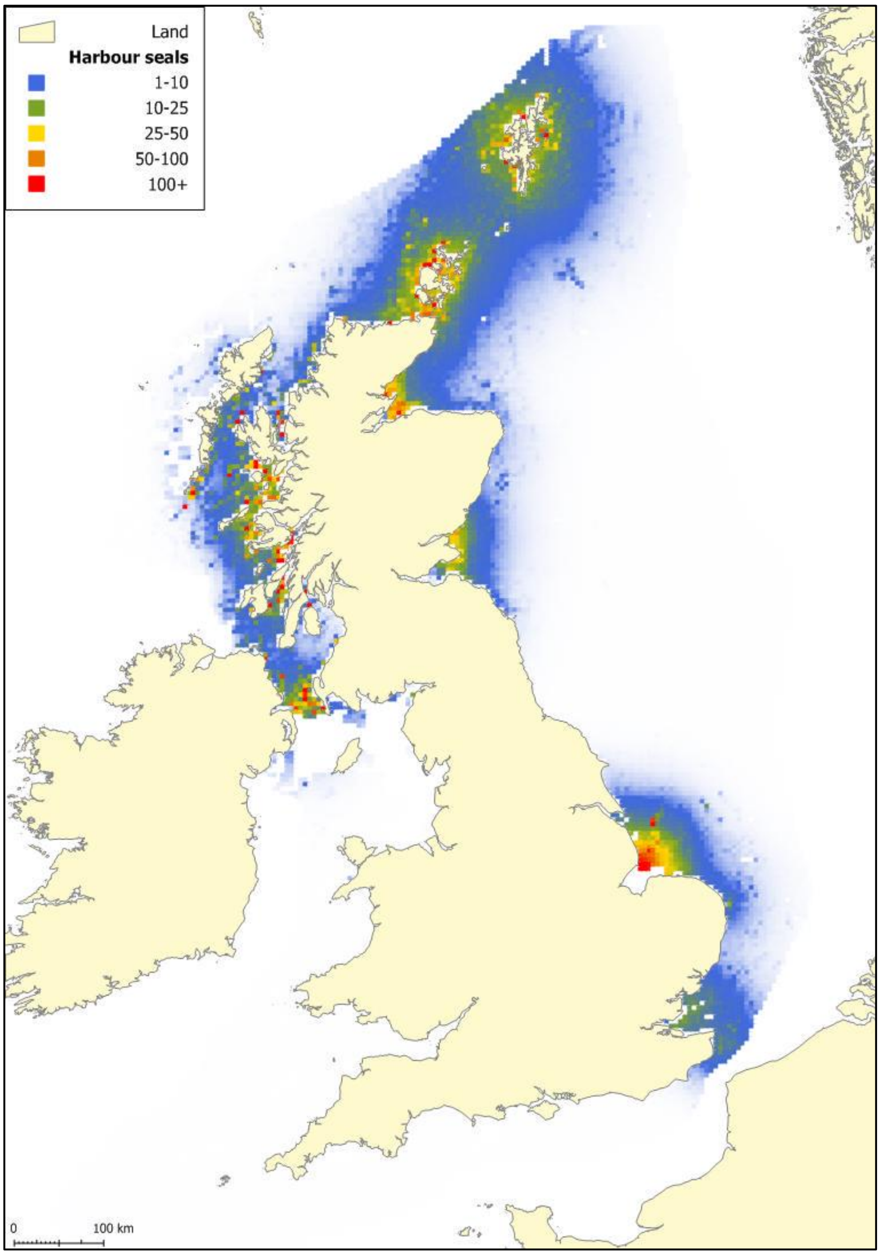

Figure 7.4. Harbour seal habitat preference showing the predicted number of seals in each 5x5km^2 grid square. E.g. a yellow square denotes between 25 and 50 seals are within that grid cell.

7.5 Conclusions

Habitat models performed well when fitting the development and validation data, and were used to produce maps of grey and harbour distributions including data-sparse or unobserved regions (see report on Data-sparse regions in task MR5.1.2 in this Report).

Both grey and harbour seals show a preference for shallower water. Grey seals prefer areas where the water column is mixed all year, with a near bottom temperature of 9.7°C (higher than in other studies but this was a yearly average). Harbour seals prefer areas with a near bottom salinity of 33.7 psu (approximately the salinity of sea water) and increasing sea-floor slope. Harbour seals spend much of their time close to the coast, where mixing of the water column (that may influence prey distributions) is known to be primarily driven by salinity (density) (Scott *et al.,* 2010). Water column mixing, near bottom temperature and salinity, and sediment may all be associated with the distribution and concentration of prey that are utilised by grey or harbour seals. Furthermore, harbour seals are known to meet the basic sensitivity requirements to salinity for chemosensory orientation (Sticken &

Dehnhardt, 2000) and so could use salinity to navigate. However, the biological mechanisms that drive the spatial distribution of seals in relation to the abiotic environmental variables in this study are not yet well understood and will not be discussed in greater detail in this report.

It will be possible to update the maps by incorporating additional movement and terrestrial count data in future, and further covariates could also be added to the models if new environmental data are made available. The existing models could be used to make predictions about changes to seal distributions under changing conditions such as (1) local seal populations increasing or declining; (2) environmental variables such as sea bottom temperature or salinity varying due to climate change.

7.6 References

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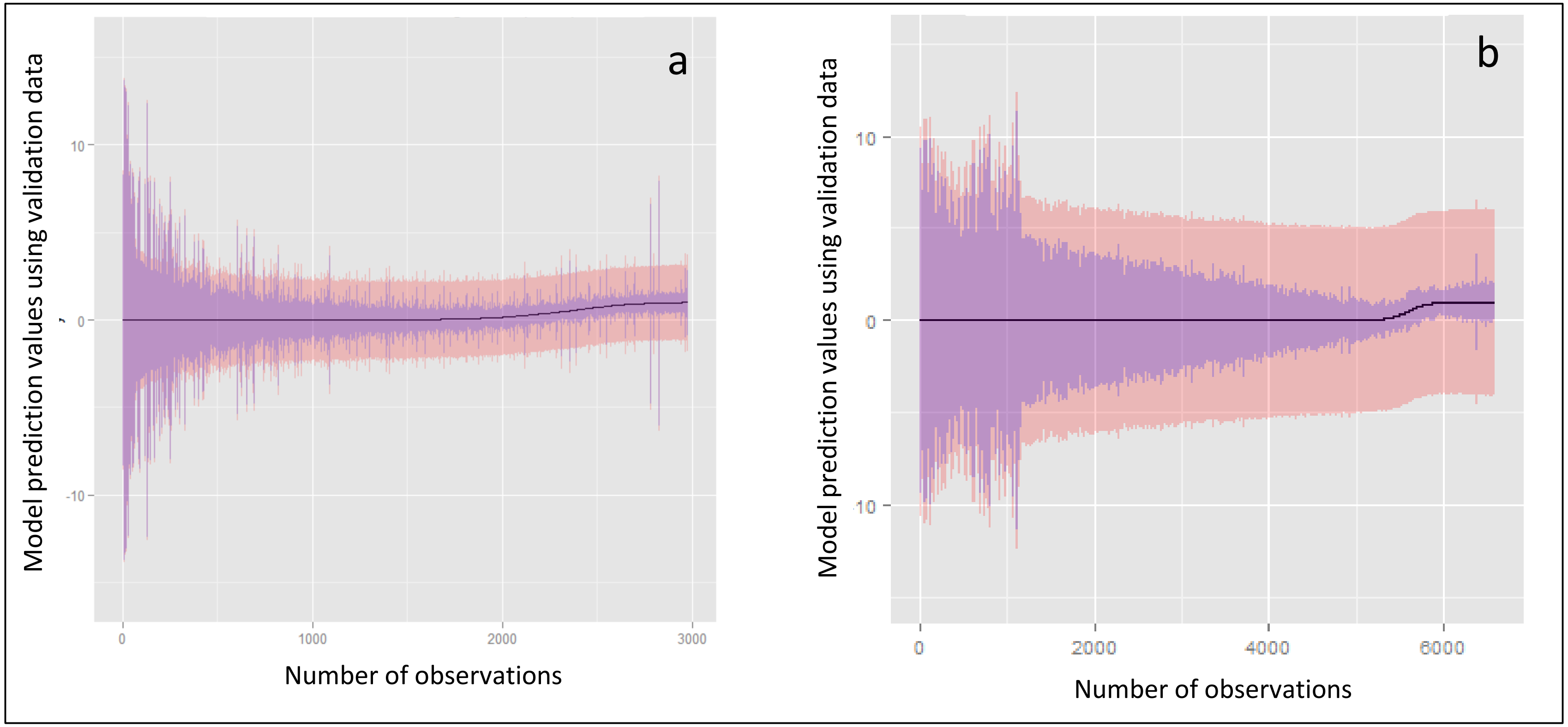
7.7 Appendix

Appendix Table 1 Summary of transformed covariates offered to the grey and harbour seal models.

Covariate name	Data set	Data source	Date	Original scale and projection	Processing	Data type
biodist	Geodesic distance (km) (distance to haul-out)	User defined	2013	5x5km^2 grid squares, Transverse Mercator UTM30N WGS1984	Step Gaussian moving window approach.	5x5km^2 grid squares, Transverse Mercator UTM30N WGS1984, in km, all positive values.
bathy	Seabed depth (m)	EDINA/SeaZone	2009	Vector 10m resolution, lon/lat WGS1984		Continuous surface, Transverse Mercator UTM30N WGS1984, in km, can take any value.
cosaspect	Mean seabed aspect (radians) from -1 (south) to 1 (north)	EDINA/SeaZone	2009	3x3km^2 grid squares, lon/lat WGS84	Derived from Bathymetry on 3x 3km^2 scale.	Continuous surface, Transverse Mercator UTM30N WGS1984, in km, -1 to 1.
sinaspect	Mean seabed aspect (radians) from -1 (west) to 1 (east)	EDINA/SeaZone	2009	3x3km^2 grid squares, lon/lat WGS84	Derived from Bathymetry on 3x 3km^2 scale.	Continuous surface, Transverse Mercator UTM30N WGS1984, in km, -1 to 1.
slope	Seabed slope (incline) (Degrees)	EDINA/SeaZone	2009	3x3km^2 grid squares, lon/lat WGS84	Derived from Bathymetry on 3x 3km^2 scale.	Continuous surface, Transverse Mercator UTM30N WGS1984, in km, positive values.
sandprop **gravelprop**	Sediment type including CO_3 concentration.	British Geological Survey (Digibath 250)	NA	Lon/lat WGS1984	Simplified Folk classification data supplemented with additional data from US Navy and point samples. Data kriged to provide continuous coverage. Include CO_3 concentrations.	Sand, gravel, and mud as proportions of sediment (mud was excluded due to reciprocity), 0 to 100 allowed.
nbt	Monthly mean near seabed potential temperature (°C)	MyOcean	Aggregated from 01/01/1990 to 31/12/2004	12x12km^2 resolution, surface to 5000m, lon/lat WGS 1984	Each response point (presence/pseudo-absence) is matched with closest month stamp from nbt covariate.	12x 12km^2 grid squares, Transverse Mercator UTM30N WGS1984, in km, positive values.

nbs	Monthly mean near seabed salinity (psu)	MyOcean	Aggregated from 01/01/1990 to 31/12/2004	12x12km^2 resolution, surface to 5000m, lon/lat WGS 1984	Each response point (presence/pseudo-absence) is matched with closest month stamp from nbs covariate.	12x 12km^2 grid squares, Transverse Mercator UTM30N WGS1984, in km, positive values.
thst	Thermal stratification (°C)	MyOcean	Aggregated from 01/01/1990 to 31/12/2004	12x12km^2 resolution, surface to 5000m, lon/lat WGS 1984	Monthly mean sea surface potential temperature – Monthly mean near seabed potential temperature. Each response point (presence/pseudo-absence) is matched with closest month stamp from thst covariate.	12x 12km^2 grid squares, Transverse Mercator UTM30N WGS1984, in km, negative and positive values.
sast	Salinity stratification (psu)	MyOcean	Aggregated from 01/01/1990 to 31/12/2004	12x12km^2 resolution, surface to 5000m, lon/lat WGS 1984	Monthly mean sea surface salinity – Monthly mean near seabed salinity. Each response point (presence/pseudo-absence) is matched with closest month stamp from sast covariate.	12x12km^2 grid squares, Transverse Mercator UTM30N WGS1984, in km, negative and positive values.
springtidal	Spring mean tidal stratification (m^{-2} s^3)	Proudman Oceanographic Laboratory. Depth (mean sea level) derived from US Naval Oceanographic Office DBDB0-V-Version 4.2.	2008	12x12km^2 resolution, Transverse Mercator UTM31N WGS1984	Log_{10}(depth / Peak flow for a mean spring tide)^3)	Transverse Mercator UTM30N WGS1984, in km.
neaptidal	Neap mean tidal stratification (m^{-2} s^3)	Proudman Oceanographic Laboratory. Depth (mean sea level) derived from US Naval Oceanographic Office DBDB0-V-Version 4.2.	2008	12x12km^2 resolution, Transverse Mercator UTM31N WGS1984	Log_{10}(depth / Peak flow for a mean neap tide)^3)	Transverse Mercator UTM30N WGS1984, in km.



Appendix Figure 1. Ordered fitted values using validation data showing 95% CI using fixed effects variance (purple) and random effects variance (pink) for (a) grey seals; and (b) harbour seals.