

JNCC Report No: 602

Review of analytical approaches for identifying usage and foraging areas at sea for harbour seals

Esther L. Jones, Sophie Smout, Deborah J. F. Russell, Eunice H. Pinn & Bernie J. McConnell

January 2017

© JNCC, Peterborough 2017

ISSN 0963-8901

For further information please contact:

Joint Nature Conservation Committee Monkstone House City Road Peterborough PE1 1JY www.jncc.Defra.gov.uk

This report should be cited as:

Jones, E.L., Smout, S., Russell, D.J.F., Pinn, E.H. & McConnell, B.J (2017). Review of analytical approaches for identifying usage and foraging areas at sea for harbour seals. *JNCC Report No. 602.* JNCC, Peterborough.

JNCC EQA Statement:

This report is compliant with the JNCC Evidence Quality Assurance Policy <u>http://jncc.Defra.gov.uk/default.aspx?page=6675</u>.

The report was reviewed by the Interagency Marine Mammal Working Group which comprises of expert staff from JNCC, SNH, NRW, NE and DAERA.

Executive summary

The purpose of this report is to build upon the outputs of work undertaken by the Sea Mammal Research Unit (SMRU, University of St Andrews) funded by the Department of Energy and Climatic Change (DECC) and the Scottish Government, in order to draw these strands of work together with the aim of identifying whether discrete and persistent foraging areas for harbour seals (*Phoca vitulina*) can be identified in the UK marine area.

A usage map of harbour seal at-sea distribution is presented in order to identify important atsea areas for the species. Usage is the estimate of the instantaneous density of seals at sea. This is based upon movement data derived from 277 telemetry tags deployed between 2003 and 2013, combined with terrestrial haul-out count data from 1996 to 2013. These data were collected by two tag types: Satellite Relay Data Loggers (SRDL) that use the Argos satellite system for location estimation and data transmission, and GPS phone tags that use the GSM mobile phone network for data transmission. The usage map extends to the limit of UK harbour seal movements and has a spatial resolution of 5km x 5km. Seal usage within the 5km x 5km cells is estimated (using current and historical data where appropriate) for the year 2013. The data do not support breaking down this usage map by year, season, or by the intrinsic properties of seal age or sex. Uncertainty is incorporated into the usage map estimation so that 95% confidence intervals of individual cell usage are available.

Regional significance is demonstrated by dividing the usage map into five Harbour Seal Areas (HSAs). Within each HSA, grid cells are ranked in descending order based on the estimated usage in each cell. Grid cells are selected, beginning with the most intensively used cells, until 10% of the total usage of each HSA is included. This is repeated in 10% increments (up to 90%) of individual HSA usage and the resulting maps are presented. Usage maps could be made more accurate with strategically-located future deployments of tags. This would also help indicate whether high usage areas are persistent in the long term. The usage maps are weighted by the terrestrial distribution of harbour seals surveyed during the moult (August) period. However, there may be redistribution over the rest of the year so synoptic haul-out counts outside the moult period are needed to test whether this is a significant issue. Usage maps present a 'snapshot' of seal usage: they show the estimated number of seals per grid square at any instant in time, in this case the year is 2013.

Estimating activity-unclassified usage is informative for management, since it integrates all activities (all of which are considered to be essential for harbour seals) into one simple index. There may be added value in classifying activity because it would allow activity-specific management. For instance, changes in prey abundance and distribution may be important in areas where foraging dominates, but less important in areas used primarily for travelling. By contrast, in some cases disturbance may have more serious implications in travelling areas; if only one travelling route connects a haul-out and offshore foraging area then disturbance on such routes, for example during wind farm construction, may cause barriers to movement.

A State Space Modelling (SSM) framework was developed that uses track speed and tortuosity, and diving behaviour to disaggregate foraging, travelling and resting activities. Using this framework, it was demonstrated that data collected using SRDL tags are not suitable for estimation of activity states in harbour seals (e.g. foraging); only data from GPS phone tags are of the high temporal resolution required to define activities. There are no usage maps of these activities currently available. However, activity-specific locations of tagged individuals from a DECC-funded study at The Wash were overlaid onto local population usage. This simple comparison indicates that offshore high usage areas, in this region at least, are typically associated with a relatively high density of foraging locations. Such a comparison would not be appropriate elsewhere because other regions for which

GPS data are available are dominated by complex coastlines encompassing multiple haulout sites. In such regions usage in a given at-sea grid cell results from tracks emanating from multiple haul-out site cells; the usage resulting from each haul-out site cell is then weighted by the population size of that haul-out site cell. Therefore a comparison of the locations of tagged individuals with population level usage would not be appropriate. Such a comparison is possible for The Wash because it comprises a small group of isolated haulout site cells meaning that both population level usage and foraging locations emanate from the same sites.

Extensive work would be required to use the activity data to quantify key foraging areas. Even though the activity-unclassified usage maps included data from SRDL tags, a lack of telemetry data associated with haul-out site cells meant that 48% of the total harbour seal usage had to be predicted based on the relationship between usage and distance to haulout sites for those haul-out site cells for which telemetry data were available. This percentage would increase with the exclusion of SRDL data, and predictions based on distance to haul-out sites would be inappropriate for predicting foraging areas. Thus, habitat preference analyses, for which environmental covariates are linked to foraging, is likely to be the most suitable way to in predict key foraging areas.

Contents

1	Inti	roduction	1
2	Est	timating at-sea usage for UK harbour seals	4
	2.1	Methods	5
	2.1	.1 Mapping	5
	2.1	.2 Population data	6
	2.1	.3 Movement data	6
	2.1	.4 Positional corrections	8
	2.1	.5 Interpolation	9
	2.1	.6 Haul-out detection	9
	2.1	.7 Haul-out site aggregation	9
	2.1	.8 Trip detection	9
	2.1	.9 Kernel smoothing	9
	2.1	.10 Information content weighting	10
	2.1	.11 Population scaling	10
	2.1	.12 Population uncertainty	11
	2.1	.13 Individual-level uncertainty	11
	2.1	.14 Null Model	12
3	lde	ntifying high-use areas at sea for UK harbour seals	12
	3.1	Defining appropriate geographical regions for assessment	12
	3.2	Analytical approach	14
	3.3	Results: the most intensively-used areas	15
4	lde	entifying harbour seal foraging areas	19
	4.1	Telemetry data	19
	4.2	State assignment	19
	4.3	Temporal resolution	20
	4.4	Currents: movement in hydro-space	20
	4.5	Habitat preference modelling	20
	4.6	Overlaying foraging locations on usage maps	20
5	Dis	scussion	24
	5.1	Usage maps	24
	5.2	Identification of foraging areas	25
	5.3	Relevance to the identification of harbour seal foraging areas throughout the UK.	26
6	Ac	knowledgements	27
7	Re	ferences	28

8	Appendix	. 3	1
---	----------	-----	---

1 Introduction

Harbour seals (*Phoca vitulina*) are one of two resident seal species around the UK. Scotland holds approximately 79% of the UK harbour seal population, with 16% in England and 5% in Northern Ireland. Harbour seals are widespread around the west coast of Scotland and throughout the Hebrides and Northern Isles. On the UK east coast, their distribution is more restricted with concentrations in the major estuaries of the Thames, The Wash, Firth of Tay and the Moray Firth. Adults weigh 80-100kg, with males being slightly larger than females and both sexes have a typical lifespan of 20-30 years (SCOS 2015). Harbour seals are central place foragers, spending time on land between foraging trips at sea. They spend the majority of their time within 50km of the coast (Jones *et al* 2015a). Their diet varies seasonally and regionally with a range of prey including sand eel (*Ammodytes spp*), gadids, flatfish (*Pleuronectidae*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), octopus and squid (*Cephalopoda*) (Wilson & Hammond 2015). Harbour seals haul out for extended periods to breed in June and July, and moult in August. Mothers give birth to single pups and lactate for approximately 24 days until weaning (Muelbert & Bowen 1993). Pups shed their white coat *in utero* and can swim and dive within hours of birth.

The 1992 Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC), otherwise known as the 'Habitats Directive', is one of the main policy drivers for nature conservation in European waters including the UK. Seals are also protected under the Conservation of Seals Act 1970 (England and Wales), the Marine (Scotland) Act 2010 and The Wildlife (Northern Ireland) Order 1985. As part of the UK's legal obligations, a coherent European ecological network of Special Areas of Conservations (SACs) should be established, composed of sites hosting the habitat types listed in Annex I and the species listed in Annex II of the Habitats Directive. These sites are expected to enable the habitat types and the species concerned to be maintained or, where appropriate, restored at a favourable conservation status in their natural range [Article 3(1)]. Article 4(1) states 'for animal species ranging over wide areas these sites shall correspond to the places within the natural range of such species which present the physical or biological factors essential to their life and reproduction. For aquatic species which range over wide areas, such sites will be proposed only where there is a clearly identifiable area representing the physical and biological factors essential to their life and reproduction'. These aguatic species include harbour seals.

At the 2009 Atlantic Biogeographic meeting, the European Commission concluded that the UK was 'insufficient moderate' for the designation of haul-out areas for harbour seals, meaning that one or a few additional sites (or maybe extension to existing sites) were required. At the meeting, the Sound of Barra was specifically mentioned as needing designation for the species. This site has subsequently become an SAC and the UK is now considered sufficient for haul-out areas (Figure 1a). In 2009, the Commission also concluded that there was 'scientific reserve' for feeding areas, meaning that a definite conclusion on sufficiency was not possible at that time and that there was a need to investigate and/or clarify further. The scientific reserve is still in place today. Currently, the UK has 12 SACs graded A-C for harbour seals (Figure 1a) and 17 graded D.

This report has been undertaken as a contribution to considering the scientific reserve for harbour seal feeding areas at sea. Most surveys of harbour seals are carried out in August, during their annual moult. At this time, harbour seals tend to spend longer at haul-out sites and the greatest and most consistent counts of seals are found ashore. This provides a minimum estimate of population size. Scaling this by the estimated proportion hauled out produces an estimate of total population size (for further details see SCOS 2015).

Since 1988, the Sea Mammal Research Unit's (SMRU) surveys of harbour seals around the Scottish coast have been carried out on an approximately five-yearly cycle. Exceptions are the Moray Firth (between Helmsdale and Findhorn), and the Firth of Tay and Eden Estuary SAC, which have been surveyed annually since 2002 (Duck *et al* 2015) (see Figure 1b). Surveys carried out in 2006 revealed significant declines in harbour seal numbers in Shetland, Orkney and elsewhere along the UK coast. Between 2007 and 2009, SMRU surveyed the entire Scottish coast including a repeat survey of some parts of Strathclyde and Orkney. In 2010, Orkney was surveyed again to determine whether previously observed declines had continued. The next complete survey of Scotland began in 2011 and was due for completion in 2015. A complete survey of Northern Ireland and the Republic of Ireland was carried out in 2011 and 2012.

In England, the Lincolnshire and Norfolk coast holds approximately 90% of the English harbour seal population and is usually surveyed twice annually during the August moult. Since 2004, additional breeding season surveys (in early July) of harbour seals in The Wash (which lies within the August survey area) were undertaken for Natural England. The Suffolk, Essex and Kent coasts were last surveyed by SMRU during the breeding season in 2011 and during the August moult.

These surveys reveal that harbour seal populations have been in decline in some areas around the UK since 2000. The population estimate for 2013 was 36,500 (approximate 95% Cl 29,900 - 49,700) (Duck *et al* 2014), and the species is considered to have an unfavourable conservation status in UK waters (JNCC 2013). Reduced juvenile survival and fecundity have been identified as proximate causes of the decline in the Moray Firth, north east Scotland (Matthiopoulos *et al* 2014). An ongoing investigation by SMRU into the decline of harbour seals around Scotland has identified other possible causes of the decline to include interactions with grey seals (*Halichoerus grypus*) (indirectly through competition for resources and/or directly through predation) (Brownlow *et al* 2016) and exposure to toxins from harmful algae (Jensen *et al* 2015).

This report describes an analytical approach used to estimate synoptic UK harbour seal atsea usage, based on telemetry-derived movement data and on terrestrial haul-out surveys. An example of ongoing studies into the identification of harbour seal foraging areas is presented for The Wash. More detailed technical descriptions of the analytical methodology can be found in Jones *et al* (2015a) and Russell *et al* (2015). Review of analytical approaches for identifying usage and foraging areas at sea for harbour seals



Figure 1a. Locations of current UK SACs with marine components where harbour seals, as an Annex II species, are the primary reason or qualifying feature for site selection.

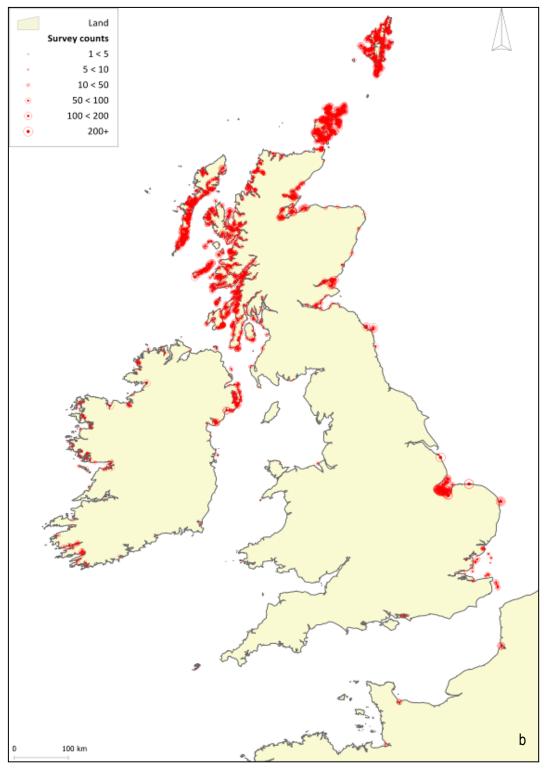


Figure 1b. Harbour seal haul-out sites identified through terrestrial surveys. Adapted from Figure 2b in Jones *et al* (2015a).

2 Estimating at-sea usage for UK harbour seals

Broad-scale maps identifying the intensity of space-use at sea for harbour seals were developed for the Scottish Government under the Marine Mammal Scientific Support Programme MMSS/001/11 and delivered in 2014. The resulting publication (Jones *et al* 2015a) provides the basis for the usage maps in this report.

The maps were based on long-term telemetry data from tagging studies conducted at many different sites around the UK, up to 2013. Male and female animals (aged one or more) were included in the analysis. Tags provided information on at-sea and haul-out site locations during the months that the tags remain attached.

A brief summary of the methods used to produce seal usage maps follows and a more detailed account can be found in section 2.1. Full details of the analytical methodology are available in Jones et al (2015a). For every haul-out site that had associated survey count data and seal movement data, kernel smoothing was used to map individual patterns of movement, which were then combined to map general patterns of usage associated with that site (Figure 2, boxes 1, 2 and 3). Only a sample of animals within the population were tagged and there are a large number of haul-out sites around the UK coast. For some haulout sites where seals were present onshore during count surveys, there were no associated telemetry data. For these sites, a model was used to estimate at-sea distribution based on a general analysis of the telemetry data from other haul-out sites to predict the distribution of seals based on distance to coast and haul-out site. This is referred to as the "null model" (Figure 2, box 7). Usage from separate haul-out sites, based on the null model or on kernel smoothing, was then combined to estimate UK at-sea usage over the study area, taking account of the number of animals counted at each site during surveys (Figure 2, boxes 4 and 8). For a site where many animals were known to haul out, observed movement patterns from telemetry associated with that site would therefore be more influential in determining the pattern of the overall usage map than movements from a low-population haul-out site.

The resulting maps are usage surfaces, where the value in any one grid cell represents the expected number of seals in that cell. In simple terms, if the ocean was instantaneously drained and snapshots immediately taken in every grid cell, the number of seals counted in any one grid cell would be the usage for that cell. Estimates of usage were calculated by grid square so that numbers for any grid cell (and corresponding colour scale) will depend on the grid resolution. If larger grid squares are used, then higher numbers are expected in each grid square. This is an important consideration if usage maps produced at different spatial resolutions are to be compared. Uncertainty was propagated throughout the analysis to produce 95% confidence intervals for the usage estimates, for every grid cell (Figure 2, boxes 5 and 6).

2.1 Methods

Figure 2 shows a schematic flowchart of the analytical processes used to estimate spatial usage by UK harbour seals. The steps involving calculation of uncertainty based on individual variation in patterns of usage and on variability in the count data are also shown.

2.1.1 Mapping

All maps were projected using Universal Transverse Mercator 30° North, World Geodetic System 1984 datum (UTM30N WGS84) using a grid of 5km x 5km. Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data from NOAA were used in all figures showing the UK coastline (available from <u>www.ngdc.noaa.gov/mgg/shorelines/gshhs.html</u>). Analyses were conducted using R 3.1.2 (R Core Team 2014) and GIS software Manifold 8.0 (Manifold Software Ltd 2013).

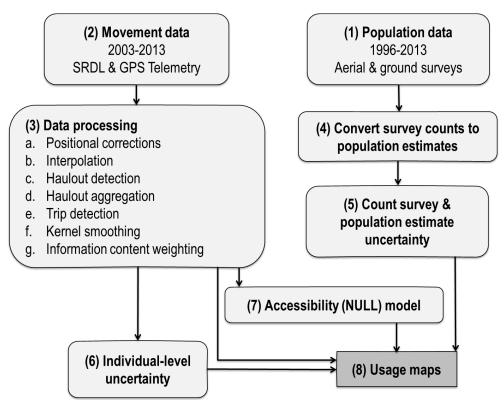


Figure 2. Flowchart showing the analytical methodology used to produce harbour seal usage maps. Adapted from Figure 1 in Jones *et al* (2015a).

2.1.2 Population data

Harbour seals are surveyed during their moult in August when the greatest numbers of animals haul out on land for an extended period. During aerial surveys all seals along a specified coastline are counted and coordinates are recorded to an accuracy of approximately 50m. Surveys take place within two hours of low tide when low tide is between 12:00 and 18:00 hours (Thompson *et al* 2005). Survey effort is variable between regions and all available data between 1996 and 2013 (the most contemporary data available) were used. Ground- and boat-based count data collected by other organisations were also used in the analysis. All sources of data collection are summarised in Table 1.

2.1.3 Movement data

Adult and sub-adult (i.e. any animal more than one-year-old) seals (n=277, 168 male; 109 female) were tagged between 2003 and 2013, in locations around the UK (see Table 2 and Figure 3). Between 2003 and 2007, Satellite Relay Data Loggers (SRDL) were deployed that use the Argos satellite system for location estimation and data transmission. Between 2006 and 2013, GPS phone tags that use the GSM mobile phone network were deployed (McConnell *et al* 2004). Telemetry data are irregular in time and prone to error. These data were initially cleaned to remove implausible values and then interpolated to produce regularised tracks.

Table 1. Summary of harbour seal terrestrial surveys. Unless specified otherwise in the description,	
all surveys took place during August. Adapted from Table 1 in Jones et al (2015a).	

Area surveyed	Method	Description	Data used
Scotland	Aerial survey (helicopter)	Both species surveyed every 1 to 5 yr using SMRU protocol	1996–2013
Moray Firth, Firth of Tay, Donna Nook, The Wash in East Anglia, Thames estuary	Aerial survey (fixed-wing)	Both species surveyed annually using SMRU protocol	1996–2013
Chichester & Langstone harbour	Ground counts through Chichester Harbour Authority	Harbour seals surveyed annually	1999–2012
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 & 2010
Republic of Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol	2003*
Northern France	Ground counts with extrapolation (Hassani <i>et al</i> 2010)	Harbour seals surveyed annually	1996–2008

*2011 and 2012 survey data were not available at the time of map production.

Table 2. Summary of harbour seal telemetry deployments by year. Adapted from Table S2 in Jones *et al* (2015a).

Year	Tag type	Number of tags	Sex ratio (M:F)	Mean tag lifespan (days)	Tagging locations
2003	SRDL	26	11 :15	161	W Scotland, Orkney & N coast, Shetland, SE England
2004	SRDL	29	15 :14	116	W Scotland, Orkney & N coast, Shetland, SE England
2005	SRDL	21	12 :9	94	W Scotland, Moray Firth, SE England
2006	SRDL / GPS	25 / 30	36 :19	90	Western Isles, Moray Firth, SE England, Ireland, France, N Ireland
2007	SRDL / GPS	1/8	5 :4	108	Moray Firth, N Ireland, Ireland, France
2008	GPS	15	14 :1	129	France
2009	GPS	10	3 :7	84	W Scotland, Moray Firth, W England & Wales
2010	GPS	10	8 :2	92	N Ireland
2011	GPS	31	22 :9	96	W Scotland, Orkney & N coast, E Scotland
2012	GPS	68	40 :28	77	W Scotland, Orkney & N coast, E Scotland, SE England
2013	GPS	3	2 :1	56	E Scotland
TOTAL		277	168:109	mean=100	

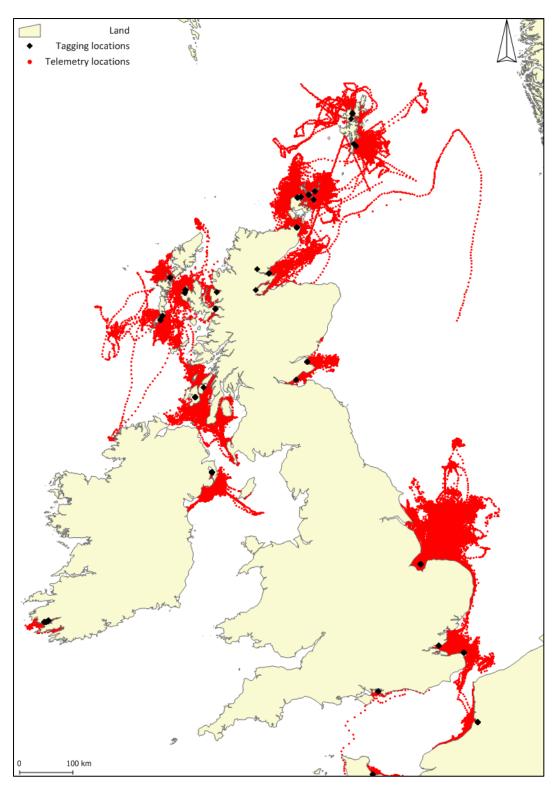


Figure 3. Telemetry deployments for harbour seals around the UK showing tagging locations (black diamonds) and telemetry locations (red points). Adapted from Figure 3b in Jones *et al* (2015a).

2.1.4 **Positional corrections**

Locations derived from Argos-based SRDL can have significant error, varying from 50m to >2.5km. 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*

1992). Observation model parameters were provided by the location quality class errors from Vincent *et al* (2002), and process model parameters were derived from the average speeds of all higher accuracy GPS tags. The majority of GPS locations have an expected error of \leq 55m (Dujon *et al* 2014), however occasional outliers were excluded based on thresholds of residual error and number of satellites.

2.1.5 Interpolation

SRDL movement data were interpolated to two-hour intervals using output from the Kalman filter and merged with linearly interpolated GPS data that had been regularised to two-hour intervals. A regular grid of 5km resolution was created to encompass all telemetry data; 5km was selected based on the computational trade-off between the resolution and spatial extent of the final maps. The patterns of movement of the tagged animals were assumed to be representative of the whole population (Lonergan *et al* 2011). Tag deployment occurs outside breeding and moulting seasons, and the tags will fall off when animals moult, if not before. Although telemetry data were collected year-round, harbour seal data collection occurred primarily between January and June.

2.1.6 Haul-out detection

Haul-out events for both SRDL and GPS tags were defined as starting when the tag sensor had been continuously dry for 10min and ending when the sensor had been continuously wet for 40s. Haul-out events were assigned a location by matching their date and time with that of the track records.

2.1.7 Haul-out site aggregation

Haul-out sites (defined by the telemetry data as any coastal location where at least one haulout event had occurred) were aggregated into the 5km × 5km cells as defined above. Haulout events occur on land or intertidal sandbanks. Haul-out site cells were associated with a terrestrial count in order to scale the analysis to the population level. First, telemetry haul-out sites were linked to terrestrial counts based on matching their grid cells. Second, if no match could be found, the nearest valid haul-out site cell visited by the animal either directly before or after the unmatched haul-out site event was chosen. Third, if an animal had never been to a haul-out site cell with associated terrestrial data during the time it was tagged, count information was assigned from the nearest haul-out site cell based on Euclidean distance.

2.1.8 Trip detection

Seals moved between different haul-out sites. The movements of individuals at sea were divided into trips, defined as the sequence of locations between haul-out events. Each location in a trip was assigned to a haul-out site cell. After spending time at sea, an animal could either return to its original haul-out site cell (classifying this part of the data as a return trip) or move to a new haul-out site cell (giving rise to a transition trip). Transition trips were divided temporally into two equal parts, and the corresponding telemetry data were attributed to the departure and termination haul-out site cells.

2.1.9 Kernel smoothing

Telemetry data are locations recorded at discrete time intervals. To transform these into spatially continuous data representing the proportion of time animals spent at different locations, the data were kernel smoothed. The KS library in R (Chacón & Duong 2010) was used to estimate spatial bandwidth of the 2D kernel applied to each animal/haul-out site map using the unconstrained plug-in selector ('Hpi') and kernel density estimator ('kde') to fit a

usage surface. Kernel smoothing can be sensitive to the choice of smoothing parameter and serial correlation in the observations. However, thinning the data to eliminate autocorrelation would have meant a significant loss of information. Instead, the average tag duration (100 days) was determined to be long enough to counteract bandwidth sensitivity (Blundell *et al* 2001; Fieberg 2007). Only at-sea locations were smoothed because haul-out events were at fixed locations and known without uncertainty at the scale of the analysis. Therefore, haul-out event locations were incorporated back into the maps as discrete grid cell usages.

2.1.10 Information content weighting

To account for differences in tag operation duration, an Index of Information Content was derived (see Jones *et al* 2015a, Supplementary Material). This process ensured the importance of animals with short tag-lifespans was reduced and animals with heavily auto-correlated location data were not overrepresented. A 'discovery' rate was determined, defined as the total number of new grid cells visited as a function of tag lifespan, and modelled using generalised additive models (Wood 2006, 2011). Explanatory covariates were tag lifespan and type of tag (SRDL or GPS). Each animal/haul-out event map was multiplied by a normalised discovery rate (termed an 'information content weighting') and all maps connected to each haul-out site cell were aggregated and normalised to one.

2.1.11 Population scaling

The harbour seal population in each haul-out site cell was estimated from terrestrial count data, which were rescaled to allow for the proportion of animals that were at sea when surveys were carried out. Using mean haul-out probabilities over all available months and their variances, a distribution of population estimates was derived ranging from the value of each terrestrial count (minimum population size) to 100 times the count (maximum population size). A likelihood distribution of estimates. The spatial extent of annual terrestrial counts varied considerably and inter-region counts were seldom contemporary. In addition, the harbour seal population has varied, at different geographical scales, over the period covered by this analysis. To obtain a single population estimate for each haul-out site cell from the bootstrapped estimates, a decision tree (Figure 4) was used to produce population estimates and variances.

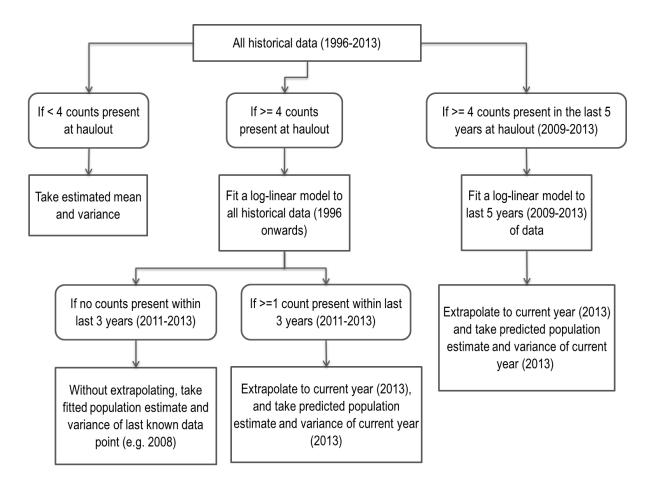


Figure 4. Decision tree flow chart showing how the population estimates depend on the terrestrial count data available. Here 'haul-out' refers to a haul-out site cell. Adapted from Figure S4 in Jones *et al* (2015a).

2.1.12 Population uncertainty

Several types of uncertainty are associated with counts from terrestrial surveys and scaling to the population level. Observational errors occur in surveys due to varying weather conditions, accuracy in recording animal locations, and possible disturbance to animals during surveying. Sampling errors occur because surveys, by their nature, are instantaneous counts in time. These errors were mitigated as much as possible through survey design and repeat surveying, and errors were modelled based on the mean proportion of time harbour seals spent hauled out, with corresponding standard errors (Matthiopoulos 2011; Lonergan *et al* 2011).

2.1.13 Individual-level uncertainty

Individual-level uncertainty accounted for differences in the magnitude of data collected by an animal over its tag lifespan and for variation in the operational settings of the tag itself. Variance was modelled using data-rich haul-out site cells (determined experimentally to be those sites which had \geq 7 animals associated with them). Variance was estimated using linear models with explanatory covariates of sample size (number of animals at the haul-out site) and mean usage by seals. The models predicted variance for data-poor and null usage sites (where population data existed but movement data did not (see section 2.1.14)).

Within-haul-out site cell, variance was estimated for null usage sites by setting the sample size of the uncertainty model to zero. Individual and population-level variances were

combined to form uncertainty estimates for the usage maps. Usage and variance by haul-out site cell were aggregated to a total usage and variance maps. Estimates of haul-out site cell usage were then added to at-sea usage to generate maps of total usage.

2.1.14 Null Model

For haul-out site cells that had terrestrial counts but no associated telemetry data, usage was estimated on the basis of accessibility. A model of decay of usage with increasing distance from the haul-out site cell was used, based on the whole telemetry data set for the UK. To ensure the spatial extent of the analysis was not restricted by the availability of environmental data, simple generalised linear habitat models (McCullagh & Nelder 1989) were built using the two covariates of geodesic distance to haul-out site and Euclidean distance to land (Bailey *et al* 2014). The predicted usage for each haul-out site cell was normalised and weighted by the mean proportion of time animals spent not hauled out. Mean and variance were scaled to population size by combining each one with the population mean and variance estimates of each haul-out site cell, and these were aggregated to the total usage map. Harbour seals distribute themselves widely along the coast. Therefore, tagging effort was concentrated over a relatively small area compared to the species distribution on land. This, combined with harbour seal abundance in west Scotland and Ireland, which have long complex coastlines, meant the null map models contributed 48% of the total usage.

3 Identifying high-use areas at sea for UK harbour seals

A harbour seal usage map, at the whole-UK scale, was produced (Figure 5). This was then used to define areas that are of particular regional importance to harbour seals. The first step involved setting broad local areas, termed Harbour Seal Areas (HSAs), within which locations of high usage should be identified (section 3.1 below). The second step (section 3.2) required a consistent protocol for processing the usage maps to indicate areas of high seal usage.

3.1 Defining appropriate geographical regions for assessment

For the purposes of this report it was agreed with the IAMMWG¹ that dividing the UK usage into regions should be carried out in a biologically appropriate way. Harbour seals are concentrated into three regions around the UK (Scotland, Northern Ireland and east England) and this was used as the primary split. HSAs in Scotland were sub-divided according to the largest aggregations of animals in west Scotland, Orkney and Shetland, and the Moray Firth (Figure 6). HSAs included the majority of seal usage in each area, and the at-sea usage map was visually inspected to determine the seaward extent of each HSA.

¹ Inter-Agency Marine Mammal Working Group, which comprises JNCC, SNH, NE, NRW, DAERA and invited independent experts.

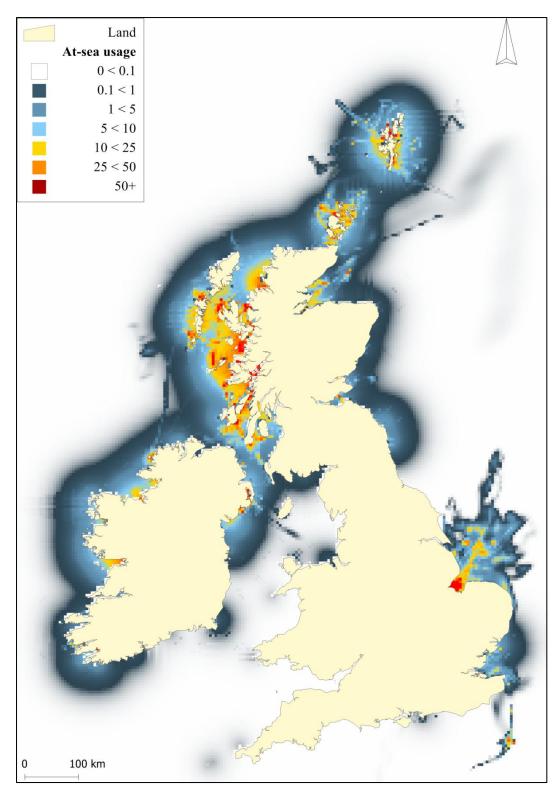


Figure 5. Predicted number of harbour seals at sea in each 5km x 5km grid square. Adapted from Figure 4b in Jones *et al* (2015a).

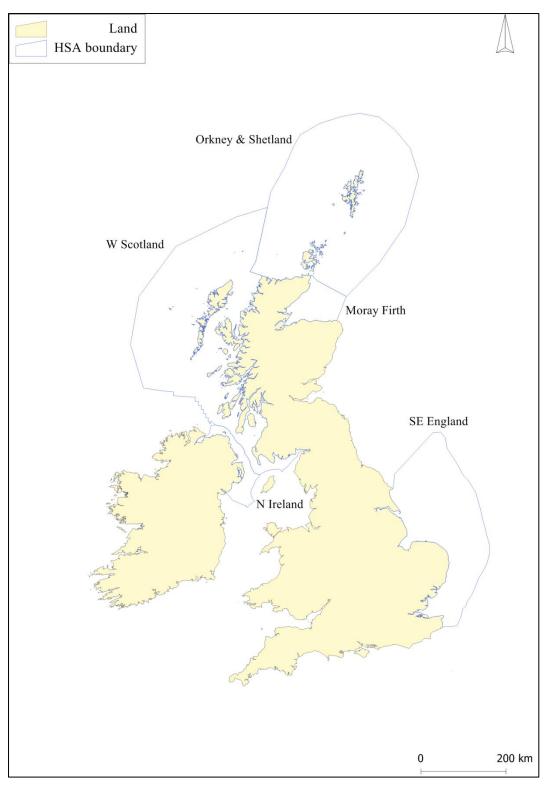


Figure 6. Harbour Seal Areas (HSA) utilised for this analysis.

3.2 Analytical approach

Within each HSA, grid cells were ranked in descending order based on the estimated usage in each cell. Grid cells were selected, beginning with the most intensively used cells, until 10% of the total usage of each HSA was included. The number of seals in the selected area

was calculated for each HSA, along with 95% confidence limits. This protocol was repeated in 10% increments from 10% to 90% of the total usage in each HSA.

3.3 Results: the most intensively-used areas

Figures 7, 8 and 9 show high-use 'at-sea' areas corresponding to 10, 20 and 50% of total seal usage within each HSA. The remainder of the 10 to 90% series percentile total usage maps are shown in the Appendix (Figures 11 to 16). The colour scale on these maps represents the estimated number of seals at any instant in each 5km x 5km grid cell. The estimated number of seals within the designated areas is calculated, and the total population estimates in each HSA, along with associated 95% confidence intervals are given. Many of the grid cells identified are close to the coast, where seals spend much of their time hauled out. In east England, the area selected close to the coast (defined as within 10km from the coastline) has been previously designated in The Wash and North Norfolk Coast SAC (Figure 1). However, in east England (and the Moray Firth and Orkney to some extent), areas of high usage were also identified away from the coast (Figure 9). In these areas, harbour seals utilise offshore sandbanks that may be associated with foraging (Tollit et al 1998). Many of the areas around the complex coastlines of Orkney, Shetland, and west coast of Scotland are identified as high usage, with some grid cells identified further from the coast in Orkney and Shetland. In Northern Ireland, areas of high at-sea usage closely overlap with existing SACs in Strangford Lough and Murlough (Figure 9; see Figure 1a for SAC locations).

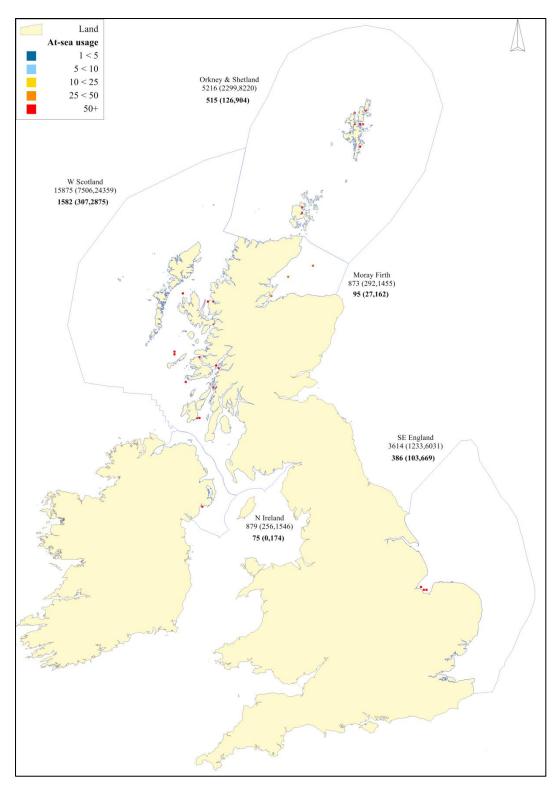


Figure 7. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>10% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

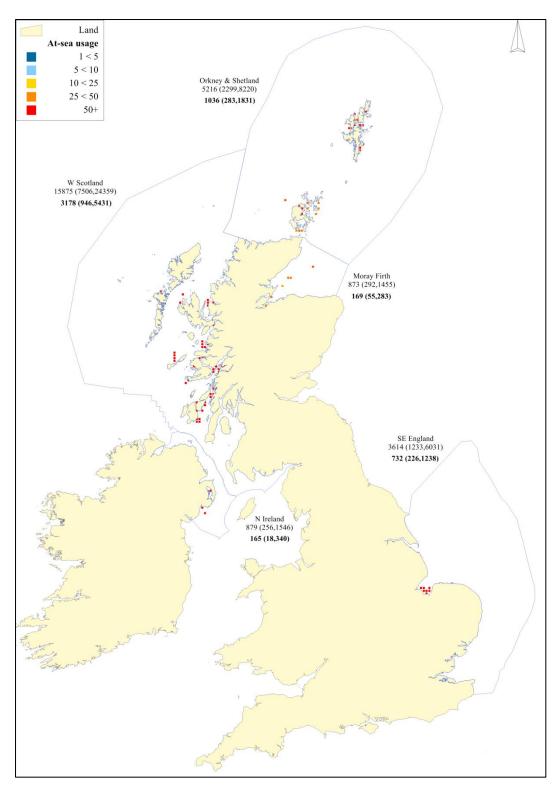


Figure 8. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>20% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

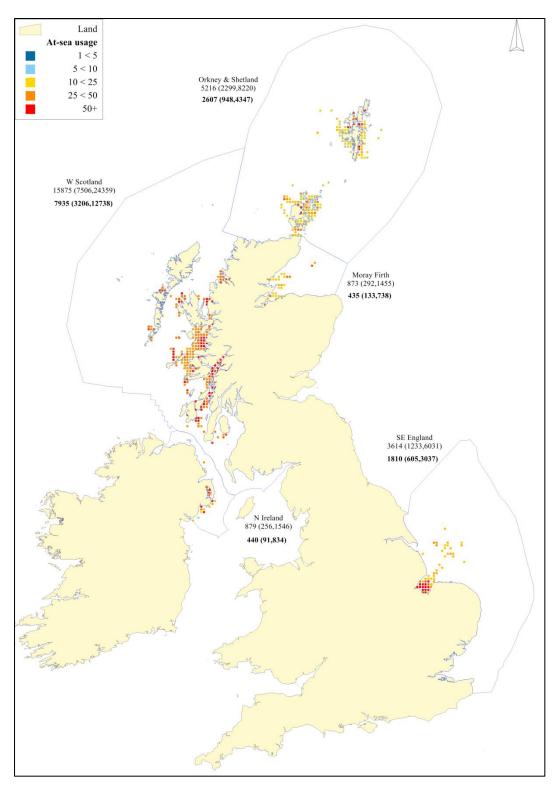


Figure 9. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>50% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

4 Identifying harbour seal foraging areas

A framework for estimating seal activity budgets using telemetry data was developed as part of a study commissioned by DECC (Russell & McConnell 2014). Resting and diving intervals were assigned using behavioural data and then, using a state-space model, diving intervals were split into foraging and travelling (McClintock *et al* 2013; Russell *et al* 2015). The temporal resolution at which activities were classified was dependent on the tag type (SRDL or GPS) and settings (see 4.1 Telemetry data). In this report the states assigned to regularised telemetry data on a two-hour resolution were compared visually with the local usage map for The Wash, east England.

4.1 Telemetry data

SMRU telemetry tags collect both locational and behavioural data. The tags collect data for each dive and haul-out event, but the tags do not successfully transmit all data. The tags also transmit summary data; the proportion of time the tag has been dry (associated with haul-out), wet but above the tag-specific depth threshold (at-surface) and diving (below the depth threshold) within a defined period of time (two, four or six hours depending on the tag settings). Summary data were used to define whether an interval should be assigned to resting or diving. The temporal resolution at which states (resting, foraging and travelling) can be defined was limited by the resolution of the summary data. Summary periods were six hours for SRDL tags, and two or four hours for GPS tags. To allow the use of data from all tags, in Russell *et al* (2015) states were defined at a resolution of six hours. In more recent studies (Russell 2015, 2016), only data from GPS phone tags with two-hour summary periods were considered and thus activities were defined on a two-hour resolution.

4.2 State assignment

Resting can occur on land (a haul-out event) or on the surface of the sea; resting at sea is likely associated with digestion (Sparling *et al* 2007). Analysis of the summary data revealed that the maximum percentage of time harbour seals can spend under water is 88.8% of a two-hour period due to having to come to the surface to replenish oxygen stores between dives. Diving behaviour is thus composed of 11.2% of time on the surface (surface overhead) and the rest underwater. An interval was classified as diving if more than 50% of it was spent engaging in diving behaviour (including the surface overhead). In other words, if over 44.4% of the interval was recorded as diving by the tag ((100-11.2)/2) then the interval was assigned to the diving state. Harbour seals dive when travelling and foraging, thus the locational data were then used to estimate the probability of a diving interval being associated with foraging or travelling.

Locational data were input into a Bayesian state-space model, within which speed and turning angle were used to estimate the probability that an interval was associated with foraging or travelling. Relatively slow, tortuous movements are associated with area restricted search, thus the state exhibiting these characteristics was assumed to be foraging and the state characterised by faster more directed movements was assumed to be travelling. It is important to bear in mind that the state estimates of "foraging" and "travelling" are labels that are assumed to correspond to the two movement types observed. Within the confines of the modelling framework, it was necessary to assume that an interval encompasses only one state, i.e. seals do not switch between foraging and travelling within an interval.

4.3 Temporal resolution

On a six-hour resolution, activity budgets were defined for 126 harbour seals, but for 25 (c. 20%) of these, separate foraging and travelling states could not be defined (Russell et al 2015). This was likely due to switches in behaviour during intervals; in most regions of the UK, harbour seals forage close to the coast and thus are unlikely to engage in travelling periods that are long enough to result in an interval being assigned to travelling. Thus the inability to distinguish between foraging and travelling is likely to be most pronounced for individuals which exhibited short trips. Due to likely bias in presenting results for the individuals for which foraging and travelling could be distinguished, results were only reported in a region for which foraging and travelling could be defined for almost all individuals (28 of 30 for south-east Scotland; Russell et al 2015). Due to the potential switches in behaviour, even for this region activity budgets may not have been accurate. To investigate whether a two-hour resolution of activity budgets would be more suitable, DECC and Scottish Government funded a study to define activity budgets using data from GPS tags for which summary periods were on a two-hour resolution. Foraging and travelling could be distinguished for a higher proportion of individuals (c. 90%) than was possible at a sixhour resolution (c. 80%; Russell 2015). These results demonstrate that, for harbour seals, a two-hour resolution is more appropriate when assigning activities. Preliminary activity data on a two-hour resolution, based only on GPS tags deployed in The Wash (Russell 2016), are presented in this report, see section 4.5 below.

4.4 Currents: movement in hydro-space

The impact of tidal current speed and direction on the assignment of intervals to foraging and travelling, was investigated (Russell 2015). The software "Polpred" (http://noc.ac.uk/using-science/products/software/polpred/polpred) provides predictions of current direction and speed (water displacement). These were used to calculate the active movement of seals through the water (in hydro-space). Between 3.7 and 8.5% (95% Cls) more intervals were assigned as foraging when seal movements were considered in hydro-rather than geo-space. However, there are caveats associated with defining activities in hydro-space, most notably the unknown error associated with the current data used. Error levels will be affected by the temporal resolution of the telemetry data, the spatial resolution of the current data and the degree of mismatch between the surface current data used and the currents at the depth of the seals in the water column (Russell 2016).

4.5 Habitat preference modelling

Habitat preference analyses, funded by DECC, were conducted to compare the drivers of foraging locations versus all at-sea locations (Russell & McConnell 2014). Preliminary results suggested that there was little difference between the environmental covariates driving the foraging and overall at-sea distributions of harbour seals. However, it is likely that these results were impacted by the difficulties in assigning foraging and travelling periods at a two-hour resolution.

4.6 Overlaying foraging locations on usage maps

There is only one region, The Wash, for which visual comparisons of foraging and travelling locations with usage maps are appropriate (Figure 10). The Wash comprises a small group of isolated haul-out site cells meaning that both population level usage and foraging locations emanate from the same sites (see Discussion). Elsewhere in the UK, this approach would not be appropriate because, for regions where GPS data are available, the coastlines are very complex and encompass multiple haul-out sites. The Wash and North Norfolk Coast SAC encompasses a large and increasing population of harbour seals. In a DECC funded

study, 24 GPS tags were deployed on harbour seals in The Wash and activity budgets of these individuals were estimated (Figure 10; Russell 2016). Usage from The Wash was estimated using telemetry data from 43 individuals (19 SRDL tags and 24 GPS tags). Foraging (Figure 10b) and travelling (Figure 10c) locations from the 24 GPS tags were overlaid onto the usage maps.

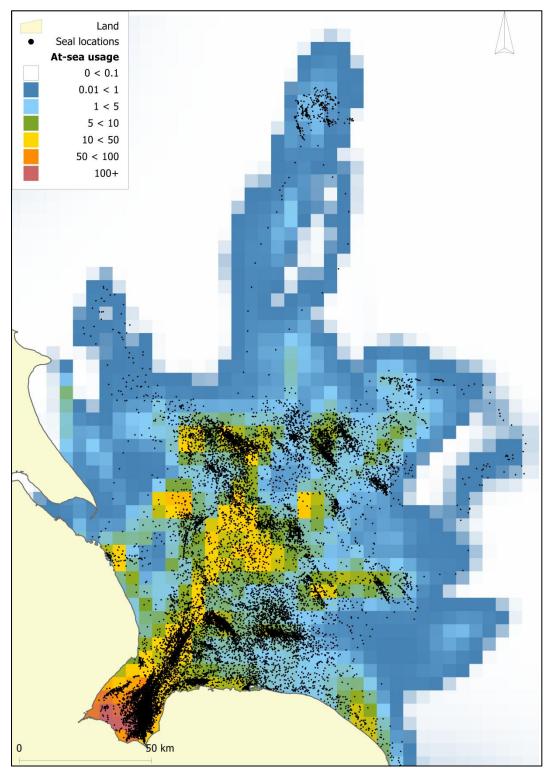


Figure 10a. Estimated population level usage of harbour seals in The Wash overlaid with all telemetry locations (at a two-hour resolution) from the 43 tagged individuals used to estimate usage.

Review of analytical approaches for identifying usage and foraging areas at sea for harbour seals

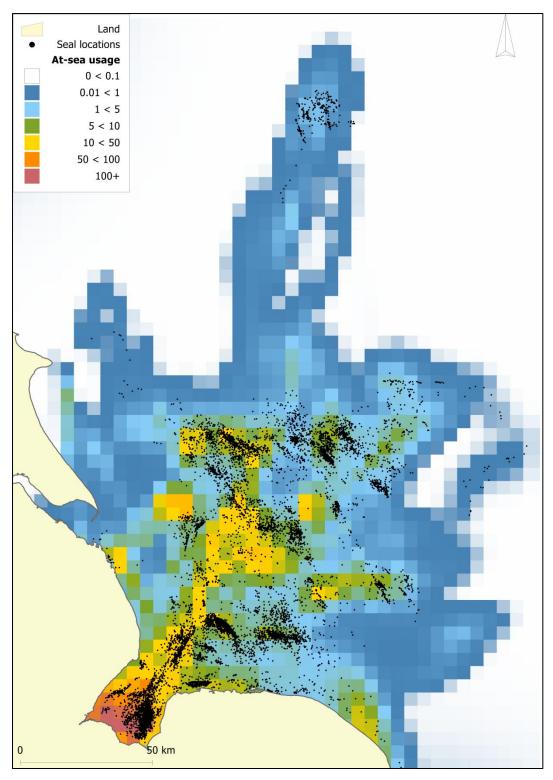


Figure 10b. Estimated population level usage of harbour seals in The Wash produced using data (SRDL and GPS) from 43 individuals. The foraging locations estimated on a two-hour resolution using GPS data from 24 individuals are overlaid (see section 4.6 for more details).

Review of analytical approaches for identifying usage and foraging areas at sea for harbour seals

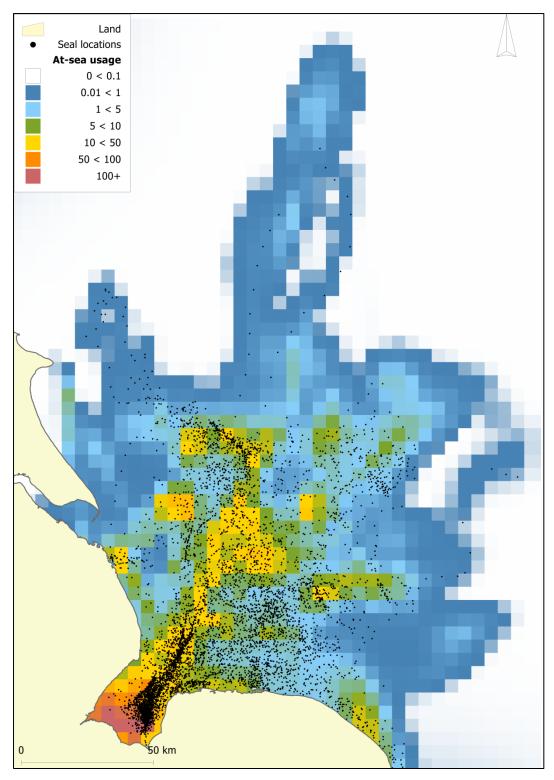


Figure 10c. Estimated population level usage of harbour seals in The Wash produced using data (SRDL and GPS) from 43 individuals. The travelling locations estimated on a two-hour resolution using GPS data from 24 individuals are overlaid (see section 4.6 for more details).

5 Discussion

5.1 Usage maps

The density of UK harbour seals was modelled and usage maps were created, with associated uncertainty. This usage modelling combined both terrestrial haul-out site surveys and telemetry data. Usage maps were then overlaid with bespoke HSAs so that high levels of within-region usage could be identified. Within each HSA areas were identified that contained 10, 20 and 50% of the most intensively used cells.

Usage maps summarise a large, long-term telemetry data set, which include data from many different studies carried out over decades around the UK. The maps were not subdivided by yearly or seasonal factors or by intrinsic covariates (such as mass, age class or sex), since the available data did not have detailed coverage across the full range of these factors and covariates, and their possible combinations, e.g. movement data from all major haul-out sites in every season and year were not available. With the telemetry and survey data currently available, the generation of overall usage patterns does not take these factors and covariates into account.

Since many seal haul-out site cells lacked matching telemetry data, the use of a "null model" was necessary to estimate at-sea usage by seals using those cells. Maps for some areas were therefore not well informed by telemetry data and were based on general properties of seal movement (null models). Wider confidence intervals reflected greater uncertainty in these areas, such as parts of the west coast of Scotland.

The null model included only spatial covariates and did not make use of habitat variables such as sediment type because this would have required covariate data that were continuous over the full spatial extent of the study area: these were not available. Region-specific habitat-preference models for harbour seals may result in null models with greater predictive power, but this would require substantial further development. For example, habitat preference may vary from one region to another if seals are exploiting different prey assemblages, which may also change over time.

In addition to amalgamating seasonal changes in haul-out site specific movement patterns, it should be noted that the haul-out site survey data are concentrated around the moult period in August, and thus any geographic redistribution over the remainder of the year is not taken into account. Despite these important caveats, the usage maps represent the best estimate of the at-sea usage of UK harbour seals and the regional grouping into HSAs accentuates locally-high usage at a regional level.

The processes involved in producing population level usage limit the appropriateness of a visual comparison between the telemetry tracks and usage. Figure 10a shows estimated harbour seal usage in The Wash, overlaid with the locations of 43 tagged seals. As expected, high concentrations of telemetry locations are associated with high usage. However, there are also areas with high and low usage despite relatively low and high numbers of locations, respectively. This mismatch is driven by two processes involved when using telemetry data to estimate population level usage. First, some telemetry tags may last much longer than others, giving many more locations. To avoid usage being strongly influenced by individuals for which there is a long time series of data, tracks are weighted to ensure all individuals contribute equally. Thus areas with large numbers of points which are only due to one individual may be areas of low population level usage. Second, usage is weighted by the population of the haul-out sites. Thus if there are multiple haul-out sites within a region, an individual that uses a large haul-out site represents a relatively large population and their use of an area will result in relatively high population level usage. This

mismatch is limited in The Wash because it comprises a small group of isolated haul-out site cells and thus both population level usage and telemetry locations emanated from the same sites. Such a mismatch will be exacerbated when considering regions such as the west and north coasts of Scotland which have complex coastlines encompassing multiple haul-out sites.

5.2 Identification of foraging areas

The usage maps do not take account of differences in behaviour; areas may be used by the seals for different purposes such as travelling or foraging. State-space modelling (SSM) methodology offers an approach to classifying track data into different activities (Russell *et al* 2015). The usage maps encompass both SRDL and GPS telemetry data, but reliable designation of foraging locations are only available for data collected by those GPS tags for which summary data are available on a two-hour resolution.

As discussed in section 5.1, The Wash is the only region for which a comparison of the locations of tagged individuals with population level usage is appropriate. Notwithstanding the caveats associated with comparing population usage (see section 5.1) with the tracks of individual seals, activity-specific locations from 26 individuals tagged with GPS tags were overlaid onto the population level usage generated using data from the 26 GPS tags and an additional 17 SRDL tags. Areas with high usage are largely associated with a high density of foraging locations (Figure 10b) whereas travelling locations are more dispersed and show less spatial structure (Figure 10c). An exception to this pattern is at the entrance to The Wash, which is a travelling corridor for harbour seals hauling out at this SAC. This simple comparison indicates that offshore high usage areas, in this region at least, are usually associated with foraging. This finding was supported by preliminary results from habitat preference analyses for the North Sea (section 4.5) which suggested similar drivers of both foraging and overall distributions at sea, indicating that their distributions are similar.

Foraging areas have not been identified per se and extensive work would be required to do so both in terms of accurately defining activity states for all GPS data and in using these data to predict population level foraging usage. Currently, activity states cannot be reliably estimated for areas of high current; these are often areas of conservation interest due to their potential for tidal developments. Further work is required to determine how suitable the available current data are for defining movements in hydro-space and more generally whether estimates of foraging in geo- or hydro-space are more accurate. The reliance on null usage to estimate overall usage means that it would be inappropriate to generate foraging usage maps in the same way. Null usage is predicted based on the relationship between usage and distance to haul-out sites for those sites for which telemetry data are available. A lack of telemetry data associated with haul-out sites means that null usage accounts for 48% of the overall harbour seal usage. A previous study (Russell et al 2015) demonstrated that data collected using SRDL tags are not suitable for estimation of activity states in harbour seals (e.g. foraging). The exclusion of SRDL data would mean that, compared to overall usage, a higher percentage of foraging usage would have to be made up of null usage.

Predictions of foraging usage, based on such a simple relationship between foraging usage and distance to haul-out sites, are likely to be inaccurate and prohibit the identification of discrete foraging areas. Despite the caveats (see section 5.1), habitat preference analyses may be most suitable in predicting key foraging areas. Foraging habitat preference analysis was conducted for the North Sea area but was hampered by the inability to reliably distinguish foraging and travelling for data collected by SRDL (see section 4.5). Habitat preference analysis would involve quantifying the association between environmental covariates and foraging, to allow predictions of foraging usage to be made, including foraging usage resulting from individuals hauling out at sites for which there are no GPS telemetry data.

Estimating all-activity usage is informative for management, since it integrates all activities (all of which are considered to be essential for harbour seals) into one simple index. There may be added value in classifying activity because it would allow activity-specific management. For example, changes in prey abundance and distribution may be important in areas where foraging dominates, but less important in areas used primarily for travelling. In contrast, in some cases disturbance may have more serious implications in travelling areas; if there is only one travelling route between a haul-out and offshore foraging areas, disturbance on such routes (e.g. during wind farm construction) may cause barriers to movement. Quantifying connectivity between foraging areas and between haul-out sites and foraging areas, whilst of relevance to conservation management, was outside of the scope of this report. However, this should be a priority for future scientific research.

5.3 Relevance to the identification of harbour seal foraging areas throughout the UK

This report summarises selected parts of the Marine Mammal Scientific Support MMSS/001/11 programme commissioned by Scottish Government and also draws on data from DECC-funded projects. This report reflects the current status of synoptic assessment of UK harbour seal usage, and it provides a regional (The Wash) comparison between usage maps and localised foraging behaviour identified by state-space modelling. This comparison highlighted the strong association between usage and areas with a high density of foraging locations, suggesting that, in general, high usage will correspond to key foraging areas, especially offshore.

In order to improve the spatial coverage of the telemetry data and to distinguish the effects of season and individual covariates on usage, more tagging is required. In particular data-sparse regions with relatively few tags deployments have been identified as:

- Central mainland Shetland (east and west coasts)
- South-west Orkney (Scapa Flow),
- Summer Isle, north-west Scotland where there are few telemetry data within 50km of the area,
- South Uist, Outer Hebrides, West Scotland and Inner Hebrides (from southern Skye to Isle of Mull).

For a discussion of telemetry data-sparse regions see Jones *et al* (2015c). The investigation of seasonal effects also requires haul-out site surveys to be carried out during periods outside the August moult. In addition, due to regional population declines, areas such as Abertay has not contributed strongly to harbour seal usage in UK waters over recent years due to the now small number of harbour seals using haul-out sites there. Tagging seals in such areas may be a priority for other reasons, such as investigations into the causes of decline, but will not significantly affect local seal usage maps (Jones *et al* 2015b).

Usage maps present a 'snapshot' of seal usage: they show the estimated number of seals per grid square at any instant in time. Such maps do not indicate the rate at which animals move through an area. This issue might be important if some areas are used by a large number of seals which travel through them swiftly: in such areas, the instantaneous usage of animals might not be high, but a large number of animals might be exposed to risk if some fixed hazard is located there (such as a tidal turbine). In future work, explicit modelling of seal movements may be needed to build on existing understanding of habitat usage in order to evaluate the impact of such risks. Agent or individual based models have proved

successful in exploring the potential impacts of human activities on porpoises (Nabe-Nielsen *et al* 2014) and their further development for central place foragers such as harbour seals would be of value in planning the conservation of UK seals.

6 Acknowledgements

Historical telemetry and population data were funded by Chichester Harbour Conservancy; Department for Energy and Climate Change; Department of Arts, Heritage, Gaeltacht and the Islands; Industry Nature Conservation Association; Langstone Harbour Authority; Marine Current Turbines Ltd; Marine Scotland; National Environmental Research Council; Natural Resources Wales; Northern Ireland Environment Agency; Royal Society for the Protection of Birds; Scottish Natural Heritage; SMRU Consulting; Welsh Assembly Government; Zoological Society of London.

This report was funded by the Joint Nature Conservation Committee on behalf of the UK's Statutory Nature Conservation Bodies.

7 References

Bailey, H., Hammond, P.S. & Thompson, P.M. 2014. Modelling harbour seal habitat by combining data from multiple tracking systems. Journal of Experimental Marine Biology and Ecology. 450:30–39.

Blundell, G.M., Maier, J.A.K. & Debevec, E.M. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs. 71:469–489.

Brownlow, A., Onoufriou, J., Bishop, A., Davison, N. & Thompson, D. 2016. Grey seal (*Halichoerus grypus*) infanticide and cannibalism may indicate the cause of spiral lacerations in seals. PLoS ONE. 11:1-14.

Chacón, J.E. & Duong, T. 2010. Multivariate plug-in bandwidth selection with unconstrained pilot bandwidth matrices. Test. 19:375–398.

Duck, C.D., Morris, C.D. & Thompson, D. 2014. The status of UK harbour seal populations in 2013, including summer counts of grey seals. SCOS-BP 14/03, 107-133. *Special Committee on Seals: Scientific Advice on Matters Related to the Management of Seal Populations 2014.* Sea Mammal Research Unit, University of St Andrews, St Andrews.

Duck, C.D., Morris, C.D. & Thompson, D. 2015. The status of UK harbour seal populations in 2014, including summer counts of grey seals. SCOS-BP 15/04, 92-118. *Special Committee on Seals: Scientific Advice on Matters Related to the Management of Seal Populations 2015.* Sea Mammal Research Unit, University of St Andrews, St Andrews.

Dujon, A.M., Lindstrom, R.T. & Hays, G.C. 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. Methods in Ecology and Evolution. 5:1162–1169.

Fieberg, J. 2007. Kernel density estimators of home range: smoothing and the autocorrelation red herring. Ecology. 88:1059–1066.

Hassani, S., Dupuis, L., Elder, J.F., Caillot, E., Gautier, G., Hemon, A., Lair, J.-M. & Haelters, J. 2010. A note on harbour seals (*Phoca vitulina*) distribution and abundance in France and Belgium. NAMMCO Scientific Publications. 8:107-116.

Jensen, S.-K., Lacaze, J.-P., Hermann, G., Kershaw, J., Brownlow, A., Turner, A. & Hall, A. 2015. Detection and effects of harmful algal toxins in Scottish harbour seals and potential links to population decline. Toxicon. 97:1–14.

JNCC. 2013. European Community Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora. Third Report by the United Kingdom under Article 17. Conservation status assessment for Species: S1365 - Harbour seal (*Phoca vitulina*). JNCC, Peterborough. 20pp.

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.J. & Matthiopoulos, J. 2015a. Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. Marine Ecology Progress Series. 534:235–249.

Jones, E.L., Smout, S. & McConnell, B.J. 2015b. Review the extent of how new survey data affect usage estimates. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MMSS/001/11 MR 5.1, St Andrews, 2pp.

Jones, E.L, Smout, S., Morris, C.D. & McConnell, B.J. 2015c. Determine data sparse regions. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MMSS/001/11 MR 5.1, St Andrews, 12pp.

Lonergan, M., Thompson, D., Thomas, L. & Duck, C. 2011. An Approximate Bayesian Method Applied to Estimating the Trajectories of Four British Grey Seal (*Halichoerus grypus*) Populations from Pup Counts. Journal of Marine Biology. 2011:1–7.

Manifold Software Ltd. 2013. Manifold System Ultimate Edition 8.0.28.0. Hong Kong.

Matthiopoulos, J., Cordes, L., Mackey, B., Thompson, D., Duck, C., Smout, S., Caillat, M. & Thompson, P. 2014. State-space modelling reveals proximate causes of harbour seal population declines. Oecologica. 174:151–162.

Matthiopoulos, J. 2011. How to be a Quantitative Ecologist, 1st ed. Wiley & Sons.

McClintock, B., Russell, D.J.F., Matthiopoulos, J. & King, R. 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology. 94:838–849.

McConnell, B.J., Beaton, R., Bryant, E., Hunter, C., Lovell, P. & Hall, A.J. 2004. Phoning home - A new GSM mobile phone telemetry system to collect mark-recapture data. Marine Mammal Science. 20:274–283.

McConnell, B.J., Chambers, C. & Fedak, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science 4:393–398.

McCullagh, P. & Nelder, J.A. 1989. Generalized Linear Models. Chapman & Hall, London.

Muelbert, M.M.C. & Bowen, W.D. 1993. Duration of lactation and post weaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. Canadian Journal of Zoology. 71:1405–1414.

Nabe-Nielsen, J., Sibly, R.M., Tougaard, J., Teilmann, J. & Sveegaard, S. 2014. Effects of noise and by-catch on a Danish harbour porpoise population. Ecological Modelling. 272: 242-251.

R Core Team. 2014. R: A language and environment for statistical computing. Vienna, Austria.

Royer, F. & Lutcavag, M. 2008. Filtering and interpreting location errors in satellite telemetry of marine animals. Journal of Experimental Marine Biology and Ecology. 359:1–10.

Russell, D.J.F. & McConnell, B.J. 2014. Seal at-sea distribution, movement and behaviour. Report to DECC (URN: 14D/085).

Russell, D.J.F. 2015. Activity classification using state space modelling.Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MMSS/001/11 MR 5.2, St Andrews, 10pp.

Russell, D.J.F., McClintock, B.T., Matthiopoulos, J., Thompson, P.M., Thompson, D., Hammond, P.S., Jones, E.L., MacKenzie, M.L., Moss, S. & McConnell, B.J. 2015. Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals. Oikos.

124/11:1462-1472.

Russell, D.J.F. 2016. Activity Budgets: Analysis of seal behaviour at sea. Draft report for the Department of Energy and Climate Change (OESEA-15-66).

SCOS. 2015. Scientific advice on matters related to the menagement of seal populations: 2015. Sea Mammal Research Unit, University of St Andrews, St Andrews, 211pp.

Sparling, C.E., Fedak, M.A. & Thompson, D. 2007. Eat now, pay later? Evidence of deferred food-processing costs in diving seals. Biology Letters. 3:95–99.

Thompson, D., Lonergan, M. & Duck, C. 2005. Population dynamics of harbour seals *Phoca vitulina* in England : monitoring growth and catastrophic declines. Journal of Applied Ecology. 42:638–648.

Tollit, D.J., Black, A.D., Thompson, P.M., Mackay, A., Corpe, H.M., Wilson, B., Parijs, S.M., Grellier, K. & Parlane, S. 1998. Variations in harbour seal *Phoca vitulina* diet and divedepths in relation to foraging habitat. Journal of Zoology. 244:209–222.

Vincent, C., McConnell, B.J., Ridoux, V. & Fedak, M.A. 2002. Assessment of SRDL Location Accuracy From Satellite Tags Deployed on Captive Gray Seals. Marine Mammal Science. 18:156–166.

Wilson, L.J. & Hammond, P.S. 2015. Harbour seal diet composition and diversity. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. MMSS/001/11 CSD 3.2, St Andrews, 74pp.

Wood, S.N. 2006. Generalized Additive Models: an Introduction with R. Chapman & Hall, London.

Wood, S.N. 2011. Fast stable restricted maximum liklihood and marginal liklihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology). 73:3–36.

8 Appendix

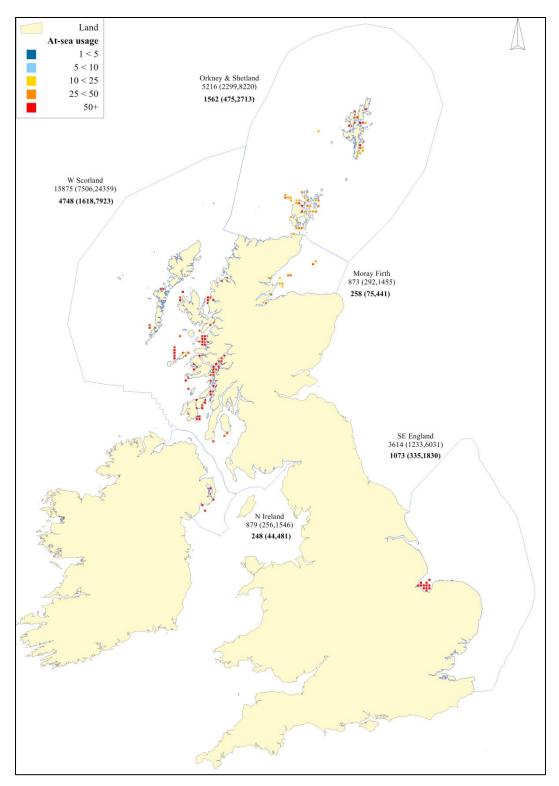


Figure 11. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>30% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

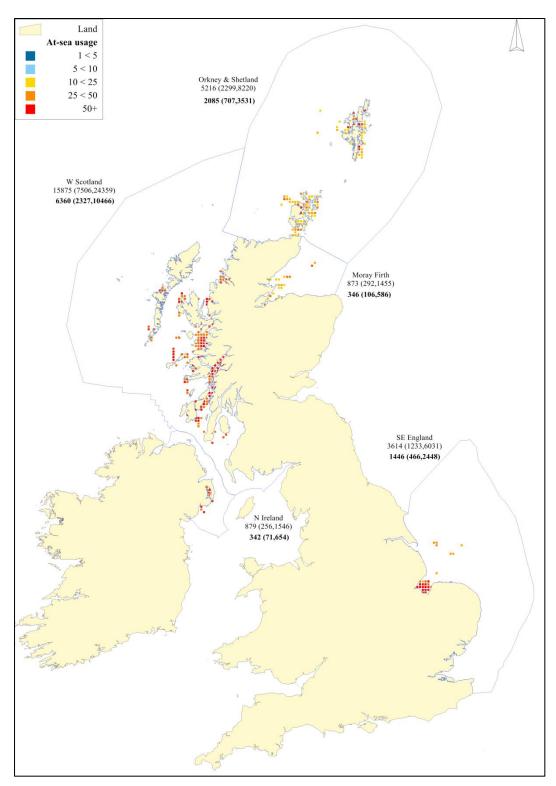


Figure 12. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>40% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

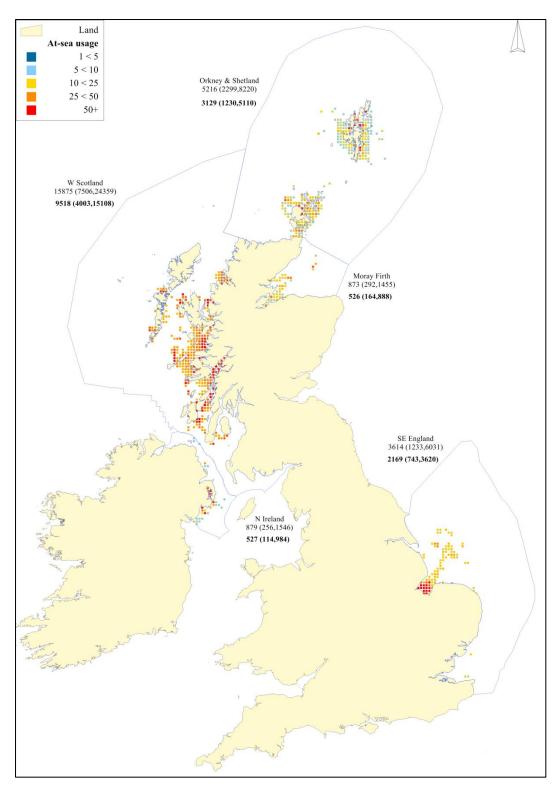


Figure 13. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>60% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

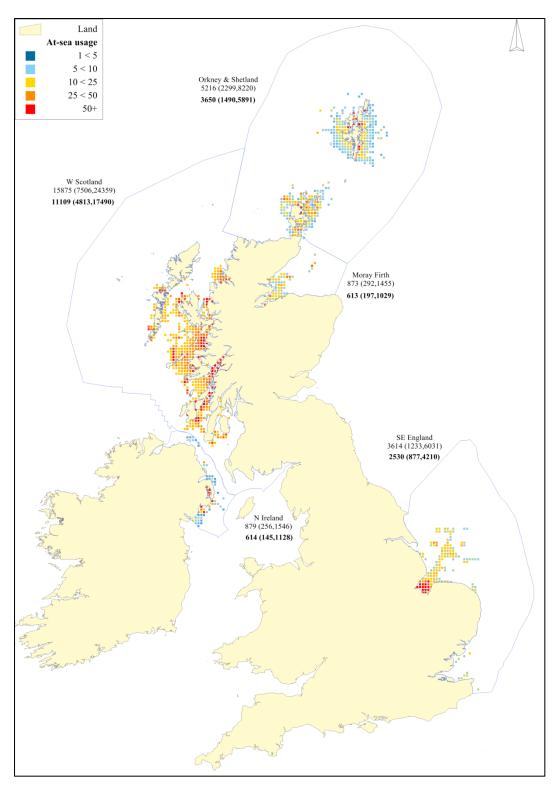


Figure 14. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>70% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

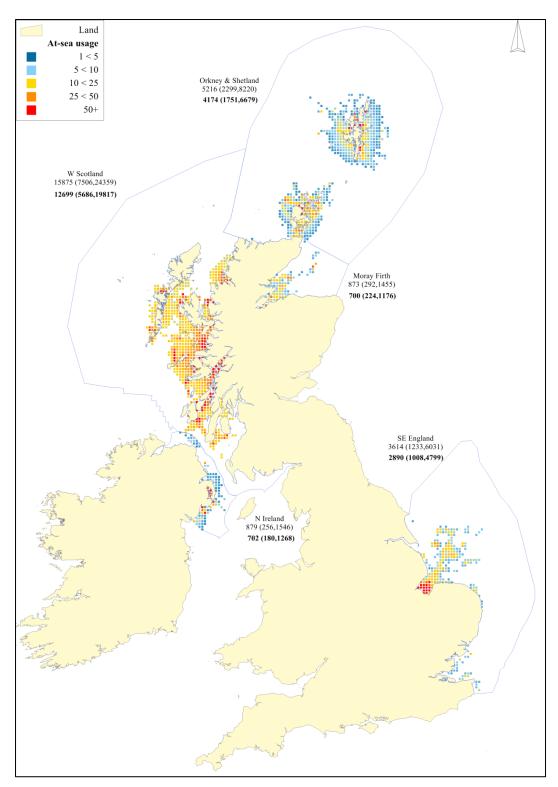


Figure 15. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>80% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).

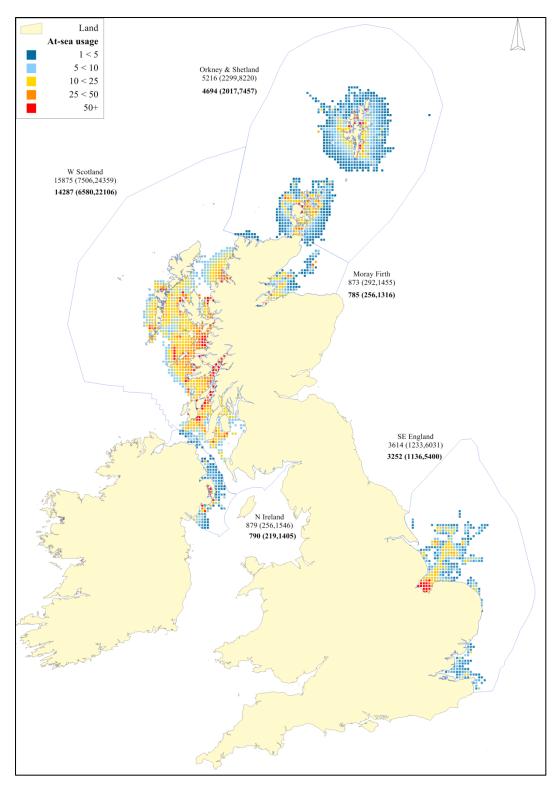


Figure 16. Harbour seal at-sea usage showing grid cells (in colour) where an area containing <u>90% of</u> <u>usage</u> in the most intensively used cells is selected in each HSA. Usage is defined as the predicted number of seals in each 5km × 5km grid square. Numbers below each HSA label denote the total estimated population of harbour seals in each HSA (with 95% confidence intervals in brackets). Bold numbers show the mean population estimate of the selected usage (with 95% confidence intervals in brackets).