Marine Mammal Scientific Support Research Programme MMSS/001/11

Grey and harbour seal density maps

Task MR 5 (part)

Sea Mammal Research Unit
Report to
Scottish Government

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Version 1500

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1 Version Log

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1.0	07/12/12	**EJ**, BM, CS, JM	First draft sent to Steering Group.
500	27/02/13	EJ, **BM**, CS, JM	Revised in response to Steering Group comments on v1.0
1000	11/03/13	EJ, **BM**, CS, JM	Revised in response to Steering Group comments on v500
1500	20/3/13	AJH, JK	Final minor comments and typographical errors corrected v1000

2 Executive summary

1. The purpose of this report is to describe seal density maps, produced by the Sea Mammal Research Unit, University of St Andrews as a deliverable of Scottish Government Marine Mammal Scientific Support Research Programme MMSS/001/11.

2. This report outlines how the maps can be interpreted and the extent of their limitations with a set of caveats. Appendix 1 describes methodology and software used.

3. Grey seal (*Halichoerus grypus*) telemetry data from 1991-2011 and harbour seal (*Phoca vitulina*) telemetry data from 1991-2012 were combined with count data from 1988-2012 to produce UK-wide maps by species of estimated density and associated confidence intervals.

4. The usage maps are available for download as GIS shape files from the Marine Scotland Interactive website (http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/Themes).

3 Contents

4 Background

In order to assess the likelihood of interactions between marine mammals and the development of offshore renewables, it is necessary (though not sufficient) to examine spatial overlap. Mapping the spatial distribution of UK seals has been the subject of previous funding rounds from both the UK and Scottish Governments. These have supported the development of analytical methods for the 2D mapping of harbour and grey seal at-sea usage. In this report we bring together, for the first time, spatial estimates of grey and harbour seal density. In addition we provide indicators of the confidence we have in these estimates.

This report describes the seal density maps, produced by the Sea Mammal Research Unit, University of St Andrews as a deliverable of Scottish Government Marine Mammal Scientific Support Research Programme (MMSS/001/11). Grey seal (*Halichoerus grypus*) telemetry data from 1991-2011 and harbour seal (*Phoca vitulina*) telemetry data from 1991-2012 were combined with haul out count data from 1988-2012 to produce UK-wide maps by species of estimated density and associated confidence intervals. It is hoped that these data will assist both licencing proposals and assessment procedures.

These usage maps are freely available in a variety of geo-referenced formats from the Marine Scotland Interactive website (http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/Themes). This report outlines how the maps can be interpreted, their limitations and their caveats. The Appendix covers in greater detail the methodology and software used.

5 Introduction

5.1 Seal density

The maps developed and presented here show at-sea and hauled-out distributions of grey and harbour seals around the UK. They can be used in assessments where seal distributions need to be considered; for example, when considering extent and placement of a Marine Protected Area (MPA), or assessing potential impacts of offshore renewable energy developments. They show broad-scale species distribution around the UK, at a fine-scale resolution of 5x5km.

The maps are grouped by species into mean “at-sea” density (seals per 5x5km cell), showing marine distribution, and mean “total” density, which combines at-sea and hauled-out densities. We recommend “at-sea” maps should be used when only the marine environment is being considered; for example as inputs into collision or underwater acoustic models. “Total” maps are more appropriate when considering terrestrial disturbance.

Density maps use aggregated telemetry data scaled to population-levels using trends in count data, which provide a stable, long-term analysis of species distribution. To scale up to population level, land counts are used, which take account of inter-annual variability by using data from multiple years. In contrast, characterisation surveys at haul-out sites carried out through the year can capture intra-annual fluctuations in counts, although these will be over a shorter time period than the 20+ years of counts used in the density maps.

5.2 Confidence levels

Upper and lower 95% confidence intervals of the means of density estimates are provided in separate maps. These show confidence in our estimate of the *mean* of the density in each cell - rather than showing the actual day to day variability in density.

There is higher uncertainty in the mean in an area if:

- the number of tagged animals represents a small sample size compared to the population-level, or
- there are limited or no telemetry data, and so density is modelled (see Appendix - Accessibility models), or
- there are highly varying counts in the survey data between years.

Therefore, uncertainty can be used as an additional assessment tool to indicate whether further data collection and / or analysis should be carried out in the form of characterisation surveys.

Analytical methodology for estimating uncertainty was identical for both species (see Appendix – Quantifying uncertainty). However, spatial and temporal tagging and count survey effort varied between the species (see Appendix -Tables 2-4), which means that even when grey and harbour seals were found in similar locations, they did not have the same levels of uncertainty associated with them due to variation in the underlying data.

The total usage over larger, aggregated areas can be estimated by summing the means for the grid cells it contains. There are two approaches to estimate our confidence in this aggregated mean density:

- If the uncertainty in the estimates for individual cells is considered to be independent, the variance for a combination of cells can be estimated by summing the variances for the usages within the individual cells (each of which is approximately the square of one quarter of the difference between the lower and upper bounds of its confidence interval). The confidence interval for the mean density of the combined area can then be approximated as two standard errors, which is the square root of the variance, either side of the total best estimate. However, in many areas, the uncertainty in estimates for neighbouring cells cannot be considered independent because a large part of it comes from the spatial smoothing within the model.

- A more conservative approach would be to use the sum of the lower bounds for the individual cells as the lower bound for the whole area. This is likely to overestimate the size of the confidence interval, because it ignores both the different data points contributing to each square's usage estimate and the gradual decay, with distance, in the spatial correlations implicit in the model's structure.

We recommend the second approach. Although it may overestimate confidence intervals, it does not make the assumption that the density of individual cells is independent.

5.3 Updating usage maps

The maps show estimated species distributions of grey and harbour seals. Because they synthesise over 20 years of telemetry and survey count data, they integrate changes in the long-term population dynamics and so will not change dramatically in the short-term. However, it is reasonable to assume that species distribution will vary temporally and where SMRU have on-going projects to tag seals and carry out haul-out surveys, these new data will be incorporated into the maps when they are refreshed. It is important to note that the underlying telemetry data were collected for various purposes and so sampling effort and data-poor regions will still exist in future. It is planned that the maps should be updated every 2-3 years to allow new data to be incorporated. Meanwhile the maps presented here provide a stable view.

6 Frequently asked questions

Q. Is usage the same as density?

A. *Yes, usage maps represent estimated density of the expected population of seals in each 5x5km grid square.*

Q. What units are the maps measured in?

A. *The maps can be interpreted as the* <u>*mean*</u> *density of seals in each 5x5km grid square over the year. For example, a green square denotes a* <u>*mean*</u> *density of between 5 and 10 seals per 5x5km cell. The upper and lower* <u>*confidence intervals*</u> *relate to our confidence in this* <u>*mean*</u>*.*

Q. Does the predicted at-sea density take into account animals that may be hauled out or does it assume all animals in the population are at-sea?

A. *The analysis takes into account that a proportion of animals are hauled-out at any one time. The maps represent the estimated population of seals at-sea and not the proportion of the population hauled-out.*

Q. Does the density represent a particular age or sex group of animals?

A. *Telemetry data were aggregated to create a density map of each species (*see Appendix, Table 2 and Table 3*). 234 grey seal tracks were used, of which the* male to female ratio was 111:123 and 177 of the tagged animals were adults and 57 were moulted pups. 196 harbour seal tracks were used; the known male to female ratio[1] was 81:95 and 190 were adults and 6 were weaned pups.

Q. Does density represent a particular time of year?

A. *Density is represented throughout the year. Both species of seal moult annually; female grey seals moult in January and February and males between February and April; harbour seals moult in August and September. Telemetry tags are placed on seals' neck pelages and secured with epoxy resin. The tags fall off when animals moult and so tend to be put on well before the moult or just afterwards to maximise tag lifespan. Therefore, there is limited*

[1] Sex data were missing in 20 seals

location data available during the moult season of each species.

Q. Do the maps represent current population estimates?

A. *No, the maps use population estimates taken from a likelihood distribution that is biased towards more temporally recent counts (see* Appendix - Aerial survey & population level*). However, this will not match with current (2012) population estimates.*

Q. How are missing data handled?

A. Clearly, not every 5x5km coastal cell is surveyed every year to count seals hauled out. Thus both spatially and temporally there will be missing count data. However, the analysis reflects the most complete counts that are available.
In 5x5km coastal cells where hauled out seals were counted, but where no tagged animals ever visited, a null model approach is used to estimate at sea usage (see Appendix, Accessibility models).

7 Usage maps

Figures 1-12 show the total (at-sea and hauled-out) and at-sea estimated densities of grey and harbour seals around the UK, and their associated upper and lower 95% confidence intervals. The maps can be interpreted as the average number of seals in each 5x5km grid square at any point in time. For example, a green square denotes, on average, between 5 and 10 seals will be within that grid square at any point in time.

The majority of usage is concentrated around Scotland, reflecting the distribution of seals around the UK (90% of grey seals and 79% of harbour seals live and/or breed in Scotland; SCOS, 2012). The broad-scale, high resolution of the maps means that fine-scale features can be seen. So, although the maps do not distinguish between activity budgets of animals, the high offshore density areas seen throughout the maps are most likely to be foraging patches.

Grey and harbour seal density maps

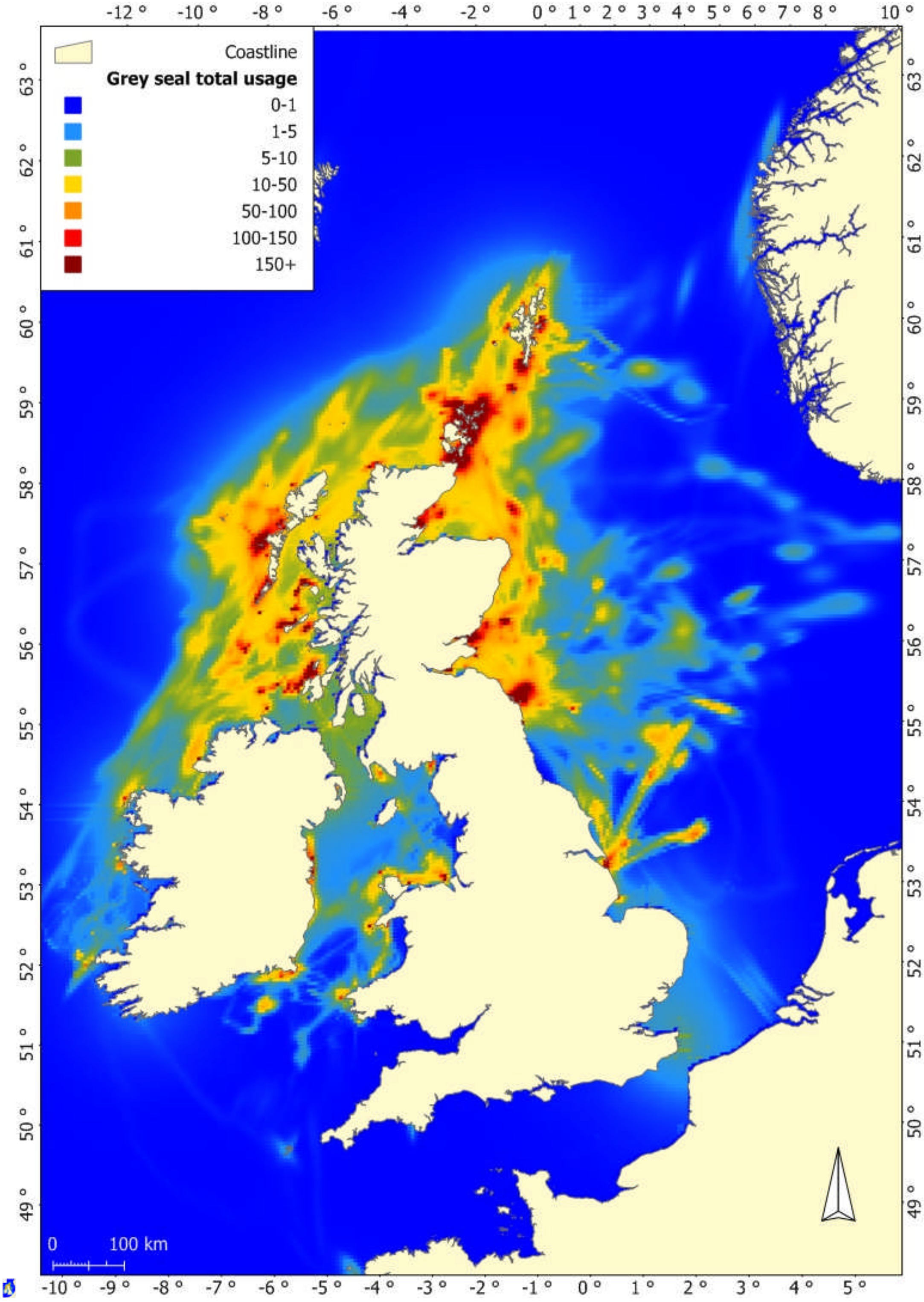

Figure 1. Estimated total density of grey seals around the UK.

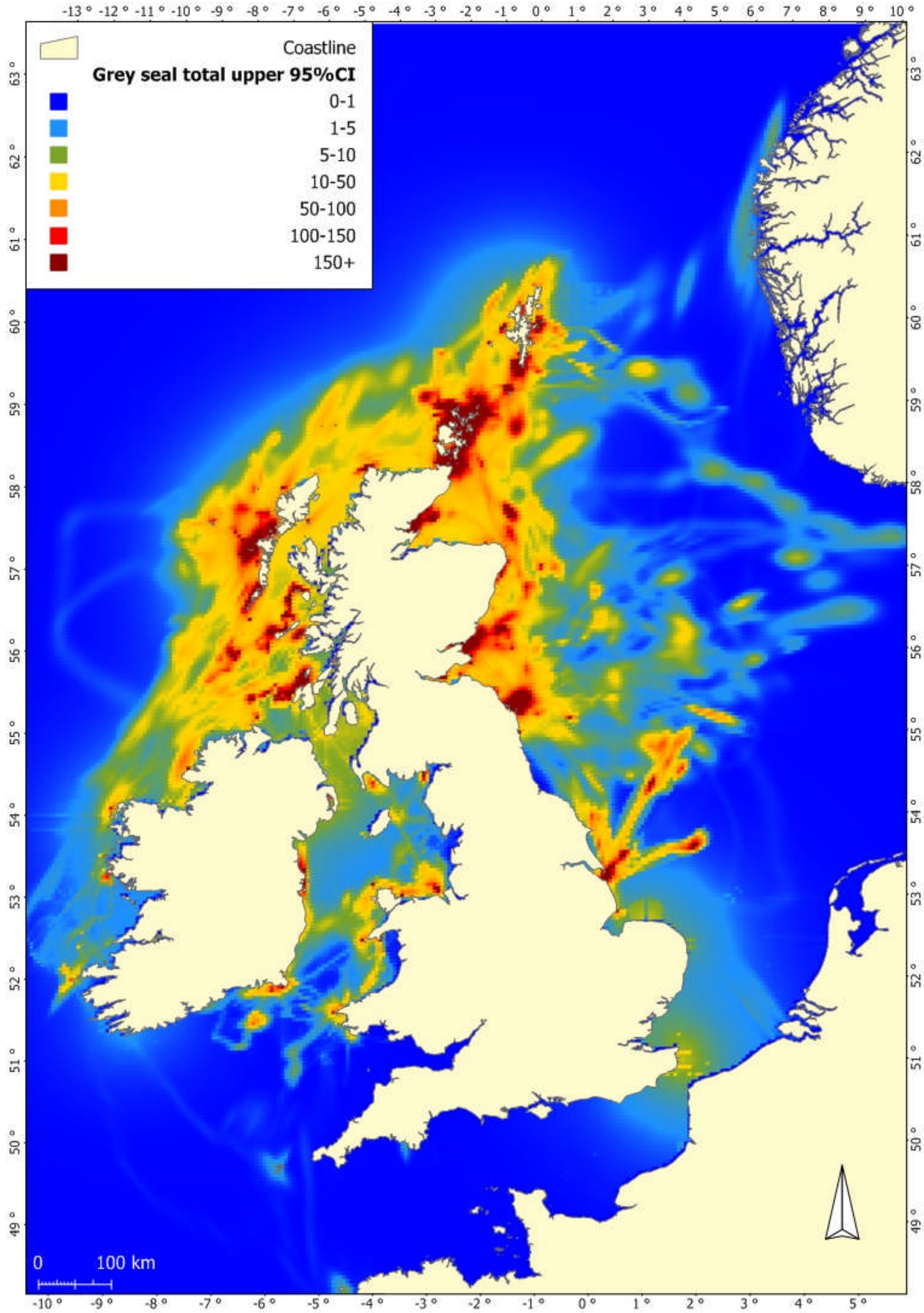

Figure 2. Upper 95% confidence intervals of total estimated density of grey seals around the UK.

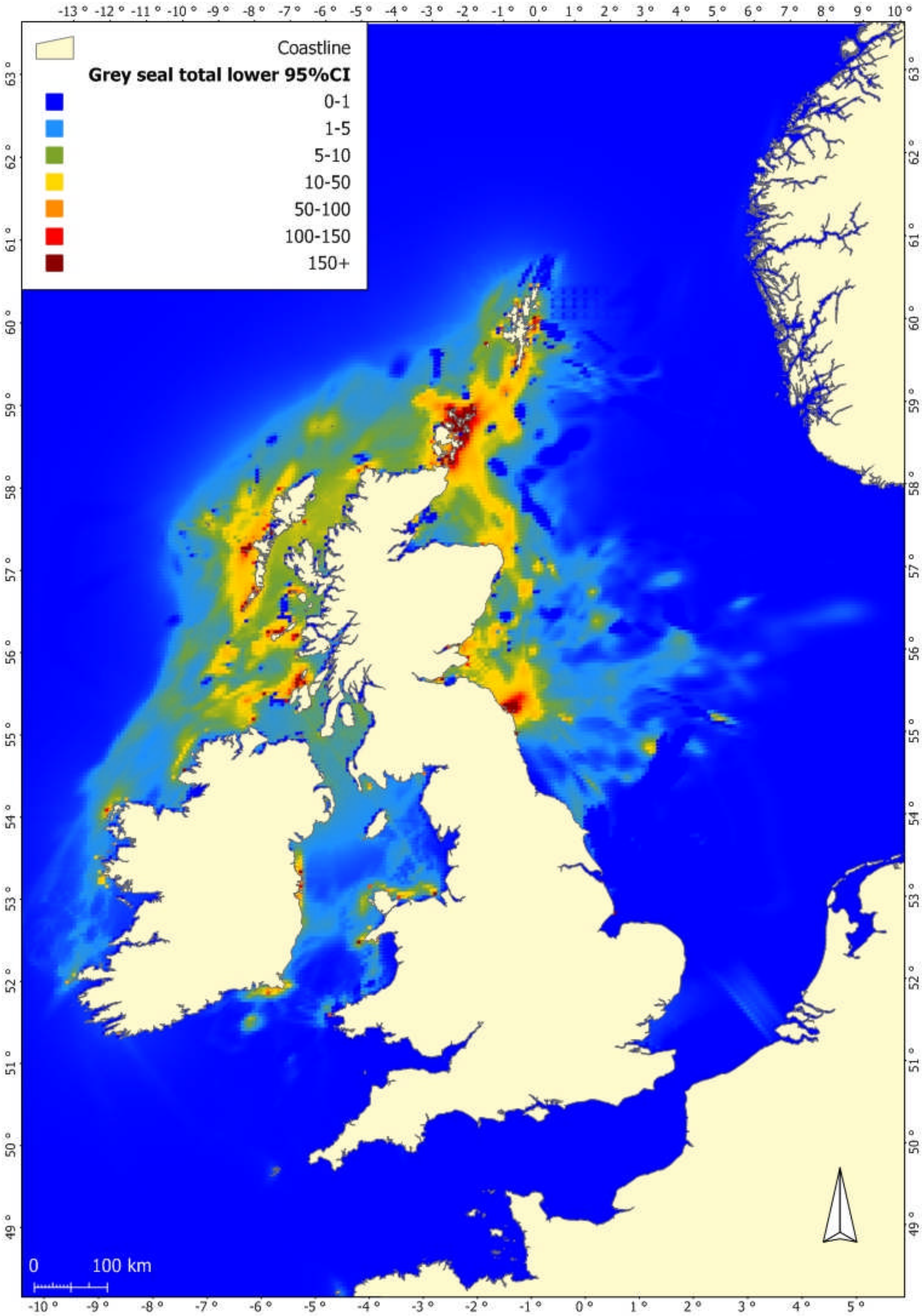

Figure 3. Lower 95% confidence intervals of total estimated density of grey seals around the UK.

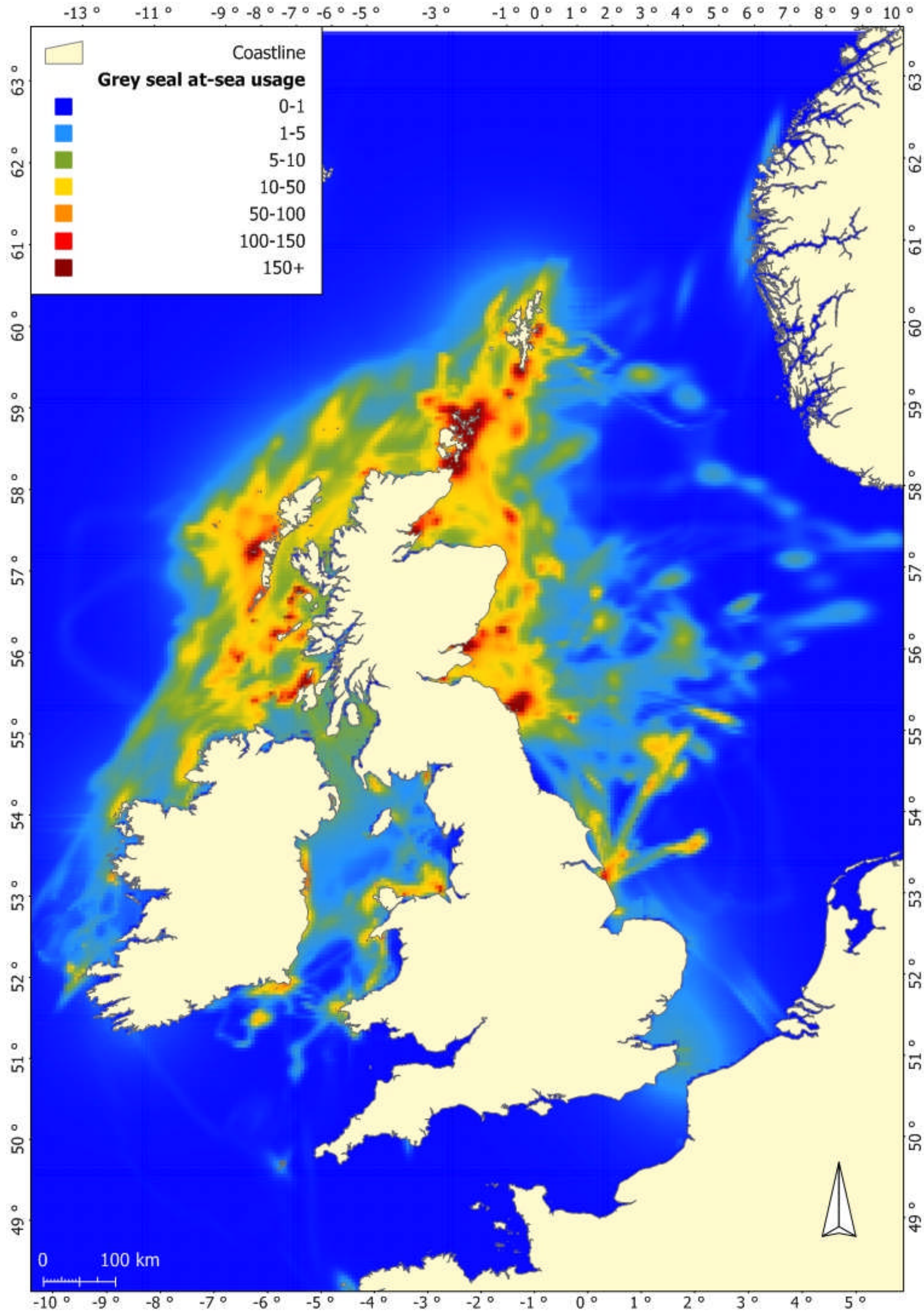

Figure 4. Estimated at-sea density of grey seals around the UK.

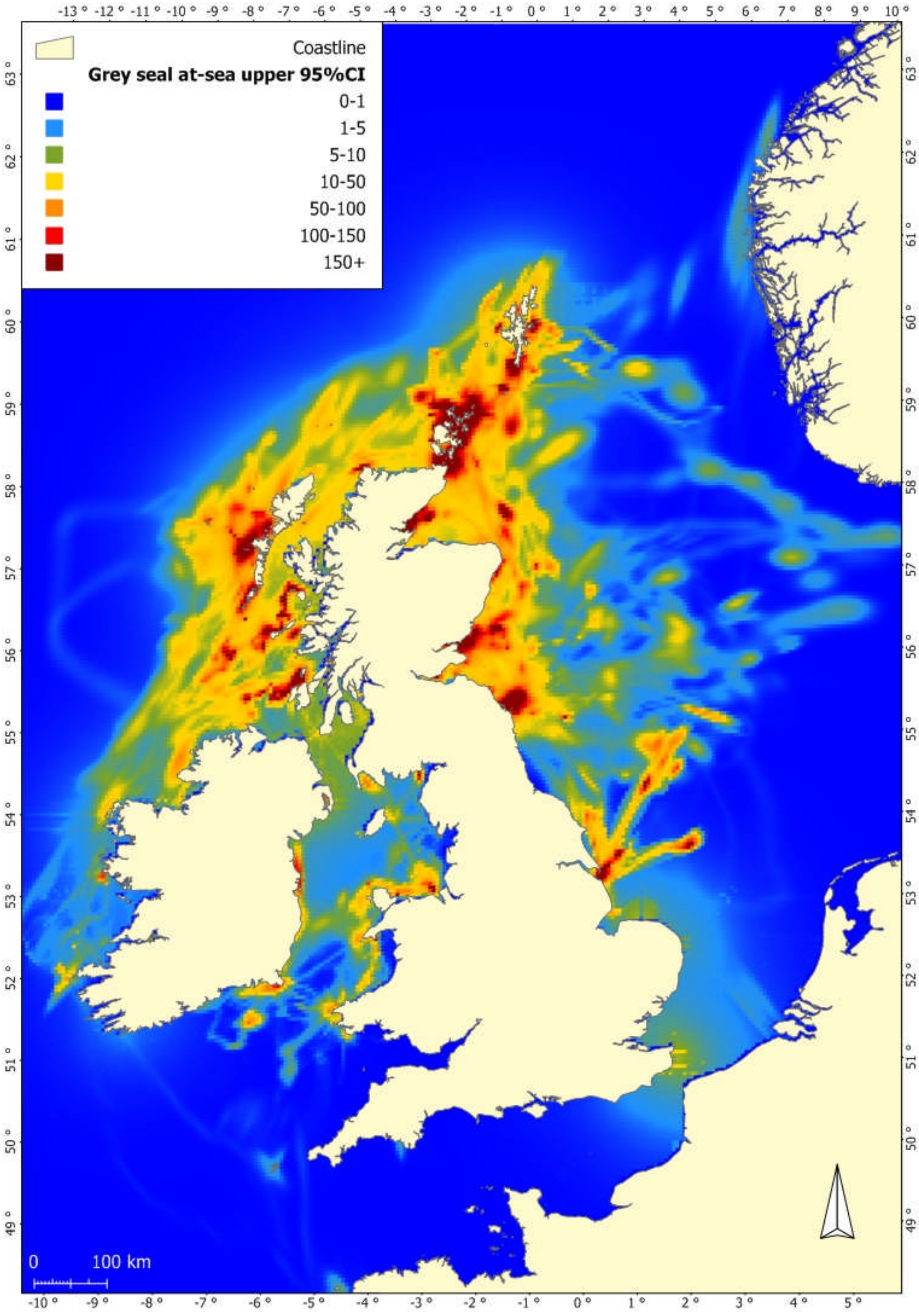

Figure 5. Upper 95% confidence intervals of at-sea estimated density of grey seals around the UK.

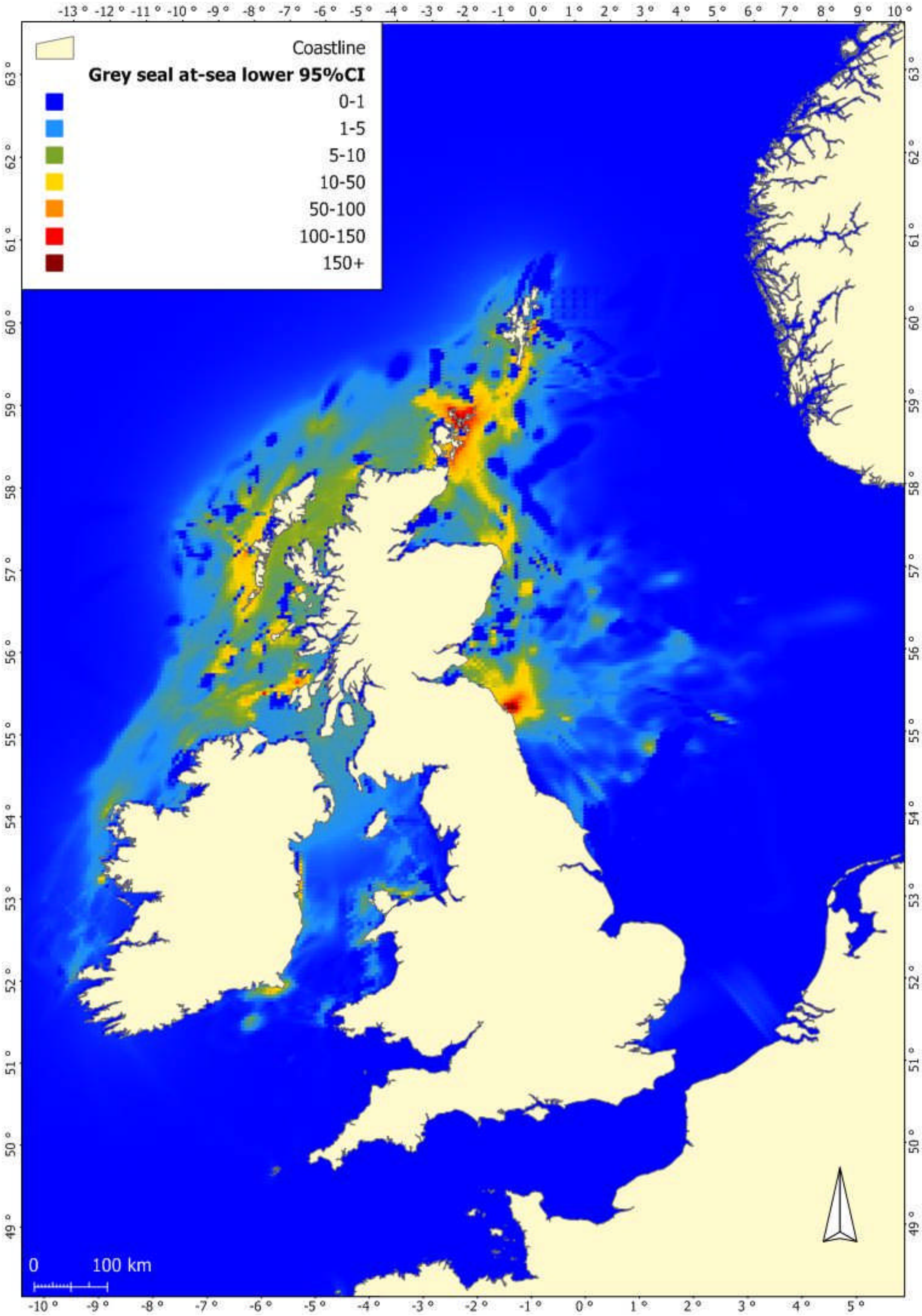

Figure 6. Lower 95% confidence intervals of at-sea estimated density of grey seals around the UK.

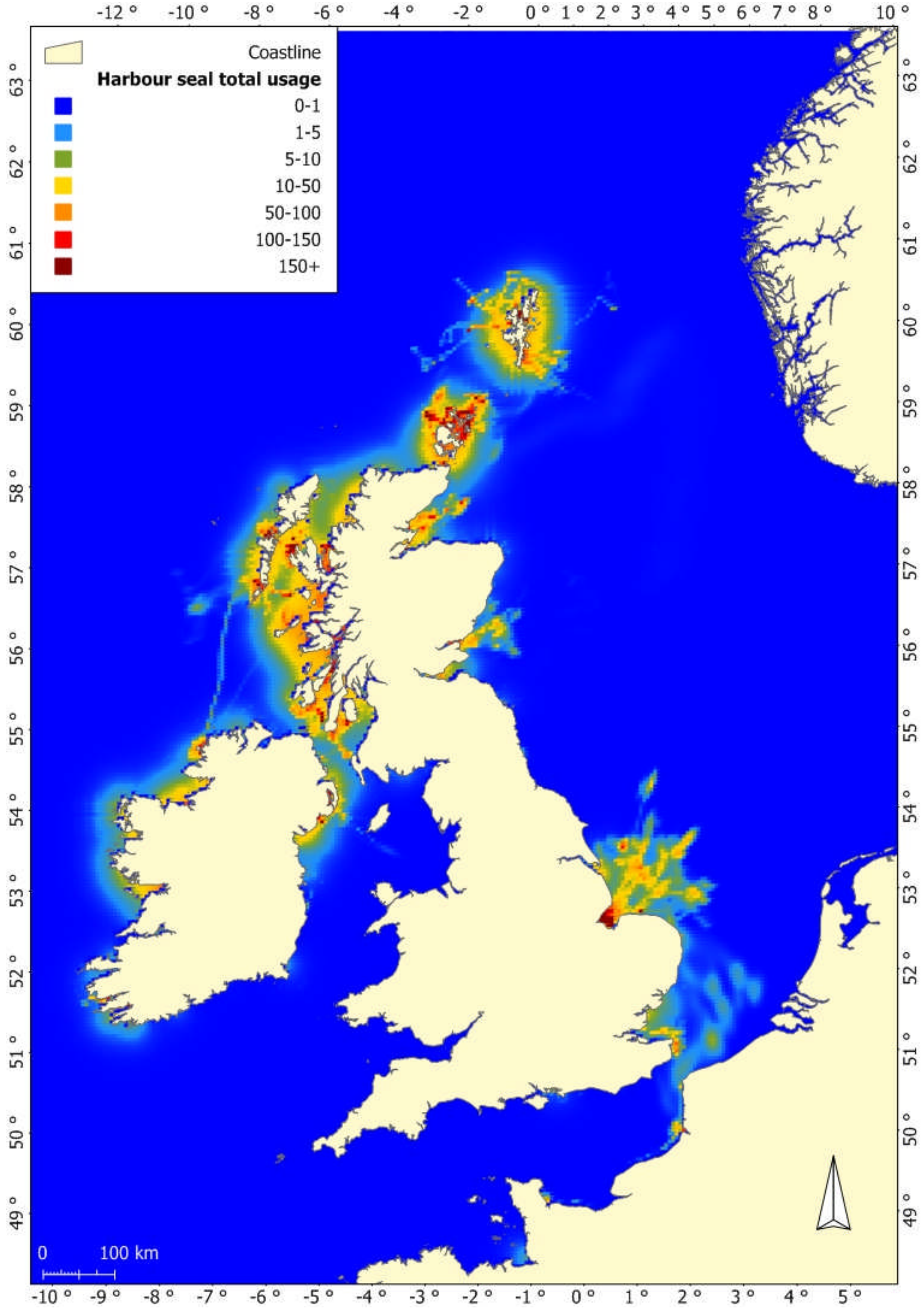

Figure 7. Estimated total density of harbour seals around the UK.

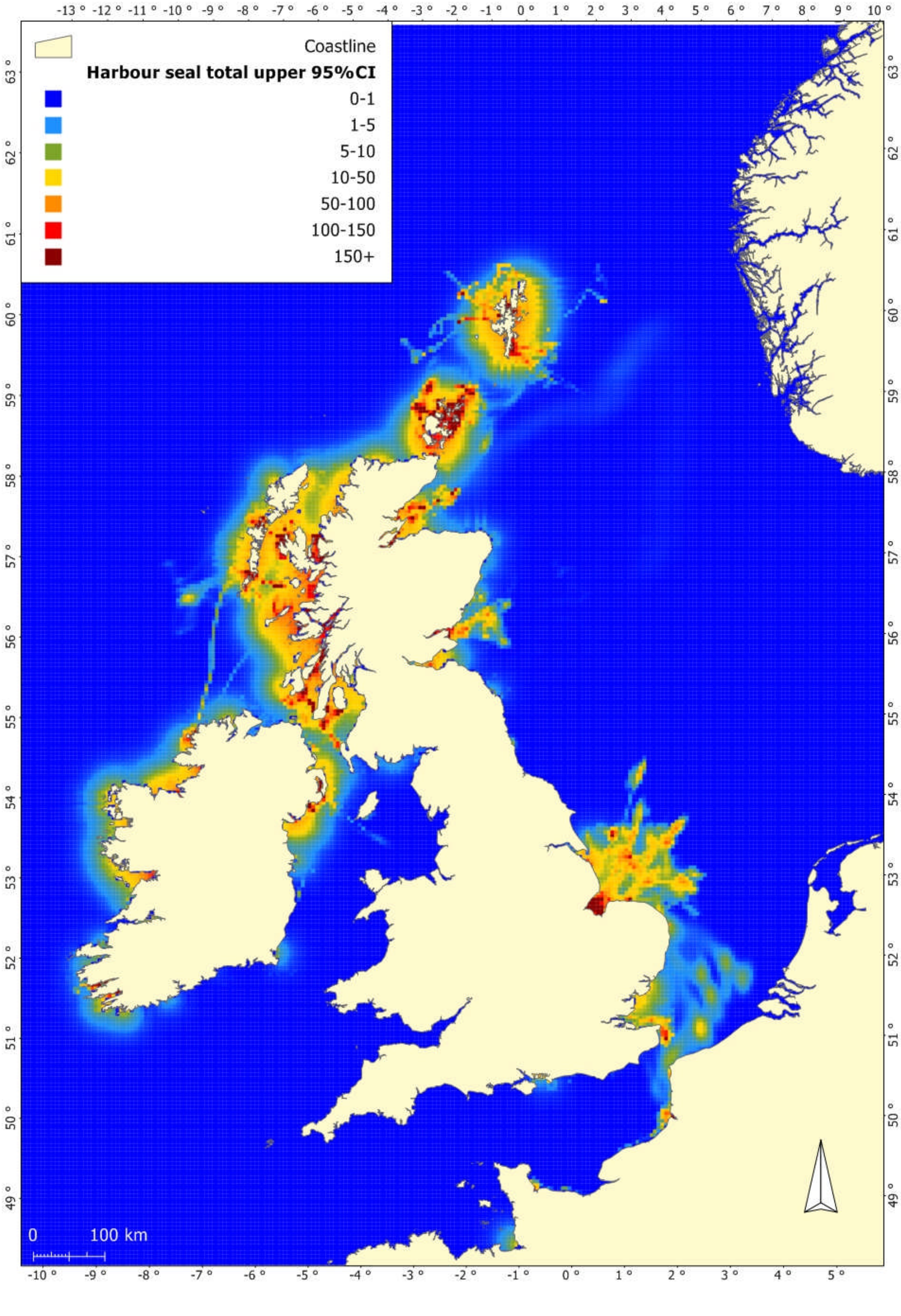

Figure 8. Upper 95% confidence intervals of total estimated density of harbour seals around the UK.

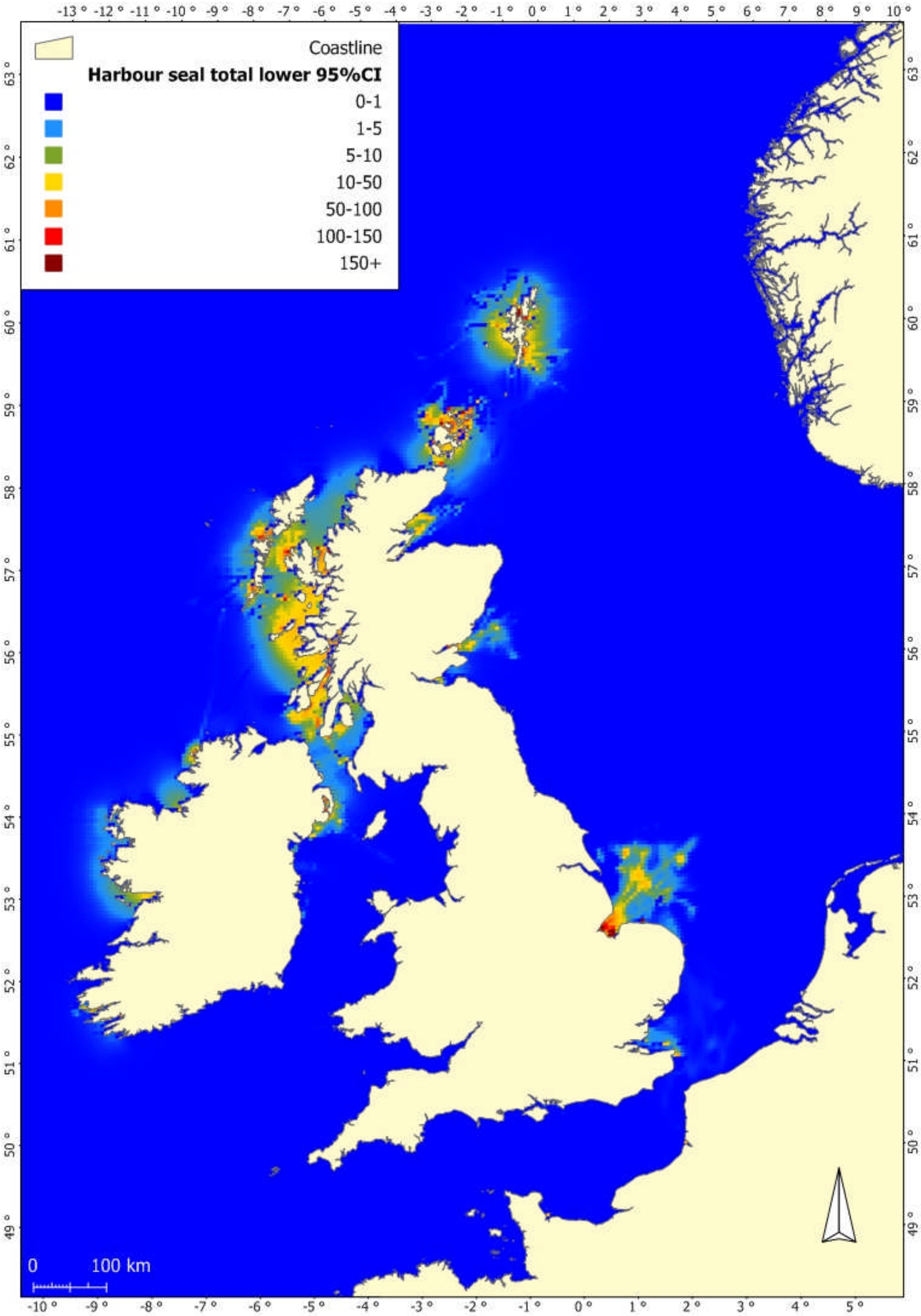

Figure 9. Lower 95% confidence intervals of total estimated density of harbour seals around the UK.

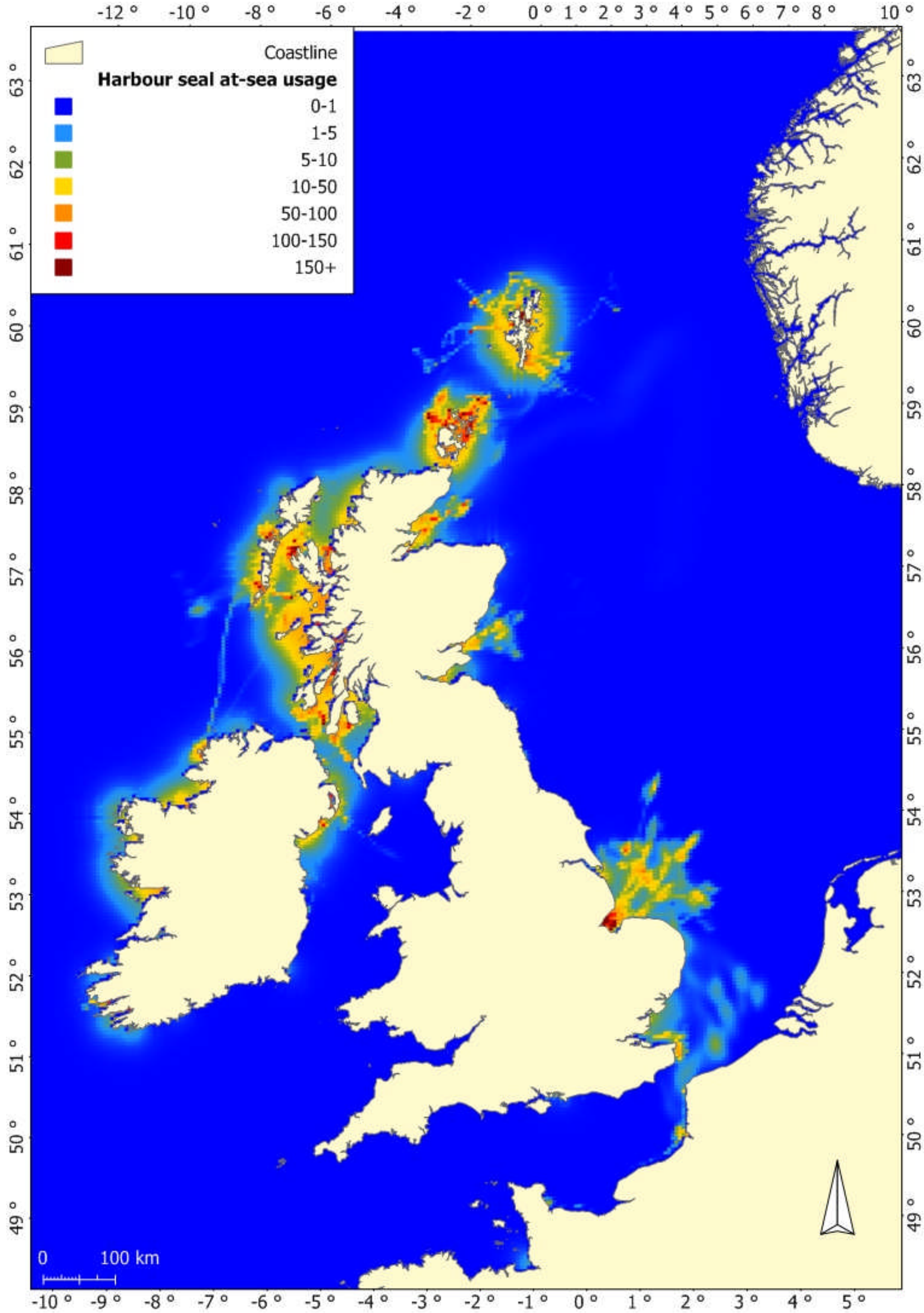

Figure 10. Estimated at-sea density of harbour seals around the UK.

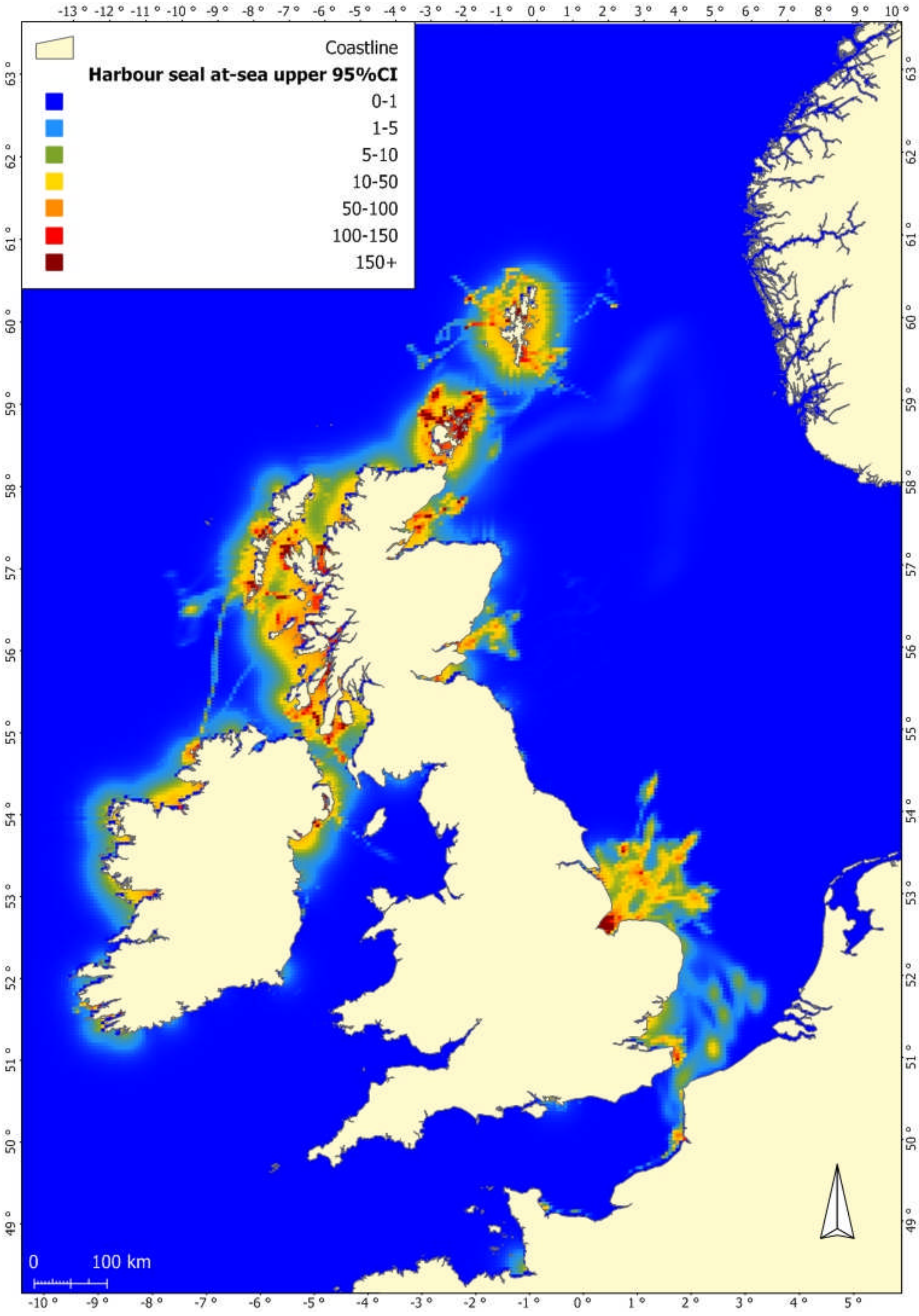

Figure 11. Upper 95% confidence intervals of at-sea estimated density of harbour seals around the UK.

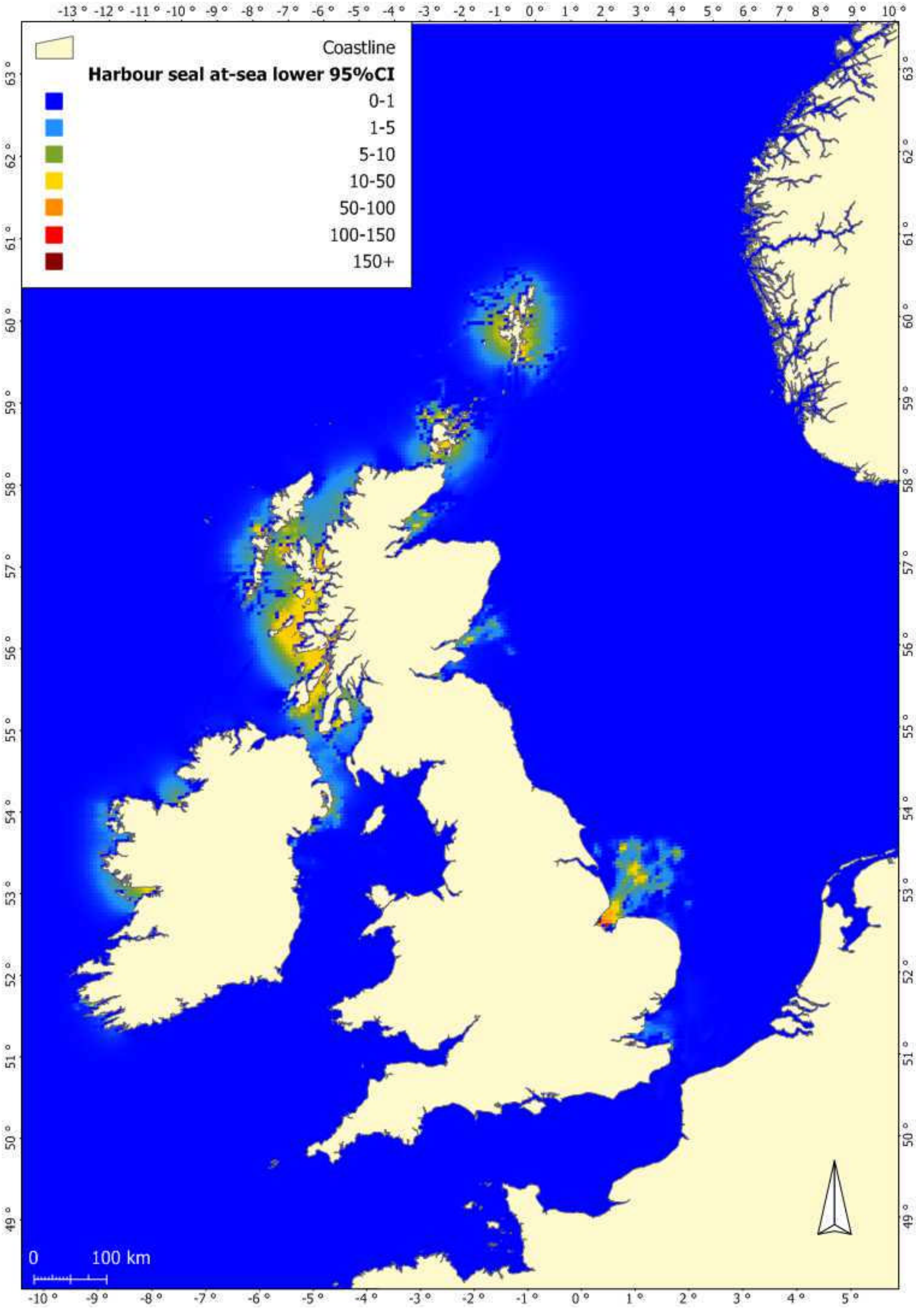

Figure 12. Lower 95% confidence intervals of at-sea estimated density of harbour seals around the UK.

8 Caveats and limitations

8.1 Map Projection

Maps were gridded as 5x5km cells on a Universal Transverse Mercator 30°N World Geodetic System 1984 (UTM30N WGS84) projection. The supplied GIS files can be readily re-projected.

8.2 Survey count data

Survey count data were assimilated from various data sources, including aerial and ground counts, which used different data collection protocols (see Appendix, Table 1).

A single count was assigned to each haul-out site for each year where data were present from 1988-2012. Within-cell temporal variability in counts was incorporated into the usage model and is shown as increased uncertainty.

Spatial data coverage shown in Appendix, Figure 13 shows all the data available at the time of map production (December 2012). However, due to uneven survey effort, there are data-poor regions of known grey seal usage such as the south-west coast of England and North Rona off the north of Scotland. With the exception of harbour seal count data from northern France, data from countries outside the UK where seals haul-out such as Norway, were not included in the analysis, which could underestimate density in those areas (distant from the UK).

8.3 Telemetry data

Telemetry data spanned 21 years. Within this time tag design improved and over the last eight years higher accuracy and location rate GPS tags have superseded Argos satellite-based SRDL tags. We were able to combine data from different tag types by:

- regularising tracks to a common time frame,
- smoothing Argos-based locations to reduce track error,
- weighting individual animals by information content (see Appendix – Information content weighting) to account for differences in individual tag durations.

8.4 Spatial marine distribution

We assumed the spatial distributions of both species were in equilibrium to allow telemetry data to be aggregated across years and produce UK-wide maps. Whilst this assumption may not hold in localised areas where population dynamics have altered since the telemetry data were collected, at a broad-scale this is a reasonable assumption.

8.5 Temporal variation

The distribution of grey and harbour seals varies seasonally and possibly annually. However, in order for grey and harbour seal density maps to be compared directly, August survey counts were used for both species. This corresponds to the timing of the regular and synoptic harbour seal moult surveys that are undertaken by SMRU. At the same time grey seals that are hauled out are also counted. For grey seals, this timing corresponds to approximately 1-3 months before they congregate at breeding sites.

Telemetry data spanned all months for both species but with variable sampling effort. Grey and harbour seals have similar lifecycles including yearly moulting and breeding, which happen at different times of the year for each species. Because tags fall off during moulting and animals are not usually tagged during breeding, telemetry data are limited to between July and October for grey seals, and December and April for harbour seals. Grey seals form highly aggregated hauled-out colonies when they are breeding (and to a lesser extent when they are moulting) in a clockwise-cline around the UK between September and December. The limited tag data from the grey seal breeding seasons should not affect population-level density distribution as current research shows grey seals may go to a site to breed but return after several weeks to their original haul-out region (Russell *et al.*, 2012 in review).

8.6 Population structure

The factors of age and sex were aggregated to provide the most complete spatio-temporal coverage of species distribution around the UK. The breakdown of these factors in the telemetry data that are analysed is shown in Tables 2 and 3 of the Appendix.

9 References

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10 Appendix– Methods

This appendix provides a detailed breakdown of how the usage maps were created.

10.1 Available data

10.1.1 Count Data

Grey and harbour seals were censussed by SMRU during August when harbour seals are found in moulting aggregations and grey seals are dispersed on haul-outs along the coast. An entire coastline is surveyed and counts are marked using OS Landranger maps (1:50,000) to within an accuracy of 50m. Surveys take place between 08:00h and 18:00h within 2 hours of low tide (Lonergan *et al.,* submitted; Thompson *et al.*, 2005; Lonergan *et al.*, 2007). Table 1 shows the surveys used in the analysis. Figure 13 shows the locations of aerial survey and ground counts used, colour coded by region.

Area surveyed	**Method**	**Description**	**Data used**
Scotland	Aerial survey (Helicopter)	Both species surveyed annually using SMRU protocol.	1996-2010
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.	1988-2009
Northern Ireland	Aerial survey (Helicopter)	Both species surveyed annually using SMRU protocol.	2002
Strangford Lough, Northern Ireland	Aerial survey (Helicopter)	Both species surveyed annually using SMRU protocol.	2006, 2007, 2008 and 2010.
Republic of Ireland	Aerial survey (Helicopter)	Both species surveyed annually using SMRU protocol.	2003
Chichester and Langstone harbour	Ground counts through public sightings and by Chichester Harbour Authority.	Annually, harbour seals only.	1999-2011
North Wales	Ground counts (Westcott & Stringell , 2004)	Grey seals only, counts extended over 12 months.	2002, 2003
Ramsey Island, South Wales	Ground counts	Grey seals only in August	2008-2012
Baie de Somme, Baie de Veys, and Baie de Monte Saint Michel, France	Ground counts with extrapolation (Hassani *et al.*, 2010).	Annually, harbour seals only.	1986-2008

Table 1. Summary of surveys used in the analysis.

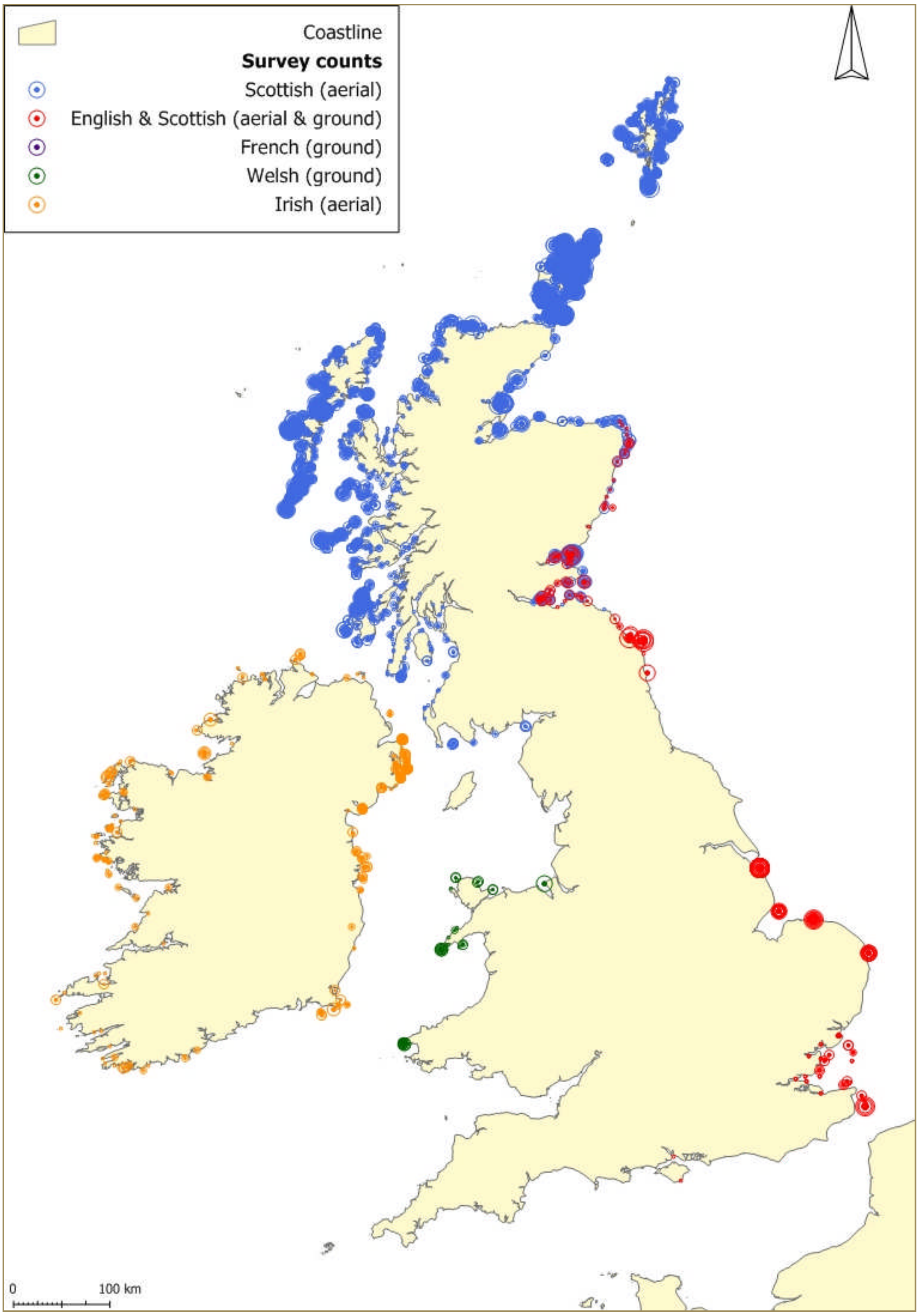

Figure 13a. Survey haulout counts of grey seal counts between 1986 and 2012, colour-coded by region. A single count was estimated for each location using data from multiple years – the symbols are scaled by this count. Plotting neighbouring counts can give the impression of symbol smudging.

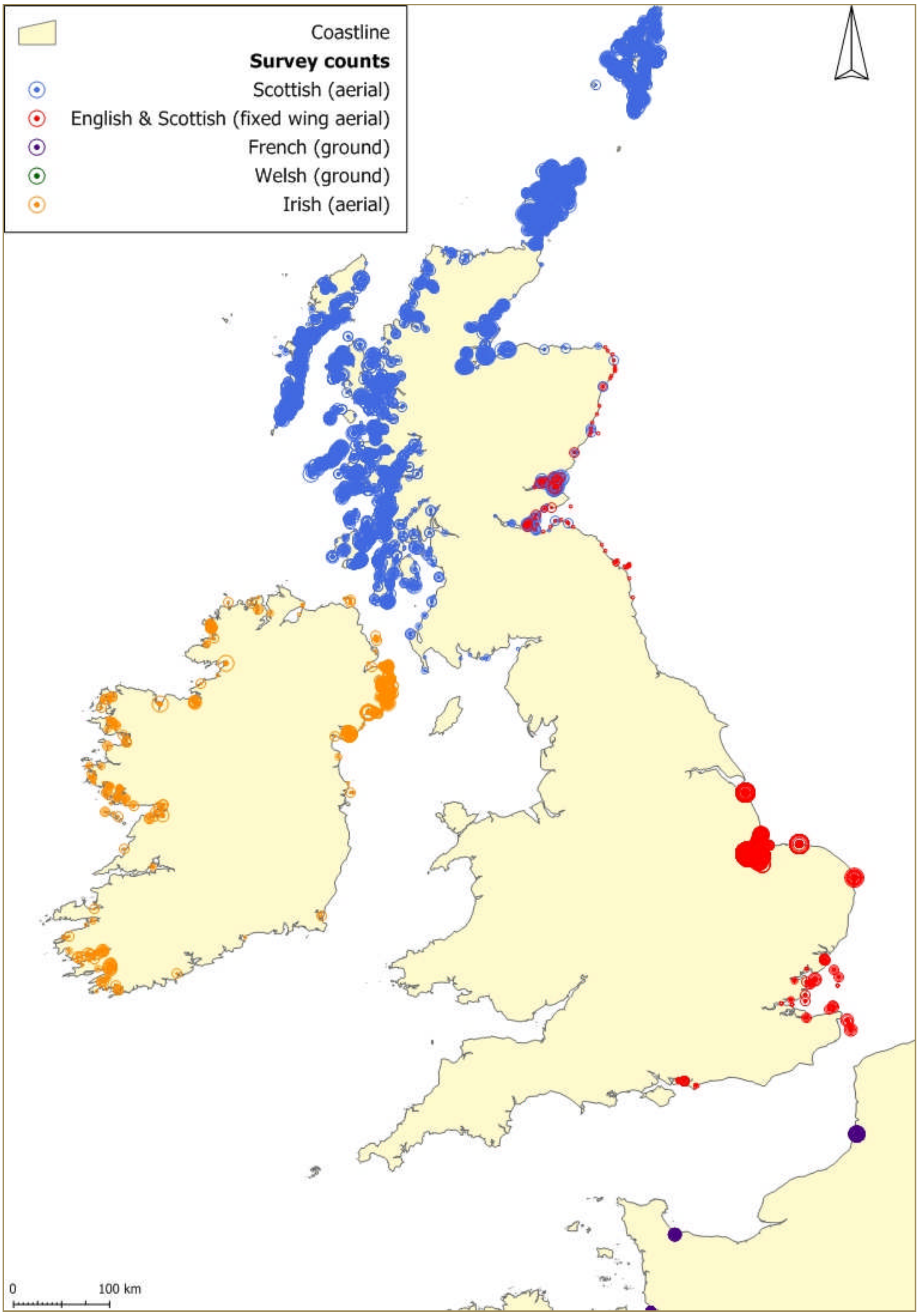

Figure 14b. Survey haulout counts of harbour seal counts between 1986 and 2012, colour-coded by region. A single count was estimated for each location using data from multiple years – the symbols are scaled by this count. Plotting neighbouring counts can give the impression of symbol smudging.

10.1.2 Telemetry

Telemetry data from grey and harbour seals have been collected by SMRU since 1988 from two types of logging devices: Satellite Relay Data Logger (SRDL) tags developed by SMRU use the Argos satellite system and were deployed between 1988 and 2010. GPS phone tags that use the GSM mobile phone network with a hybrid Fastloc GPS protocol (McConnell *et al*., 2004) have been deployed since 2005. Telemetry data were selected from the SMRU database by species and processed through a set of data-cleansing protocols to remove null and missing values, duplicated records and ineligible data (Russell *et al.*, SCOS briefing paper 11/17). Because the analysis characterises total species distribution, data were not disaggregated by sex or age.

234 grey seal tracks were included (**Table 2**), tagged between 1991 and 2011. The male to female ratio was 111:123; 177 of the tagged animals were adults and 57 were moulted pups.

Year	Tag type	Number of tags	Sex ratio (m:f)	Age (adult:pup)	Mean tag lifespan (days)
1991	SRDL	5	4 :1	5 : 0	106
1992	SRDL	12	8 :4	12 : 0	107
1993	SRDL	3	2 :1	2 : 1	93
1994	SRDL	4	2 :2	0 : 4	59
1995	SRDL	21	15 :6	15 : 6	92
1996	SRDL	20	8 :12	20 : 0	59
1997	SRDL	8	4 : 4	8 : 0	76
1998	SRDL	24	17 :7	24 : 0	145
2001	SRDL	11	6 :5	1 : 10	141
2002	SRDL	9	4 :5	2 : 7	108
2003	SRDL	22	14 :8	22 : 0	119
2004	SRDL	28	11 :17	28 : 0	154
2005	SRDL	9	5 :4	9 : 0	145
2006	SRDL	2	1 :1	2 : 0	66
2008	SRDL / GPS	10 / 9	9 :10	19 : 0	186
2009	GPS	12	2 :10	7 : 5	180
2010	GPS	24	10 :14	0 : 24	142
2011	GPS	1	1 :0	1 : 0	210
		234	**111 : 123**	**177 : 57**	**Mean=127**

Table 2. Summary of grey seal telemetry tracks used in the analysis.

196 harbour seal tracks were used (**Table 3**), tagged between 2001 and 2012. The known male to female ratio was 81:95[2]; the majority (190) of the tagged animals were adults and 6 were pups.

[2] Sex data are missing in 20 seals

Year	Tag type	Number of tags	Sex ratio (m:f)	Age (adult:pup)	Mean tag lifespan (days)
2001	SRDL	10	5 :5	10 : 0	130
2002	SRDL	5	4 :1	5 : 0	136
2003	SRDL	36	15 :21	36 : 0	147
2004	SRDL	35	19 :16	29 : 6	117
2005	SRDL	21	12 :9	21 : 0	94
2006	SRDL / GPS	25 / 26	33 :18	51 : 0	92
2007	SRDL / GPS	1 / 1	1 :1	2 : 0	95
2008	GPS	14	0 : 14	14 : 0	133
2009	GPS	10	3 :7	10 : 0	84
2010	GPS	10	8 :2	10 : 0	92
2011	GPS	1	0 :1	1 : 0	61
2012	GPS	1	1 :0	1 : 0	41
		196	**81 : 95**	**190 : 6**	**Mean=112**

Table 3. Summary of harbour seal telemetry tracks used in the analysis. Sex data are missing in 20 seals.

Table 4 shows the number and proportion of tracks tagged in each Seal Management Region (Scottish Government, 2011) and additional regions defined by the authors.

Management region	GREY SEALS		HARBOUR SEALS	
	Number of tracks	Proportion of tracks	Number of tracks	Proportion of tracks
E Scotland	58	25%	25	13%
France	2	1%	14	7%
Ireland	7	3%	13	7%
Moray Firth	5	2%	12	6%
NE England	28	12%	22	11%
Orkney & N coast	30	13%	15	8%
SE England	8	3%	4	2%
Shetland	7	3%	33	17%
W Highlands	34	15%	15	8%
Wales	30	13%	26	13%
Western Isles	25	11%	17	9%
Grand Total	**234**		**196**	

Table 4. Number and proportion of animals tagged in each region by species.

Figure **15** shows the geographical locations of grey and harbours seal tracks used in the analysis.

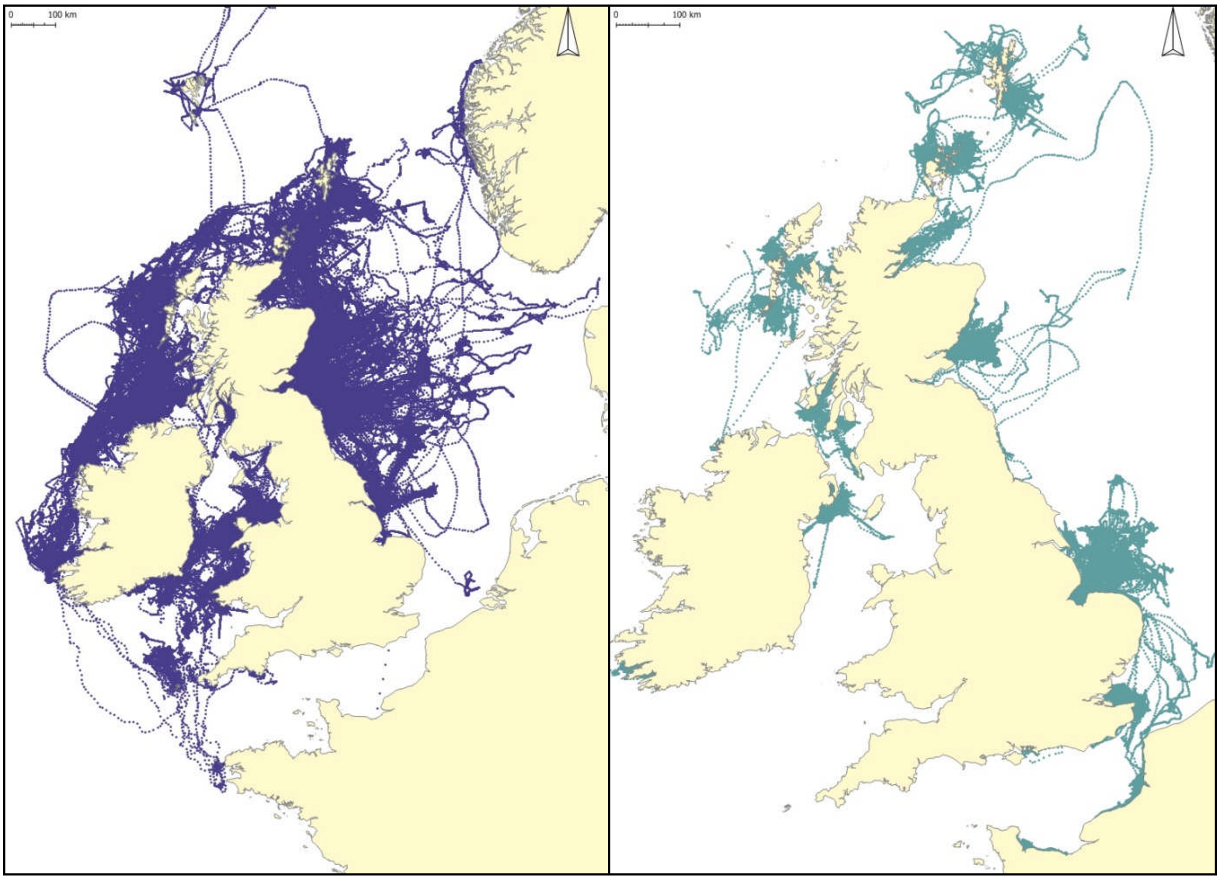

Figure 15. Telemetry tracks: (L) Grey seal and (R) harbour seal tracks between 1991 and 2012.

10.1.3 Coastline

GSHHS 2.2.0 fine (f) resolution L1 data (Wessel & Smith, 1996) available to download from NOAA was used as the coastline layer in the usage maps.

10.2 Software

The statistical package R version 2.15.2 (R Development Core Team, 2012) was used for data processing and analysis. GIS software Manifold version 8.0 (Manifold, 2012) was used to produce the maps. All maps are in Universal projection Transverse Mercator zone 30^{0} North (UTM30N), datum World Geodetic System 1984 (WGS84).

10.3 Spatial extent

Data were gridded into 5x5km squares. The limits of the maps were defined by the spatial extent of the telemetry data.

10.4 Treatment of positional error

Positional error, varying from 50m to over 2.5km (Argos User's Manual, 2011), affects all SRDL telemetry points leading to a loss in fine-scale detail. The range of positional error is defined by the number of uplinks received during a satellite pass. Errors are assigned to six location classes: '0', '1', '2' and '3' indicate four or more uplinks have been received for a location, 'A' denotes three uplinks, and 'B' denotes two uplinks (Vincent *et al*., 2002). Because seals spend the majority of their time underwater, uplink probability is reduced and so over 75% of the telemetry data have location class error 'A' or 'B'.

There are many approaches to addressing the problem of location error, ranging from simple moving average smoothers to elaborate state-space models, but none have offered a comprehensive solution combining automation, computational speed, precision and accuracy. We developed a Kalman filter (Royer & Lutcavage, 2008; Patterson *et al.*, 2010; Roweis & Ghahramani, 1999) using a linear Gaussian state-space model to obtain location estimates, accounting for observation error. This provides flexibility and fast processing times. SRDL data were first speed-filtered (McConnell *et al*., 1992) using a *maximum speed parameter* of 2ms^{-1} to eliminate outlying locations that would require an unrealistic travel speed. Observation model parameters were provided by the location class errors described above, and process model parameters were derived from Vincent *et al*. (2002).

GPS tags are more accurate than SRDL tags, and 95% of these data have a distance error of less than 50m. However, occasional errors do arise and these data were excluded from the analysis by removing data with 'residuals' that were either 0 or greater than 25, and removing locations based on fewer than 5 satellites (for further details see: Russell *et al.*, SCOS briefing paper 11/17).

10.5 Haul-out detection

SRDL and GPS telemetry tags record the start of a haul-out event once the tag sensor has been continuously dry for 10 minutes. This event ends when the tag has been continuously wet for 40 seconds. Haul-out event data were combined with positional data and assigned to geographical locations. In the intervening period between successive haul-out events, a tagged animal was assumed to be at sea.

10.6 Haul-out aggregation

Haul-out sites (defined by the telemetry data as any coastal location where at least one haul-out event had occurred) were aggregated into 5x5km cells. 5km was determined by the computational trade-off between the resolution and spatial extent of the final maps. Haul-out events are mostly coastal locations, but also occur at sea, possibly due to seals hauling-out on sandbanks or isolated rocks, or because the placement of a tag on an animals' neck means that the tag registers as dry when the seal is in fact just resting on the surface. Haul-out sites were assigned to a terrestrial count to scale up to population size.

10.7 Trip detection

As seals spend time on land and at-sea, the behaviour that links these two aspects are individual trips from their haul-out to locations at-sea. This also provides a mechanism to scale up from individual animal movement to population spatial distribution by linking the survey count data to telemetry data when seals haul-out.

Individual movements at sea were divided into trips, defined as locations between haul-out events. Return trips have the same departure and termination haul-out site, whereas during transition trips, seals haul-out at a different termination site to the departure site after a period at sea. A haul-out site was assigned to each location in a trip. Return trips were attributed to the departure haul-out. Transition trips were divided temporally into two equal parts and the haul-out. Corresponding telemetry data were attributed to departure and termination haul-outs.

10.8 Kernel smoothing

Telemetry data are positional locations at discrete time intervals. To transform these into spatially continuous data representing the proportion of time animals spend at different locations we used kernel smoothing. The KS (Chacon & Duong, 2010; Duong & Hazelton, 2003; Wand & Jones, 1994; Wand & Jones, 1995) library in R was used to estimate the spatial bandwidth of the 2D kernel applied to the telemetry data using the unconstrained plug-in selector ("Hpi") and kernel density estimator "kde" to fit the usage surface.

10.9 Information content weighting

To account for individual variation in the telemetry points collected from each animal, indexes of information content were devised using data from the whole of the UK. This approach reduced the importance of data-poor animals, whilst simultaneously not overstating the contribution of animals with heavily auto-correlated observations. For each species, models were built using a response variable of rate of discovery, defined by the number of new 5km grid cells an animal visits during the lifespan of the telemetry tag. This rate was modelled as a function of the number of received telemetry locations for an animal, tag lifespan and whether the tag was SRDL or GPS. The intercept was set to zero and a Poisson distribution with a log-link function was used within a Generalised Additive Model (GAMs) framework utilising the R library MGCV (Wood, 2011; Wood, 2006).

Figure **16a** shows a boxplot of grey seals tag type vs. discovery rate for total usage. The mean number of grid cells discovered throughout a tag's lifespan are shown by red triangles (SRDL = 121, GPS = 311). A Welch two-sample t-test gave a significant difference between the means at a 95% confidence level. This was driven by a significantly higher tag lifespan (Figure **16b**; SRDL= 2896 hours, GPS = 3875 hours), and higher uplink rate per hour (Figure **16c**; SRDL= 0.36, GPS = 1.22). The SRDL tags show smaller variation in the number of locations per hour because they were regularised at 2 hourly intervals, as well as keeping the original locations in the data.

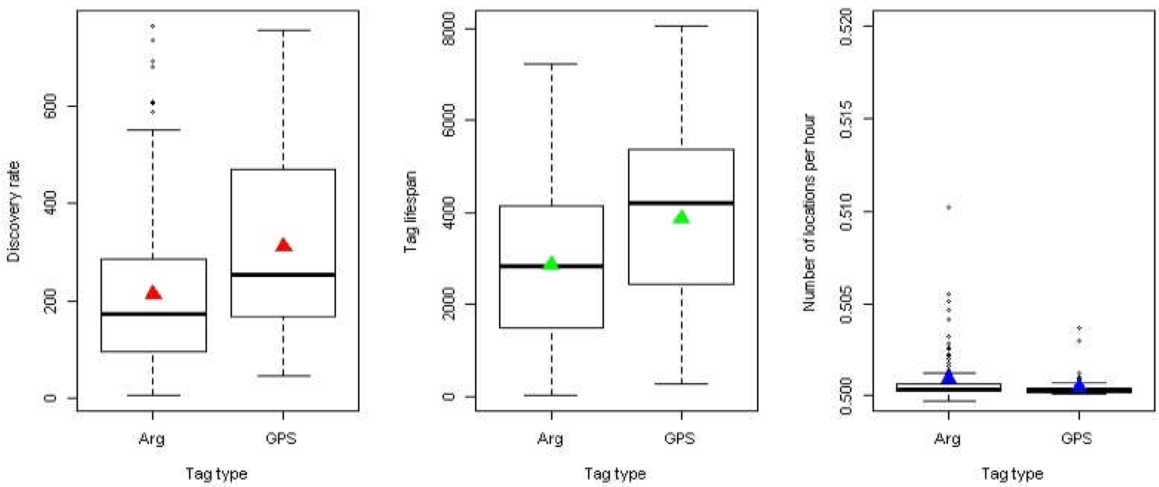

Figure 16. Boxplots showing significant differences between tag types for grey seals. Coloured triangles represent mean values, thick black lines are median values, boxes are interquartile ranges, and dotted lines show minimum and maximum values. (L-R): a. Discovery rate; b. Tag lifespan; c. Number of locations per hour.

Figure **17a** shows a boxplot of harbour seals tag type vs. discovery rate for total usage. The mean number of grid cells discovered throughout a tag's lifespan are shown by red triangles (SRDL= 67, GPS = 18). A Welch two-sample t-test gave a significantly higher mean for SRDL data at a 95% confidence level. This was partly influenced by a significantly higher tag lifespan (Figure **17b**; SRDL= 2987 hours, GPS = 2169 hours) although the GPS tags have a higher uplink rate per hour (Figure **17c**; SRDL= 0.45, GPS = 0.85).

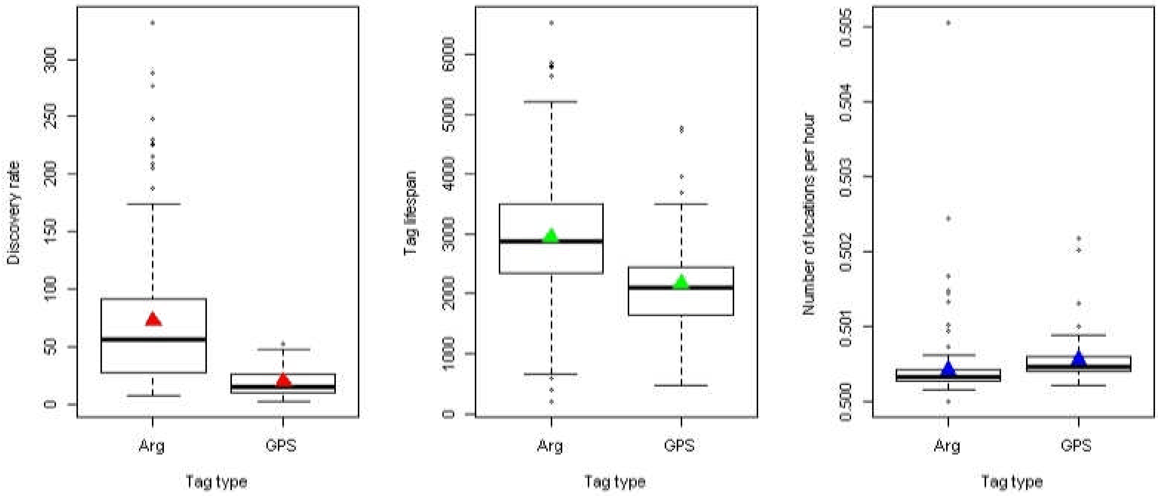

Figure 17. Box plots showing significant differences between tag types for harbour seals. Coloured triangles represent mean values, thick black lines are median values, boxes are interquartile ranges, and dotted lines show minimum and maximum values. (L-R): a. Discovery rate; b. Tag lifespan; c. Number of locations per hour.

Number of locations, tag lifespan, and tag type (SRDL or GPS) were significant and explained 43.2% and 27.9% of variation in the data for grey and harbour seals respectively. Figure **18a** and Figure **19a** show total usage fitted values vs. observed discovery rate. Figure **18b**, Figure **19b**, Figure **18c** and Figure **19c** show the GAM smoothing curves for tag lifespan and number of telemetry locations.

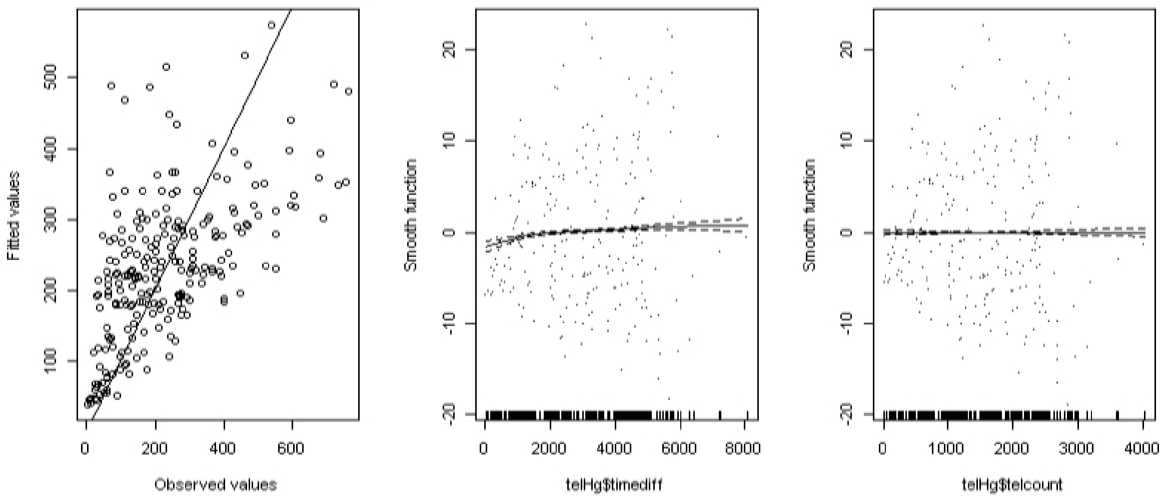

Figure 18. GAM model deriving 'information content' by individual grey seal. (L-R): a. Observed vs. fitted values; b. Tag lifespan smoothing curve; c. Number of telemetry locations smoothing curve.

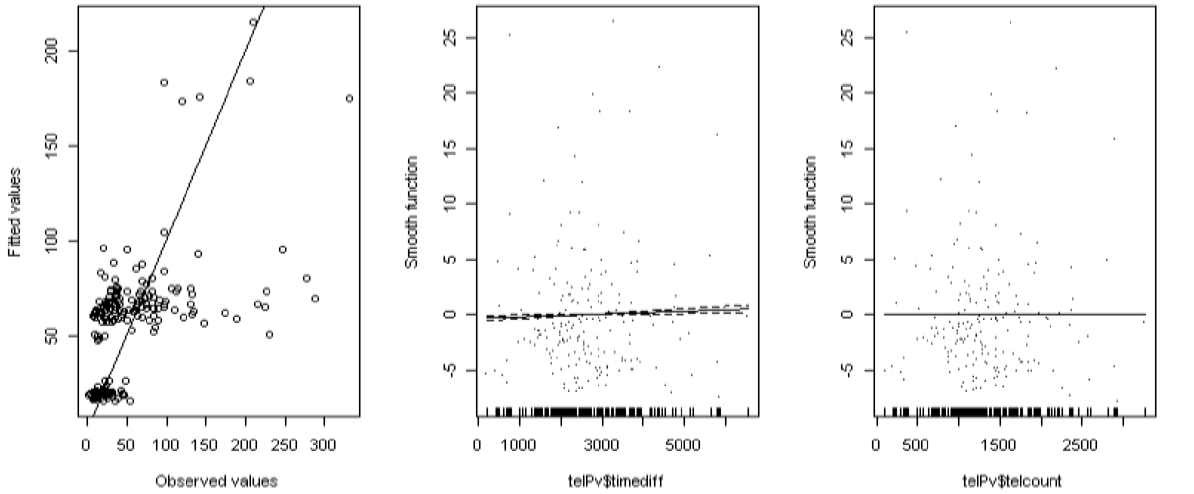

Figure 19. GAM model deriving 'information content' by individual harbour seal. (L-R): a. Observed vs. fitted values; b. Tag lifespan smoothing curve; c. Number of telemetry locations smoothing curve.

Fitted values were normalised and used to weight the contribution of different animals to estimate usage associated with each haul-out location.

10.10 Accessibility models

To account for areas in the maps where aerial survey data were present but telemetry data were not, null maps of estimated density were produced for each species. GLMs were used to model the number of telemetry locations associated with each haul-out. This count was modelled using at-sea distance from the haul-out to represent accessibility by animals to each haul-out, and the distance to the shore to represent accessibility to the coast. A sub-sample of tracks from each species was selected and quasi-Poisson distributions with log link functions were fitted. Figure **20** shows the observed vs. fitted number of telemetry locations associated with each haul-out for (a) grey seals and (b) harbour seals.

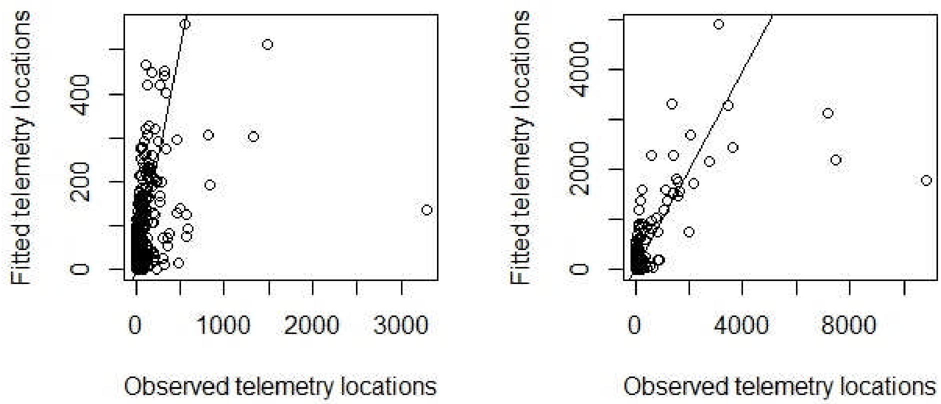

Figure 20. GLM models deriving null usage. Observed number of telemetry locations vs. fitted locations for: a. Grey seals; b. Harbour seals.

10.11 Quantifying uncertainty

Several types of uncertainty were accounted for at individual animal and population level.

10.11.1 Within haul-out

For each species, Linear Models (LMs) were built to estimate variance. All haul-outs with more than 7 animals associated with them were used. The response variable was log (variance) and covariates were sample size (number of animals associated with a haul-out) and log (estimated mean density of seals weighted by information content). At-sea kernel smoothed densities were bootstrapped 500 times for each haul-out, and log (sample size) was sampled with replacement to produce estimated log (variance) and log (mean densities). The models used both covariates without an interaction term and explained 100% of the variation in the data. Estimated mean densities in the null maps were produced by setting sample size to 0 in the uncertainty model to reflect that no tagged animals went to these haul-outs.

10.11.2 Aerial survey & population level

Sampling error and population uncertainty were accounted for by using a derived likelihood density distribution and applying this to each haul-out site based on a given population estimate and the aerial survey counts.

Parameters for the beta function in the likelihood function were calculated using the mean proportion of time each seal species spends hauled-out along with their corresponding confidence intervals (Lonergan *et al.,* submitted; Lonergan *et al.*, 2011).

$$\alpha = \frac{\mu}{\sigma^2}(\mu - \mu^2 - \sigma^2) \quad \text{and} \quad \beta = \frac{1-\mu}{\sigma^2}(\mu - \mu^2 - \sigma^2)$$

Where:
μ = mean seal population hauled-out at any point in time
σ^2 = variance in seal population hauled-out at any point in time

The density distribution likelihood distribution was then derived as:

$$Likelihood = \frac{\prod_{k=N_i-m_{ij}-1}^{N_i-m_{ij}+\beta-1} k}{\prod_{k=N_i+1}^{N_i+\propto+\beta-1} k}$$

Where:
N_i = Seal population of i^{th} haul-out
m_{ij} = Number observed on i^{th} haul-out on j^{th} survey

Population mean and variance of each haul-out site were estimated by sampling with replacement from the likelihood density and taking the mean and variance from that sample.

Population and within haul-out means and variances for each haul-out were combined using formulas for the sum of independent variables.

$$mean = E(X) \times E(Y)$$

$$variance = (E(Y) \times E(Y) \times Var(X)) + (E(X) \times E(X) \times Var(Y)) + (Var(X) \times Var(Y))$$

10.12 Analysis

To create maps of total usage all grey and harbour seal telemetry data from the SMRU database were processed through a series of data cleansing protocols to remove unusable data. SRDL data were spatially interpolated to 2 hour intervals using a Kalman filter and merged with GPS data, which were also interpolated to 2 hours. A grid consisting of 5km squares was created to extend to the limits of the telemetry tracks and overlaid onto the data. Haul-out detection and aggregation were applied to the data at 5km resolution. After spending time at sea an animal could either return to its original haul-out (classifying this part of the data as a return trip), or move to a new haul-out (giving rise to a transition trip).

At-sea data (i.e. when animals were not hauled-out) were then kernel smoothed. A bandwidth was estimated for each animal. Each animal/haul-out combination was kernel smoothed using the estimated bandwidth to produce separate animal/haul-out association distribution maps.

Each animal/haul-out map was multiplied by the normalised Information Content Weighting and all maps connected to each haul-out were aggregated and normalised. Within haul-out uncertainty was predicted and the aggregated usage map and this uncertainty were combined with the previously estimated population mean and variance. The mean usage was then multiplied by the total proportion of time animals spent not hauled-out to calculate at-sea usage only. Usage and variance by haul-out were aggregated to a total at-sea usage and variance map for each species. Hauled-out usage was then added to construct total usage.

Null maps were constructed for each haul-out with no associated telemetry data. The null models were fitted for each species to estimate usage, then normalised, and weighted by the mean proportion of time animals spend not hauled-out. Within haul-out variance was estimated by setting the sample size of the uncertainty model to 0. The mean and variance were scaled to population size by combining with the population estimate mean and variance of each haul-out. These were aggregated to the total usage map for each species.