

# Seal at-sea distribution, movements and behaviour

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## Report to DECC

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## 2 Executive Summary

The Department of Energy and Climate Change (DECC) Offshore Energy Strategic Environmental Assessment (SEA) programme requires robust evidence to inform DECC policy development and execution.

Funded by multiple agencies, the Sea Mammal Research Unit, in collaboration with others, has deployed around 600 telemetry tags on harbour (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the UK over the last 25 years. The objective of this project was to consolidate these data to allow combined analyses for the production of a high quality information base on the at-sea distribution, movements and behaviour of UK seals in the form of peer-reviewed papers.

To this end, all data were collated and consolidated into a managed database. Protocols were developed to clean all historical and incoming telemetry data in a consistent and effective manner. Protocols are also in place that ensures telemetry tags are monitored in real time. These procedures facilitate the use of telemetry data in a standardised format for various projects.

Three main areas were addressed in the subsequent data analyses. First the foraging distribution of grey seals was related to their breeding distribution. Second, using a state-space model we improved on current methods for defining activity budgets in seals by categorising four states: hauled out, resting at-sea, diving and foraging, and we related these budgets to intrinsic (sex, age), time invariant (region) and time variant (day of the year, time of day) covariates. Finally, we investigated the foraging habitat preference of both species.

Grey seals are capital breeders; they accumulate resources for breeding during the majority of the year and then do not forage while suckling their pups. Thus understanding where the effects of any given at-sea impact may be reflected in a breeding population ashore (especially at European and other conservation sites) is critical. This requires quantification of the movement of female grey seals between the foraging and breeding seasons. Along with survey count data in both seasons, telemetry data on regional transitions of individuals allowed quantification of regional transition rates between foraging and breeding seasons. We found that between 21 and 58% of females used different regions for foraging and breeding. For these animals any impacts of their environment, including anthropogenic effects, on reproductive success will not be apparent in the region of impact. Taking the estimated transition probabilities into account is particularly important when assessing the potential impact of off-shore developments on animals which breed on conservation sites such as Special Areas of Conservation.

The activity budgets of both grey and harbour seals in the UK were quantified using telemetry data from 63 and 126 individuals, respectively. Complete activity budgets, encompassing activity at-sea and on land, had never been quantified for these species. Previous investigations of at-sea activity budgets in grey seals elsewhere have defined only two activities: foraging and travelling. However, both species dive to forage and travel and we found that prolonged periods of non-diving behaviour was evident in both species, possibly related to food digestion. Without taking into account such non-diving behaviour, the proportion of time spent foraging and travelling may be incorrectly estimated and subsequently important foraging areas may be incorrectly defined. Thus in this study, behavioural data were used to define activities: resting behaviour (hauled out on land or at-surface

in the sea) and diving. Movement data was then used to split diving into either foraging behaviour (which was defined by slow tortuous movements) or travelling (faster, more direct movement).

We found that both species spent a similar proportion of time in the four states (hauled out, at-surface, foraging and travelling) but that their drivers differed. For example, the proportion of time resting in harbour seals, but not in grey seals, varied regionally. In grey seals the probability of foraging varied seasonally with both sex and age. To allow inclusion of data from both ARGOS and phone tags, the interval for which we defined states was 6 hours. To permit further investigation of activity budgets and increase the use of the results for other projects such as the building of energetic models, these models should be rerun on a finer time resolution with data from phone tags. Most phone tag data are from harbour seals and defining activity budgets on a finer temporal resolution is particularly important for this species as they engage in shorter trips than grey seals. It should be noted that for grey seals it is currently not possible to define high temporal resolution activity budgets (and thus determine the impact of the temporal resolution of the data on grey seal activity budgets) due to a lack of recent and thus high (temporal and spatial) resolution telemetry data. The activity budget data will be used to delineate the at-sea usage developed in the Scottish Government Project by activity state.

Habitat preference analyses allow an understanding of the environmental drivers of a species' distribution. In turn, this enables management to be concentrated in the most appropriate areas. Previous studies on habitat preference in UK seals have focussed on grey seals only and were based on all at-sea locations. However, as central place foragers seals travel between land and foraging sites, and so preference for certain environments is likely to be related to activity state. For instance foraging habitat preference is likely to be related to the influence of the environment on distribution or catchability of prey species. Environmental drivers may include sediment type, depth and sea temperature. Such preference may not be evident when travelling. Thus in this project we examined habitat preference for both species using two types of data: (1) all at-sea locations and (2) only foraging locations. In both species and using both data types, all covariates were retained to explain at-sea distribution: distance from haul-out, depth, sediment type and sea temperature. However the shape of the relationship between the covariates and at-sea distribution differed between species and in grey seals differed with data type. In harbour seals which have shorter trips, there was little difference in results with data type. However, this result may be partly because of the temporal resolution of the activity data and thus should be reinvestigated once activity budgets are defined on a 2 hour resolution.

### **3 Introduction**

As part of the DECC's Offshore Energy Strategic Environmental Assessment programme (SEA), studies have been commissioned to ensure that there is robust evidence on which to base the relevant assessments. The Sea Mammal Research Unit (SMRU) has extensive telemetry data holdings relating to UK seals. These data have been summarised in a number of bespoke reports to DECC (available at <http://www.bgs.ac.uk/data/sea/>). However there is a need to provide a more comprehensive analysis of the data in order to increase their utility in scientific understanding, conservation and supporting assessments and consent decisions. Furthermore the publication of

such analyses through the peer-review system adds authority to their findings. The specific analyses considered here relate to the at-sea distribution, movements and behaviour of both harbour (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the UK.

In the UK, SMRU started deploying telemetry tags (excluding VHF) on seals in 1988 and since then have deployed around 600 such tags there. Data recorded includes information on location and, in most cases, detailed behavioural information. Behavioural data comprise the timing of individual haul-out events and detailed individual dive information (timing and depth profiles). The quantity and quality of data received from tags is dependent on the tag type and transmission channel. Two data relay channels are used: the Argos satellite system and the mobile phone network (SMRU GPS/GSM phone tags). Argos tags are of two types: SMRU Satellite Relay Data Logger (SRDL) and Wildlife Computer (WLC) Spot tags. SMRU SRDL and GPS/GSM tags collect similar types of data, but data relayed from GPS/GSM tags comprise better quality, more frequent locations and a more complete set of behavioural data. WLC Spot tags provide at-sea locations and so can be useful for looking at at-sea distribution and survival, but they provide no detailed individual dive data and limited information about haul-out activities and so cannot readily be utilised for studies on activity budgets.

The deployment of tags has involved various funding agencies, including DECC, to answer various methodological, ecological and applied questions (peer reviewed publications: Thompson *et al.* 1989, 1996, 1997, 1998; McConnell *et al.* 1999, 2004; Matthiopoulos *et al.* 2004; Aarts *et al.* 2008; Cunningham *et al.* 2009; Sharples *et al.* 2009, 2012; Patterson *et al.* 2010; Lonergan *et al.* 2009, 2011, 2012). Therefore, the number of seals tagged varied by species, year, region and age. Furthermore, the set up and tag type, which can affect the biological interpretation of telemetry data has changed with project and through time.

This aim of this project was to "Collate and interpret tagging information for grey and harbour seal at-sea distribution, movements and behaviour". To this end a post-doctoral fellowship was awarded to the Sea Mammal Research Unit, University of St Andrews. At a similar time funding from the Scottish Government was also awarded to SMRU to produce at-sea usage maps of grey and harbour seals that haul-out in the British Isles

(<http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/Themes/seal-density>).

The concurrent running of both projects, employing two research fellows, Debbie JF Russell (DECC funded) and Esther Jones (Scottish Government funded) allowed synergistic collaboration between the projects.

In this document we summarise the results of this project. The aim was to publish a series of papers that address the overall aims of the project. Currently some outputs are published, whilst other are in press or in the final stages of preparation. Rather than repeat the content of these papers here we summarise their findings by quoting their abstracts.

## 4 Project Outputs

There were two principle aims. The first was to collate and quality control the seal telemetry holdings in SMRU. The second was to carry out a series of investigations that, as well as being of intrinsic biological interest in their own right, relate to the policy requirements of DECC.

We include in this section, a summary of data holdings held by SMRU.

### 4.1 Collate and quality control telemetry data

As outlined in the Introduction, SMRU holds telemetry data from over 600 deployments on UK grey and harbour seals. Whilst these data were stored securely in an Oracle database, it was evident that considerable effort was required before they could be efficiently and confidently used in any meta-analysis. Two tasks were identified: data collation and quality control in the form of data cleansing procedures. In addition to serving this project directly, these tasks resulted in a secure and efficient database and set of procedures to facilitate any future analysis in an efficient manner. Procedures were established to apply data collation and cleansing to new telemetry data.

#### 4.1.1 Data collation

Whilst the historical telemetry data were stored in bespoke, and highly structured Oracle database tables, there was a need to develop a robust link to the biological details of each seals deployment.

A database, named Bioracle, was developed that contains data on all telemetry deployments. This includes information about the individual animals (including morphometrics) and tracks. More general information on tagging location and tag parameters is also included. Due to the multiple projects and people involved, such data were previously not stored centrally. Such a database has allowed efficient use of the data by SMRU personnel.

In conjunction with this database, a Capture database was developed which includes a record for each capture of a seal (except the long term grey seal breeding monitoring sites at North Rona and the Isle of May). This database includes records of all flipper tags (applied and recaptures).

Both databases were developed by and continue to be managed by DJF Russell. In interests of continuity, BJ McConnell retains overall responsibility for both databases which are now documented and securely archived.

#### 4.1.2 Data cleaning protocols

Tag data can have two types of error. Location data from both ARGOS and GPS/GSM tags contain, to varying degrees, error and some erroneous locations. Second, the dates of the first and last transmission in each deployment may not match to duration of useful data from the tag. For example a seal track could include pre-deployment test data or data acquired after the tag had been shed from a seal. This procedure is referred to as data clipping. A protocol was thus required to allow data to be cleaned in a consistent manner.

#### 4.1.2.1 Argos tag location error

Locations obtained by Argos have error of between 250m and over 1500m (Argos User Manual, 2011). Locations which require unrealistic speeds of movement (McConnell *et al.* 1999) are excluded. The remaining locations are smoothed using a Kalman Filter developed within the Scottish Government Project (see Jones *et al.* 2012 in Appendix IV).

#### 4.1.2.2 GPS/GSM phone tag location error

These tags use Fastloc GPS technology to provide frequent (up to 90 per day) and, for the most part, GPS quality location fixes. However, erroneous points still occur. Using test data at a known location collected before deployment, distance error was related to the number of satellites used in transmission and a diagnostic variable returned by the location fixing algorithm termed the 'residual error value'. This allowed erroneous GPS locations in the telemetry data to be removed using thresholds of number of satellites and residual error (see Russell *et al.* 2011 in Appendix II).

#### 4.1.2.3 Data clipping and monitoring of new data

Tags can cease transmission because of mechanical or software failure; battery exhaustion; or because the tag is submerged underwater after falling off an animal or on a submerged dead animal. Alternatively, a tag can transmit false data (i.e. data that does not relate to a seal that is alive). This can occur when a tag has fallen off on a haul-out or is on a dead animal at a haul-out. It can be difficult to identify false data because animals can remain stationary on land for prolonged periods when breeding. Furthermore, a tag can fall off at a haul-out and still transmit what appears as dives due to the tidal cycle.

Active tag monitoring allows: (1) the end date of the data to be recorded accurately (excluding false data); (2) any issues with the tags to be identified as soon as possible; (3) stationary tags to be located and recovered from haul-outs. Locating such tags means we can determine whether the tag is on a dead animal. If on a dead animal, in the case of trauma, we can use the telemetry data to try to identify where and why the animal died. If the tag is not on an animal, we can download any data that was not transmitted (i.e. fill data gaps), investigate the tag as to why it fell off (e.g. due to moult or an attachment issue) and then reuse the tag.

Active tag monitoring has been set-up and is managed by DJF Russell. It has already resulted in the recovery of five tags, providing additional data and allowing tag re-use.

## 4.2 Summary of data holdings

Here we summarise the data holdings from seals tagged in the UK by SMRU and Paul Thompson, University of Aberdeen. We include data from all telemetry tags attached on the back of the neck (i.e. we exclude WLC flipper tags), that had a duration of over 10 days and were not placed on rehabilitated animals or pups released from a captive facility. Overall 269 such tags have been deployed on grey seals between 1988 and 2010 (Table 1; Figure 1) with 69 of these deployed on moulted pups at breeding sites. Deployed tags transmit data for up to a year (Figure 2) but for adults the number of tags that have been active during the first part of the year is low due to the moult (Figure 3). The resulting tracks from the tags show grey seals range far from land and pups may have more long ranging movements than adults (Figure 4).

We also present data from harbour seals from 344 deployed tags since 2001 (Table 2). The majority of these are from adults (Figure 5) but we also have data from 48 WLC Spot tags deployed on pups in 2007. Tag durations are similar to grey seals except for some of the WLC Spot tags on pups which lasted longer (Figure 6). In the case of harbour seals, the amount of data on non-pups is lowest between July and September (Figure 7) due to the moult. The maps of the tracks show that harbour seals have a more coastal distribution than grey seals and do not travel as far from haul-outs (Figure 8). The WLC neck tags deployed on pups were for survival purposes and only transmitted locations once every three days and thus were not included in the maps.

The locations of each deployment are available as shapefiles and the maps of the tracks are available as geo-referenced tiff files (see section 9).

## 4.3 Analyses and Communication

Three aspects of movement and behaviour of UK seals were selected for study. They were selected on the basis that they satisfied some of the requirements of DECC and were attainable using the resources available. As additional aspect, seal distribution at sea, was led by E Jones, funded by the Scottish Government. The four aspects are described in the next subsections.

The primary outputs of the analyses are communicated as peer-reviewed publications (this section). In addition other reports and presentations are listed in Section 4.3.2. Currently two peer-reviewed papers are published with the remaining three in preparation.

### 4.3.1 Publications

#### 4.3.1.1 *Linking terrestrial sites with foraging sites*

The relationship between where grey seals forage and breed in not known. Such information enables the determination of where the effects of any given at-sea impact (during the foraging phase) may be reflected on breeding population ashore. This is of particular relevance in monitoring the putative effects of at-sea disturbance on breeding sites designated as Special Areas of Conservation.

#### **Status of peer reviewed publication 1: published**

**Russell, DJF , McConnell, BJ , Thompson, D , Duck, CD , Morris, C , Harwood, J & Matthiopoulos, J 2013, 'Uncovering the links between foraging and breeding regions in a highly mobile mammal' *Journal of Applied Ecology* , vol 50, no. 2, pp. 499-509.**

<http://onlinelibrary.wiley.com/doi/10.1111/1365-2664.12048/abstract>

#### Summary

1. The annual cycle of many animals is characterized by the need to satisfy different life history priorities, often requiring seasonal movements. For such species, investigating carryover effects (such as the year-long drivers of breeding success) and managing protected areas effectively, relies on quantifying these movements. Here, we model the seasonal movements of the UK population of grey seals *Halichoerus grypus* and show how insights from the model can improve its management.



2. We fit a hidden process model to two types of information – regional population redistribution and individual movements – to estimate the seasonal transition probabilities of breeding female grey seals among four regions around the UK.

3. We found that between 21% and 58% of females used different regions for breeding and foraging.

4. For our study period, we detected an increase in the breeding performance of animals that foraged in the Hebrides and South-East Coast.

5. Grey seal Special Areas of Conservation (SACs) were designed to encompass a significant proportion of the UK breeding population: ~ 40% of the breeding females in our study area. Of the females breeding on SACs, only 15% breed in Northern Scotland, but up to 50% forage there. Our results indicate that, by only considering the breeding distribution of females that breed in SACs, the impact of anthropogenic activities on nearby SACs may be overestimated, whereas impacts on remote SACs may be underestimated.

6. *Synthesis and applications.* By quantifying the link between the foraging and breeding distributions of grey seals, management of breeding populations can be focused on the foraging regions where the resources necessary for reproduction are acquired. The construction of marine developments is dependent on demonstrating that they will not have an adverse effect on the integrity of Special Areas of Conservation (SACs), and we have shown that this requires consideration of the seasonal transition probabilities estimated in this study. Our specific results provide support for management strategies that jointly consider SACs and Marine Protected Areas (MPAs). More generally, we prescribe combinations of data on population size, breeding performance and individual movement that can enable our framework to be applied to seasonally migrating species.

#### 4.3.1.2 Activity budgets

The time budgets of grey and harbour seals at-sea can be assigned to foraging and travelling based on the movement characteristics. Such models can be improved by incorporating both activity and movement data into state-based models to define a complete time budget of four states: resting at-sea, hauled out on land, foraging and travelling. Once defined such budgets can be modelled with regard to intrinsic (species, sex, age), time invariant (region) and time variant covariates (time of day, day of year).

#### Status of peer reviewed publication 2: published

**McClintock, BT , Russell, DJF , Matthiopoulos, J & King, R 2013, ' Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets ' *Ecology* , vol 94, no. 4, pp. 838-849.**

<http://www.esajournals.org/doi/abs/10.1890/12-0954.1>

#### Summary

Recent technological advances have permitted the collection of detailed animal location and ancillary biotelemetry data that facilitate inference about animal movement and associated behaviours. However, these rich sources of individual information, location, and biotelemetry data, are typically analysed independently, with population-level inferences remaining largely post hoc.

We describe a hierarchical modelling approach, which is able to integrate location and ancillary biotelemetry (e.g., physiological or accelerometer) data from many individuals. We can thus obtain robust estimates of (1) population-level movement parameters and (2) activity budgets for a set of behaviours among which animals transition as they respond to changes in their internal and external environment. Measurement error and missing data are easily accommodated using a state-space formulation of the proposed hierarchical model. Using Bayesian analysis methods, we demonstrate our modelling approach with location and dive activity data from 17 harbour seals (*Phoca vitulina*) in the United Kingdom. Based jointly on movement and diving activity, we identified three distinct movement behaviour states: resting, foraging, and transit, and estimated population-level activity budgets to these three states. Because harbour seals are known to dive for both foraging and transit (but not usually for resting), we compared these results to a similar population-level analysis utilizing only location data. We found that a large proportion of time steps were mischaracterized when behaviour states were inferred from horizontal trajectory alone, with 33% of time steps exhibiting a majority of dive activity assigned to the resting state. Only 1% of these time steps were assigned to resting when inferred from both trajectory and dive activity data using our integrated modelling approach. There is mounting evidence of the potential perils of inferring animal behaviour based on trajectory alone, but there fortunately now exist many flexible analytical techniques for extracting more out of the increasing wealth of information afforded by recent advances in biologging technology.

**Status of peer reviewed publication 3: in preparation**

**Russell DJF, McClintock B, Matthiopoulos J, Thompson P, Thompson D, Hammond P, Jones E, MacKenzie M, Moss S, McConnell BJ. Comparative influence of intrinsic and extrinsic drivers on activity budgets in sympatric grey and harbour seals**

Summary

Investigating activity budgets require a continuum of behaviours to be categorised into distinct states using direct or remote observations. Even with such observations, one type of movement or behaviour (e.g. diving) may encompass multiple states (e.g. travelling and foraging). We addressed this by combining behavioural and location data from telemetry tags deployed on 63 grey seals (*Halichoerus grypus*) and 126 harbour seals (*Phoca vitulina*) within a state-space model to define population-level activity budgets in the UK. The large sample size allowed us to investigate how time spent in four states (resting on land, resting at-sea, foraging and travelling) was influenced by intrinsic and extrinsic covariates. The activity budgets of the increasing grey seal population were similar to that of the decreasing harbour seal but the proximate drivers differed with harbour seals appearing more sensitive to extrinsic factors, most notably time of day and region. For both species, we demonstrate that resting (prolonged surface activity) occurred at foraging patches, likely for food digestion. For grey seals, we found sex-specific seasonal trends in juveniles demonstrating that differences in activity are not simply driven by differing reproductive investment. In agreement with other studies on harbour seals, haul-out probability was highest in the second half of the day and in the summer. However, the drivers of these temporal patterns likely differed as the latter, but not the former, trend was also reflected in time spent resting at-sea suggesting an overall change in preference to rest or dive, rather than an increased preference to haul out *per se*. We caution against using activity budgets as indicators of population health as we found no link with either

condition or regional population trajectories. More generally we have demonstrated a framework for using both behavioural and movement data to categorise activity budgets and for analysing the resulting data.

#### 4.3.1.3 *Habitat preference*

Previously habitat preference analysis has been conducted using all at-sea activity. This includes foraging, travelling and resting at-sea locations. Better estimates of foraging habitat preference may be produced by only considering foraging locations.

#### **Status of peer reviewed publication 4: in preparation**

**Russell DJF, McConnell BJ, Jones E, McClintock B, Thompson D, Hammond P, Thompson P, Moss S, Matthiopoulos J. Foraging habitat preference in two sympatric seal species.**

#### Summary

Investigating activity budgets requires a continuum of behaviours to be categorised into distinct states using direct or remote observations. Furthermore, one type of movement or behaviour (e.g. diving) may encompass multiple states (e.g. travelling and foraging). We addressed this by combining behavioural and location data from telemetry tags deployed on 63 grey seals (*Halichoerus grypus*) and 126 harbour seals (*Phoca vitulina*) within a state-space model to define population-level activity budgets in the UK. The large sample size allowed us to investigate how time spent in four states (resting on land (hauled out), resting at sea, foraging and travelling) was influenced by seasonal, intrinsic (age, sex) and extrinsic covariates (time of day, region, tag parameter settings). We demonstrate that resting at sea (prolonged surface activity) was prevalent in both species and occurred both inshore near haul-outs and offshore between foraging intervals, potentially serving differing functions. The activity budgets of both species were similar and in both species were influenced by all considered covariates demonstrating the importance of both intrinsic and extrinsic factors in determining activity budgets. However, the influence of covariates on aspects of the allocation of activity budget varied markedly between the species. We found no link between significant regional patterns in activity budgets and regional population trajectories and thus we caution against using activity budgets as indicators of population health. More generally we have demonstrated a framework for using both behavioural and movement data to categorise activity budgets and identifying the factors that drive them.

#### 4.3.1.4 *Distribution*

Population level at-sea distribution maps were generated for both grey and harbour seals. This incorporated both the telemetry and aerial survey count data.

#### **Status of peer reviewed publication 5: in preparation**

**Jones EL, McConnell BJ, Hammond PS, Duck CD, Morris CD, Thompson D, Russell DJF, Vincent C, Cronin M, Sharples RJ, Matthiopoulos J. Large-scale patterns of space use in sympatric marine predators.**

## Summary

The seas around the UK are populated by two pinniped species, grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*). Although it is not uncommon for both species to aggregate (haul-out) at the same locations on shore, it has long been suspected that they use space at sea in different ways. To obtain an overview of these spatial patterns it is necessary to estimate the distributions of the species over large scales and in fine resolution. Here, we set out to quantify the spatial distributions of these two sympatric species in the seas around the UK. A main challenge was to integrate broad-scale high resolution spatio-temporal data of varying types within a time-efficient framework. Density estimation was chosen as an expedient approach over other possible methodologies. More popular methods such as regression modelling have extensive processing times when fine-scale detail needs to be retained. Climate envelope modelling uses coarse-scale data with poor coverage around the coastline where seals spend much of their time, leading to an underestimate in usage. Long-term datasets of individual tracking data and partial haul-out count data were linked and scaled to provide population level insights. This framework provided a mechanism to account for imbalances in sampling effort and observation error within the data, and to develop a modelling solution for missing observations. Uncertainties were propagated through the analysis and quantified as prediction error for our final results. The methodology developed here can be used for other terrestrial and marine animals where similar partial spatial datasets are available. By comparing the spatial distributions we found clear evidence that the two species exploit their marine environment differently and exhibit geographic spatial partitioning: grey seals have more homogeneous usage near-shore, transit between haul-outs using large-scale interconnected networks, and spend time 15% of their time far-offshore. By contrast, harbour seals persist in discrete metapopulations displaying heterogeneous usage and staying within 50km of the coast. However, an exception to this behaviour can be seen where grey and harbour seals are geographically mutually exclusive, and in this case harbour seals switch to grey seal usage strategy. By comparing the spatial distributions we found evidence that the two species exploited their marine environment differently: grey seals transit between haul-outs using large-scale interconnected networks, and spend time 15% of their time far-offshore. By contrast, harbour seals persist in discrete regional populations, usually staying within 50km of the coast. Management recommendations were to ensure conservation efforts for harbour seals are concentrated within 50km of the coastline, and that the two subpopulations that are increasing in west Scotland and east England are adequately protected. For grey seals, future marine spatial planning should take into account their high usage far offshore and their use of interconnected networks between foraging and haul-out regions.

### 4.3.2 Other communications

The following reports were generated:

- Russell DJF (2011). Harbour seal telemetry data relating to potential wind farms: Docking Shoal, Race Bank and Dudgeon. Report to DECC.
- Russell DJF, Jones E, Matthiopoulos J, Duck C, Morris C & McConnell BJ (2011). SMRU seal telemetry data holdings. SCOS Briefing paper 11/16. (Appendix I)
- Russell DJF, Matthiopoulos J & McConnell BJ (2011). SMRU seal telemetry quality control process. SCOS Briefing paper 11/17. (Appendix II)

- Russell DJF & Lonergan M (2012). Short note on grey seal haul-out events at-sea. SCOS Briefing paper 12/07. (Appendix III)
- Jones EL, McConnell BJ, Duck CD, Morris CD, Hammond PS, Russell DJF & Matthiopoulos J (2012). Marine distribution of grey & harbour seals around the UK. SCOS Briefing paper 12/06. (Appendix IV)

The following presentations were given:

- SMRU seminar, 2011  
Russell *et al.*, Analysis of seal telemetry data
- MASTS annual conference, 2011  
Russell *et al.*, Linking breeding and foraging regions in a spatially segregated population
- Special Committee on Seals, 2012  
Russell *et al.*, Grey seal activity budgets.
- DECC meeting, London, 2013  
Russell *et al.*, Seal distribution and Ecology.

## 5 Acknowledgements

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## 6 References

- Aarts G, MacKenzie M, McConnell B, Fedak M & Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31, 140-160.
- Argos User Manual (2011).  
Downloaded from [www.argos-system.org/html/userarea/manual\\_en.html](http://www.argos-system.org/html/userarea/manual_en.html)
- Cunningham L, Baxter JM, Boyd IL, Duck CD, Lonergan M, Moss SE & McConnell B (2009) Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 19, 398-407.
- Lonergan M, Duck C, Moss S, Morris C & Thompson D (2013) Rescaling of aerial survey data with information from small numbers of telemetry tags to estimate the size of a declining harbour seal population. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 23, 135-144.
- Lonergan M, Duck CD, Thompson D, Moss S & McConnell B (2011) British grey seal (*Halichoerus*

- grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. *ICES Journal of Marine Science*, **68**, 2201-2209.
- Loneragan M, Fedak M & McConnell B (2009) The effects of interpolation error and location quality on animal track reconstruction. *Marine Mammal Science*, **25**, 275-282.
- Matthiopoulos J, McConnell B, Duck C & Fedak M (2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *Journal of Applied Ecology*, **41**, 476-491.
- McConnell B, Bryant E, Hunter C, Lovell P & Hall A (2004) Phoning home - A new GSM mobile phone telemetry system to collect mark-recapture data. *Marine Mammal Science*, **20**, 274-283.
- McConnell BJ, Fedak MA, Lovell P & Hammond PS (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, **36**, 573-590.
- Patterson TA, McConnell BJ, Fedak MA, Bravington MV & Hindell MA (2010) Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. *Ecology*, **91**, 273-285.
- Russell DJF, Matthiopoulos J & McConnell BJ (2011). SMRU seal telemetry quality control process. *SCOS Briefing paper 11/17*.
- Sharples RJ, Mackenzie ML & Hammond PS (2009) Estimating seasonal abundance of a central place forager using counts and telemetry data. *Marine Ecology Progress Series*, **378**, 289-298.
- Sharples RJ, Moss SE, Patterson TA, Hammond PS (2012) Spatial Variation in Foraging Behaviour of a Marine Top Predator (*Phoca vitulina*) Determined by a Large-Scale Satellite Tagging Program. *PLoS ONE* 7(5): e37216.
- Thompson PM, Fedak MA, McConnell BJ & Nicholas KS (1989) seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology*, **26**, 521-535.
- Thompson PM, Mackay A, Tollit DJ, Enderby S & Hammond PS (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **76**, 1044-1053.
- Thompson PM, McConnell BJ, Tollit DJ, Mackay A, Hunter C & Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. *Journal of Applied Ecology*, **33**, 1572-1584.
- Thompson PM, Tollit DJ, Wood D, Corpe HM, Hammond PS & Mackay A (1997) Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology*, **34**, 43-52.

## 7 Tables

**Table 1.** Telemetry tags deployed on grey seals in the UK where duration was greater than 10 days.

region	age	YEAR																			Total		
		1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	2000	2001	2002	2003	2004	2005	2008	2009		2010	
West England & Wales	pup																			5	12	17	
	1+															17							17
West Scotland	1+															21	12						33
Western Isles	pup								8														8
	1+								15	4						15							34
North Coast & Orkney	pup																					14	14
	1+						2			8		7											17
Shetland	1+										7												7
Moray Firth	1+					5																	5
East Scotland	pup													11	10								21
	1+			2			2		5	9	10		1		4	1	3	9				47	
Northeast England	pup							5	4													9	
	1+				5	7					2		4						10			28	
Southeast England	1+	1	1															10				12	
<b>Total</b>		<b>1</b>	<b>1</b>	<b>2</b>	<b>5</b>	<b>12</b>	<b>9</b>	<b>4</b>	<b>23</b>	<b>17</b>	<b>11</b>	<b>24</b>	<b>4</b>	<b>12</b>	<b>10</b>	<b>40</b>	<b>30</b>	<b>14</b>	<b>19</b>	<b>5</b>	<b>26</b>	<b>269</b>	

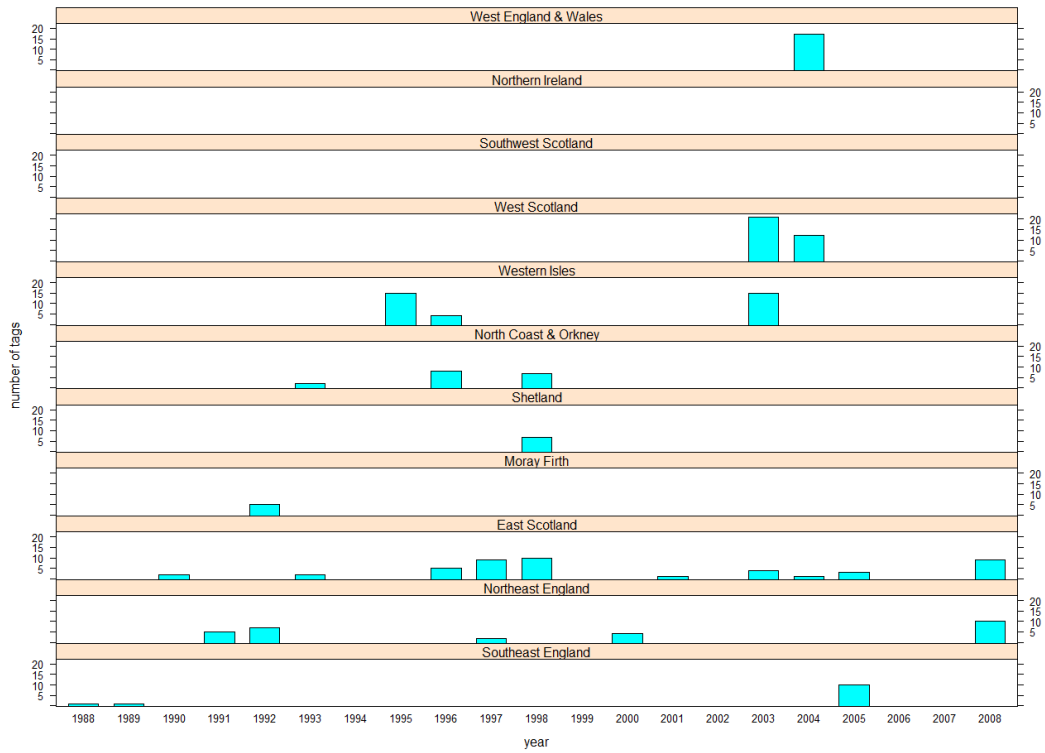
**Table 2.** Telemetry tags deployed on harbour seals in the UK where duration was greater than 10 days.

region	age	year											Total	
		2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011		2012
West England & Wales	1+									5				5
Northern Ireland	1+						12		9		12			33
West Scotland	pup							24						24
	1+			6	9	8				1		15	14	53
Western Isles	1+						20							20
North Coast & Orkney	pup							24						24
	1+			7	8							14	17	46
Shetland	1+			8	7									15
Moray Firth	1+				5	5	1	1		5				17
East Scotland	1+	10	5	10					6			5	6	42
Southeast England	1+			5	11	8	9						32	65
<b>Total</b>		<b>10</b>	<b>5</b>	<b>36</b>	<b>40</b>	<b>21</b>	<b>42</b>	<b>49</b>	<b>15</b>	<b>11</b>	<b>12</b>	<b>34</b>	<b>69</b>	<b>344</b>

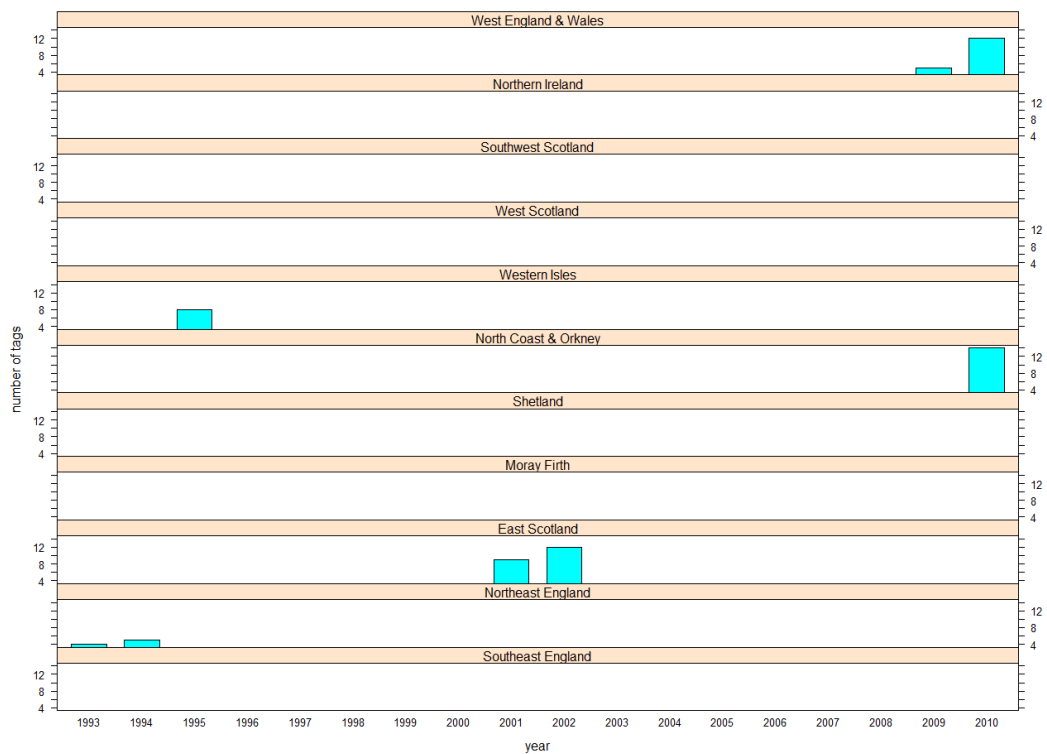


## 8 Figures

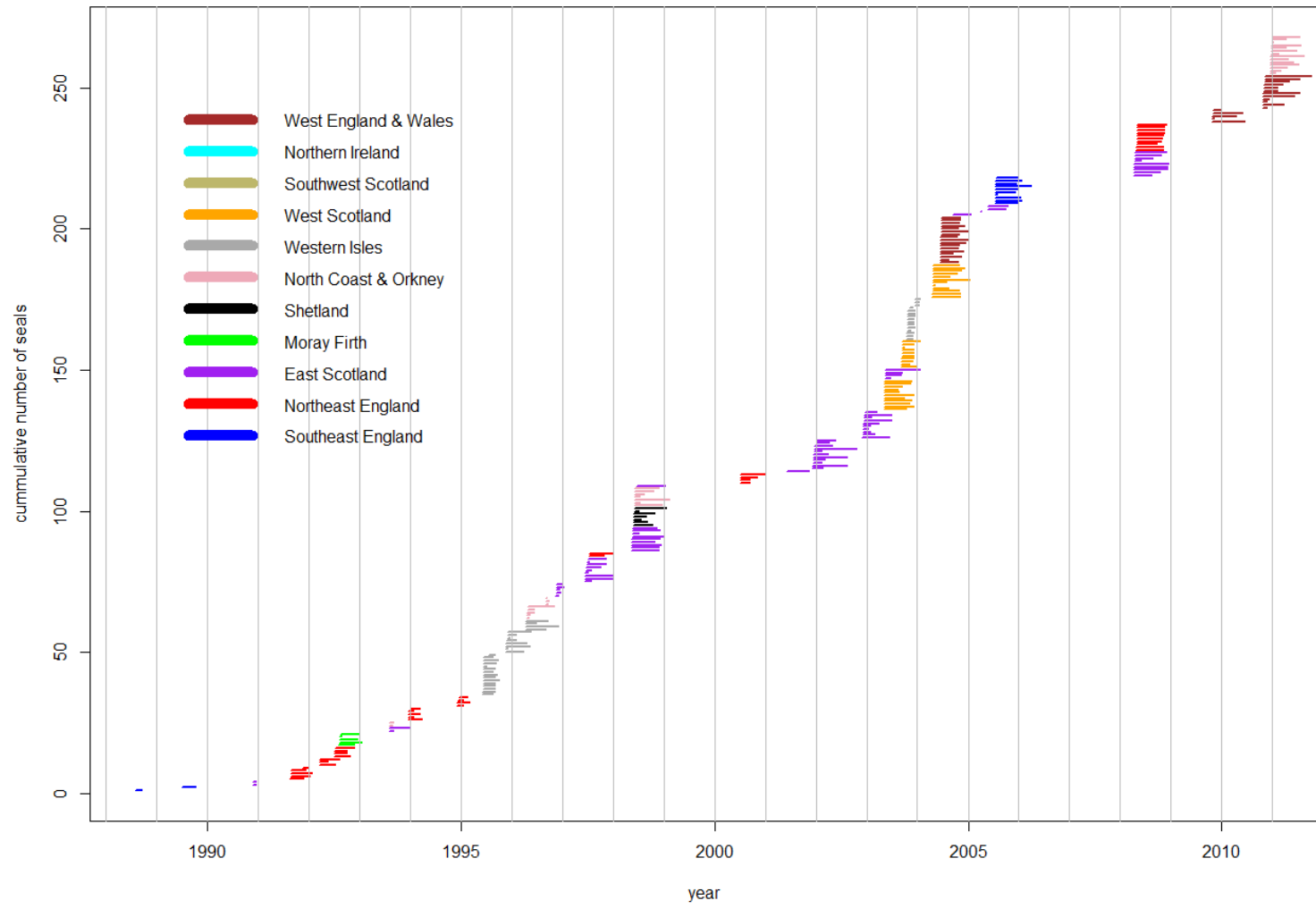
(a)



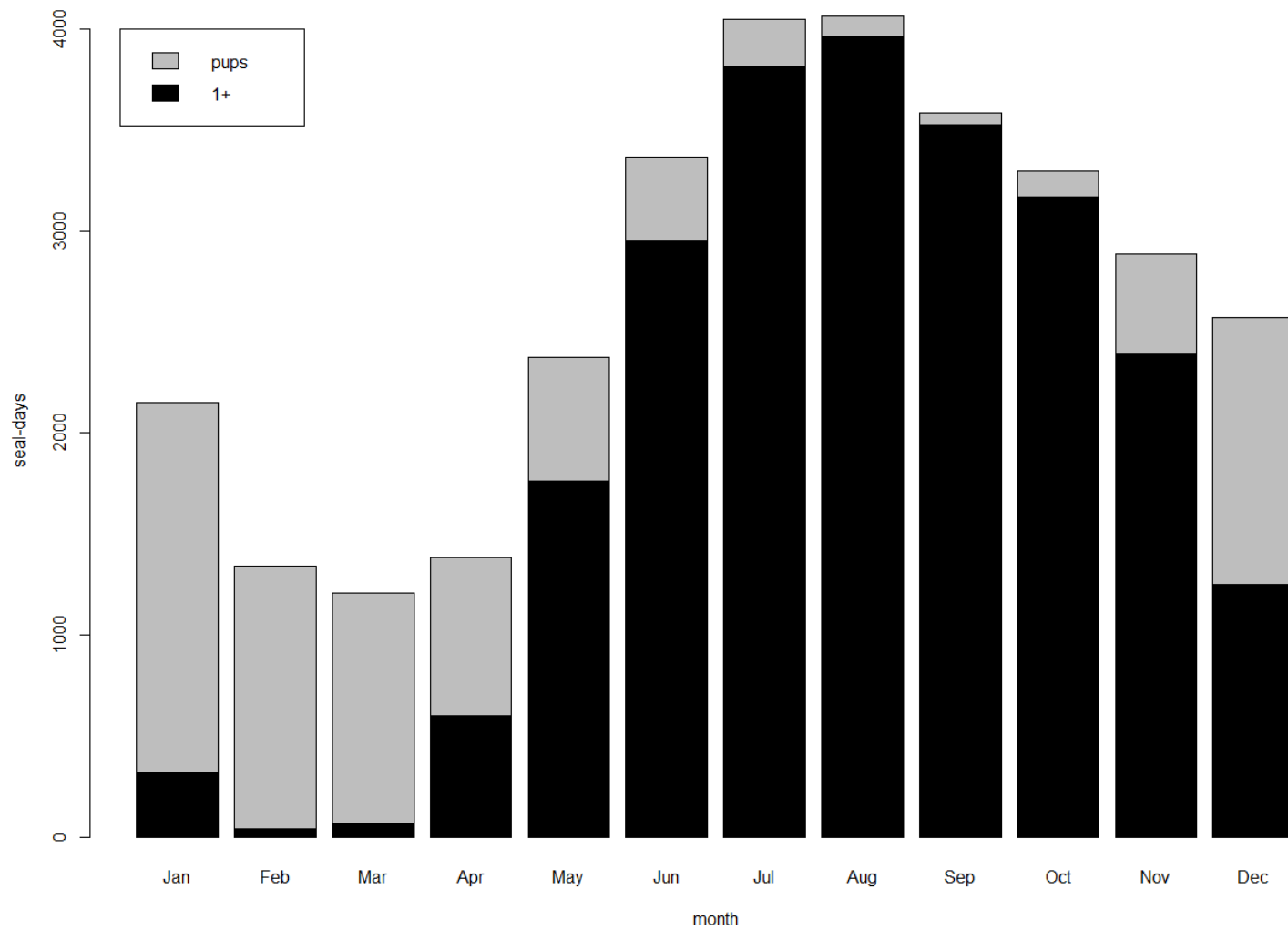
(b)



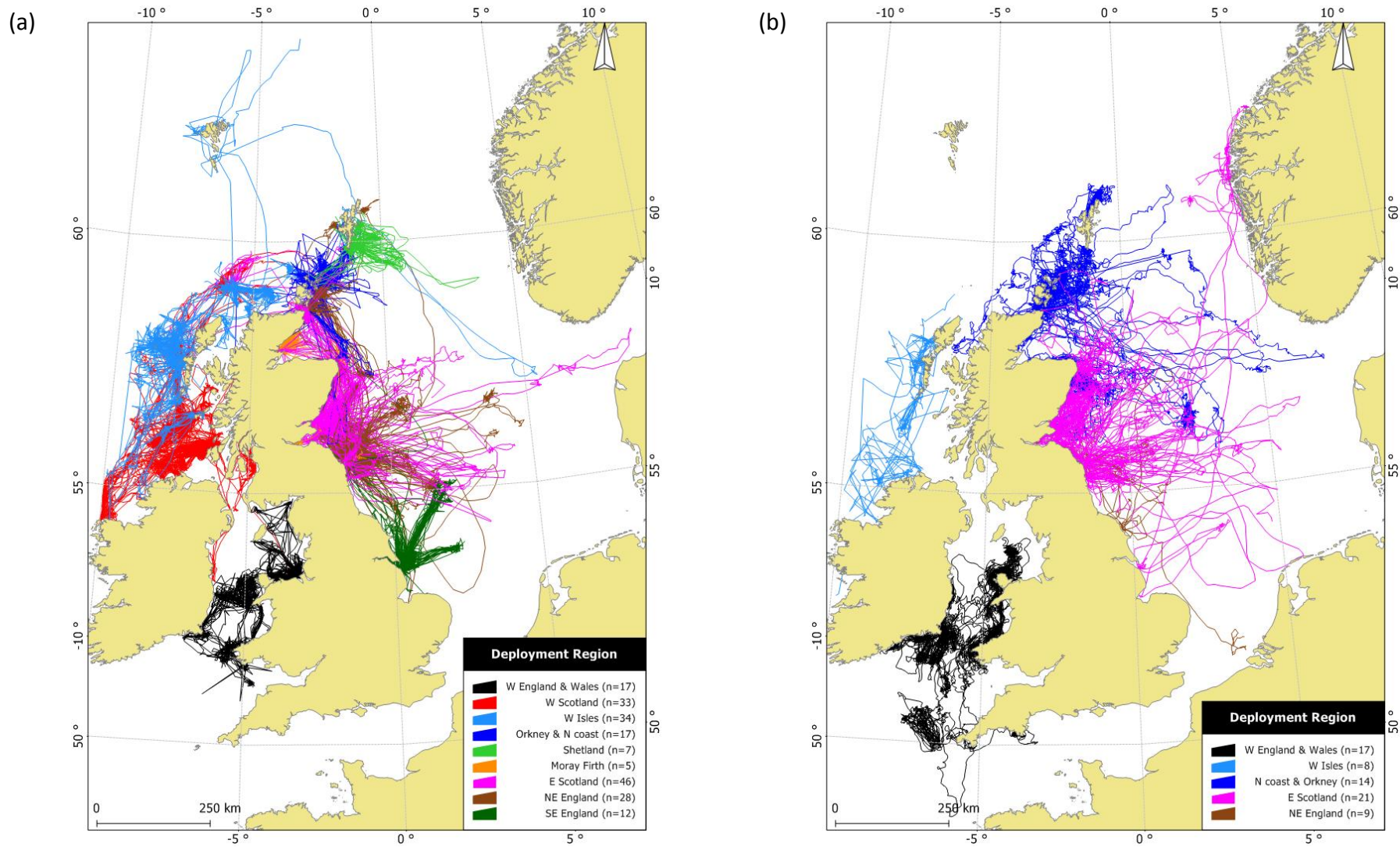
**Figure 1.** Telemetry tags deployed on grey seals aged one year or over (a) and pups (b), in the UK where duration was greater than 10 days.



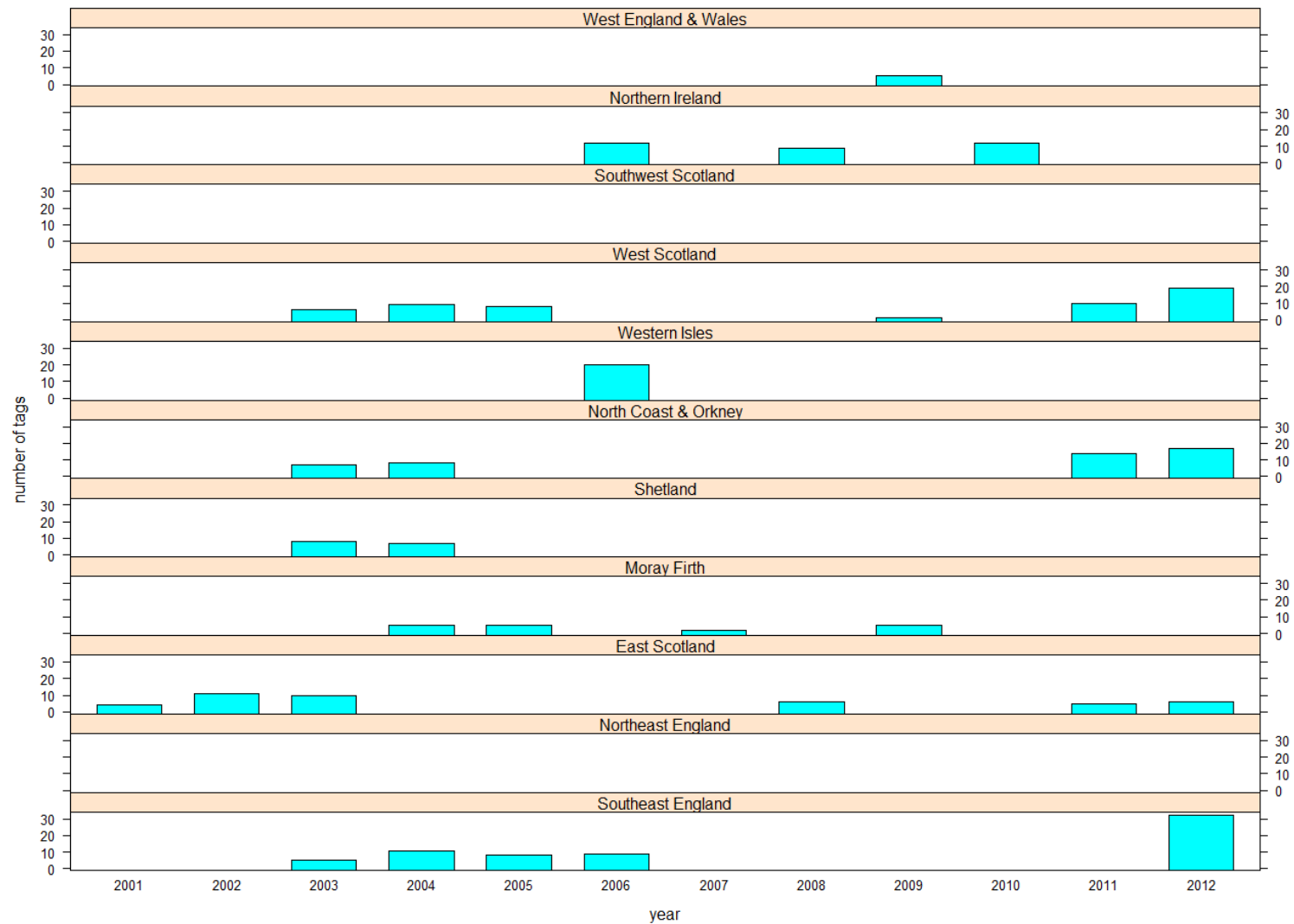
**Figure 2.** Grey seal cumulative tagging effort over time by region showing tag duration.



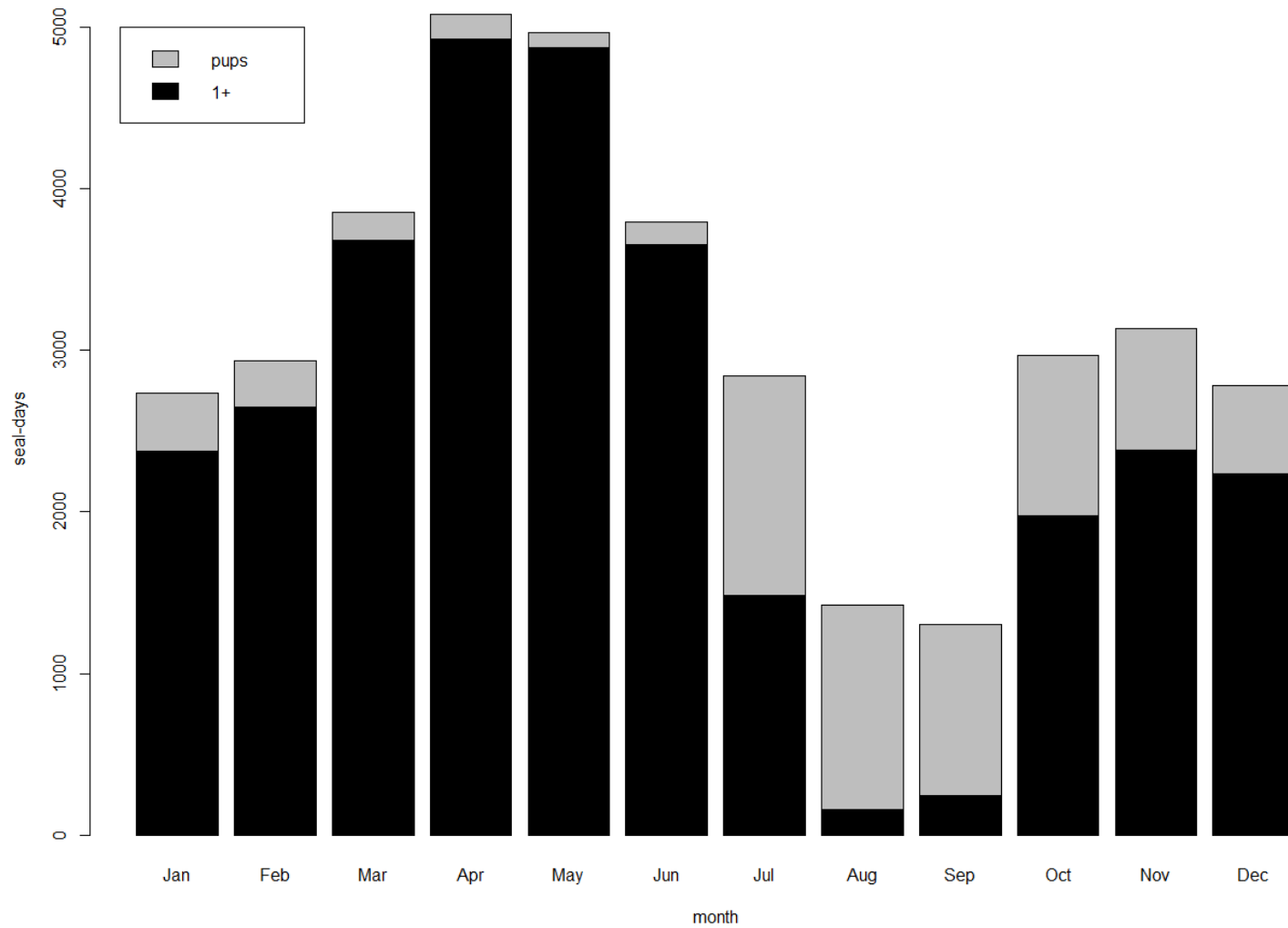
**Figure 3.** Number of days of telemetry data by month for grey seals.



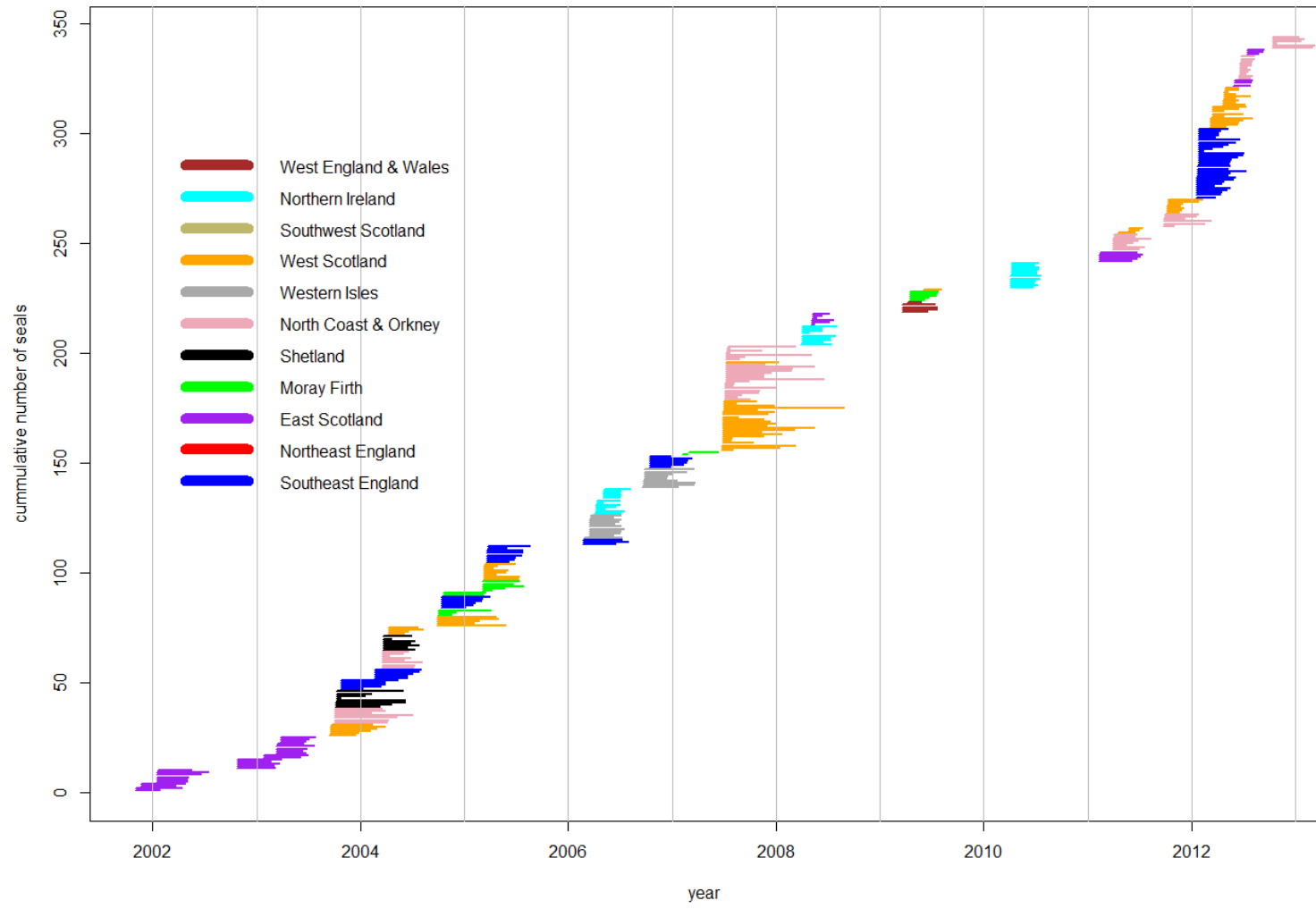
**Figure 4.** Telemetry tracks by deployment region for grey seals aged one year or over (a) and pups (b). Projection is Universal Transverse Mercator zone 30N. These are available to download as a geo-referenced tiff file (see Section 9).



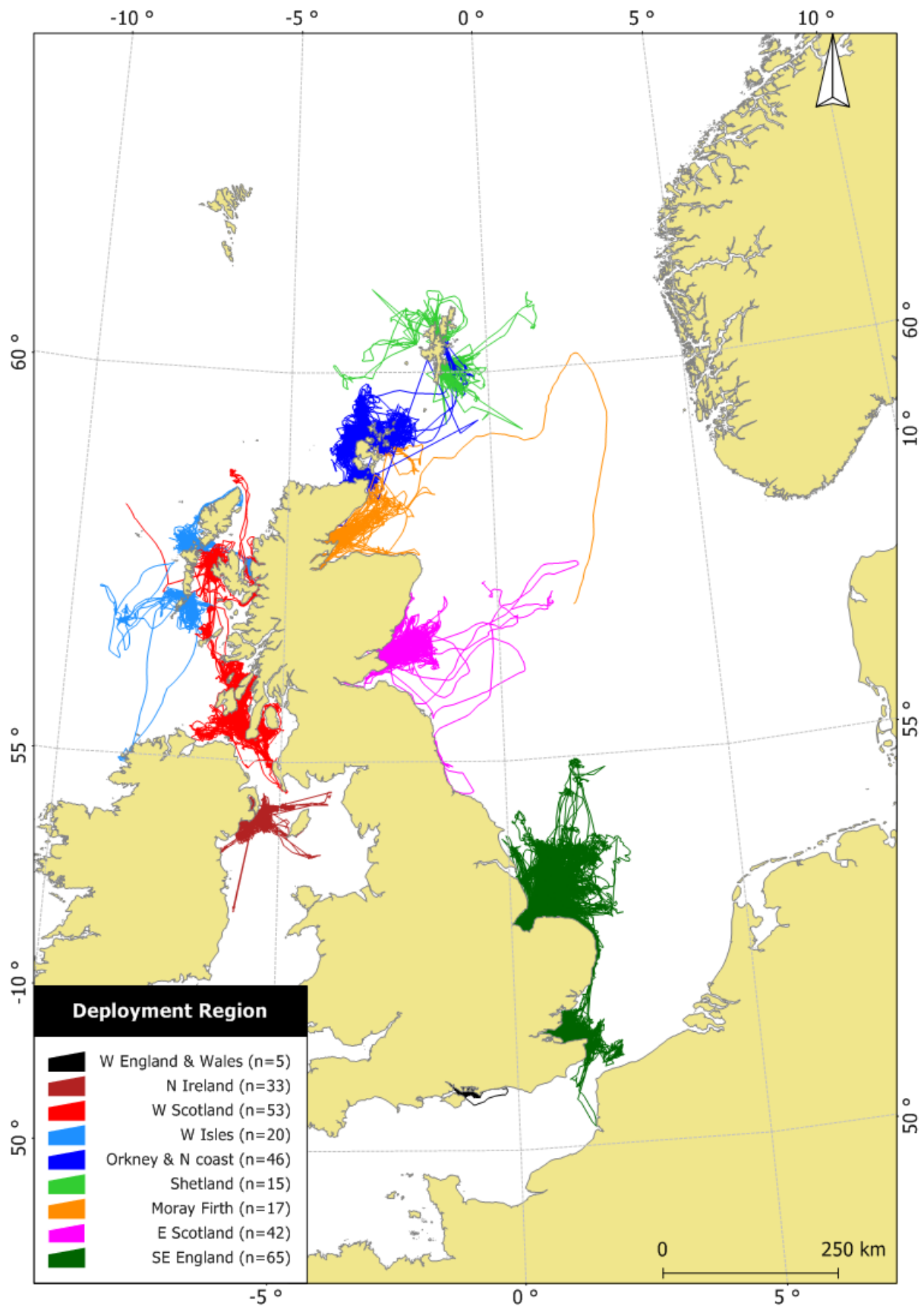
**Figure 5.** Telemetry tags deployed on harbour seals aged one year or over in the UK where duration was greater than 10 days.



**Figure 6.** Number of days of telemetry data by month for harbour seals.



**Figure 7.** Harbour seal cumulative tagging effort over time by region showing tag duration.



**Figure 8.** Telemetry tracks by deployment region for harbour seals aged one year or over. Projection is Universal Transverse Mercator zone 30N. This is available to download as a geo-referenced tiff file (see Section 9).



## 9 Downloadable files

These files are available at <http://www.bgs.ac.uk/data/sea/>. Upon their use, please reference this report.

### 9.1 Deployment Location

To aid interpretation of the tracking data (Figures 4 and 8), we have provided the location of tag deployments as well as tag type which is indicative of the quality and resolution of data transmitted (Section 3). The tag types are "GPS/GSM", "DUAL" (GPS/GSM and SRDL), "SRDL" and "WLC".

The following files are available:

grey\_seal\_1+\_deployments

grey\_seal\_pup\_deployments

harbour\_seal\_1+\_deployments

harbour\_seal\_pup\_deployments

All files are in longitude latitude coordinates (WGS 1984).

During a deployment, tags are often deployed at multiple locations. Thus the deployment locations shown are the approximate and as such the centre of islands where animals were tagged is shown rather than the individual tagging sites.

### 9.2 Tracks

The telemetry data in the form of tracks (Figure 4 and 8) are also available in the form of geo-referenced tiff files. These can be used as a layer in GIS software to allow overlay with areas of interest such as proposed marine renewable development sites.

The following files are available:

grey\_seal\_1+\_tracks (Figure 4a)

grey\_seal\_pup\_tracks (Figure 4b)

harbour\_seal\_1+\_tracks (Figure 8)

Projection: Universal Transverse Mercator zone 30N

## Appendix I

## **Russell DJF, Jones E, Matthiopoulos J, Duck C, Morris C & McConnell BJ**

### **SMRU seal telemetry data holdings**

NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION OF THE AUTHOR

## **Introduction**

SMRU started deploying telemetry tags on seals in 1988 and since then there have been around 600 such tags deployed in the UK. In this paper, we summarise the usable data resulting from these deployments. Data recorded includes information on location and, in some cases, activities. Activity data comprise of data on time hauled out; at the surface; and diving. Data received from tags are dependent on the tag type and transmission mechanism. There are two types of data transmission: through the Argos satellite system or mobile phone network (SMRU GPS/GSM phone tags). SMRU Argos SRDL and SMRU GPS/GSM tags produce similar types of data, but data from GPS tags comprise better quality and more frequent locations and a more complete set of activity data. Wildlife Computer Argos Spot (WLC) tags have also been deployed. For the most part WLC tags they have been deployed on the back of the head of seals, as for other telemetry tags. They provide at-sea locations, but no detailed dive and haulout information and so are useful for looking at at-sea usage but cannot readily be utilised for studies into activity budgets. However, in 2009, 25 flipper WLC tags were deployed on Harbour seals in order to look at haulout frequency and duration. These tags did not transmit at-sea location data.

Tagging effort is dependent on funding and thus is irregular in time and space. Therefore, the number of seals tagged varies by species, year, region and age. In this Briefing Paper, for the most part, data are presented regionally. In Scotland, we have used the seal management regions defined by the Scottish Government. For the rest of the UK, these regions are Northern Ireland, North-East England (Border to Hartlepool), South-East England (Hartlepool to Dover), South England (Dover to Land's End) and Wales.

## **1. Grey seals**

Useful telemetry data exist from almost 300 deployments on grey seals (figure 1, figure 2). Data from ten deployments were excluded from the holdings catalogue as the data were not usable. Tagging of adults has been carried out across the UK (figure 1a) with particularly large numbers (over 35 and over 26, respectively) in the Abertay and Farnes areas. Pups have been tagged in the Outer Hebrides (Monach Isles), North Scotland, East Scotland (Isle of May), North-East England (Farne Islands), and Wales (figure 1b).

To produce comprehensive UK-wide usage maps, telemetry and aerial survey data were combined (SCOS-BP 11/14). In these analyses, ideally each haulout area should be represented by telemetry data. As grey seals often use more than one haulout, many haulouts in addition to where animals were tagged are represented in the data. However, there are still spatial gaps in our knowledge of usage. Scottish aerial survey data from 1996-2009 were used and weighted linearly, giving increasing importance to more recent data (SCOS-BP 11/14). Figure 3 shows raw telemetry tracks from 180 animals tagged in Scotland between 1995 and 2010, which have been through data quality control processing and correction (SCOS-BP 11/15; Royer and Lutcavage, 2008). The figure includes grey seal haulout sites that were recorded during August aerial surveys but were not visited (to within 5km) by any tagged grey seal. Figure 3 also shows current and proposed wind farm developments. The most significant telemetry data gaps are in South Orkney, Northern Scotland, and part of the Western Isles (North-East Lewis and South Uist).

To address other research questions, finer scale spatio-temporal data are essential. These questions

could include investigation of how seal activity budgets vary through space and time. Due to the individual variability of seals, large sample sizes may be required for spatio-temporal analysis. However, there are some areas for which we can attempt to investigate temporal trends. Tags have been deployed, on seals of age 1+ in multiple years in certain regions (figure 2a): West Highlands (2 years), Western Isles (3 years), Orkney and North Coast (3 years), East Scotland (12 years), North-East England (5 years) and South-East England (3 years). Within years, tags have been deployed in different areas allowing investigation of patterns in behaviour across space. For example, grey seals were tagged in the Western Highlands and Western Isles in 2003; and East Scotland and North-East England in 2008. Tags have also been deployed on pups at breeding colonies in multiple years (figure 2b): East Scotland (2 years) and Wales (2 years). In 2010 pups were tagged both in Orkney and Wales.

Figure 4 illustrates the number of tags deployed by region, time and their duration. Figure 5 shows the seasonal distribution of number of seal-days of data. This figure clearly shows the lack of data for adult grey seals during the moult. Some of the tags deployed on pups in late 2010 are currently active and thus the end date has not been calculated for these animals. For the purposes of figures 4 and 5 their end date has been arbitrarily set as the end of 2010.

## 2. Harbour seals

Harbour seal tagging effort on seals age 1+ has been spread across the UK (figure 6a, figure 7a), with particularly high effort in Strangford Loch, Orkney, Abertay and The Wash. Data from seven tags were excluded as they were not usable. Pups have also been tagged at some locations, including the Inner Hebrides and Orkney (figure 6b, figure 7b). Tagging of harbour seals only started in 2001 but the number of tags deployed is almost as high as for grey seals due to consistently high effort in recent years.

Filling in spatial gaps in historical telemetry data will also inform comprehensive usage maps for harbour seals. Figure 8 shows raw telemetry tracks

from 163 animals tagged in Scotland between 2001 and 2010, and went through the same processing and correction as the grey seal data. The figure includes harbour seal haulout sites that were recorded during August aerial surveys but were not visited (to within 5km) by any tagged harbour seal. Figure 8 also shows current and proposed wind farm developments. The most significant telemetry data gaps are in West Shetland, South-West Orkney, part of the Western Isles (North-East Lewis, South Uist and Rona), and areas of the West Highlands (Inner Sound, Coll, West Mull and Loch Linnhe). Additionally, the proposed wind farm development off Tiree is situated in a data poor area.

Comparisons of seal behaviour and usage between years may be possible (figure 7a) with tags (which transmit location data) being deployed on age 1+ seals in multiple years in Northern Ireland (three years), Western Highlands (four years), Orkney and North Coast (three years), Shetland (two years), Moray Firth (four years), East Scotland (five years) and South-East England (four years). However, in some cases tags were deployed in different areas of these large regions, making data between years non comparable at a fine scale. Due to recent increase in tagging effort there are also possibilities for comparing harbour seal activity between regions within years; 2003, 2004, 2005, 2006, 2008, 2009 and 2011. For pups, there have been tags deployed in the West Highland region and Orkney (figure 7b) in 2007, allowing behavioural comparisons between these two groups. Although there have been tags deployed on pups in the Wash, these were pups rehabilitated by the RSPCA.

Figure 9 shows the number of tags deployed by region, time and their duration. Figure 10 shows the seasonal distribution of number of seal-days of data. There are fewer data for seals age 1+ in the third quarter of the year due to their moulting season. In figures 9 and 10, data from tags deployed in 2011 are not included because most of these tags are currently active and so the data has not gone through data quality control process.

## References

Royer F. & Lutcavage M. (2008). Filtering and interpreting location errors in satellite telemetry of marine animals. *Journal of Experimental Marine Biology and Ecology*. 359:1-10.

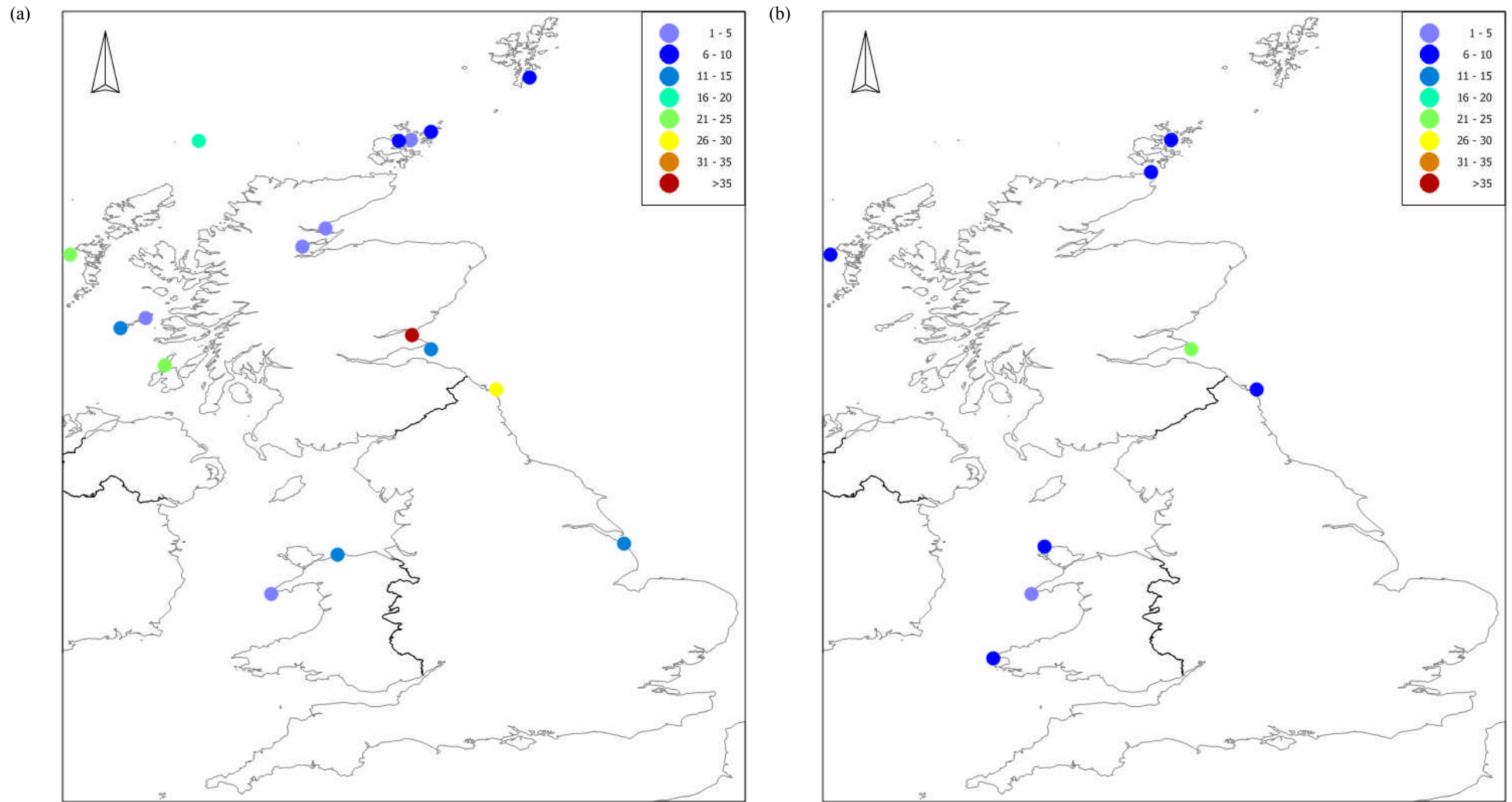


Figure 1. The distribution tags deployed on grey seal of age year 1+ (a) and moulted pups (b). All locations are approximate. Seven of the animals tagged near St Andrews were seals (age 1+) released from the SMRU pool facility.



(b)



Figure 2. The region and years of tagging of grey seals aged 1+ (a) and moulted pups (b).



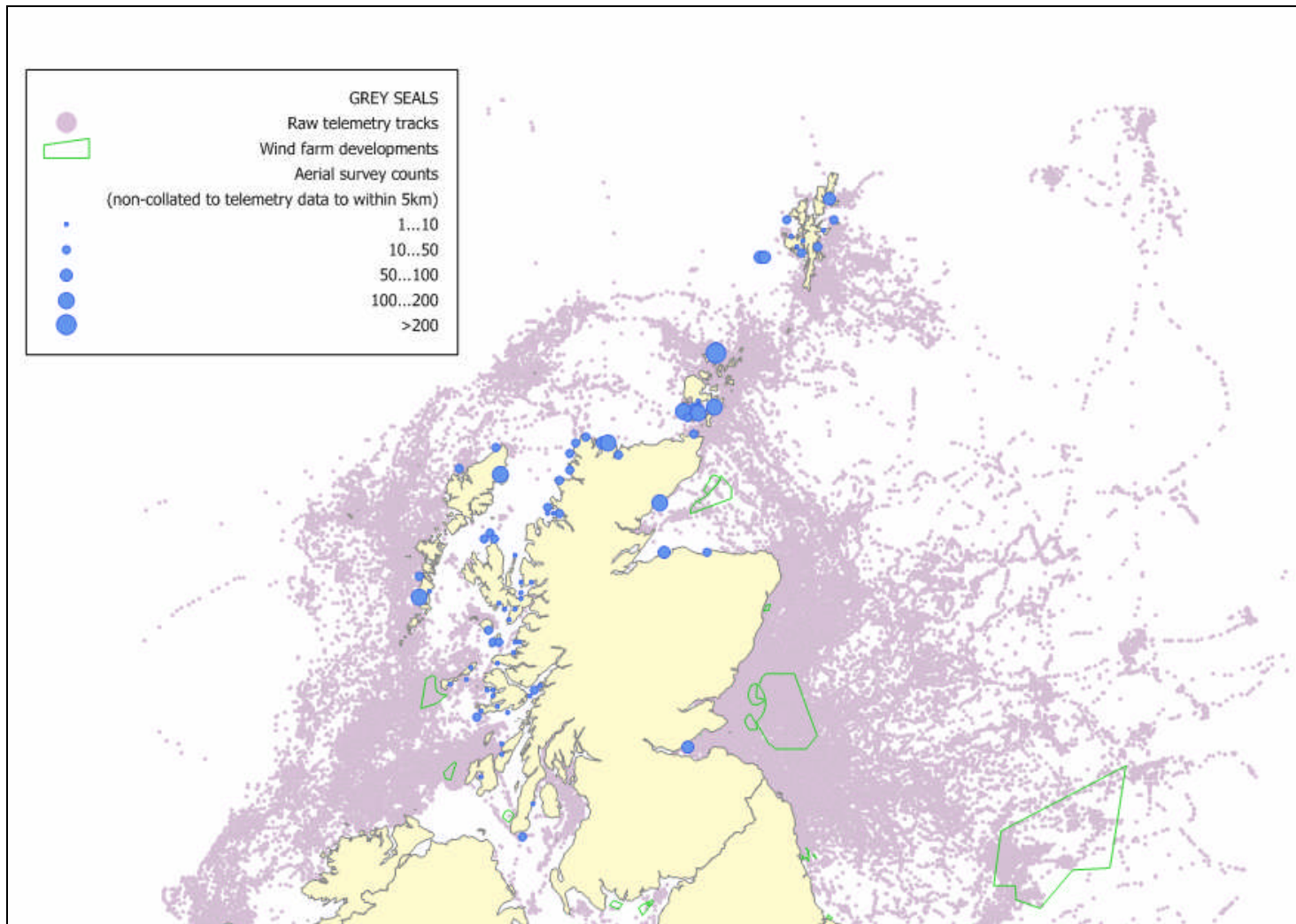


Figure 3. Grey seal raw telemetry tracks (purple), non-collated (with telemetry data) Scottish aerial survey count data (blue), proposed and current wind farm developments (green outlines). © 2011 Crown Estates.

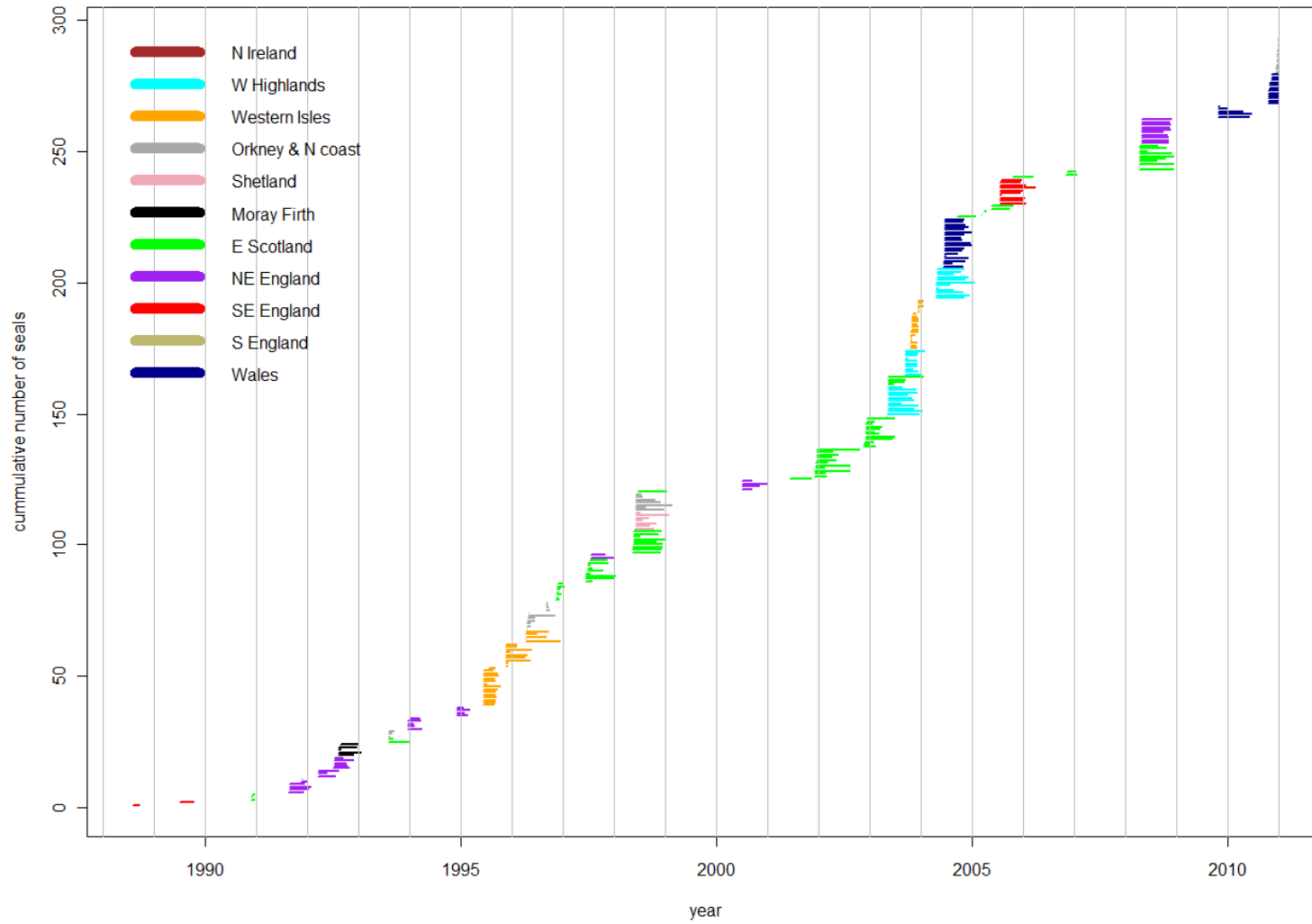


Figure 4. The cumulative number of grey seals tagged by SMRU, with their duration and region also indicated.

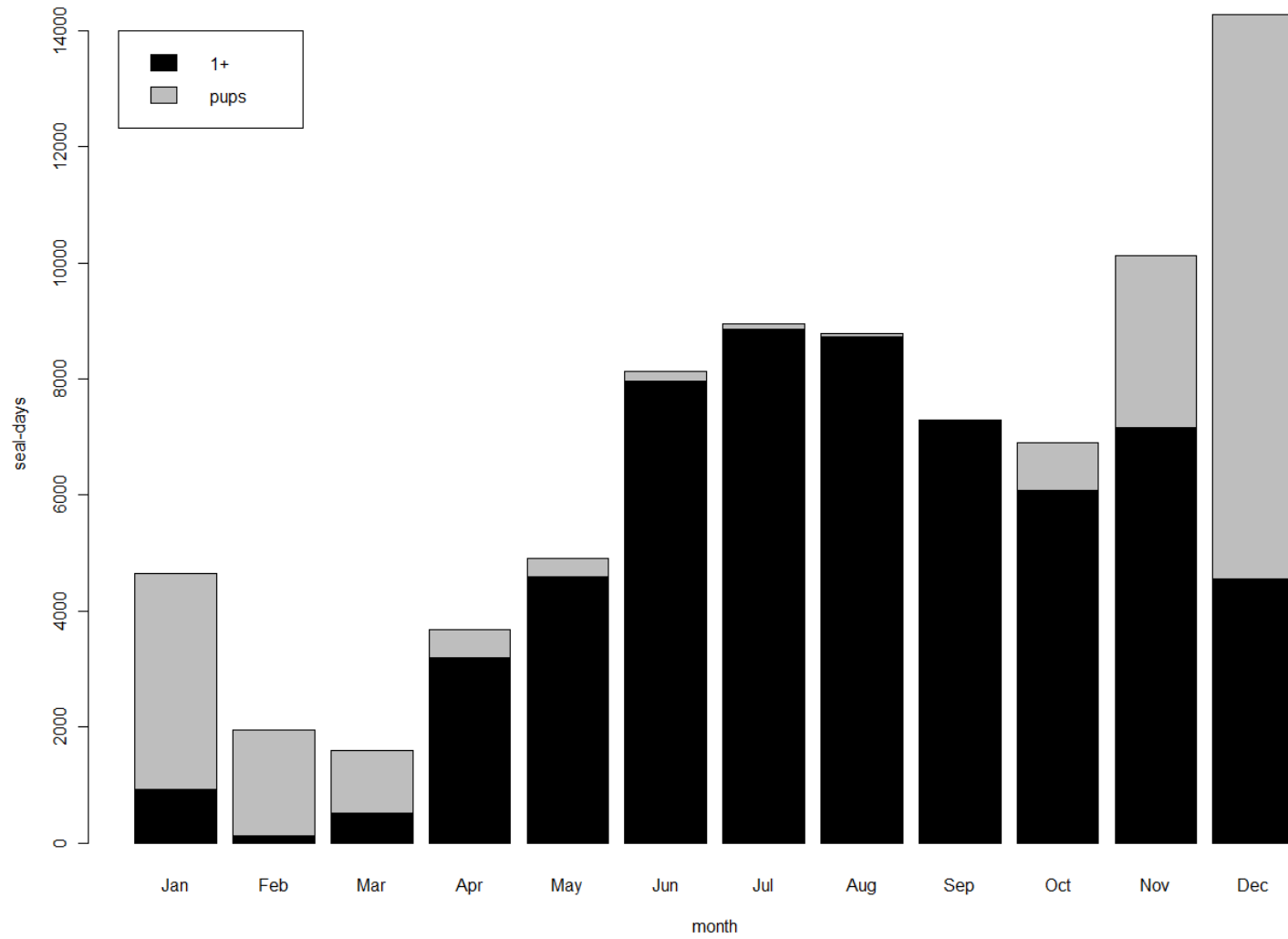
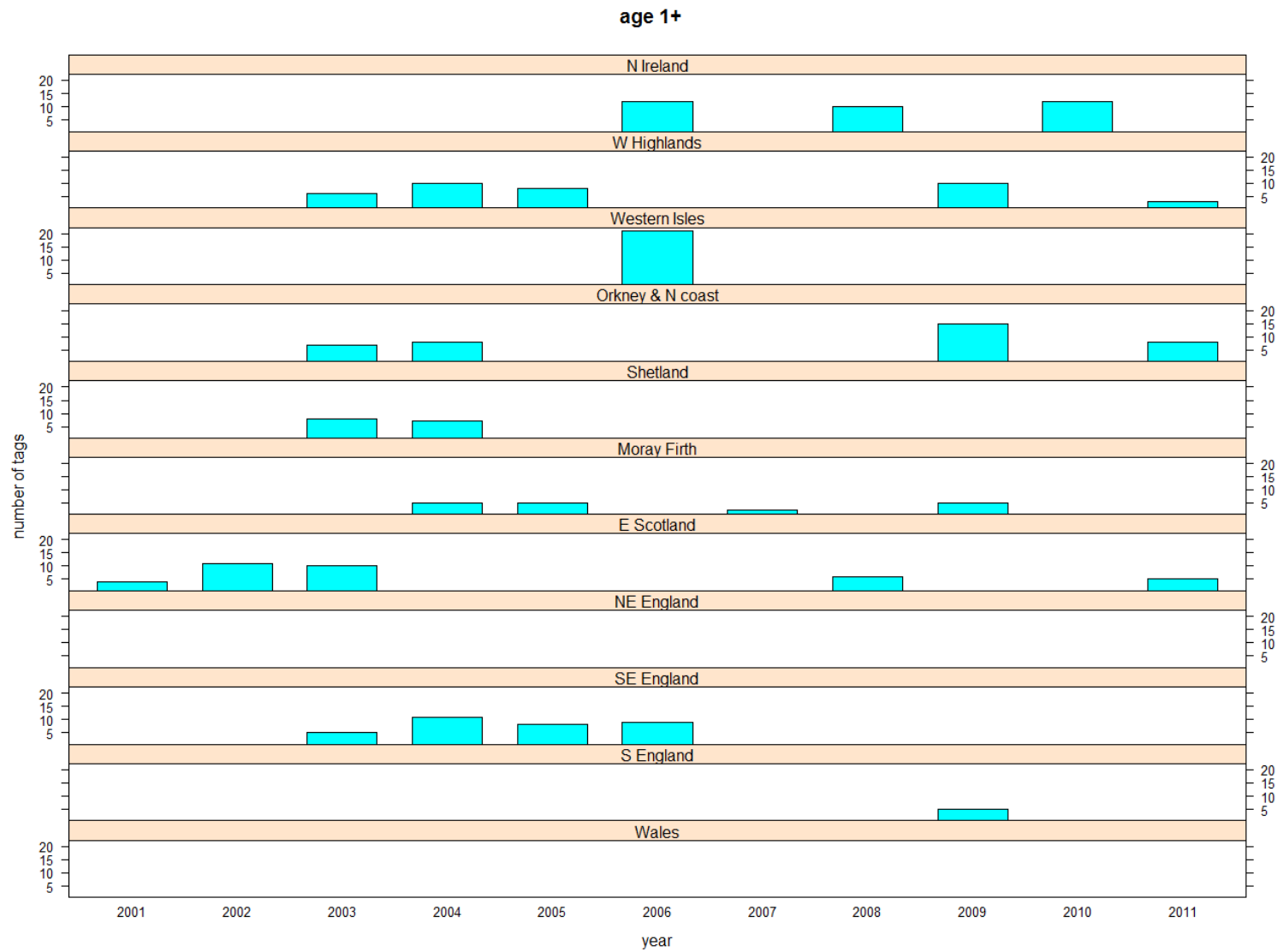


Figure 5. The number of seal-days of data per month, for grey seals, grouped by age.



(a)



(b)

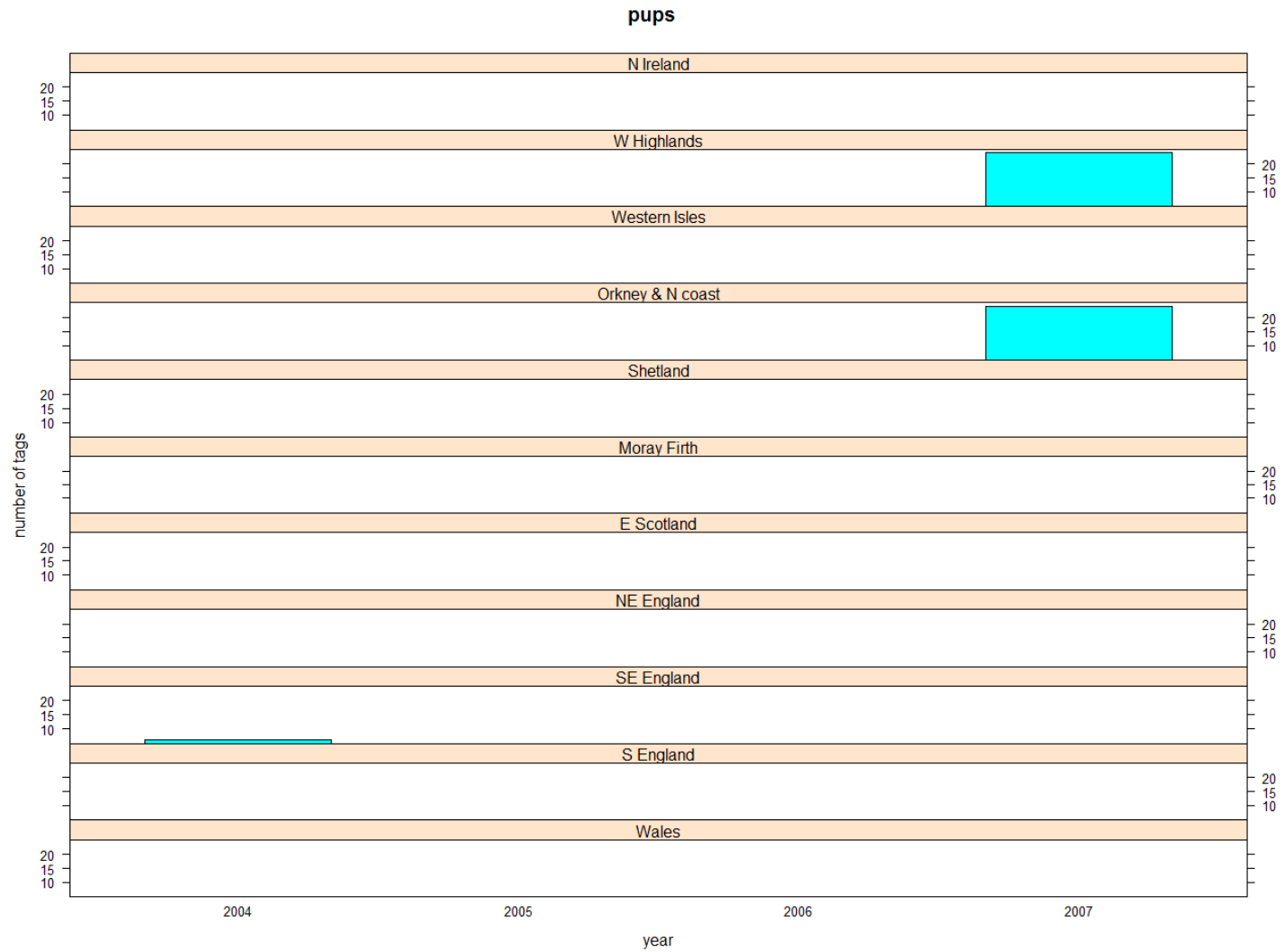


Figure 7. The region and years of tagging of harbour seals aged 1+ (a) and moulted pups (b). In 2009, tags deployed on age 1+ in the Inner Hebrides and Orkney were flipper Spot tags and thus there was no at-sea location data for these tags. All tags deployed on pups in 2007 were Spot tags deployed on the animal's head; these provide at-sea location data but no activity data.

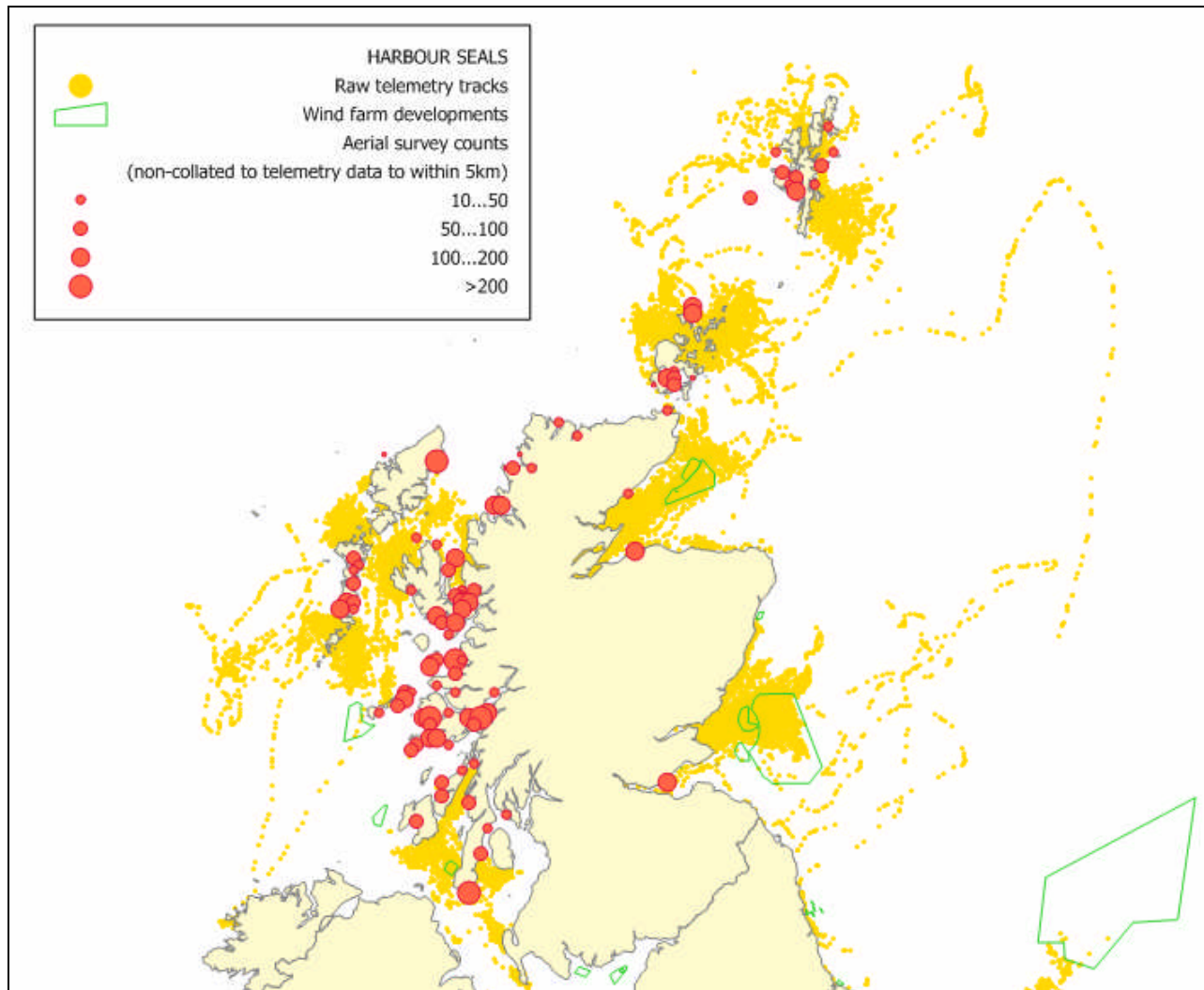


Figure 8. Harbour seal raw telemetry tracks (yellow), non-collated (with telemetry data) Scottish aerial survey count data (red), proposed and current wind farm developments (green outlines).  
© 2011 Crown Estates.

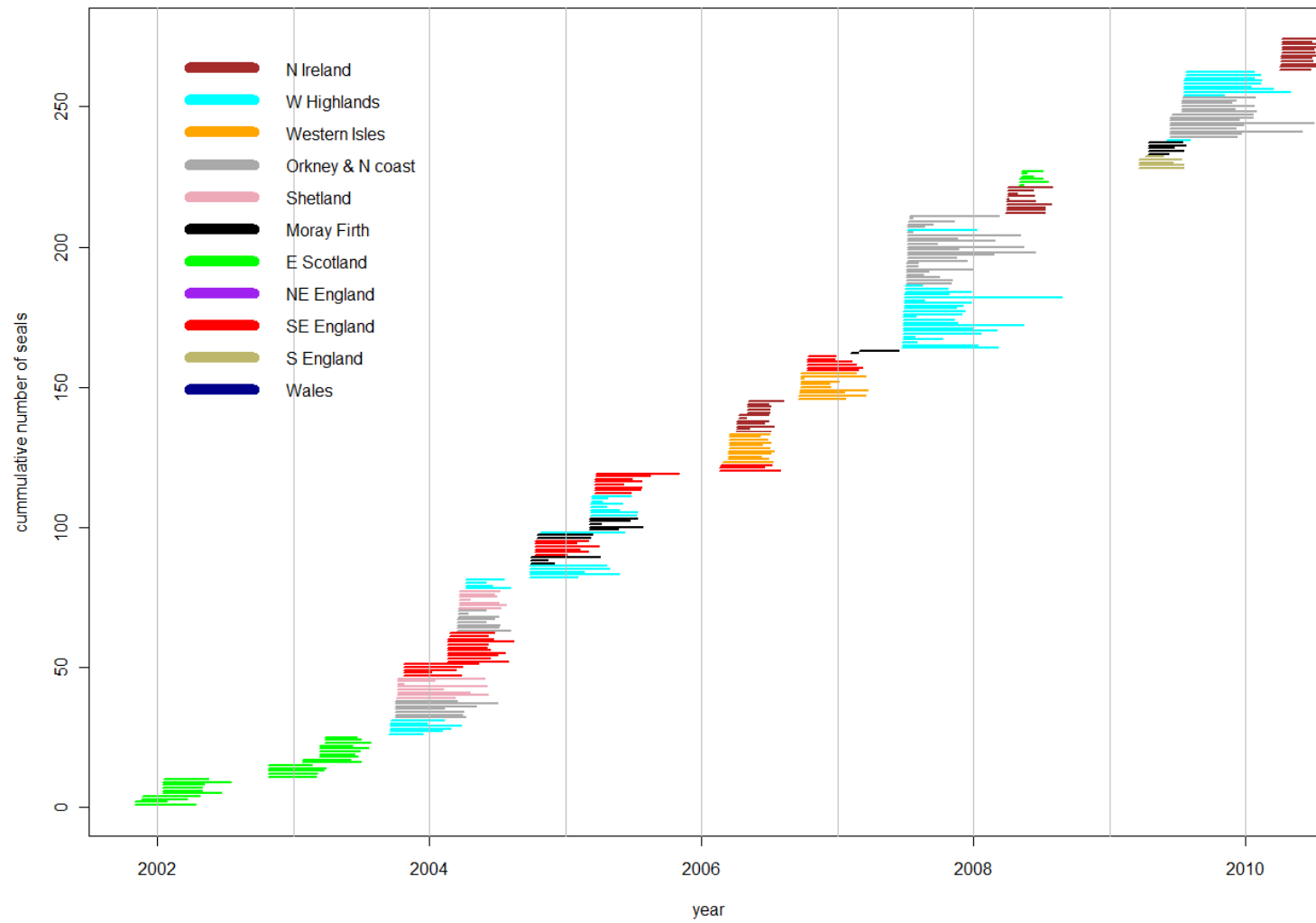


Figure 9. The cumulative number of harbour seals tagged by SMRU, with their duration and region also indicated.



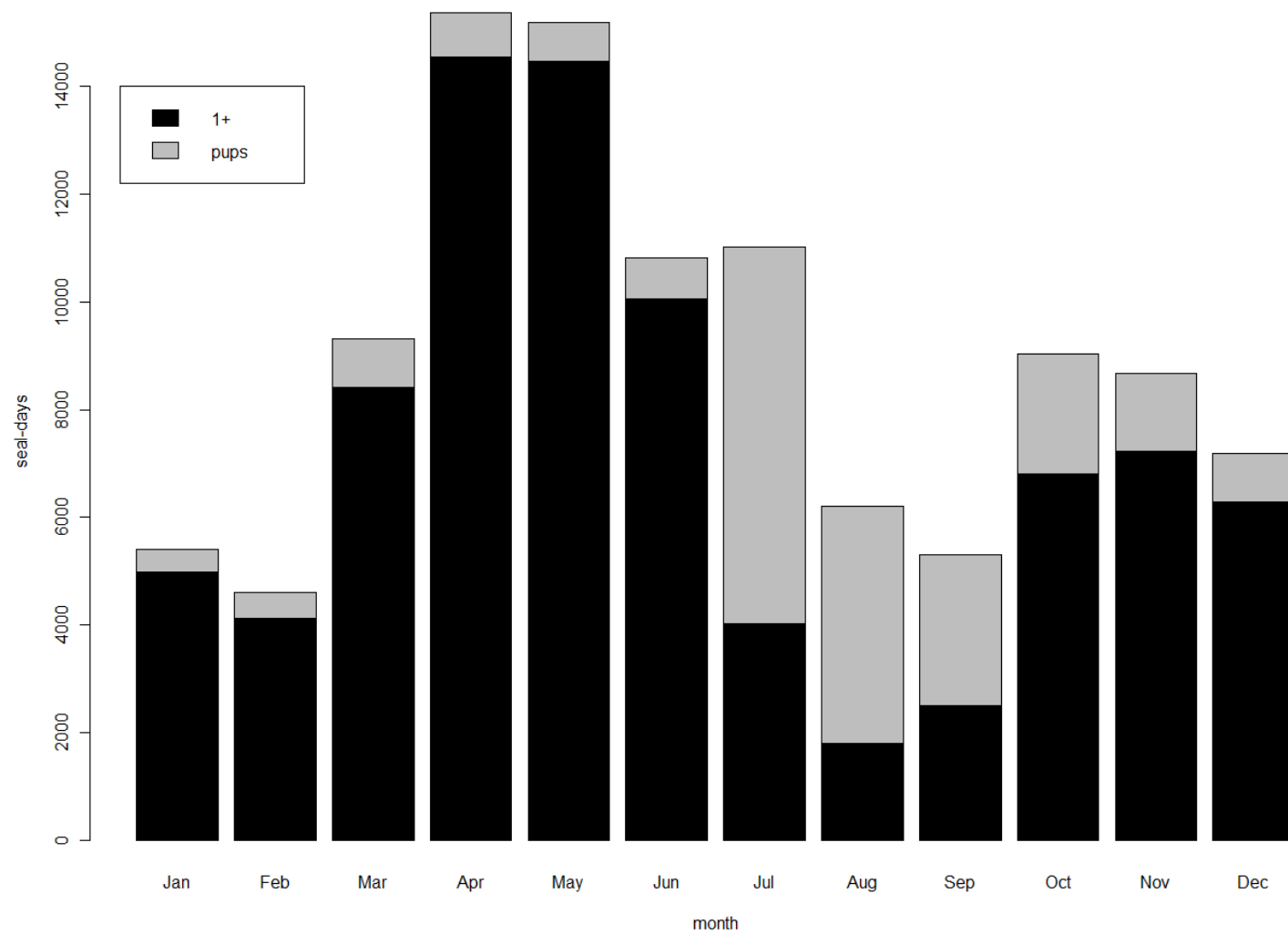


Figure 10. The number of seal-days of data per month, for harbour seals, grouped by age.

## Appendix II

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## Russell DJF, Matthiopoulos J & McConnell BJ

### SMRU seal telemetry quality control process

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION OF THE AUTHOR

#### Introduction

Approximately 600 tags have been deployed on seals in the UK. A protocol was required to filter historical and new telemetry data in an effective and consistent way. There were two parts to filtering process: location fixes associated with large distance error were removed and useful start and end dates were defined. There are essentially two types of data transmission for such tags (Box 1) which affect the protocol for filtering the resulting data: those which transmit through the Argos satellite system and those which transmit through the mobile phone system (SMRU GPS/GSM phone tags). The former can be further split into two tag types: SMRU Satellite Relay Data Logger (SRDL) and Wildlife Computer Spot tags (WLC). SRDL tags transmit activity data as well as location fixes. Activity data comprise haulout data; at surface data; diving data and summary data. Summary data record the proportion of time spent hauled out, at surface and diving in a predefined period (between two and six hours).

Box 1. Tag descriptions.

#### 1) Argos

Locations obtained by Argos have error of between 250m and over 1500m (Argos User Manual, 2011).

#### a) SMRU Satellite Relay Data Logger (SRDL)

These tags relay data via the Argos system. However the data flow bottleneck of the satellite system results in a sample (c. 10%) of all data stored for transmission being successfully relayed. These tags transmit detailed individual dive and haulout information.

b) Wildlife Computer Spot tags can be deployed in two ways depending on the research questions being investigated. For the most part, as in SRDL

and GPS tags, WLC tags have been deployed on the back of the head of seals. These tags provide at-sea location data and have been used in studies of survivorship and at-sea association of grey seals. They are smaller and cheaper than SRDL tags, but detailed dive or haulout information is not readily available for these tags. In contrast, 25 tags were deployed on the flippers of harbour seals in summer 2009. These tags did not transmit at-sea locations, but rather transmitted data on haulout frequency and duration.

#### 2) SMRU GPS/GSM phone tags

These tags use Fastloc GPS technology to provide frequent and, for the most part, GPS quality location fixes. Near complete sets of high quality dive and haulout records are stored and relayed through the mobile phone system.

### 1. Location Fixes

First, erroneous location fixes, defined as having unacceptable location uncertainty, were excluded from our telemetry database. These fixes were identified in one of two ways, dependent on the tag type. For Argos tags, location fixes were filtered by an algorithm described by McConnell *et al.* (1992) using a maximum speed parameter of  $2 \text{ ms}^{-1}$ . This resulted in the masking of locations which would require an unrealistic travel speed from the last location. The remaining telemetry locations were corrected for positional error using a linear Gaussian state space Kalman filter (Royer & Lutcavage, 2008). The filter has been developed in-house as part of a Scottish Government funded project (SCOS-BP 11/14).

#### 1.1 GPS test data

GPS location fixes are obtained using a hybrid Fastloc protocol. Whilst most of the locations are of GPS quality, there are occasional large errors. It was thus essential to develop an automated strategy by which these points were excluded without the removal of excessive useful data. Three potential variables could have been used: speed (as with Argos data); the number of working GPS satellites within view of the tag; and the value of residual error (residuals) associated with each location fix. Residuals are a measure of the difference between the locations, converged upon in one location fix.

The use of speed to filter location fixes was inappropriate for GPS locations for two reasons. First, the frequency of GPS locations (up to 90 per day) was much higher than that of Argos locations (c. 10 per day). Seals can swim at speeds in excess of  $2 \text{ ms}^{-1}$  for limited periods, thus valid GPS locations were likely to be excluded using this method. Second, the GPS tags have been deployed in areas of high tidal activity (34 tags deployed in Strangford Lough). Such water movement could cause prolonged travelling speeds in excess of  $2 \text{ ms}^{-1}$  being recorded.

Tags were tested before deployment on seals to ensure the tags were working satisfactorily. In most of these tests, the tags were placed at a known location and the data received checked. These test datasets enabled us to examine the use of number of satellites and residuals in data filtering. The number of working GPS satellites in view of the tag affect the quality of location fixes. Increased number of satellites results in increased location accuracy (Bryant, 2007). Although there were seal telemetry location fixes generated using less than five satellites, there were no test data for which the number of satellites was under five. Location fixes from less than five satellites are associated with high location error (Bryant, 2007, figure 1) and thus these were excluded from the telemetry data prior to analysis.

In contrast with number of satellites, the role of residuals in outlining erroneous point was less well defined. We investigated the role of residuals and number of satellites ( $>5$ ) in location error, using tag

test data at a known location. Residuals of 0 were excluded prior to data investigation as they indicate that the location algorithm failed to converge and thus defaulted to the home longitude and latitude. This home location was usually the deployment location; given to assist the algorithm in focusing its search for a location.

By the end of 2010, 113 SMRU GPS tags had been deployed on grey and harbour seals in the UK. Test data were available for 87 of these tags, resulting in 3494 location fixes (excluding records with no date/location stamp). For 23 of the deployed GPS tags, the distribution of residuals was unusual in comparison to the other tags. Thus test data for these tags were analysed separately (see 1.1.2). For test data, at a known location, the distances between the true location of the tag and the location fixes were calculated (distance error).

#### 1.1.1 Majority of test data

We examined the relationship between residuals and distance error (figure 2). There were two clumps of data, one from residuals primarily below 25 and one over 185. It was clear that the residuals in the second clump indicate high distance error and thus unreliable locations. The lowest residual associated with an extreme distance error (223 km), had a value of 186.4. Obviously this extent of inaccuracy was not acceptable and thus residuals over 185 (distance errors of between 0.084 and 910.1 km) were excluded (3.69% of the test data). These exclusions resulted in the remaining data shown in figure 3. Due to the small number (nine) of data which had residuals between 25 and 185, it was not possible to make conclusions as to the distribution of distance error for this range of residuals. Thus any data, with residuals of 25 and over, were excluded. In total 96% of the test data were retained.

The data retained after the first stage of filtering consisted of location fixes with residuals between 0 and 25 (exclusive). The relationship between number of satellites and distance error (figure 4) illustrates that if high location accuracy was required then a subset of location fixes, based on number of satellites, could be used. However, in general number of satellites was not necessary in

defining accuracy because most of the data (95%) has a distance error of less than 50m.

### 1.1.2 Unusual tags

There were 23 deployments which had a different distribution of residuals from the majority of tags. These unusual distributions of residuals were associated with particular tags, rather than deployment locations. These tags were among the first GPS deployments and included all those deployed in Strangford Loch in 2006 (deployment gp4). Some of these tags were involved in deployment pv12g. The following individual tags also displayed the same unusual distribution of residuals: pv18g-G150-06, pv19g-Opal-06, pv19g-Phil-06, pv19g-Ross-06 and pv20g-Adam-06. As well as unusual residuals, some of the tags in deployment pv12g did not work properly and thus their data were excluded from the catalogue of SMRU data holdings (SCOS-BP 11/15). Of the 23 unusual tags, there were four for which there was test data at a known location.

The relationship between residuals and distance error was of a similar structure to that of the other tags (figure 5). High residuals (over 1000) indicated highly inaccurate locations and the lower residuals indicated more accurate locations, with no or a weak relationship between residuals and distance error, within the cluster of lower residuals (figure 6). However, the lower cluster of residuals extended to 125 and the mean distance error for this cluster was higher than for the majority of tags. Due to the lack of data between 125 and 1000, all location fixes with residuals of 125 or over were excluded (figure 6). Within the retained data ( $0 < \text{residuals} < 125$ ), the most inaccurate distance errors were, for the most part, related to records with only five satellites (figure 7). Thus if particularly accurate location data were required, locations fixes resulting from five satellites could be excluded.

### 1.2 Conclusion

In summary, erroneous location fixes from Argos tags were excluded using speed between location fixes. All remaining data were then Kalman filtered. For GPS data we excluded any location

fixes for which there were less than five satellites. For the majority of the GPS tags, all location fixes for which the values of residuals were 0 or equal to or over 25 were also excluded. Unusual GPS tags were identified, for which different exclusion rules apply relating to the values of residuals. For these problem tags, locations fixes associated with residuals of 0 or equal to or over 125 were excluded.

Once the filtering protocol was developed, we investigated how many seal telemetry data would be excluded using these protocols, and by other options available (table 1). The data investigated includes all deployments which ended prior to the end of 2010. We investigated the relationship between tag deployment and the proportion of data retained for harbour seal data (figure 8) and grey seal data (figure 9). The majority of GPS data for most tags were retained with the exception of the data from the unusual tags.

## 2. Adjusted start and end dates

The second stage in the filtering process involved adjusting the start and end date of the tags to ensure that only useful data from tags were retained. Location fixes were of primary importance in defining the duration of useful tag data, thus regardless of the presence of any activity data, data were excluded based on the presence of location fixes. We used three methods to adjust the start and end dates of tags. Original tag start date often reflected the date the fieldwork team left SMRU to deploy the tags. The true start date was often a few days later and could have been weeks later if an additional field trip was required to finish deploying the tags. Furthermore, tags were often switched on for sporadic testing in the lead up to deployment and any such test data needed to be excluded. Where possible, the tag deployment date recorded by the field team was used as the original start date of the tag. However, the transmission of useful data could have started days after deployment date.

Tags can stop transmitting useful data for various reasons, such as tag battery failure or damage. If a

tag was failing, it often continued to transmit but infrequently. For example, for some tags, there was one or two location fixes a few months after the end of the bulk of the data. The end date needs to be adjusted to reflect the end of the bulk of the data. Due to tag loss or animal death, some tags transmitted useless data. Confirmation of these events often required visualisation of the data in MAMVIS. MAMVIS is software (Fedak *et al.* 1996) which allows visualisation of animal tracks and behaviour, such as hauling out and diving.

## 2.1 Automated methods

We developed automated methods of adjustment of start and end dates. The adjusted start date was moved to the first day with a location fix for which there was a location fix on the following day. Similarly the adjusted end date was the latest date with a location fix for which there was a location fix on the day immediately preceding it. Some tags were programmed to transmit a location fix every three days and so for these tags the gap allowed between the first and second transmission days and between the penultimate and last transmission days, was allowed to be 3 days. These automatic adjustments of start and end date resulted in exclusion of the majority of data which was test data or at the end of the tag when it was failing. However, it did not avoid problems of gaps in transmission or data from tags which had fallen off animals on haulouts.

## 2.2 Distance checks

In some cases, tags which have fallen off an animal continued to register dives due to the tide rising and falling on haulouts. Thus for GPS tags we investigated movement in the last three days of tag data. If there was less than a kilometre of movement, we investigated the tag data using the MAMVIS software, and then adjusted end data manually, where appropriate. This was only carried out for GPS data because it was not possible with Argos data due to the high inaccuracy of location estimates.

## 2.3 Location and activity data by day

In the final stage of the filtering process, plots were generated representing the data from every tag. These plots showed the presence of location fixes, summary data, haulout data and/or diving data against Julian day. For some tags there were no summary, dive or haulout data because the tag was a Wildlife Computer Spot tag, location only tag or because some/all of the sensors were not working. Using these plots, tags were flagged if their data did not appear normal. Tags were flagged as abnormal for various reasons including if there appeared to be long gaps in location fixes or diving. Such data were then investigated in MAMVIS and the start/end dates corrected accordingly. Tags were also investigated if transmission ended during the moulting season whilst hauled out. The adjusted end date was then moved to the first day of continuous haulout, as there was no way to tell when the tag fell off.

All the above adjustments to the start and end date resulted in more useful data and although some useful data may have also have been excluded, the purpose of the exercise was to generate a workable database of useful data.

## References

- Argos User Manual (2011). Downloaded from [www.argos-system.org/html/userarea/manual\\_en.html](http://www.argos-system.org/html/userarea/manual_en.html)
- Bryant, E (2007). 2D Location Accuracy Statistics for Fastloc® Cores Running Firmware Versions 2.2 & 2.3. Technical report TR01.
- Fedak MA, Lovell P, McConnell (1996). MAMVIS: A marine mammal behaviour visualization system. *Journal of Visualization and Computer Animation* 7: 141 - 147.
- McConnell BJ, Chambers, C, Fedak MA (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4: 393 - 398.
- Royer F. & Lutcavage M. (2008). Filtering and interpreting location errors in satellite telemetry of marine animals. *Journal of Experimental Marine Biology and Ecology*. 359:1-10.

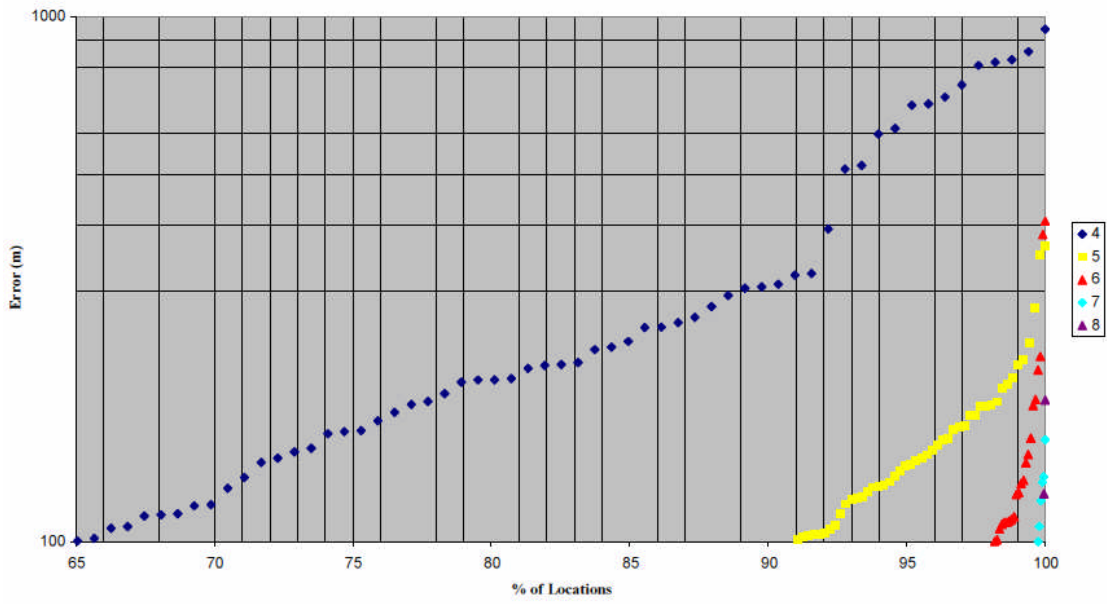


Figure 1. The cumulative distance error plot (>100m), using between four and eight satellites (from Bryant 2007).

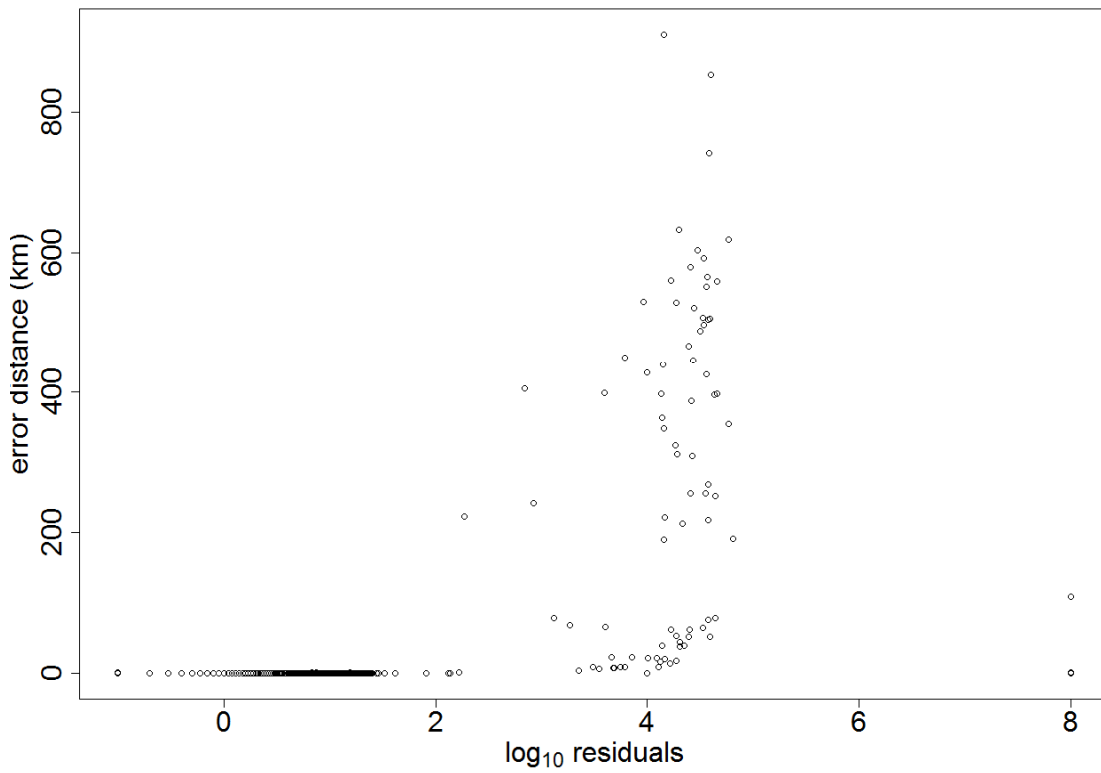


Figure 2: The relationship between value of  $\log_{10}$  residuals and distance error (km).

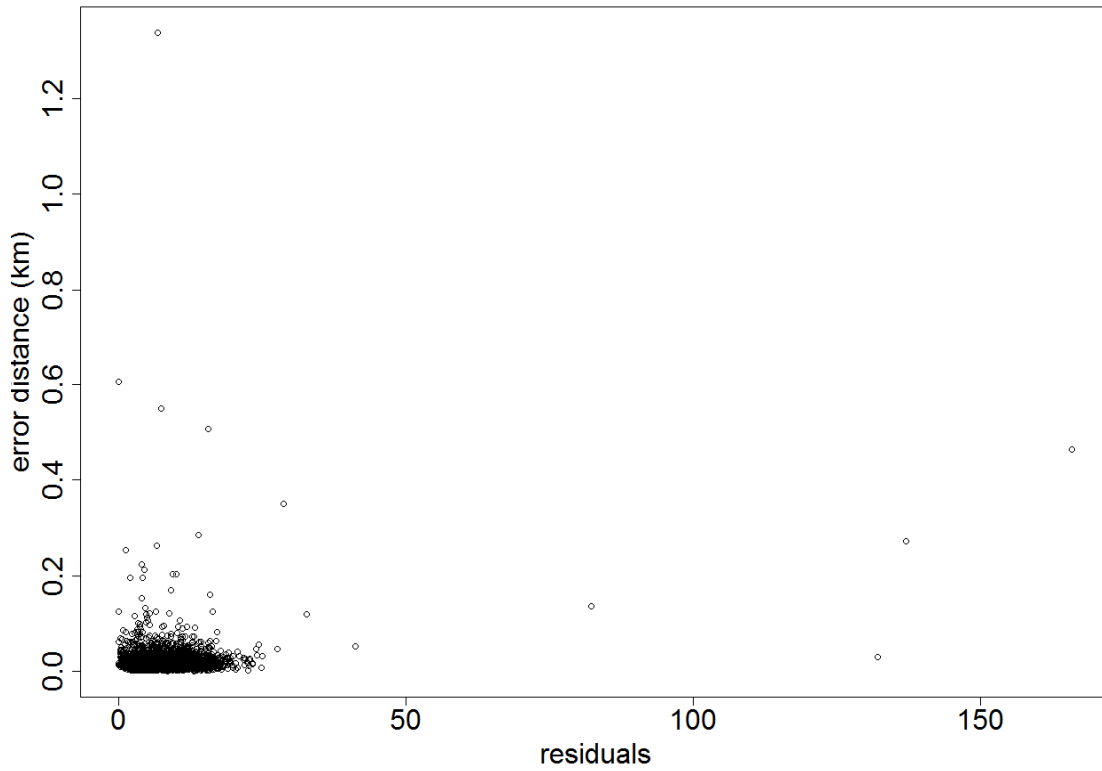


Figure 3: the relationship between residuals (up to 185) and distance error (km).

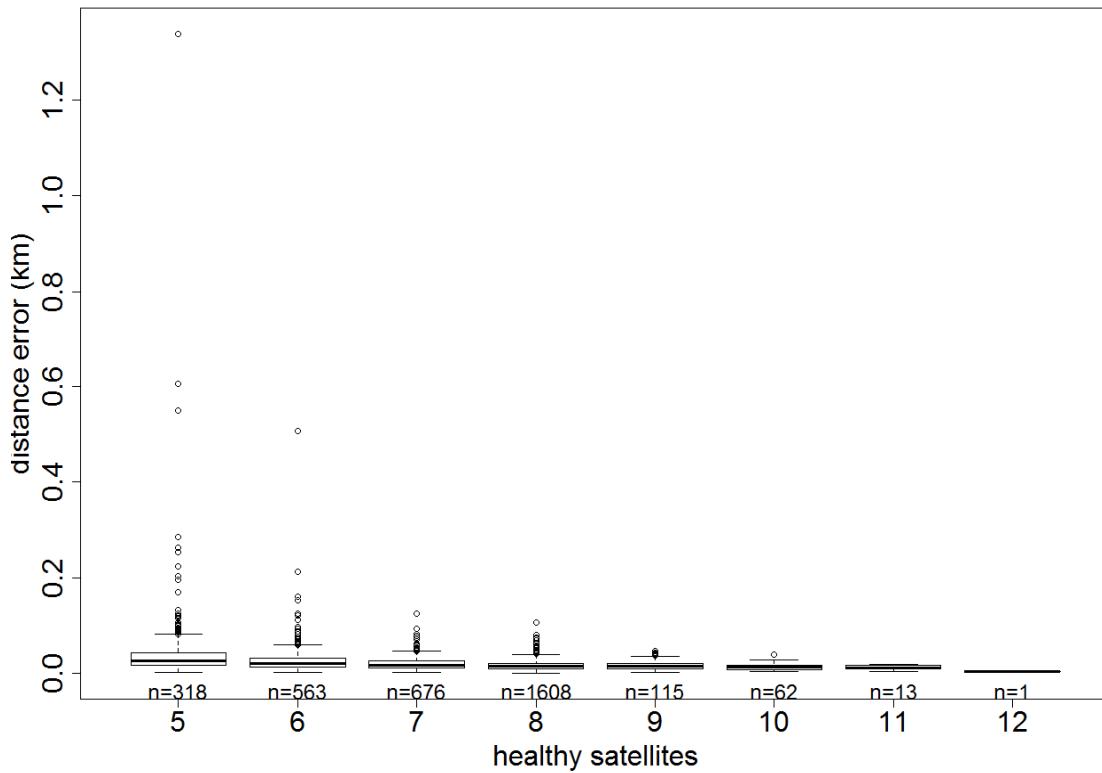


Figure 4: the relationship between number of satellites and distance error with the horizontal line indicating the median distance error; the boxes encompassing the 25th and 75th quartiles of the data; and the lines being 1.5 times these quartiles, respectively.



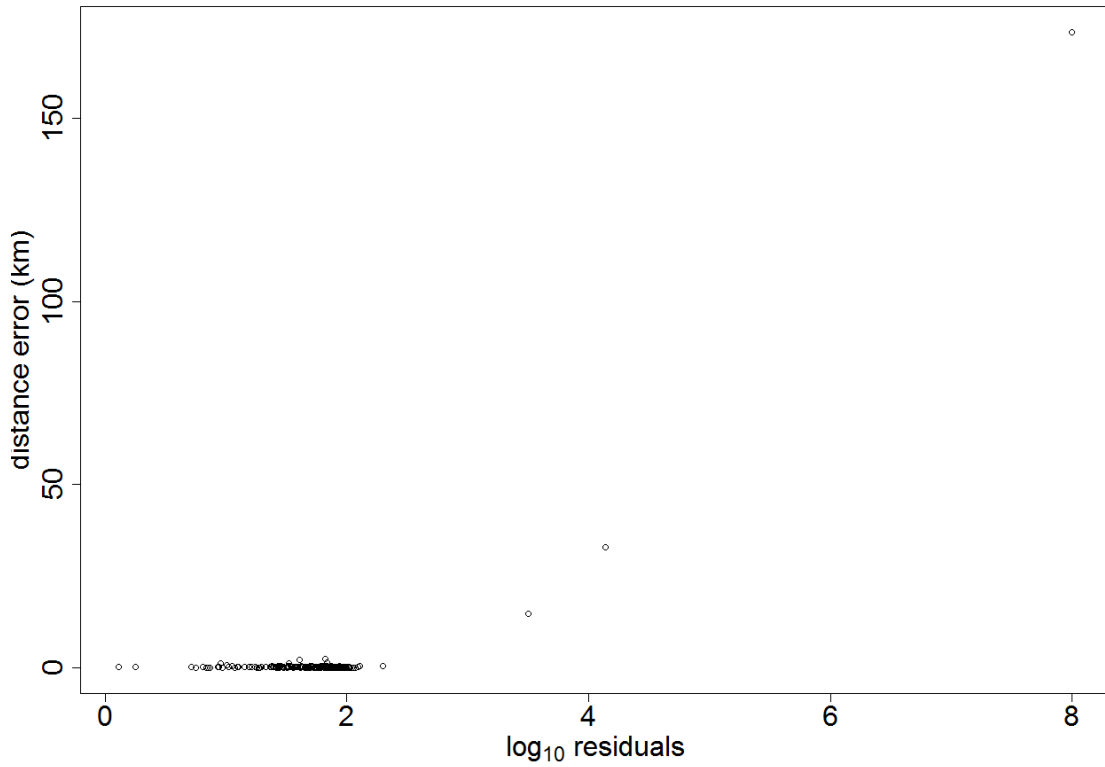


Figure 5: the relationship between  $\log_{10}$  residuals and distance error.

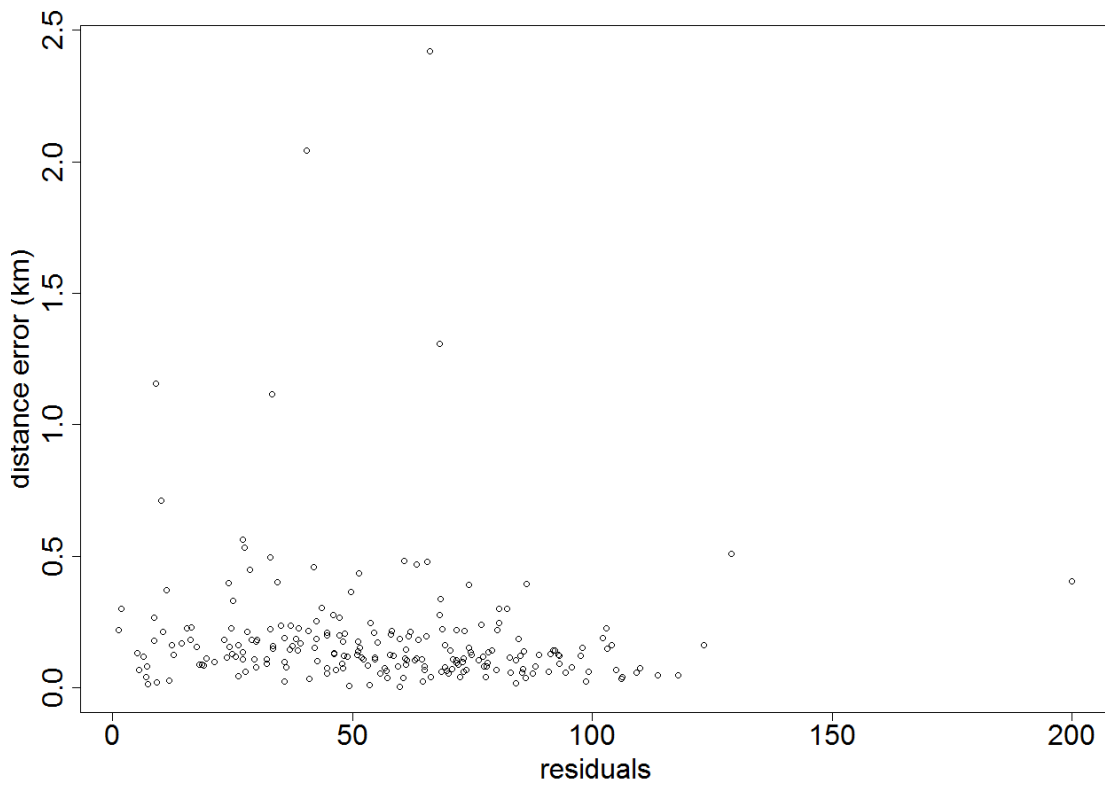


Figure 6: the relationship between residuals ( $0 < \text{residuals} < 1000$ ) and distance error.

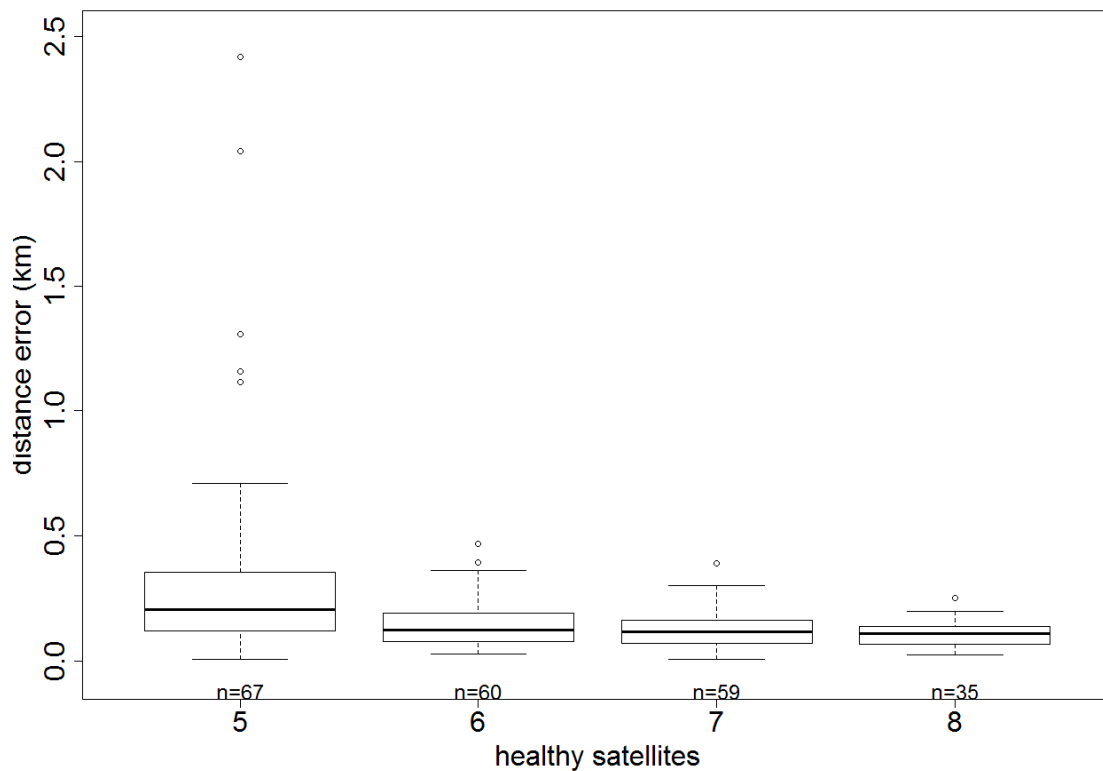
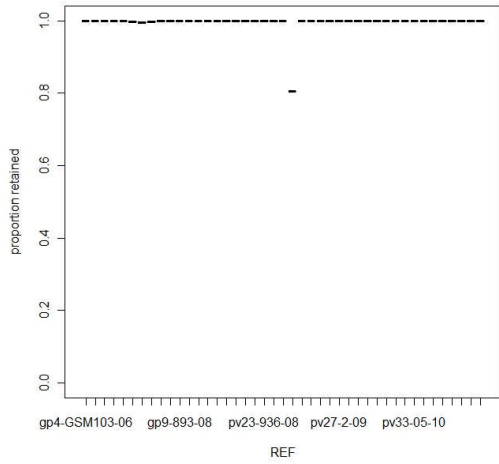


Figure 7: The relationship between the number of satellites and the distance error for retained data ( $0 < \text{residuals} < 125$ ). The horizontal lines indicate the median distance error; the boxes encompassing the 25th and 75th quartiles of the data; and the lines being 1.5 times these quartiles, respectively.

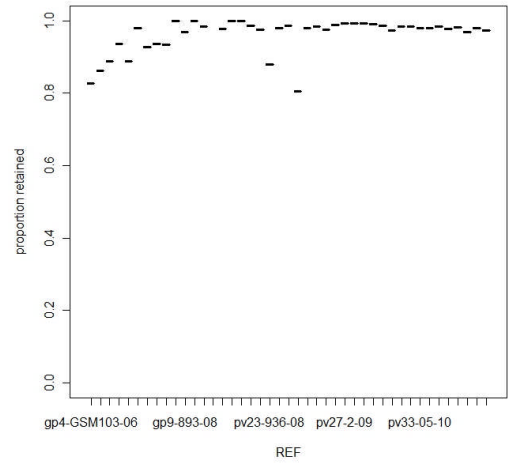
Table 1: summary of the number of location estimates remaining once certain records have been removed. In bold are the rules utilised. Hg represents grey seals and Pv, harbour seals. The unusual harbour seal data is also shown. The bottom row shows the data retained when all the appropriate rules are imposed: 5+ satellites and residuals between 0 and 25 (exclusive). For unusual residuals: residuals between 0 and 125 (exclusive).

rules	Hg records		Pv records		unusual Pv records	
	data retained	% retained	data retained	% retained	data retained	% retained
<b>Date/location non NA</b>	<b>131938</b>	<b>100</b>	<b>117363</b>	<b>100</b>	<b>30898</b>	<b>100</b>
Speed test passed	127284	96.5	114639	97.7	16603	53.7
<b>5+ satellites</b>	<b>130522</b>	<b>98.9</b>	<b>117149</b>	<b>99.8</b>	<b>28831</b>	<b>93.3</b>
<b>residuals over 0</b>	<b>131809</b>	<b>99.9</b>	<b>117251</b>	<b>99.9</b>	<b>30896</b>	<b>99.9</b>
0<Resid <1000	129447	98.1	115406	98.3	28395	91.9
0<Resid <125					<b>28169</b>	<b>91.2</b>
0<Resid <25	<b>127675</b>	<b>96.7</b>	<b>114362</b>	<b>97.4</b>	7219	23.4
<b>all rules</b>	<b>126563</b>	<b>95.9%</b>	<b>114331</b>	<b>97.4</b>	<b>27849</b>	<b>90.1</b>

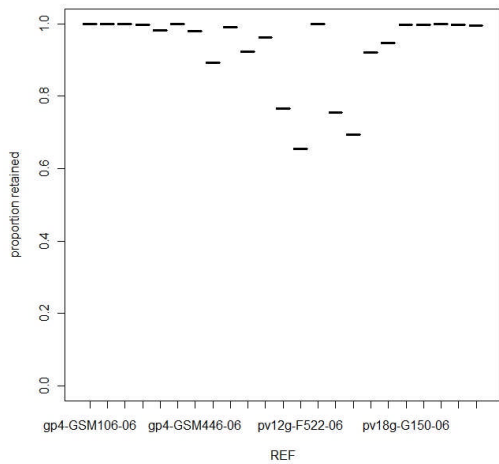
(a,i)



(a,ii)



(b,i)



(b,ii)

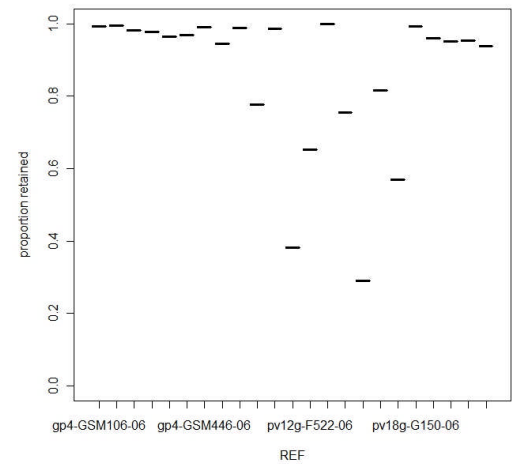
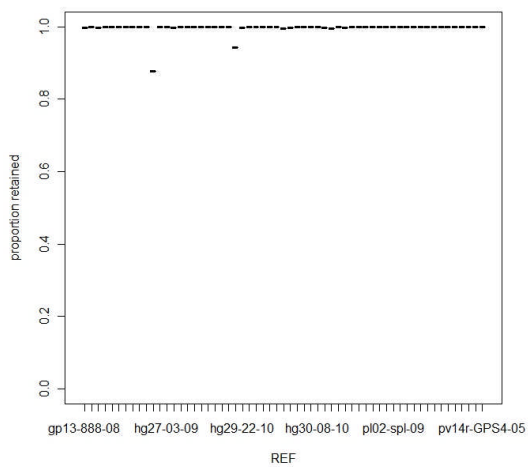


Figure 8. The proportion of harbour seal GPS location data retained per tag after the filtering process. This includes data from the majority of tags (a) and of the unusual tags (b) deployed on harbour seals. Data were retained if they were associated with five or more satellites (i) and had acceptable values of residuals (ii;  $0 < \text{residuals} < 25$  (a) and  $0 < \text{residuals} < 125$  (b)).

(a)



(b)

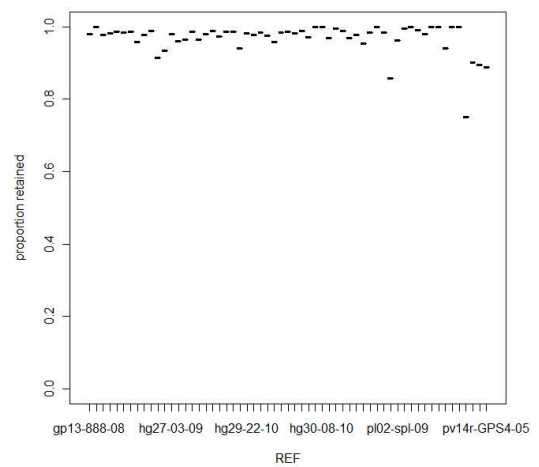


Figure 9. The proportion of grey seal GPS location data retained per tag after the filtering process. Data were retained if they were associated with five or more satellites (a) and had acceptable values of residuals (b;  $0 < \text{residuals} < 25$ ).

Table 2: The percentage of Argos location fixes excluded by the cleaning process.

rules	Hg records		Pv records	
	data retained	% retained	data retained	% retained
<b>All data</b>	<b>338994</b>	<b>NA</b>	<b>382433</b>	<b>NA</b>
<b>Date/location non NA</b>	<b>200521</b>	<b>100</b>	<b>200752</b>	<b>100</b>
<b>Speed test</b>	<b>146596</b>	<b>73%</b>	<b>146220</b>	<b>72.8%</b>

## Appendix III

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**Russell DJF and M Lonergan**  
**Short note on grey seal haul-out events at-sea**

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION OF THE AUTHOR

**Introduction**

In 2007, 2008 and 2009, the summer aerial surveys of harbour seals were extended to cover almost all grey seal haul-outs. This was undertaken to provide an estimate of grey seal abundance that was independent of the breeding season surveys, and could be used to identify whether density dependence affected fecundity or pup survival. This required the summer counts to be scaled up to population size, which was done using estimates of the proportion of time animals were hauled-out during the survey window obtained from telemetry data (Lonergan *et al.* 2011). A key assumption of this scaling is that the “haul-out events” recorded by telemetry tags indicate animals’ availability for counting. Haul-out events that occurred when seals are resting at sea, could bias the population estimate. This document examines the proportion of at-sea haul-out events in a subset of animals to investigate the likely extent of this problem.

A haul-out event is recorded when a tag’s wet/dry sensor has been dry for a period of 10 minutes and ends when the sensor has been wet for 40 seconds. The majority of telemetry tags deployed on grey seals have been Argos tags. There are three difficulties in determining the proportion of haul-out events that occur at sea: (1) When no location fix occurs within a haul-out event, haul-out locations are an interpolation between available fixes; (2) even once Kalman filtered (Royer & Lutcavage, 2008; Jones *et al.* 2011) the error in locations makes it difficult to determine whether locations near land are on land or not (3) tidal effects on the

coastline limit the precision of maps and prevent automated testing of whether locations are on land.

Here we investigate the scale of at-sea haul-out events using telemetry data from nine of the ten phone (GPS) tags that have been deployed on adult grey seals. These were deployed at Abertay, south-east Scotland in April 2008. Data from the tenth tag were excluded because it only lasted two days. Restricting the analysis to these data limited the impact of the three issues described above: (1) Phone tags transmit locations much more frequently than Argos tags thus the majority of the haul-out events from these tags contained GPS location fixes (2) The location accuracy of GPS data is much higher than for Argos with 95% of cleaned observed location fixes from these tags accurate to within 50m (Russell *et al.* 2011); (3) the limited amount of data permitted direct examination, on digital nautical charts, of haul-out events reported by the tags. Because the purpose of this analysis was to investigate the likely extent of at-sea haul-outs on the population estimates, the breeding season (September to December) was excluded from this analysis.

**Methods**

The data were cleaned by adjusting the start and end dates and excluding erroneous locations as per Russell *et al.* 2011. We also excluded all data from the 1<sup>st</sup> of September (start of the breeding season). The median duration of the resulting data was 142 days (Table 1). In some cases a proportion of random haul-

out events are not transmitted successfully. When recorded, haul-out events are numbered and this showed that 100% of the haul-out events records were received for all tags except gp13-902-08 for which 13% (17 events) were not received.

The haul-out events that contained at least one observed location were examined, with the mean of the location fixes used as an estimate of its position. These included 88% of all received haul-out events (minimum of 80% per tag) and 95% of the duration of received haul-out events. Unsurprisingly, shorter haul-out events were less likely to encompass a location (Table 1). Polygons of the British Isles (GSSH: Global Self-consistent, Hierarchical, High-resolution Shoreline Database) were initially used to automatically categorise locations within the polygon to land. For the remaining locations, nautical chart overlays were used to define areas exposed at low tide, and haul-out events were assigned as on land if they were located within these exposed areas and at-sea otherwise.

Separately, we examined haul-out events with interpolated locations to check whether there is evidence that the proportion of haul-out events without observed locations that occurs at-sea differs from that for events containing GPS fixes. Such haul-outs cannot be definitively assigned to land. However, haul-outs can be definitively assigned as at-sea if the preceding and subsequent GPS fixes are sufficiently far from the coast. To determine whether haul-out events outwith a 5km buffer of the coast could be defined as at-sea the following was considered: the distance between the interpolated location and land; the gap between the preceding observed location and the start of a haul-out event; the gap between the end of a haul-out event and the following location; and also the

maximum horizontal displacement of grey seals ( $2\text{ms}^{-1}$ ).

## Results

A third of the seals (two males and one female) had at-sea haul-out events containing observed locations (Table 1, Figure 1). More than 100 haul-out events were examined for each of the two males, and 1 and 3% of these were at sea. Two of the 25 (8%) haul-out events recorded for the female were at-sea. The percentage of haul-out time that was at-sea was less than the percentage of haul-out events at-sea in each animal, indicating that haul-out events at-sea were, on average, shorter than those on land. The mean percentage of haul-out events at-sea, over all the animals, was 1.4% and the percentage duration is 0.4%.

All but two of the interpolated haul-out locations were within the 5km buffer around the coastline. Those two haul-out events were from the same animal (ID gp13-908-08) and must have happened at-sea because they both occurred within 2.5 hours of an observed location, over 200 km from the nearest land. For gp13-908-08, assuming all other haul-out events with interpolated locations were on land, this increases the percentage of events at-sea to 4.3% and the duration to 1.6%. Overall, the percentage of haul-outs at-sea increases to 1.3% and the percentage duration remains at 0.4%.

## Discussion

These results illustrate that haul-out events do occur at-sea, but their frequency is low and their duration is on average shorter than those events on land. If these preliminary findings are representative of the wider population, haul-out events at sea will have little effect on the independent estimate of population size.

However, confidence in these conclusions is dependent on both the validity of the assumptions in this study and whether these individuals investigated here are representative of the population.

There are three obvious potential sources of bias in this study. First, the percentage of haul-out events or time at-sea was not investigated with regard to time of day, tide or time of year. These overall percentages might not be representative of behaviour during the survey windows used in Lonergan *et al.* (2011), which were two hours long during low tide in August. Second, haul-out events on areas exposed at low tide, were assigned to land on the assumption that these occurred at low tide. It is possible that some of these events actually involved animals in the water, though there is limited potential for that during the actual survey windows. Third, the 12% of haul-out events that did not encompass observed locations could not be examined in as much detail as the haul-out events with observed locations. Given that both at-sea events and events without observed locations had relatively short durations, a different proportion of such haul-outs events may be at-sea. However, at-sea haul-out events which encompassed observed locations were almost all very far from land, and all but two events without observed locations were estimated to be within 5km of land, thus it seems unlikely that such events will introduce a substantial bias. Moreover, although assuming that all haul-out events with no observed locations were at-sea would increase the proportion of at-sea events to 13% they would still only encompass 5.0% of haul-out time, further supporting the conclusion that at-sea haul-outs would have little effect on the grey seal population estimate.

There was considerable variability in the proportion of at-sea haul-outs of the nine individuals examined here. In individuals for which there was more than one at-sea haul-out event these were all on different days with only two on consecutive days (gp13-908-08). It seems likely that the probability of at-sea haul-outs is affected by individual factors such as position of the tag on the back of the neck, animal size, and behaviour as well as sea-state and other environmental conditions. There may also be regional variability in the proportion of time spent in at-sea haul-out events. The percentage of time spent non-diving at-sea varies significantly between regions, with that proportion being lower in the study region than in most other regions, (Russell, unpublished). This may or may not translate into a higher proportion of time in haul-out events at-sea.

There is no obvious reason to expect the probability of at-sea haul-outs to differ between the phone tags considered here and the Argos tags that have been used in all the other deployments on adult grey seals. While the data-transmission technology differs, they use the same wet/dry sensor and definition of a haul-out event. However, the high variability between individuals found here suggests it may be of interest to examine the data from Argos tags in order to increase the sample size and determine appropriate confidence limits around estimates of the size of this effect. The finding that all but one at-sea haul-out occurred more than 50km from land suggests that the lower precision of ARGOS locations may not be insurmountable.



## References

Jones EL, McConnell BJ, Duck C, Morris C, Matthiopoulos (2011). Special Committee on Seals (SCOS). Briefing paper.

Loneragan, M., Duck, C.D., Thompson, D., Moss, S. & McConnell, B. (2011) British grey seal (*Halichoerus grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. *Ices Journal of Marine Science*, **68**, 2201-2209.

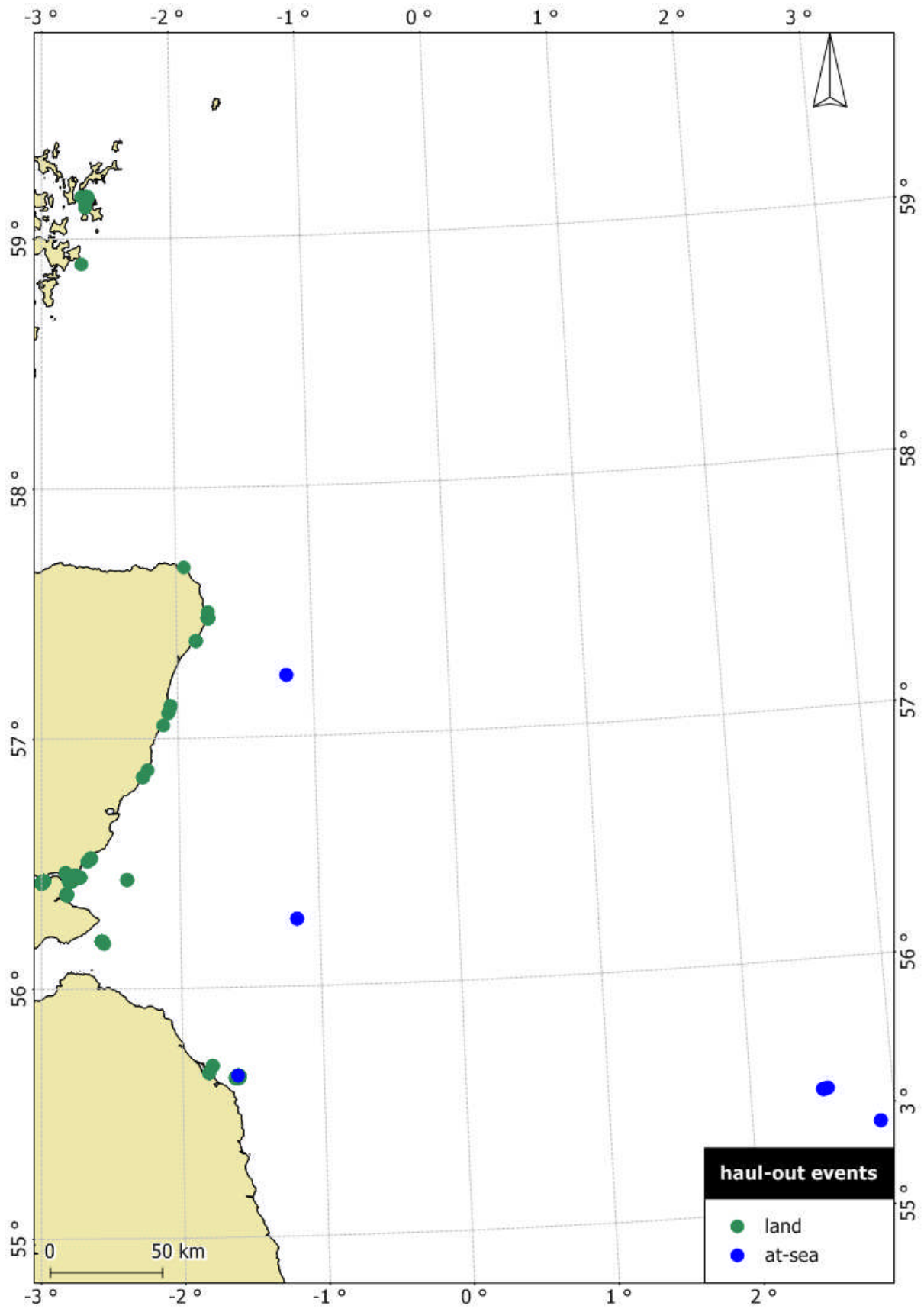
McConnell, B.J., Fedak, M.A., Lovell, P. & Hammond, P.S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, *36*, 573-590.

Royer F, Lutcavage M (2008). Filtering and interpreting location errors in satellite telemetry of marine animals. *Journal of Experimental Marine Biology and Ecology*, *359*: 1-10.

Russell DJF, Matthiopoulos J, McConnell BJ (2011). Special Committee on Seals (SCOS). Briefing paper.

Table 1. Description of haul-out events for nine phone tag seals. The haul-out events examined are those which included an observed location. Of these the number and percentage of haul-out duration at-sea is shown.

ID	sex	duration (days)	haul-out events examined			at-sea haul-out events		
			number	% of received haul-out events	total duration (hours)	number	number at-sea (%)	duration at-sea ( % )
gp13-888-08	m	144	108	80	524.54	1	0.9	0.7
gp13-897-08	f	142	87	90	510.86		0	0
gp13-902-08	m	144	115	88	620.01		0	0
gp13-904-08	f	48	25	81	102.15	2	8	1.5
gp13-908-08	m	126	118	86	604.14	4	3.4	1.1
gp13-910-08	f	142	81	95	446.33		0	0
gp13-915-08	f	144	115	83	473.59		0	0
gp13-916-08	f	144	95	94	425.24		0	0
gp13-921-08	m	131	122	94	690.31		0	0



## Appendix IV

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**Jones, E. L., McConnell, B.J, Duck, C.D., Morris, C.D., Hammond, P.S., Russell, D.J.F. & Matthiopoulos, J.**

**Marine distribution of grey & harbour seals around the UK**

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**Summary**

The way that grey and harbour seals use their marine geographical environment (i.e. spatial usage) appears to be different. When both species haul-out at similar locations, such as Orkney, harbour seals stay close to the coast and their haul-out sites, whereas grey seals move further afield. So, even though both species are characterised as central place foragers they appear to have different spatial distribution strategies. This behaviour was modelled for each species to produce UK-wide maps on a fine-scale by linking two decades of telemetry and terrestrial count data to produce population-level estimated usage. Uncertainty was propagated through the analysis and quantified as standard deviation contours on the usage maps. These provide a level of certainty and are particularly useful when focusing on fine-scale features of the maps.

**Introduction**

Fisheries have historically regarded seals as a potential threat to economically important fish stocks and a number of legislative acts now protect seal species, while working with the fishing industry to protect their livelihood. Grey and harbour seals are both listed in Annex II of the European Habitats Council Directive 1992 (EHCD) (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora) which requires member states to protect grey and harbour seals to maintain ‘favourable conservation status’, meaning that populations must have long term stability and viability, sustained natural range, and that an adequately large habitat is maintained for the population (JNCC, 2010). This has led to 24 Special Areas of Conservation (SAC) around the UK (14 in Scotland) where grey and harbour seals (as Annex II species) are the qualifying reason or feature for selection (JNCC, 2012). Marine protected area (MPA) design commonly focuses on identifying areas with a high abundance of apex predators when they are the focus of the MPA and spatial and/or temporal maps

form an accessible platform for MPA design (Hooker *et al.*, 2011). It is therefore important to provide accurate estimates of spatial usage with quantifiable precision to inform future management plans.

Likewise, recent expansion in proposed renewable energy developments of offshore tidal, wave and wind power particularly around Scotland means that spatial distribution and abundance of seals are needed as inputs into Environmental Impact Assessments when considering placement and potential impacts of commercial development.

Spatial maps provide insights into species distributional ranges, comparisons between these ranges, and provide a layer of information to link other datasets such as fisheries and prey data, enabling spatial and/or temporal overlap studies. This paper presents up-to-date fine-scale usage maps of grey and harbour seals around the UK with corresponding uncertainty estimates, utilising 20 years of telemetry and aerial survey data.

**Methods**

**Count data**

Aerial surveys are conducted each year by Sea Mammal Research Unit (SMRU) and funded primarily by the National Environmental Research Council (NERC), Scottish Natural Heritage (SNH) and Natural England (NE). Grey and harbour seals are surveyed during August when harbour seals are found in moulting aggregations and grey seals are dispersed in haul-outs along the coast.

Over a number of consecutive years the entire Scottish coastline is surveyed and counts are marked using OS Landranger maps (1:50,000) to within an accuracy of 50m. Data from 1996-2010 surveys were used in the analysis.

Fixed wing aerial surveys were also completed over selected areas of the Scottish and English east coasts funded by NERC, SNH, NE and the Department of Energy and Climate Change (DECC). The Moray Firth,

Firth of Tay, Donna Nook, The Wash in East Anglia, and the Thames estuary were surveyed and counts between 1988 and 2009 were used in the analysis.

Harbour seals in southern England around Chichester & Langstone harbours are monitored through public sightings and by the Chichester Harbour Authority. They provide a source of ground counts, and August sightings from 1999-2011 were used.

An aerial survey was conducted by SMRU in Northern Ireland in 2002, funded by the Northern Ireland Environment Agency. The same protocol was used as the Scottish aerial surveys. Additional aerial surveys were undertaken by SMRU Ltd around the Strangford Lough area in 2006, 2007, 2008 and 2010 and were funded by Marine Current Turbines Ltd. In 2003 an aerial survey of the Republic of Ireland was carried out by SMRU, funded by the Department of Arts, Heritage, Gaeltacht and the Islands.

Welsh counts were taken from Grey seal distribution & abundance in North Wales, 2002-03. The ground counts extended over all months and did not follow the same protocol as the aerial surveys.

Survey counts from France were taken from Hassani *et al.*, 2010. These are yearly ground counts of harbour seals from 1986-2008, across three locations: Baie de Somme, Baie de Veys, and Baie de Monte Saint Michel. Figures 1 and 2 show the locations of aerial survey and ground counts used, colour coded by country.

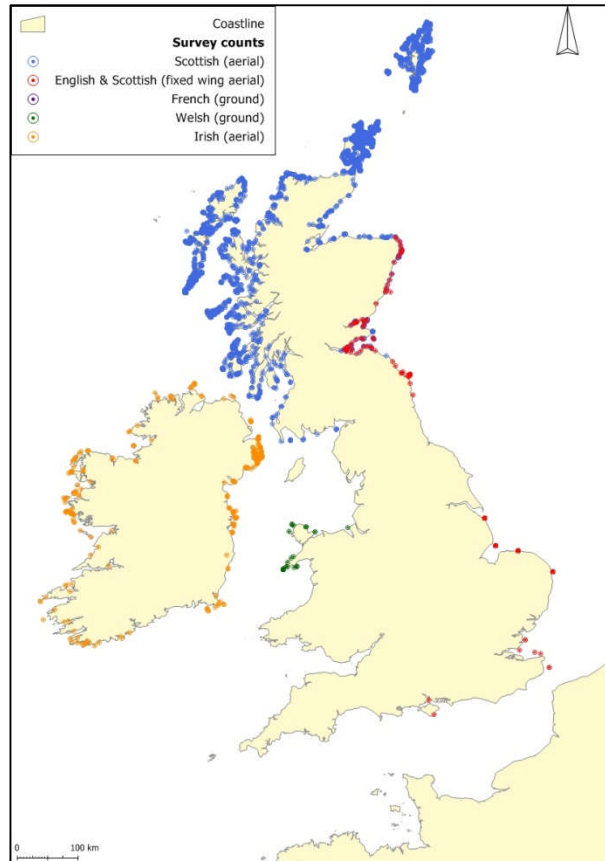


Figure 1 Grey seal aerial survey & ground counts.

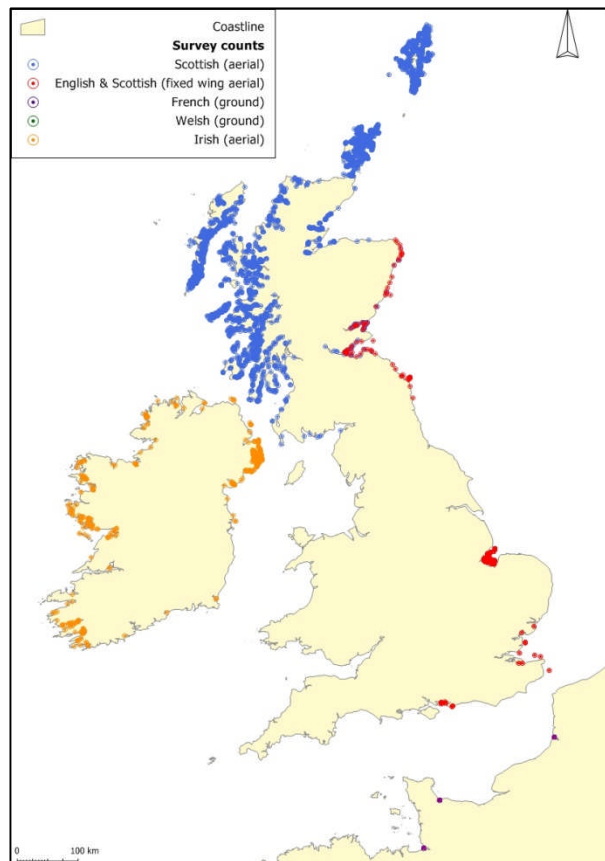


Figure 2 Harbour seal aerial survey & ground counts.

### Telemetry data

Telemetry data from grey and harbour seals have been collected by SMRU since 1988. These are 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 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). Of the 425 telemetry tracks used, 229 were from grey seals (Table 1) and 196 were from harbour seals (Table 2). All available data were used and age, sex and life-stage were not disaggregated for the purposes of the analysis.

Year	Tag type	Number of tags	Sex ratio (m:f)	Age ratio (adult:pup)
1991	Argos	5	4:1	5:0
1992	Argos	12	8:4	12:0
1993	Argos	3	2:1	2:1
1994	Argos	4	2:2	0:4
1995	Argos	20	14:6	14:6
1996	Argos	20	8:12	20:0
1997	Argos	8	4:4	8:0
1998	Argos	24	17:7	24:0
2001	Argos	11	6:5	1:10
2002	Argos	12	5:7	2:10
2003	Argos	22	14:8	22:0
2004	Argos	26	10:16	26:0
2005	Argos	9	4:5	9:0
2006	Argos	2	1:1	2:0
2008	Argos/GPS	19	9:10	19:0
2009	GPS	12	2:10	7:5
2010	GPS	20	7:13	0:20

Table 1. Summary of grey seal telemetry tracks used.

Year	Tag type	Number of tags	Sex ratio (m:f)	Age ratio (adult:pup)
2001	Argos	10	5:5	10:0
2002	Argos	5	4:1	5:0
2003	Argos	36	15:21	36:0
2004	Argos	35	18:17	30:5
2005	Argos	21	12:9	21:0
2006	Argos/GPS	52	33:19	52:0
2007	Argos/GPS	2	1:1	2:0
2008	GPS	14	7:7	14:0
2009	GPS	10	3:7	10:0
2010	GPS	10	8:2	10:0
2011	GPS	1	0:1	1:0

Table 2. Summary of harbour seal telemetry tracks used.

### Treatment of positional error

Positional error, varying from 50m to over 2.5km (Argos User's Manual, 2011), affects all Argos 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, 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. Since we are interested in large-scale population-level inferences rather than high-resolution individual-based insights we opted for a Kalman filter (Royer & Lutcavage, 2008; Patterson *et al.*, 2010; Roweis & Ghahramani, 1999) using a linear Gaussian state-space model to obtain estimates, accounting for observation error. This has been developed in-house to give flexibility and fast processing times. Argos data were first speed-filtered (McConnell *et al.*, 1992) at  $2\text{ms}^{-1}$  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 Argos 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 with less than 5 satellite fixes (Russell *et al.*, SCOS briefing paper 11/17).

### 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 (if the tag provided such information) or in an unknown state (if the tag did not).

### **Haul-out aggregation**

Haul-out sites were defined by the telemetry data as any coastal location where at least one haul-out event had occurred, aggregated into 5km square grids.

### **Trip detection**

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 for 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 corresponding telemetry data were attributed to departure and termination haul-outs.

### **Kernel smoothing**

Kernel smoothing (KS) is a statistical technique, which fits a smooth spatial usage surface to a set of positional data (Matthiopoulos, 2003). 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.

### **Information content weighting**

To account for individual variation in the telemetry points collected from each animal, indices of information content were devised using data from the whole of the UK. 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 'discovers' 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 Argos or GPS. The intercept

was set to zero and a Poisson distribution with a log-link function was used. The models used Generalised Additive Models (GAMs) utilising the R library MGCV (Wood, 2011; Wood, 2006).

Figure 3a 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 (Argos = 178, GPS = 335). 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 3b; Argos = 2896 hours, GPS = 3875 hours), and higher uplink rate per hour (Figure 3c; Argos = 0.36, GPS = 1.22). The Argos tags show smaller variation in the number of locations per hour because they were regularised at 6 hourly intervals, as well as keeping the original locations in the data.

Figure 4a 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 (Argos = 67, GPS = 18). A Welch two-sample t-test gave a significantly higher mean for Argos data at a 95% confidence level. This was driven by a significantly higher tag lifespan (Figure 4b; Argos = 2987 hours, GPS = 2169 hours) although the GPS tags have a higher uplink rate per hour (Figure 4c; Argos = 0.45, GPS = 0.85). Number of locations, tag lifespan, and tag type (Argos or GPS) were significant and explained 43.2% and 27.9% of variation in the data for grey and harbour seals respectively.

Figures 5a and 6a show total usage fitted values vs. observed discovery rate. Figures 5b, 6b, 5c and 6c show the GAM smoothing curves for tag lifespan and number of telemetry locations. Fitted values were normalised and used to weight the contribution of different animals to estimate usage associated with each haul-out location. This approach reduced the importance of data-poor animals, whilst simultaneously not overstating the contribution of animals with heavily auto-correlated observations.



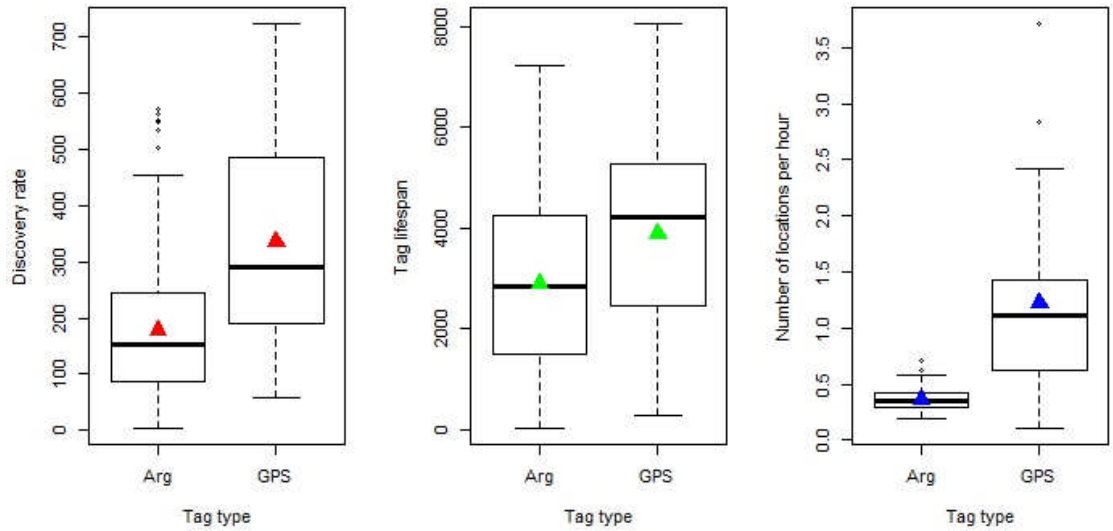


Figure 3. Boxplots showing significant differences between tag types for grey seals. Coloured triangles represent mean values, thick black lines are median values, boxes are interquartile ranges, dotted lines show minimum and maximum values. (L-R): 3a. Discovery rate; 3b. Tag lifespan; 3c. Number of locations per hour.

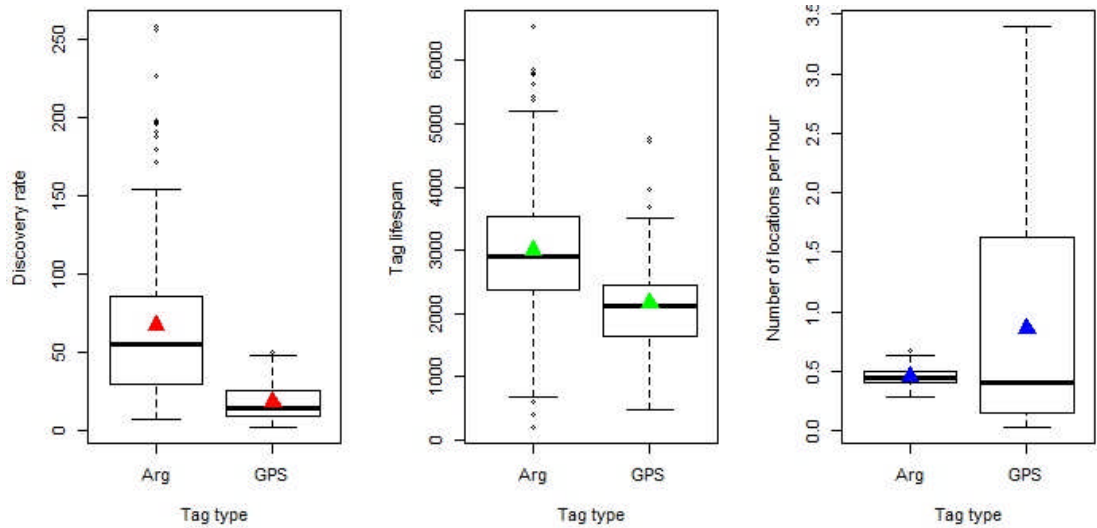


Figure 4. Boxplots showing significant differences between tag types for harbour seals. Coloured triangles represent mean values, thick black lines are median values, boxes are interquartile ranges, dotted lines show minimum and maximum values. (L-R): 4a. Discovery rate; 4b. Tag lifespan; 4c. Number of locations per hour.

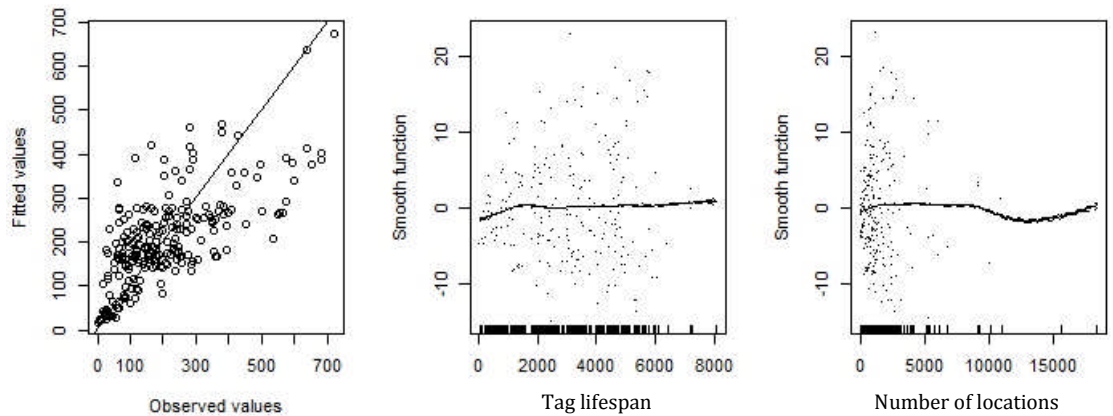


Figure 5. GAM model deriving 'information content' by individual grey seal. (L-R): 5a. Observed vs. fitted values; 5b. Tag lifespan smoothing curve; 5c. Number of telemetry locations smoothing curve.

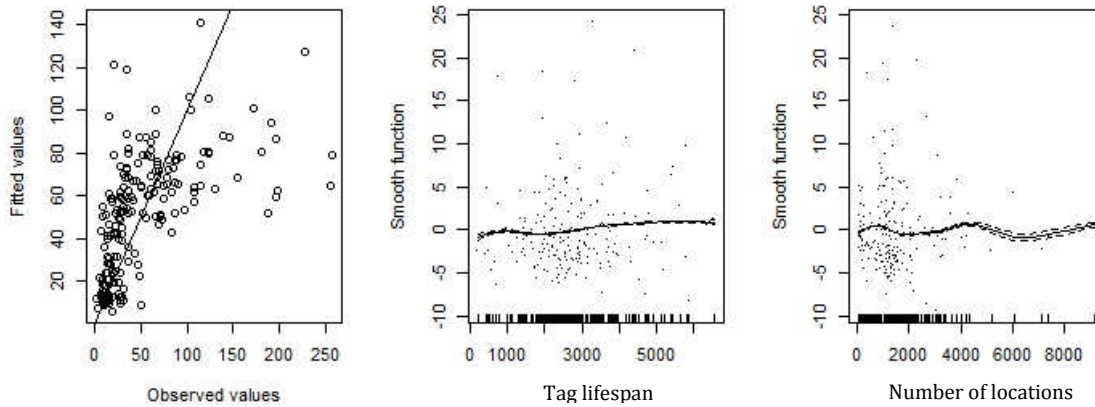


Figure 6. GAM model deriving 'information content' by individual harbour seal. (L-R): 6a. Observed vs. fitted values; 6b. Tag lifespan smoothing curve; 6c. Number of telemetry locations smoothing curve.

**NULL (accessibility) model**

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 adult tracks from each species were selected and quasi-Poisson distributions with log link functions were fitted. Figure 7 shows the observed vs. fitted number of telemetry locations associated with each haul-out for (a) grey seals and (b) harbour seals.

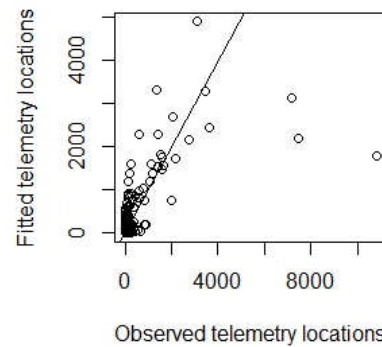
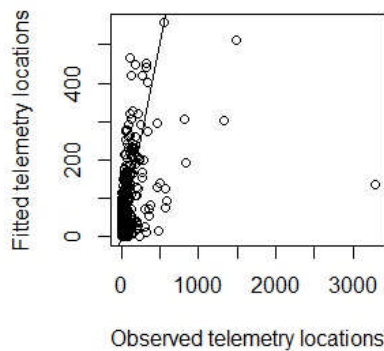


Figure 7. GLM models deriving null usage. Observed number of telemetry locations vs. fitted locations for: 7a. Grey seals; 7b. Harbour seals.



**Quantifying uncertainty**

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

**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. This was the minimum number of animals needed to bootstrap each haul-out, and was tested experimentally. The response variable was logged variance, and the covariates were: sample size (number of animals associated with a haul-out) and logged estimated mean density of seals weighted by information content. At-sea kernel smoothed densities were bootstrapped 500 times for each haul-out, and sample size was sampled with replacement and logged, to produce estimated logged variance and logged 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.

### Aerial survey & population level

Several types of uncertainty are associated with aerial surveys and scaling to population level. Observational errors occur in surveys due varying weather conditions, aircraft altitude, and accuracy in recording animal locations. Sampling errors occur because surveys by their nature are instantaneous counts in time. These errors are mitigated as much as possible through survey design and repeat surveying. Errors also occur when scaling to population estimates as a population mean haul-out percentage was used (Lonergan *et al.*, submitted; Lonergan *et al.*, 2011). These errors 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:

$\mu$  = mean seal population hauled-out at any point in time

$\sigma^2$  = variance in seal population hauled-out at any point in time

The density distribution likelihood distribution was then derived as:

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

Where:

$N_i$  = Seal population of  $i^{\text{th}}$  haul-out

$m_{ij}$  = Number observed on  $i^{\text{th}}$  haul-out on  $j^{\text{th}}$  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.

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

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

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

### Analysis

To create maps of at-sea usage all grey and harbour seal telemetry data from the SMRU database were put through a series of data cleansing protocols to remove unusable data. Argos data were spatially interpolated to 6 hour intervals using a Kalman filter and merged with GPS data.

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 at-sea 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.

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 at-sea usage map for each species.

## Results

Figure 8 shows the estimated at-sea spatial usage of grey seals around the UK. The map can be interpreted as the average number of seals in each 5km<sup>2</sup> grid square at any point in time. For example, a yellow square denotes, on average, between 25 and 50 grey seals will be within that grid square at any point in time.

White contour lines denote standard deviation from the mean as a measure of uncertainty around the estimated usage. Labels show the value of standard deviation at

each contour as the square root of the estimated variance.

The majority of usage is concentrated around Scotland, reflecting the distribution of grey seals around the UK (88% of UK grey seals breed in Scotland, SCOS 2011).

The standard deviation contours are a function of variation in aerial survey counts and the number of tagged animals associated with a haul-out. Therefore, they are a measure of aerial survey and tagging effort in each 5km<sup>2</sup> grid.

Similarly, figure 9 shows the estimated at-sea spatial usage of harbour seals around the UK with standard deviation denoted by white contour lines.

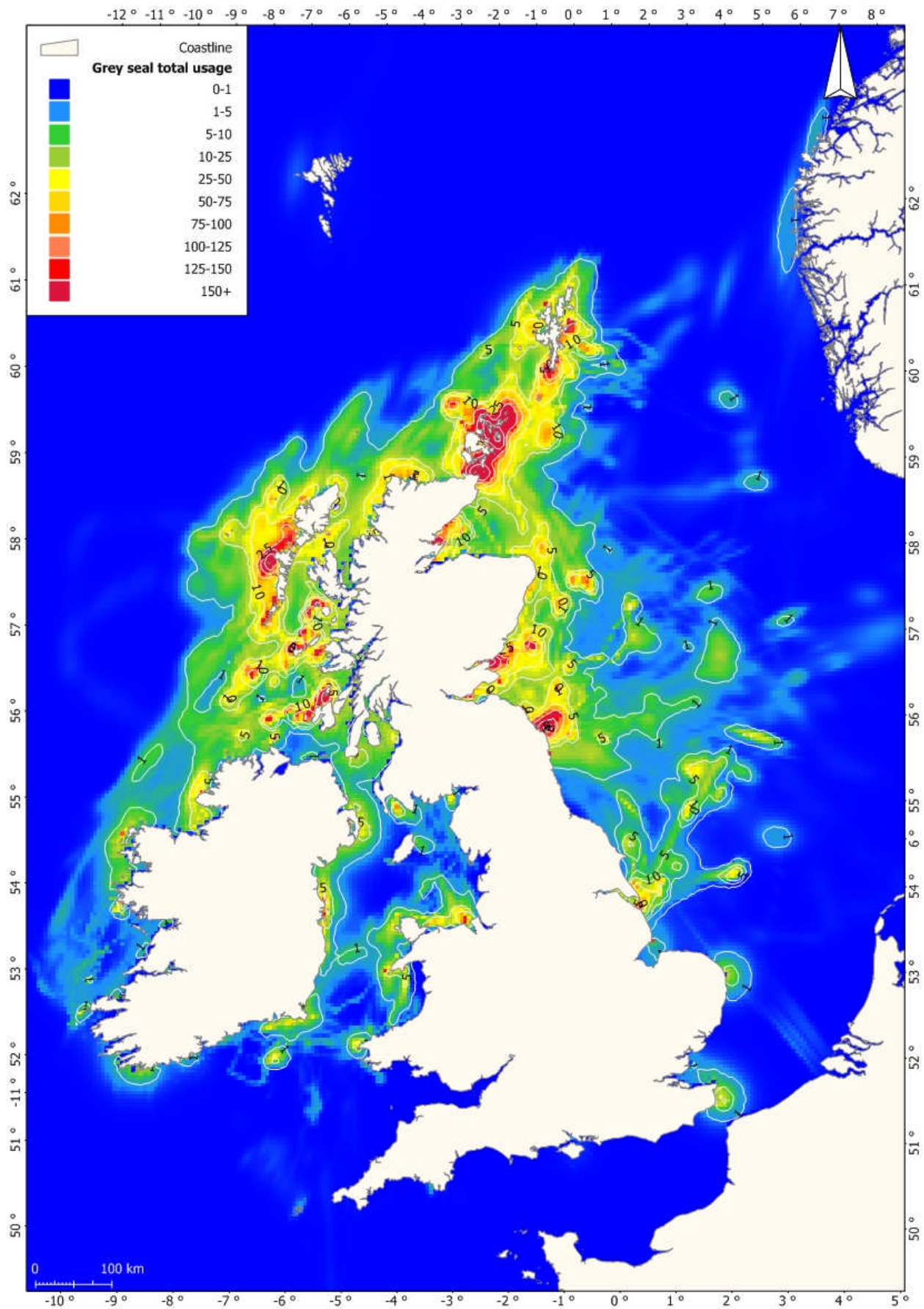


Figure 8. Estimated grey seal total (at-sea & hauled-out) usage around the UK. White contours show standard deviation from mean usage as a measure of uncertainty.

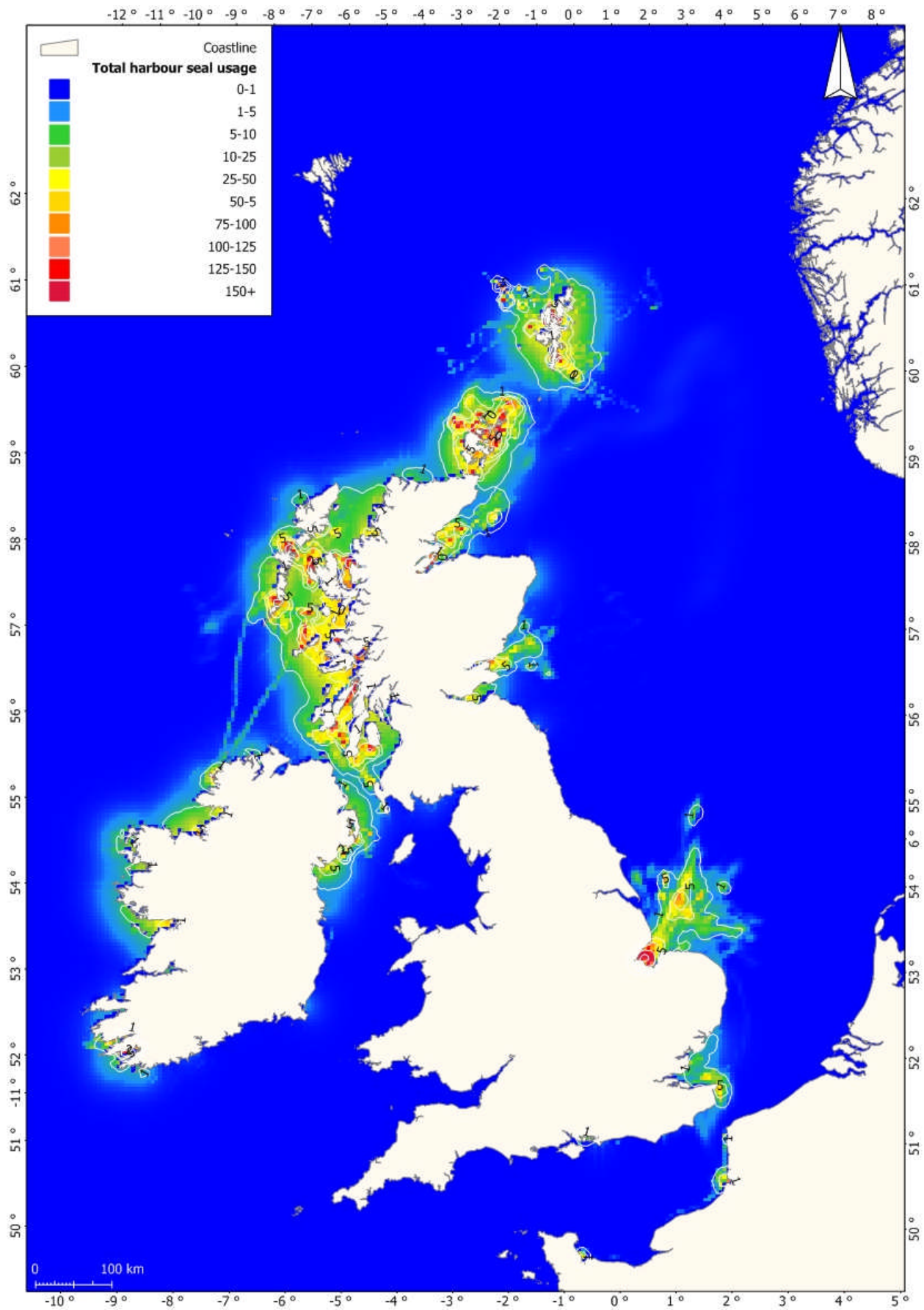


Figure 9. Estimated harbour seal total (at-sea & hauled-out) usage around the UK. White contours show standard deviation from mean usage as a measure of uncertainty.

## Discussion

The spatial extent to which harbour seals use their geographical environment at-sea appears to be less than grey seals. For instance, on the east coast of England a large colony of grey seals at Donna Nook (figure 8) regularly travel 230km out to sea from their haul-out site. In contrast, harbour seals in The Wash (figure 9), south of Donna Nook regularly travel 165km out to sea (30% less than grey seals). More generally, harbour seals spend little time at the continental shelf to the west of the UK, whereas grey seals utilise areas all along the shelf.

The telemetry movements of harbour seals underpinning the usage maps show that they although they do not travel so far offshore as grey seals (with exception of some individuals, (Sharples *et al.*, 2012)), they show considerable movement parallel to the coast, resulting in concentrated patches of high at-sea usage close to the coast. By contrast grey seals have continuous high spatial usage throughout larger areas, not only around haul-out sites, but also at-sea, indicating possible foraging patches (Thompson *et al.*, 1996).

Although the analysis does not infer changes in population dynamics through temporal representation, it shows differences in the way the two species use their marine environment, which can inform the mechanisms behind the contrasting dynamics of increasing grey seal and decreasing harbour seal populations.

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## References

- Argos User's Manual. (2011). 2007-2011 CLS.
- Chacon J.E. & Duong T. (2010) Multivariate plug-in bandwidth selection with unconstrained pilot matrices. *Test*. **19**:375-398.
- Duong T. & Hazelton M.L. (2003) Plug-in bandwidth matrices for bivariate kernel density estimation. *Journal of Nonparametric Statistics*. **15**:17-30.
- Grey seal distribution and abundance in North Wales, 2002-2003. Westcott, S.M. & Stringell, T.B. Marine Monitoring Report No: 13.
- Hassani S, Dupuis L, Elder J.F, et al. (2010). A note on harbour seal (*Phoca vitulina*) distribution and abundance in France and Belgium. *NAMMCO Scientific Publications*. **8**:107-116.
- JNCC. (2012). Accessed 19/07/12.  
<http://jncc.defra.gov.uk/ProtectedSites/SACselection/species.asp?FeatureIntCode=S1365>  
<http://jncc.defra.gov.uk/ProtectedSites/SACselection/species.asp?FeatureIntCode=S1364>
- JNCC. (2010). Accessed 19/07/12.  
<http://jncc.defra.gov.uk/page-1374>
- Lonergan, M, Duck, C, Moss, S, Morris, C & Thompson, D. (Submitted). Harbour seal (*Phoca vitulina*) abundance has declined in Orkney: an assessment based on using ARGOS flipper tags to estimate the proportion of animals ashore during aerial surveys in the moult.
- Lonergan M, Duck CD, Thompson D, Moss S & McConnell B. (2011) British grey seal (*Halichoerus grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. *ICES Journal of Marine Science*. **68**(10):2201-2209.
- Lonergan M, Duck C.D, Thompson D, et al. (2007). Using sparse survey data to investigate the declining abundance of British harbour seals. *J. Zoology*. **271**(3):261-269.
- Matthiopoulos J. (2003) Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos*. **102**(2):367-377.
- Matthiopoulos J, McConnell B.J, Duck C & Fedak M.A.(2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *Journal of Applied Ecology*. **41**(3):476-491.
- McConnell B, Beaton R, Bryant E, Hunter C, Lovell P, Hall A. (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.
- Patterson T.A, McConnell B.J, Fedak M.A, Bravington, M.V, Hindell, M.A. (2010) Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. *Ecology*. **91**(1):273-85.

- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Royer F & Lutcavage M. (2008) Filtering and interpreting location errors in satellite telemetry of marine animals. *Journal of Experimental Marine Biology and Ecology*. **359**(1):1-10.
- Roweis, S and Ghahramani, Z.(1999) A Unifying Review of Linear Gaussian Models. *Neural Computation*. **11**:305-345.
- Russell, D.J.F, Matthiopoulos, J, & McConnell, B.J. (2011) SMRU seal telemetry quality control process. *SCOS Briefing paper (11/17)*.
- Scientific Advice on Matters Related to the Management of Seal Populations (SCOS). (2011). SMRU.
- Sharples, R.J, Moss, S.E, Patterson, T.A & Hammond, P.S. (2012) Spatial Variation in Foraging Behaviour of a Marine Top Predator (*Phoca vitulina*) Determined by a Large-Scale Satellite Tagging Program. *PLoS One*. **7**(5): e37216. doi:10.1371/journal.pone.0037216
- Thompson, P.M, McConnell, B.J, Tollit, D.J, Mackay, A, Hunter, C & Racey, P.A. (1996) Comparative Distribution, Movements and Diet of Harbour and Grey Seals from Moray Firth, N. E. Scotland. *Journal of Applied Ecology*. **3**(6):1572-1584.
- Vincent C, McConnell B.J, Ridoux V, Fedak M.A. (2002) Assessment of Argos Location Accuracy From Satellite Tags Deployed on Captive Gray Seals. *Marine Mammal Science*. **22**(2):223-166.
- Wand, M.P. & Jones, M.C. (1994) Multivariate plugin bandwidth selection. *Comp Statistics*. **9**:97-116.
- Wand, M.P. & Jones, M.C. (1995) Kernel Smoothing. Chapman & Hall. London.
- Wessel, P, and Smith, W.H.F. (1996) A Global Self-consistent, Hierarchical, High-resolution Shoreline Database, *J. Geophys. Res.*, **101**, 8741-8743.
- Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Royal Stat Soc (B)*. **73**(1):3-36.
- Wood, S.N. (2006) Generalized Additive Models: an Introduction with R, CRC.