Modelling harbour seal habitat by combining data from multiple tracking systems

Helen Bailey[1,2,3*] Philip S. Hammond[4] & Paul M. Thompson[2]

[1] SMRU Ltd, New Technology Centre, North Haugh, St Andrews, Fife, KY16 9SR, UK.
[2] University of Aberdeen, Institute of Biological & Environmental Sciences, Lighthouse Field Station, Cromarty, Ross-shire IV11 8YJ, UK.
[3] Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA.
[4] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY16 8LB, Scotland, UK

* Corresponding author: Helen Bailey, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA. Tel: (1) 410-326-7284, E-mail: hbailey@umces.edu

Abstract

Technological developments over the last 20 years have meant that telemetry studies have used a variety of techniques, each with different levels of accuracy and temporal resolution. This presents a challenge when combining data from these different tracking systems to obtain larger sample sizes or to compare habitat use over time. In this study, we used a Bayesian state-space modelling approach to integrate tracking data from multiple tag types and standardize position estimates while accounting for location error. Harbour seal (*Phoca vitulina*) telemetry data for the Moray Firth, Scotland, were collated from three tag types: VHF, Argos satellite and GPS-GSM. Tags were deployed on 37 seals during 1989 to 2009 resulting in 37 tracks with a total of 2,886 tracking days and a mean duration of 87 days per track. A state-space model was applied to all of the raw tracks to provide daily position estimates and a measure of the uncertainty for each position. We used this standardized tracking dataset to model their habitat use and preference, which was then scaled by the population size estimated from haulout counts to give an estimate of the absolute number of harbour seals using different parts of the Moray Firth. As expected for a central place forager, harbour seals most frequently occurred in areas close to their inshore haulout sites. However, our analyses also demonstrated consistent use of offshore foraging grounds, typically within 30 km of haulout sites in waters < 50m deep. The use of these statistical models to integrate and compare different datasets is especially important for assessing longer-term responses to environmental variation and anthropogenic activities, allowing management advice to be based upon datasets that integrate information from all available tracking technologies.

Keywords

Density, habitat preference model, *Phoca vitulina*, spatial ecology, state-space model, and telemetry.

1. Introduction

Technological developments over the last 20 years have meant that telemetry studies have used a variety of techniques, each with different levels of accuracy and temporal resolution (e.g. Costa et al., 2010; Hazen et al., 2012a). This presents a challenge when combining data from these different tracking systems to obtain larger sample sizes or to compare habitat use over time. Such studies are important for making population level inferences and assessing the effects of environmental change. They are also of great benefit to management for informing marine spatial planning, marine protected area designations, and environmental impact assessments.

Radio and acoustic telemetry allows animals tagged with transmitters to be tracked through the use of fixed or portable directional receivers. Radio signals transmit poorly in saltwater, but have been used to track the movements of fish within rivers and streams (David and Closs, 2002; Goclowski et al., 2013; Peters et al., 2006). They have also been used on marine species that regularly return to the surface, such as seabirds and marine mammals (Culik et al., 1998; Read and Gaskin, 1985; Thompson and Miller, 1990). However, these studies were constrained by the need to make contact with the tagged animal at sea and tended to be limited in duration and to more coastal areas. The development of satellite-monitored radio tags, which allows signals to be detected and localised across the globe, has resulted in a much greater understanding of the movements of marine species, particularly farther offshore (e.g. Block et al., 2011). It has also revealed the wide extent of migrations, such as that of sea turtles across entire ocean basins (Hays et al., 2004; Nichols et al., 2000). The low spatial accuracy, with several kilometres error, for many positions at sea received through the ARGOS satellite location system has hindered its use for fine-scale studies, but this is now being overcome through the use of GPS (Global Positioning System) technologies, such as Fastloc and GSM (Global System for Mobile Communications) GPS (Costa et al., 2010; McConnell et al., 2004). These positions may be accurate to within 30 m (Cordes et al., 2011; Hazel, 2009).

Telemetry provides a valuable tool for determining spatial distributions and this can be combined with information on the environment to identify the habitat characteristics attracting animals to those locations. For example, a study combining electronic tagging data from 23 species of marine predators in the North Pacific utilised a state-space modelling framework to account for the location errors from a mixture of tag types (Argos satellite, archival geolocation and pop-up satellite archival tags), which had substantially different levels of spatial accuracy (Block et al., 2011; Winship et al., 2012). A state-space model is a time-series model that predicts the future state of a system from its previous states probabilistically and is being increasingly used in animal movement studies (Jonsen et al., 2013; Patterson et al., 2008). The relative density of predator species based on these modelled locations have been related to oceanographic variables (Block et al., 2011) and used to assess the potential effect of climate change on their distribution (Hazen et al., 2012b). Characterising habitat preferences is important for identifying high-use areas and focusing management efforts for protected species (Bailey and Thompson, 2009; Benson et al., 2011). It also plays a role in the development of habitat-based stock assessment models for fisheries and understanding predator-prey relationships (Nelson et al., 2010; Schaefer et al., 2007; Semmens, 2008).

In this study, we used the state-space model framework for analysis of movement data (Jonsen et al., 2003; 2005; Jonsen et al., 2013) to integrate tracking data for harbour seals (*Phoca vitulina*) from multiple tag types and standardize position estimates while accounting for location error. Broad-scale surveys across Scotland have revealed that harbour seals have declined significantly in most areas (Lonergan et al., 2007). They are resident in the Moray Firth throughout the year, breeding and resting on inter-tidal sandbanks in the inner Moray Firth (Thompson et al., 1996), and making regular foraging trips into the central and outer Moray Firth (Thompson et al., 1998). Protection has mainly focused on the terrestrial haulout sites, but the potential influence of food availability, predation, and competition with fishermen on the population decline has led to increased interest in their foraging areas and spatial distribution at sea (Cordes et al., 2011; Lonergan et al., 2007). Over the last 20 years, several different studies have used tracking devices to study the foraging movements of harbour seals from the Dornoch Firth and Loch Fleet (Cordes et al., 2011; Sharples et al., 2009; Sharples et al., 2012; Thompson et al., 1998; Thompson et al., 1996; Thompson et al., 1997). In this study we analysed the spatial distribution of harbour seals from these tracking studies (VHF, Argos satellite and GPS-GSM telemetry) to determine if there were any changes over time. These data were then related to environmental variables to identify the factors influencing their distribution and to characterize the habitat preferences of harbour seals.

Spatial predictions that incorporate environmental data provide a valuable tool for conservation by quantifying the relative or absolute abundance of animals within contiguous areas that may not have been evenly surveyed or where few observations exist (Cañadas et al., 2005; Forney et al., 2012). We used our habitat preference model and population abundance estimate to predict densities across the Moray Firth. This is of particular relevance to management because two sites have been proposed for offshore wind energy development in the outer Moray Firth and harbour seals are listed under Annex II of the European Commission Habitats Directive (Council Directive 92/43/EEC). This requires the designation of Special Areas of Conservation (SAC), and an assessment of the connectivity between proposed offshore wind energy sites and nearby harbour seal SACs. Our analysis of these telemetry data aimed to provide information on the origin of seals that may be encountered at the proposed wind energy sites, thereby informing assessments of the extent to which far-scale effects, such as construction noise, may overlap with areas used by harbour seals (see Thompson et al. 2013).

2. Materials and methods

2.1 Telemetry data

Telemetry data were available from 37 individual seals that were captured in either Loch Fleet or the Dornoch Firth in Scotland (Figure 1) and tagged between 1989 and 2009 (Table 1). Seals were captured using either hand nets or beach seine nets, and then sedated with ketamine hydrochloride and diazepam or Zoletil. Standard length and girth measurements were taken and the sex identified. The tags were glued to the hair on the head or neck using a fast setting epoxy resin (Fedak et al., 1983). The capture and handling of seals was carried out under licences issued from the Scottish Government and the Home Office. The capture and handling techniques are described in Thompson et al. (1992).

2.1.1 VHF telemetry

Between 1989 and 1991, 21 VHF (Very High Frequency) radio tags were attached to harbour seals to study their behaviour (Thompson et al. 1997) and foraging ecology (Thompson et al., 1998) (Table 1). Subsequent tracking of these individuals was designed to collect one position per day for six days per week. Radio-fixes were made from coastal vantage points with a three-element Yagi aerial using the null average method (Springer, 1979). The accuracy of fixes was estimated using a test transmitter, and the standard deviation of the error between estimated and true bearings used to produce 95% confidence limits for fixes on radio-tagged seals (Thompson and Miller, 1990).

2.1.2 Satellite telemetry

Between 2004 and 2007, 11 satellite relay data loggers (SRDLs) were attached to harbour seals in the Moray Firth as part of a broader study of harbour seal foraging distribution around the UK (Sharples et al., 2009) (Table 1). These SRDLs transmit data via the Argos system (McConnell et al., 1999). Service Argos allocates all positions to one of seven location classes, which describe the quality of those locations. Marine animal tracking studies using Service Argos typically result in low accuracy positions and location errors may be up to several kilometres (Costa et al., 2010).

2.1.3 GPS-GSM telemetry

In 2009, GPS-GSM tags were attached to five harbour seals in the Moray Firth to determine whether recent changes in haulout distribution were linked to changes in foraging area use (Cordes et al., 2011) (Table 1). These GPS-GSM tags combine a GPS sensor with a mobile phone GSM modem to relay data ashore (McConnell et al., 2004). As a result, they are able to produce much more frequent locations, providing a mean of 37 GPS positions per day compared to 10 Argos positions per day. They are also much higher accuracy than Argos locations (Costa et al., 2010). The mean error of GPS positions within a stationary test was 40 m (Hazel, 2009). This is approximately four times greater than the best Argos location quality. Hazel (2009) reported no appreciable directional bias in GPS error, and no significant difference between the latitudinal and longitudinal components of the linear error. Nevertheless, occasional errors may arise, and a 10 km h^{-1} speed filter was therefore applied to the tracks (Costa et al., 2010).

2.2 State-space modelling

The state-space modelling approach was based on the models developed for use with Argos satellite telemetry data (Jonsen et al., 2005; Jonsen et al., 2007). This provides a statistical framework for integrating error in the location estimates with a process model of the movement (Patterson et al., 2008). The only parameters that were changed in the models for each tracking method were the latitude and longitude estimation errors (Winship et al., 2012). For all datasets, the state-space model (SSM) was fitted using the R software package (R Development Core Team, 2008) and WinBUGS software (Lunn et al., 2000). Two chains were run in parallel for each track for a total of 20,000 Markov Chain Monte Carlo (MCMC) samples. The first 10,000 were discarded and the remaining samples were thinned, retaining every fifth sample, resulting in joint posterior distributions for each parameter based on 4,000 samples. In cases where the mean location estimate from the samples occurred on land (other than at haulout sites), we post-processed the SSM location as recommended by Hoenner et al. (2012). We used any nearby high quality Argos locations and the area within the SSM position 95% credible limits to adjust the location to the nearest appropriate position at sea. The application of a switching SSM also allows the animal's behaviour to be inferred (Jonsen et al., 2005; Jonsen et al., 2007). However, the model does not estimate behaviours well on small spatial scales when the data are not at a high temporal resolution (Breed et al., 2011). The majority of our positions were classified by the SSM as area-restricted behaviour, which was probably because of the timescale of the observations and model output relative to the spatial scale of movement, and we therefore did not use these behavioural estimates in our analysis.

For the Argos satellite telemetry data, the model by Jonsen et al. (2005; 2007) was applied to all of the raw Argos satellite positions to obtain daily position estimates and a measure of the uncertainty for each location given by the 95% credibility limits. In this model, we used the calculated parameters of a t-distribution for the latitude and longitude components of estimation by Jonsen et al. (2005). This had been based on published data on Argos location errors for each location class (3, 2, 1, 0, A, B) from captive grey seals tagged with SRDLs (Vincent et al., 2002). Following Jonsen et al. (2005), the estimation error in latitude was $\varepsilon_{i,lat} \sim t\left(0, \tau_{lat,q_i}, \nu_{lat,q_i}\right)$ where τ_{lat,q_i} is the scale parameter and ν_{lat,q_i} is the degrees of freedom for location quality class q for the i^{th} observed position, and similarly for the longitude estimation error.

For the GPS-GSM data, because the rare extreme values had been removed using the speed filter, the SSM error structure was modified from the t-distributions that had been used for each Argos location class (Jonsen et al., 2005) to a normal distribution where $\varepsilon_{i,lat} \sim N(0,\tau_{lat})$ and similarly for longitude (Breed et al., 2012). The accuracy of GPS positions is higher when locations are derived from at least 6 satellites (mean = 32 m, SD = 36.9 m) (Hazel, 2009), which was the case for the majority of locations from the GPS-GSM tagged seals. This information was used to estimate the scale parameters for the GPS errors, which were considered to be equal for latitude and longitude (Hazel, 2009).

For the VHF telemetry data, the SSM error structure was modified in a similar manner to that for the GPS data. A normal distribution was used to approximate the location error and the parameters were based on the error distribution of the 95% confidence limits for fixes. This resulted in a mean linear error of 1.66 km (SD = 0.93 km). However, the mean number of VHF positions per day was only 0.74, i.e. less than one per day. This led to high uncertainty in the output SSM daily positions and we therefore only retained those daily positions that had a corresponding VHF location to ensure that there were no spurious SSM locations.

2.3 Habitat modelling

The 95% credibility limits were used to estimate the uncertainty for each SSM position. Characterisation of these uncertainties was important for determining the scale at which movement could be related to underlying habitat variables (Patterson et al., 2010). The uncertainty in the SSM positions derived from the GPS tracks was very small because of the high frequency and accuracy of the positions, and was below the resolution of the available environmental data. A suitable grid size for averaging the environmental data was therefore chosen based on the median width of the 95% credibility limits for the Argos SSM positions (4.4 km), which had the highest uncertainty of the three tracking methods. Based on this, a grid size of 4 x 4 km was applied to the environmental data and associated with the seal positions in the habitat analysis. Grid cells within 2 km of a haulout site were removed to reduce bias towards locations where the seals were hauled out on land or resting in the water in inshore haul-out areas (Thompson et al., 1998).

The probability of harbour seal occurrence was modelled using a presence-absence approach within each of the 4 x 4 km grid cells. Any cell that contained at least one seal SSM position was coded as 1 for seal presence. Based on the average travel speed and foraging trip duration (Thompson et al., 1998), as well as the maximum duration of the tracks, all of the grid cells within the Moray Firth were considered available habitat. Cells containing no locations were therefore coded as 0 for seal absence.

A generalised additive model (GAM) with a binomial error distribution and logit link function was used to model these data. The environmental variables considered to be likely explanatory variables of seal occurrence were water depth, seabed slope, distance to the nearest haulout site, and seabed sediment type (Figure 2). Water depth and seabed slope were derived from SeaZone Hydrospatial Bathymetry (grid tiles: NW25600020, NW25600040, NW25600060, NW25800040) at a resolution of 6 arcsecond grid (approximately 180 m) and the mean depth and slope within each 4 x 4 km grid cell were calculated in ArcGIS 9.3. Similarly, seabed sediment type was obtained from SeaZone Seabed Sediment (1:250,000 scale, SeaZone Solutions Ltd., UK) as a polygon shapefile and the main sediment type identified within each 4 x 4 km grid cell. The sediment classification derives from that proposed by Folk (1954), which groups grains into mud, sand and gravel based on their size. To simplify the classification, some of the classes have been merged. This resulted in the seabed sediment categories for our grid cells being sandy mud, muddy sand, sand, gravelly sand, sandy gravel, and gravel in order of increasing grain size. When there were small sample sizes for any of these categories they were grouped with the most similar sediment category.

The water depth, seabed slope and distance to nearest haulout site were treated as continuous variables and the sediment type as a categorical variable, where the most common type (sand) was used as the reference level. Visual inspection of distributions was used to determine whether transformations of the variables were necessary or supported the removal of any outliers. Variance inflation factors were used to test for collinearity between the explanatory environmental variables; values were all less than 3, indicating there was no significant collinearity (Zuur et al., 2009). The smoother terms for the continuous variables were derived using penalized regression splines with a shrinkage term so that, for large levels of smoothing, a smoother could have 0 degrees of freedom and be effectively removed from the model (Wood 2006). The model was fitted using the R software (R Development Core Team 2008) and contributed package mgcv (Wood 2006). The GAM output was visually checked for spatial correlation by plotting the residuals against the spatial coordinates. There were no obvious clusters of negative or positive residuals, and no clear clusters of large residuals indicating that there was no significant spatial correlation (Zuur et al., 2009).

Habitat preference can be calculated as the ratio of the use of a habitat to its availability (Aarts et al., 2008). In this second model we used a case/control approach where random control points were generated to represent habitat availability. Control points were generated using the equation for accessibility calculated by Matthiopoulos et al. (2004) as $d^{-1.98}$, where d is the distance from the haulout in units of 5 km. Since we were using grid cells of 4 km, this was modified accordingly to $(0.8*d)^{-1.98}$. Each seal and control location was associated with environmental data from the corresponding 4 x 4 km grid cell. The same environmental variables were used in this method as in the probability of occurrence model.

A generalized estimating equations (GEE) model was applied to determine habitat preference (Bailey et al., 2013; Zeger and Liang, 1986). The correlation among seal locations is likely to differ from the correlation among available control points (Fieberg et al., 2010) and GEEs have the advantage that their parameter estimates and empirical standard errors are robust to misspecification of the correlation structure (Hardin and Hilbe, 2003). They also provide a population averaged inference rather than subject specific (Fieberg et al., 2009). A GEE model was applied with five times the number of control points as seal positions to ensure accurate representation of available habitat (Koper and Manseau, 2009) and an independence working correlation to avoid biased regression parameter estimators (Craiu et al., 2008). A quadratic term for water depth was included following examination of the relationships visually. The model was fitted using the contributed R package geepack version 1.0-17 (Yan and Fine, 2004).

Habitat preferences can vary among seasons as a result of changes in prey availability, activity patterns, and the demands of breeding and moulting (Thompson et al., 1989). The two analyses were therefore performed for both the entire dataset (including all months of the year) and for the subset of the data from the summer breeding period (April to July).

2.4 Harbour seal abundance on land and at sea

Estimates of the size of the Moray Firth harbour seal population were taken from Thompson et al. (1997). This population estimate was based upon breeding season counts at haul-out sites which were then scaled to total population size using telemetry data to estimate the proportion of animals not available to be counted.

To estimate the spatial distribution of harbour seals at sea within the Moray Firth, we combined these abundance data with the output from the model of probability of occurrence for the entire telemetry dataset. The GAM predicted the probability of seal occurrence in each of the 4 x 4 km cells across the Moray Firth. These probabilities were scaled to sum to one and multiplied by the total number of seals in the population, with the assumption that each individual in the population is somewhere at sea within the Moray Firth at any one instant in time. This resulted in an estimate of the number of seals likely to occur within each grid cell. This estimate is conservative in two ways to avoid underestimating the number of seals and consequently the potential impact of any offshore developments. First, we used the average population abundance estimate of 1,653 from 1993 (from Thompson et al. (1997), when the population was at a peak compared with current numbers (Cordes et al., 2011). Second, we assumed that all seals might be foraging at sea at the same time. However, a proportion of the population is hauled out on every low tide throughout the year, and many animals typically remain around haulout sites for several days between offshore foraging trips. As a result the number of seals at sea is likely only 60-90% of the total population, depending both upon season and the age and reproductive status of individual seals (Thompson et al., 1998). Although we do not formally incorporate uncertainty into our density estimate, we aimed to determine the maximum number of seals that could be impacted by the offshore development and hence used this conservative approach.

3. Results

3.1 Harbour seal locations

Tags were deployed during 1989 to 2009 resulting in 37 tracks with a total of 2,886 tracking days and a mean duration of 87 days per track (Table 1, see also Electronic Supplement 1). The SSM-derived daily locations from the seal telemetry data showed a high degree of overlap among the three tag types (Figure 1, see also Electronic Supplement 2), indicating consistency in habitat use among tagging methods and over the

20 year period. The majority of locations occurred near the haulout sites where the seals were tagged in the Dornoch Firth and Loch Fleet. There was also a large number around and to the north of the nearby headland, which has previously been identified as foraging habitat (Thompson et al., 1996; Tollit et al., 1998). The greatest dispersal was shown in the Argos satellite positions, which extended into the northeast part of the Moray Firth. An approximately equal number of males and females were tagged, and there was no significant difference in the distances travelled from the haulout sites between the two sexes (Generalised linear mixed model, with individual tracks as a random effect and male as the reference level for sex: Coefficient = -6.48, SE = 4.96, DF=35, t-value=-1.30, p-value=0.20).

3.2 Probability of occurrence model

Fitting the GAM to the full telemetry dataset revealed that the probability of harbour seal occurrence was significantly related to water depth, seabed slope and distance to nearest haulout , but not to sediment type (Table 2). The probability of seal occurrence was highest at intermediate depths (approximately 15-50 m) and decreased with increasing seabed slope (Figure 3). It was also highest within 30 km of the nearest haulout and declined rapidly beyond 100 km. Predicted probabilities of seal occurrence were highest in the inner Moray Firth, near the coast and in the northeastern part of the Moray Firth, including the proposed offshore wind energy development sites (Figure 4, see also Electronic Supplement 3).

When the GAM was fitted only to locations during the summer breeding period, the probability of harbour seal occurrence was significantly related to water depth and seabed slope (Table 3). Similar relationships were found to those from the year-round full dataset with the probabilities being highest at intermediate depths (approximately 15-50 m) and decreasing with increasing seabed slope. However, the distance to nearest haulout site was no longer statistically significant. In both cases the probability of occurrence was not significantly related to seabed sediment type, but for the year-round full dataset the best model included this variable based on the lowest Akaike's information criterion (AIC) value (Table 4). The predicted probabilities of seal occurrence were lower in the northeastern part of the Moray Firth during the summer breeding period (Figure 5).

3.3 Habitat preference model

The results of the GEE model indicated that harbour seal habitat preference was significantly related to water depth, seabed slope, distance to nearest haulout site, and sediment type (Table 5). Harbour seals significantly preferred the smaller grain size sediment of muddy sand than sand, and had a significantly lower preference for the larger grain sizes of sandy gravel and gravel. Seals preferred mid-water depths, shallow slopes and distances farther from the haulout sites compared to the distribution of control points within the study area. Habitat preference was highest in the northeastern part of the Moray Firth and also in small areas of the southeastern region (Figure 6).

The results of the GEE model for the summer breeding period indicated that harbour seal habitat preference was similarly significantly related to water depth, seabed slope, distance to nearest haulout site, and sediment type (Table 6). However, the preferred sediment types differed from that identified for the year-round full telemetry dataset. Seals significantly preferred sand over the smaller grain sizes of sandy mud and the larger grain sizes within sandy gravel and gravel sediment. They also still preferred distances farther from the haulout sites compared to the distribution of control points, but not as great as for the full dataset.

3.4 Harbour seal abundance at sea

At-sea density estimates based on the probability of occurrence model indicate that harbour seals from this population may be dispersed widely across the Moray Firth, particularly over offshore sandbanks (Figure 7). These density estimates suggest that there is variability in the importance of different parts of the sites identified for offshore wind energy development. Using the population estimate of 1,653 from 1993, when abundance was the highest over the last two decades, it was estimated that some grid cells could hold up to 7 seals, representing a density approaching 0.5 individuals per km^2.

Discussion

Telemetry data provide spatially explicit information on animal distributions and movements that can facilitate understanding their role in various ecological and evolutionary processes, as well as the impacts of anthropogenic activities (Nathan et al., 2008). In this study we integrated telemetry data from multiple tracking systems (VHF, Argos satellite and GPS-GSM) within a state-space modelling framework (Jonsen et al., 2003; 2005; Jonsen et al., 2013) to estimate habitat usage. It is typical in telemetry studies that financial and logistical constraints limit the number and type of tags that may deployed. Incorporating data from other sources allows a larger sample size to be obtained from a greater number of individuals and over a longer time period. These larger datasets may then be sufficiently representative to make inferences about the spatial distribution of the entire population, which provides valuable information for management and conservation (Matthiopoulos et al., 2004). Estimating spatially explicit densities is a critical component of assessing the number of individuals that may be impacted by anthropogenic activities and subsequently translating this into changes in fecundity and survival to predict longer-term population level impacts (Thompson et al., 2013). The calculation of absolute densities from telemetry data still requires an assessment of population abundance from other data sources. There has also been concern that the locations of tracked animals may be biased towards the tag deployment location, particularly for highly mobile species. However, statistical methods for accounting for this starting location bias in density estimates are now being developed (Whitehead and Jonsen, 2013).

Habitat preference models have been developed for many marine mammal species and is also beginning to play an important role in fisheries. This is both for the target species, through the development of habitat-based stock assessment models (Bigelow et al., 2002), and for non-target species by assessing bycatch risk (Žydelis et al., 2011), and the development of tools for bycatch reduction (Howell et al., 2008). As the amount of tracking data continues to grow, this source of data will be able to play an increasingly important role in the development of such models. Such data could also provide information on horizontal and vertical behaviours, that are often not available from other surveying methods, further informing our understanding of marine species habitat preferences and interactions with human activities.

Although different technologies have been used to track harbour seals in the Moray Firth over time, the state-space modelled daily positions indicated that there was high spatial overlap in habitat use among the three tracking methods (Figure 1). This suggests that harbour seal habitat use at sea has remained relatively similar over the 20 year period from 1989 to 2009, despite changes in abundance and distribution at breeding sites (Cordes et al., 2011). The VHF fixes were collected by triangulation from receivers on land and, unlike those from the Argos and GPS-GSM tags, were potentially constrained in their offshore extent. However, locations were still obtained on nearly all of the days for which radio fixes were attempted (Thompson et al., 1996), indicating that the seals occurred mainly within the detection range (Thompson and Miller, 1990).

All three tracking technologies indicated high use off the headland near the haulout sites in the Dornoch Firth and Loch Fleet. The area off this headland was previously identified as a high-use area and foraging habitat during both the early VHF tracking studies (Thompson et al., 1996; Tollit et al., 1998) and boat-based visual surveys (Bailey and Thompson, 2009). Our study confirms that this has persisted over time as an important foraging area. The currents around this headland combined with the sandy seabed sediment favourable for their prey, such as sandeels, may create a consistently profitable foraging ground close to the haulout site explaining its high use. The interactions between tidal currents and topographic features, such as channels and headlands, can increase the foraging success of marine predators (Zamon, 2001). Harbour seals in San Francisco Bay mainly foraged near their primary haulout sites in a narrow, deep channel (Grigg et al., 2012).

The central and northeast Moray Firth was another area of high probability of harbour seal occurrence and preferred habitat. This is also a core area for another predator, the harbour porpoise (Brookes et al., 2013). These offshore areas, farther from the haulout sites, were used more frequently than expected. However, they have a high proportion of sandy sediment with which harbour seals have been associated in other studies (e.g. Grigg et al., 2012; Härkönen, 1988). This makes it suitable habitat for the prey species sandeels and whiting (Atkinson et al., 2004; Holland et al., 2005; Tollit et al., 1998). A strong relationship has been found between the abundance of benthic prey species and the space use of harbour seals (Grigg et al., 2012). Harbour seals tracked in the western Hudson Bay tended to occur in water depths of less than 50 m and 95% of their dives were < 40 m deep (Bajzak et al., 2013).

Harbour seals, like several other pinniped species, are central place foragers, requiring haulout sites on land for resting, moulting and breeding, and dispersing from these sites to forage at sea. This limits their foraging range and, to reduce time and energy searching for prey, animals are likely to travel directly to areas of previously or predictably high foraging success where they will exhibit area-restricted search behaviour. Such behaviour has been observed in seabirds, which tend to be central place foragers during the breeding season (Pinaud and Weimerskirch, 2007). For example, northern gannets (*Morus bassanus*) during the breeding season in the western North Sea targeted particular regions for foraging, within which they searched more intensively and then commenced diving indicating prey detection (Hamer et al., 2009). The requirement for females to regularly return to their pups at the haulout site may have limited the distance they could travel and reduced their use of the outermost parts of the Moray Firth (Figure 5a). The constraint on their foraging range means that harbour seals, particularly during the breeding season, will be vulnerable to changes in prey abundance or disturbance events from human activities that could consequently impact their reproductive success (Hamer et al., 2007).

The probability of occurrence for both the entire year and only during the summer breeding season was high in the area overlapping with the proposed sites of the offshore wind energy developments. These sites were chosen in part because the wind turbines are limited by the water depth with current technologies, with the maximum depth of installation being approximately 40-50 m (Bailey et al., 2010). The noise from construction of offshore wind farms has been identified as a potential threat to harbour seals (Bailey et al., 2010; Kovacs et al., 2012) and nearshore developments have been found to affect haulout behaviour (Edrén et al., 2010; Teilmann et al., 2006). However, their behavioural reactions at sea to such sounds are still not well known (Southall et al., 2007; Tougaard et al., 2009), and the potential longer-term effects are only just beginning to be explored (Thompson et al., 2013).

In this study we used the average abundance estimate from 1993 (Thompson et al., 1997) to estimate the number of seals in each grid cell. The population has declined since then (Cordes et al., 2011) and our density estimates may therefore be an overestimate. The approach we used allows a range of density values to be easily calculated from different population abundance estimates, and for these to be updated when new abundance estimates are available in the future. In this study we chose a precautionary approach as the most appropriate to avoid underestimating the number of seals and consequently the inferred potential impacts of any human activities. These density estimates provide important information for management, and for environmental impact assessments for proposed developments and activities where it is necessary to know the number of animals that are expected to be in the area and that could potentially be harmed or disturbed (Forney et al., 2012; Thompson et al. 2013).

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Table 1: Summary of harbour seal telemetry data in the Moray Firth, Scotland. Telemetry techniques used were very high frequency (VHF) radio tracking, Argos satellite, and a Global Positioning System (GPS) sensor combined with a mobile phone Global System for Mobile Communications (GSM) modem to relay data ashore.

Tag type	**Deployment years**	**Number of tags**	**Mean duration (days)**	**Tracked months**[a]	**Sex ratio (Male:Female)**
VHF	1989-1991	21	58	May-Jul, Oct-Feb	12:9
Argos satellite	2004-2007	11	109	Mar-Jul, Sep-Apr	6:5
GPS GSM	2009	5	95	Apr - Aug	0:5
Total/Mean		**37**	**87**		**18:19**

[a] Months for which tracking data was available beginning with the time of deployment, which occurred in the spring and autumn.

Table 2: Results of the generalised additive model (GAM) for probability of harbour seal occurrence in relation to square root of water depth, square root of seabed slope, distance to nearest haulout and seabed sediment type (reference level: sand). An asterisk denotes statistical significance at 5% level and edf is the estimated degrees of freedom.

Smoother term:	**edf**	**Chi-square**	**P value**	**Overall deviance explained**
Depth	4.30	61.06	< 0.001*	35.2%
Slope	1.51	24.83	< 0.001*	
Distance to nearest haulout	6.47	16.48	0.021*	
Parametric coefficients:	**Estimate**	**Z value**	**P value**	
Intercept	-1.64	-6.24	< 0.001*	
Sediment - Muddy sand or sandy mud	0.16	0.39	0.693	
Gravelly sand	0.55	1.96	0.051	
Gravel or sandy gravel	-0.50	-1.41	0.160	

Table 3: Results of the generalised additive model (GAM) for probability of harbour seal occurrence during the summer breeding period (April to July) in relation to square root of water depth, square root of seabed slope, distance to nearest haulout and seabed sediment type (reference level: sand). An asterisk denotes statistical significance at 5% level and edf is the estimated degrees of freedom.

Smoother term:	**edf**	**Chi-square**	**P value**	**Overall deviance explained**
Depth	4.37	39.86	< 0.001*	37.7%
Slope	2.53	23.01	< 0.001*	
Distance to nearest haulout	4.68	10.65	0.065	
Parametric coefficients:	**Estimate**	**Z value**	**P value**	
Intercept	-2.82	-7.41	< 0.001*	
Sediment – Muddy sand or sandy mud	-0.15	-0.35	0.729	
Gravelly sand	0.02	-0.06	0.956	
Gravel or sandy gravel	-0.79	-1.72	0.086	

Table 4: Akaike's information criterion (AIC) values for candidate generalised additive models (GAM) for probability of harbour seal occurrence for the full year-round dataset and during the summer breeding period (April to July) in relation to square root of water depth, square root of seabed slope, distance to nearest haulout and seabed sediment type (reference level: sand). An asterisk denotes the lowest AIC value and hence the best model.

Candidate model	**Full year-round dataset**	**Summer breeding period**
s(Depth)	663.10	471.51
s(Depth)+s(Slope)	638.32	447.43
s(Depth)+s(Slope)+s(Distance to nearest haulout)	614.38	425.66*
s(Depth)+s(Slope)+s(Distance to nearest haulout)+Seabed Sediment Type	609.39*	427.69

Table 5: Results of generalised estimating equations (GEE) model for harbour seal foraging habitat preference in relation to square root of water depth, square root of seabed slope, logarithm (to the base 10) of distance to nearest haulout and seabed sediment type (reference level: sand). An asterisk denotes statistical significance at 5% level.

Term	**Estimate**	**Standard Error**	**Wald Statistic**	**P-value**
Intercept	-9.43	1.41	44.54	< 0.001*
Depth	2.04	0.46	19.22	< 0.001*
Depth^2	-0.21	0.04	29.77	< 0.001*
Slope	-1.43	0.33	18.80	< 0.001*
Distance to nearest haulout	3.86	0.54	51.27	< 0.001*
Sediment –Sandy mud	-0.08	0.72	0.01	0.908
Muddy sand	0.56	0.25	5.19	0.023*
Gravelly sand	-0.36	0.23	2.38	0.123
Sandy gravel	-1.31	0.45	8.47	0.004*
Gravel	-0.96	0.31	9.39	0.002*

Table 6: Results of the generalised estimating equations (GEE) model for harbour seal foraging habitat preference during the summer breeding period (April to July) in relation to square root of water depth, square root of seabed slope, logarithm (to the base 10) of distance to nearest haulout and seabed sediment type (reference level: sand). An asterisk denotes statistical significance at 5% level.

Term:	Estimate	Standard Error	Wald Statistic	P-value
Intercept	-9.79	2.49	15.48	< 0.001*
Depth	2.46	0.80	9.46	0.002*
Depth^2	-0.25	0.07	13.66	< 0.001*
Slope	-1.45	0.51	8.16	0.004*
Distance to nearest haulout	3.28	0.74	19.91	< 0.001*
Sediment – Sandy mud	-39.26	2.79	198.35	< 0.001*
Muddy sand	0.57	0.31	3.36	0.067
Gravelly sand	-0.76	0.42	3.26	0.071
Sandy gravel	-2.04	0.49	17.36	< 0.001*
Gravel	-1.91	0.48	15.85	< 0.001*

Figure Legends

Figure 1: Daily harbour seal state-space model (SSM) locations derived from Argos satellite (red), GPS (green), and VHF (blue) positions (circles). The haulout sites are shown as black circles.

Figure 2: Environmental variables summarized within 4 x 4 km grid cells for a) water depth, b) seabed slope, and c) seabed sediment type.

Figure 3: Generalised additive model (GAM) smoothing curves for square root of water depth (m), square root of seabed slope (degrees), and distance to nearest haulout (km) in relation to probability of seal occurrence.

Figure 4: a) Harbour seal presence from state-space model (SSM) daily positions in 4 x 4 km grid cells shown in red, and b) Generalised additive model (GAM) predicted probabilities of seal occurrence (white cells indicate no data). The two proposed offshore wind energy development sites are overlaid as solid black lines and the haulout sites as black circles.

Figure 5: a) Harbour seal presence from state-space model (SSM) daily positions during the summer breeding period (April to July) in 4 x 4 km grid cells shown in red, and b) Generalised additive model (GAM) predicted probabilities of seal occurrence (white cells indicate no data). The two proposed offshore wind energy development sites are overlaid as solid black lines and the haulout sites as black circles.

Figure 6: a) Map of harbour seal SSM daily positions and control points in 4 x 4 km grid cells, with data within 2 km of a haulout site removed from the analysis, and b) Generalised estimating equations (GEE) predicted values of foraging habitat preference (white cells indicate no data). The two proposed offshore wind energy development sites are overlaid as solid black lines.

Figure 7: Predicted numbers of harbour seals from Moray Firth haulout sites within 4 x 4 km grid cells across the Moray Firth. The two proposed offshore wind energy development sites are overlaid as solid black lines and the haulout sites as black circles.

Figure 1

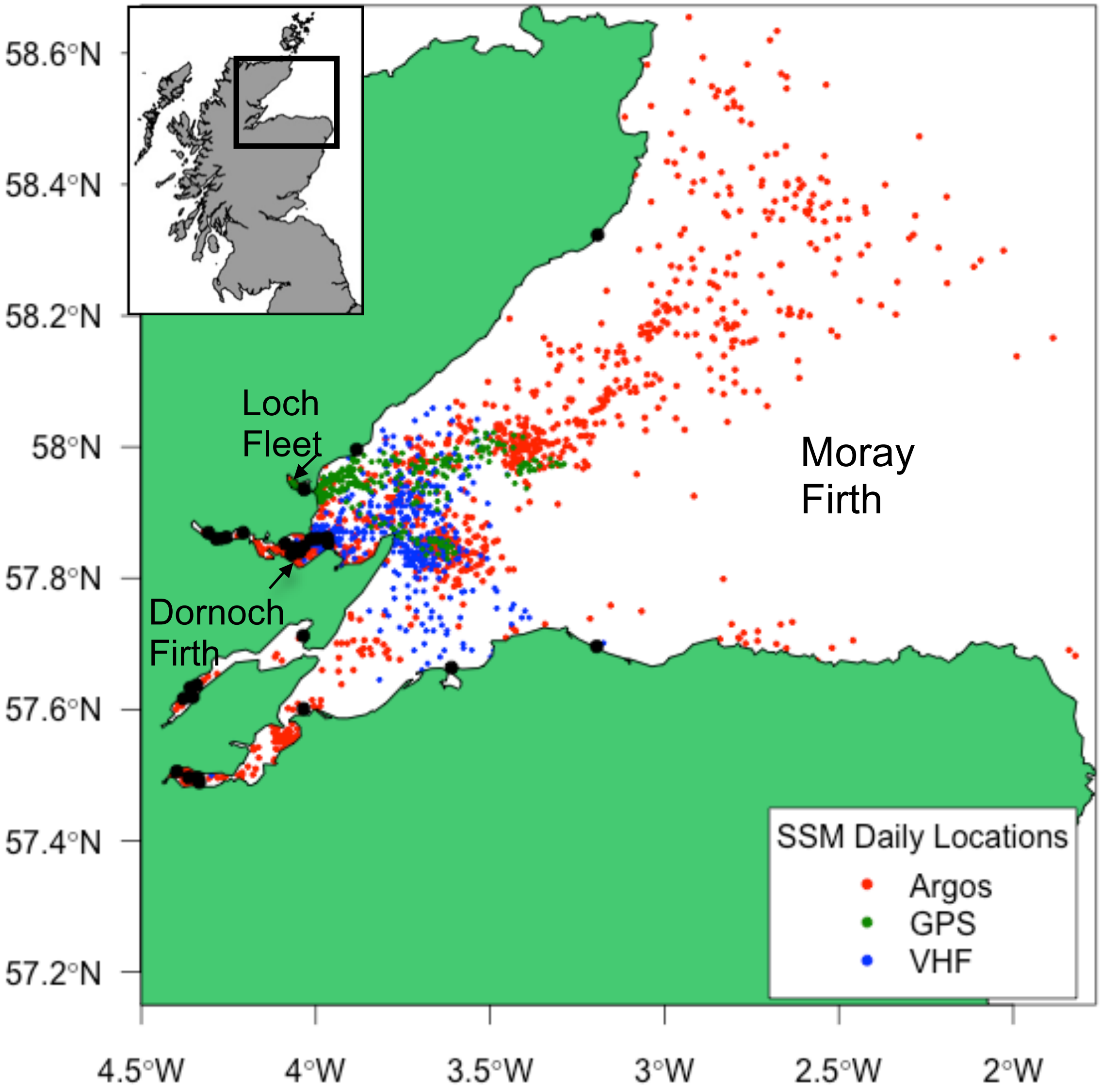

58.6°N
58.4°N
58.2°N
58°N
57.8°N
57.6°N
57.4°N
57.2°N
4.5°W
4°W
3.5°W
3°W
2.5°W
2°W
Loch Fleet
Dornoch Firth
Moray Firth
SSM Daily Locations
Argos
GPS
VHF

Figure 2

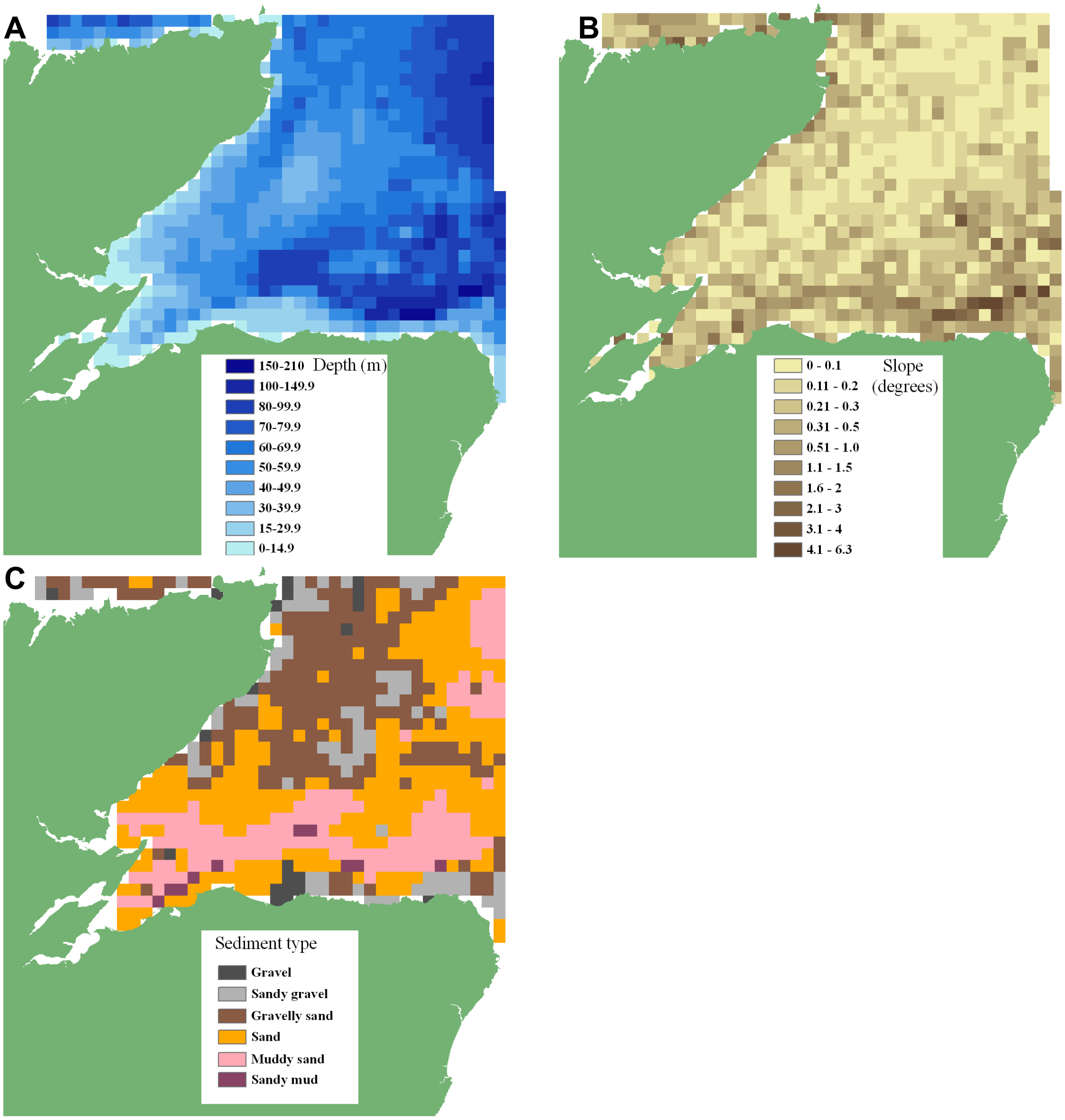

A
150-210
Depth (m)
100-149.9
80-99.9
70-79.9
60-69.9
50-59.9
40-49.9
30-39.9
15-29.9
0-14.9
B
0 - 0.1
Slope (degrees)
0.11 - 0.2
0.21 - 0.3
0.31 - 0.5
0.51 - 1.0
1.1 - 1.5
1.6 - 2
2.1 - 3
3.1 - 4
4.1 - 6.3
C
Sediment type
Gravel
Sandy gravel
Gravelly sand
Sand
Muddy sand
Sandy mud

Figure 3

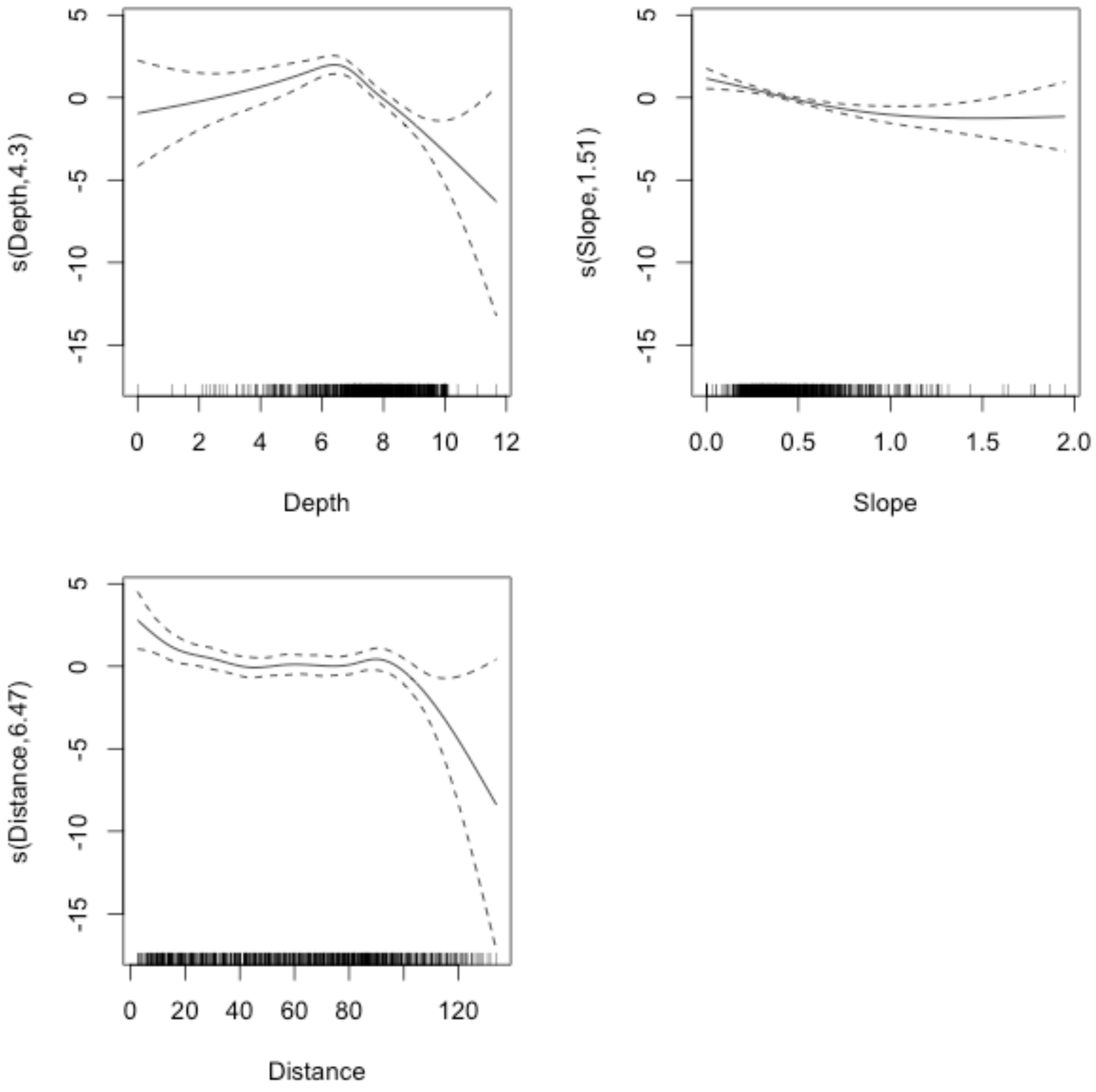

s(Depth,4.3)
5
0
-5
-10
-15
0
2
4
6
8
10
12
Depth
s(Slope,1.51)
5
0
-5
-10
-15
0.0
0.5
1.0
1.5
2.0
Slope
s(Distance,6.47)
5
0
-5
-10
-15
0
20
40
60
80
120
Distance

Figure 4

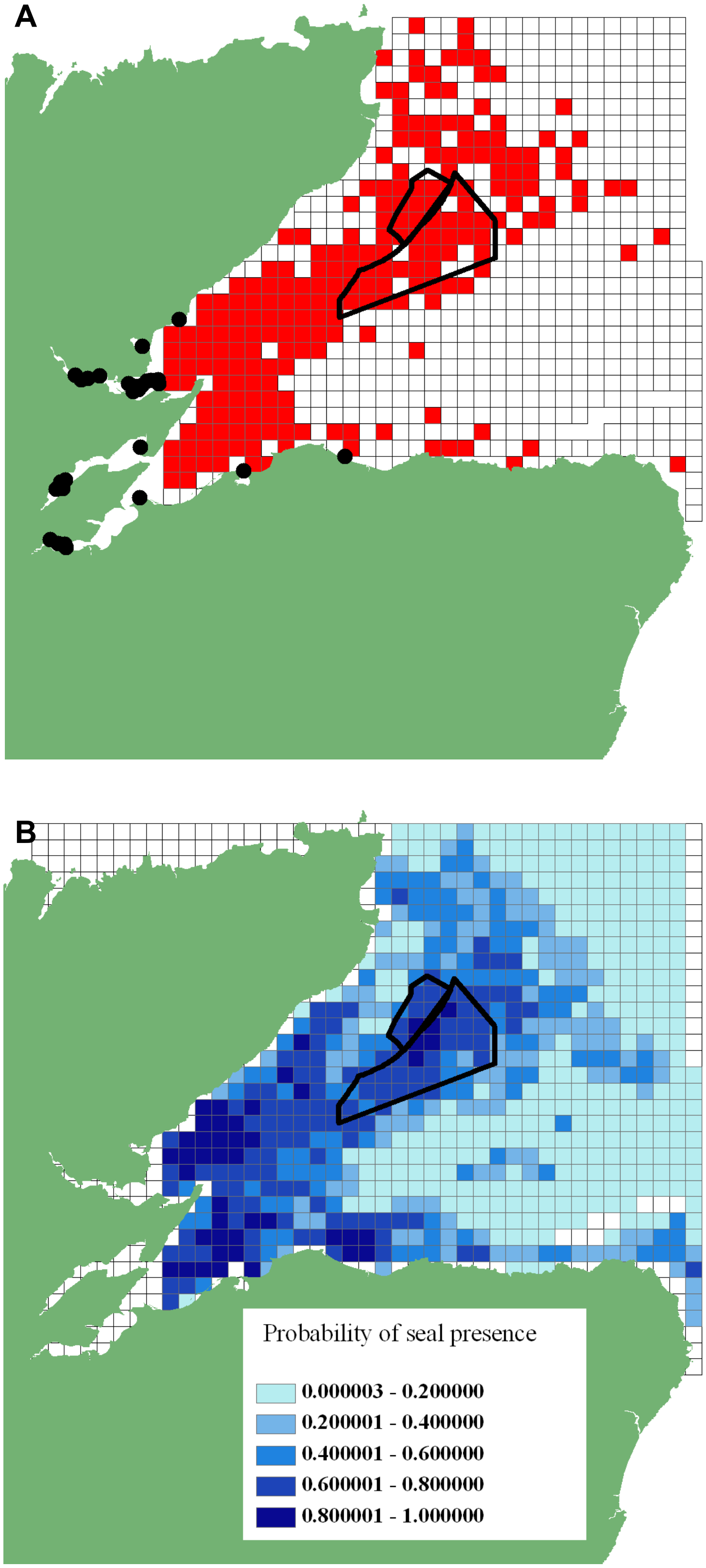

A
B
Probability of seal presence
0.000003 - 0.200000
0.200001 - 0.400000
0.400001 - 0.600000
0.600001 - 0.800000
0.800001 - 1.000000

Figure 5

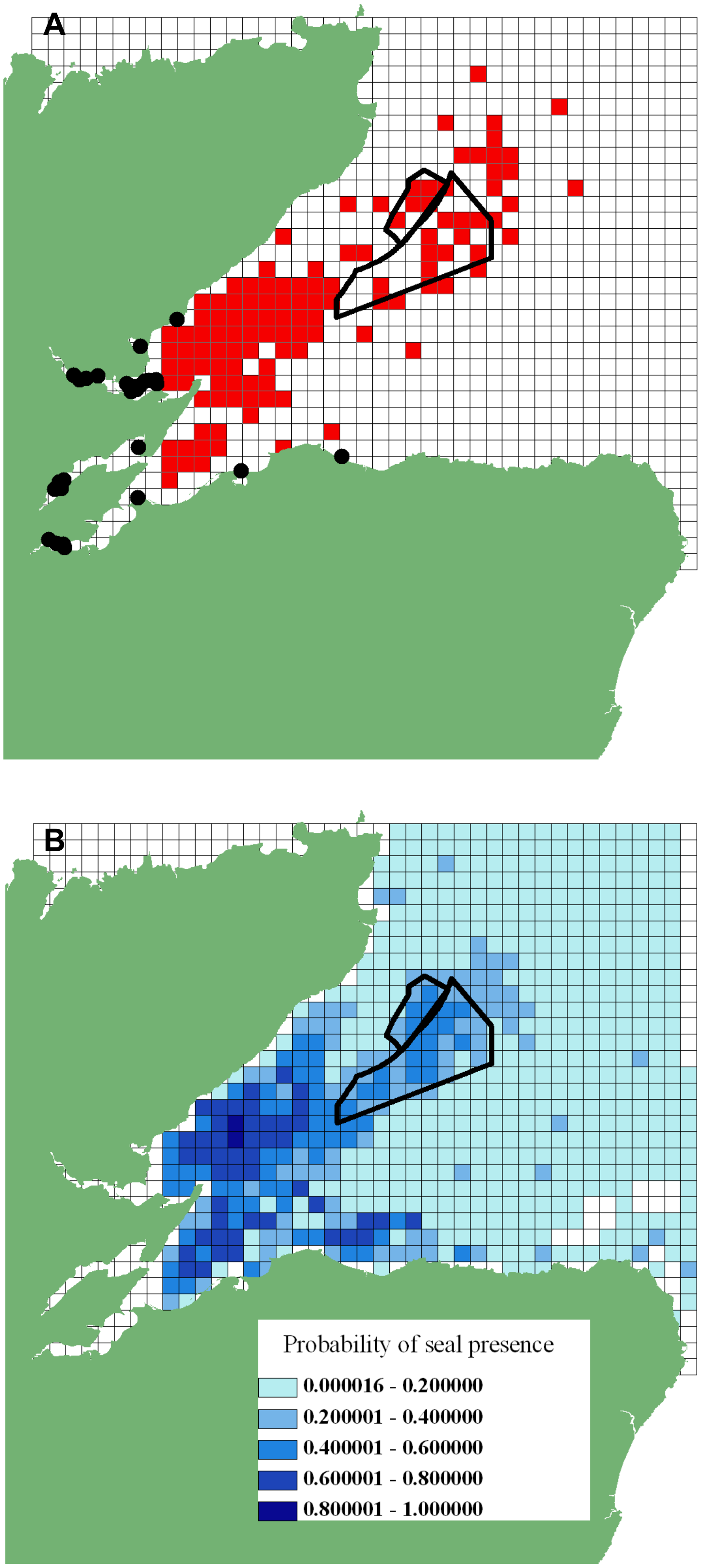

A
B
Probability of seal presence
0.000016 - 0.200000
0.200001 - 0.400000
0.400001 - 0.600000
0.600001 - 0.800000
0.800001 - 1.000000

Figure 6

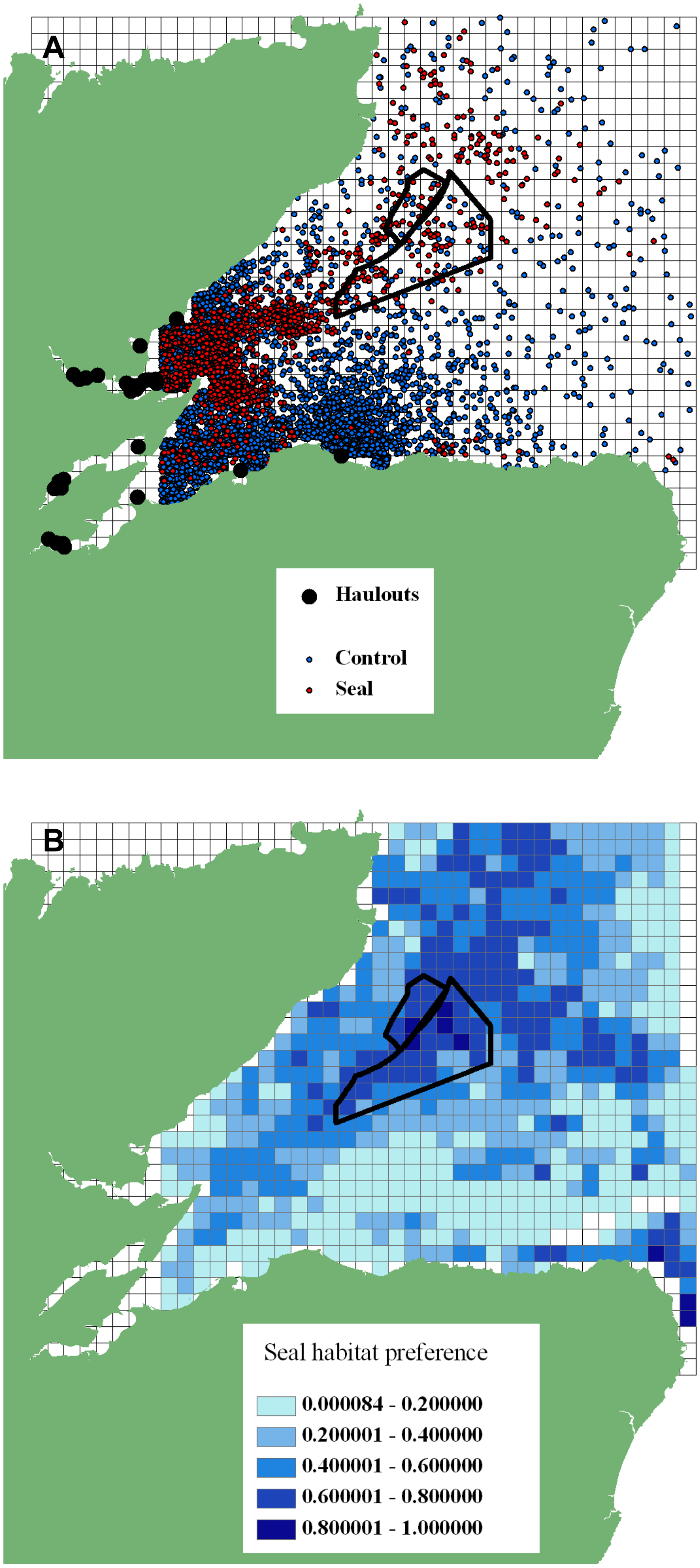
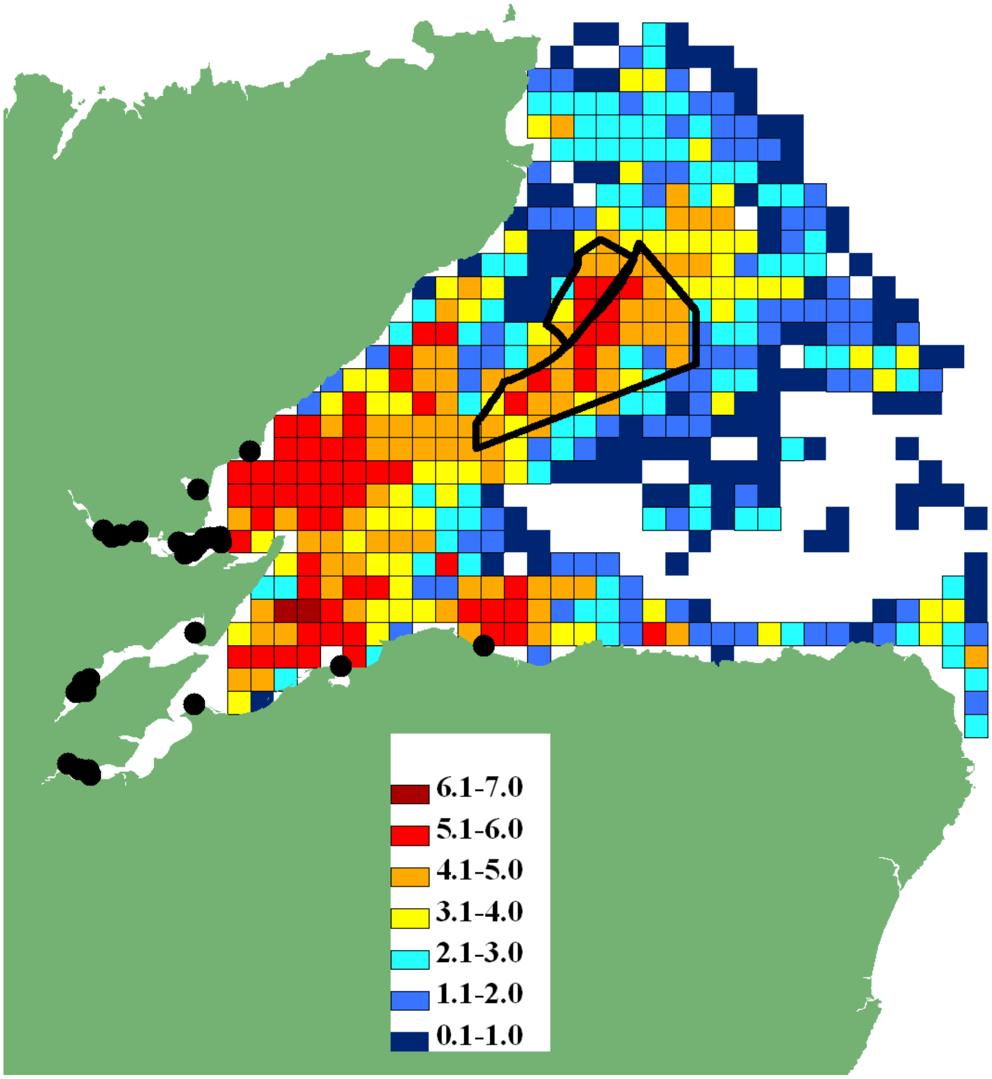

A
● Haulouts
● Control
● Seal
B
Seal habitat preference
0.000084 - 0.200000
0.200001 - 0.400000
0.400001 - 0.600000
0.600001 - 0.800000
0.800001 - 1.000000

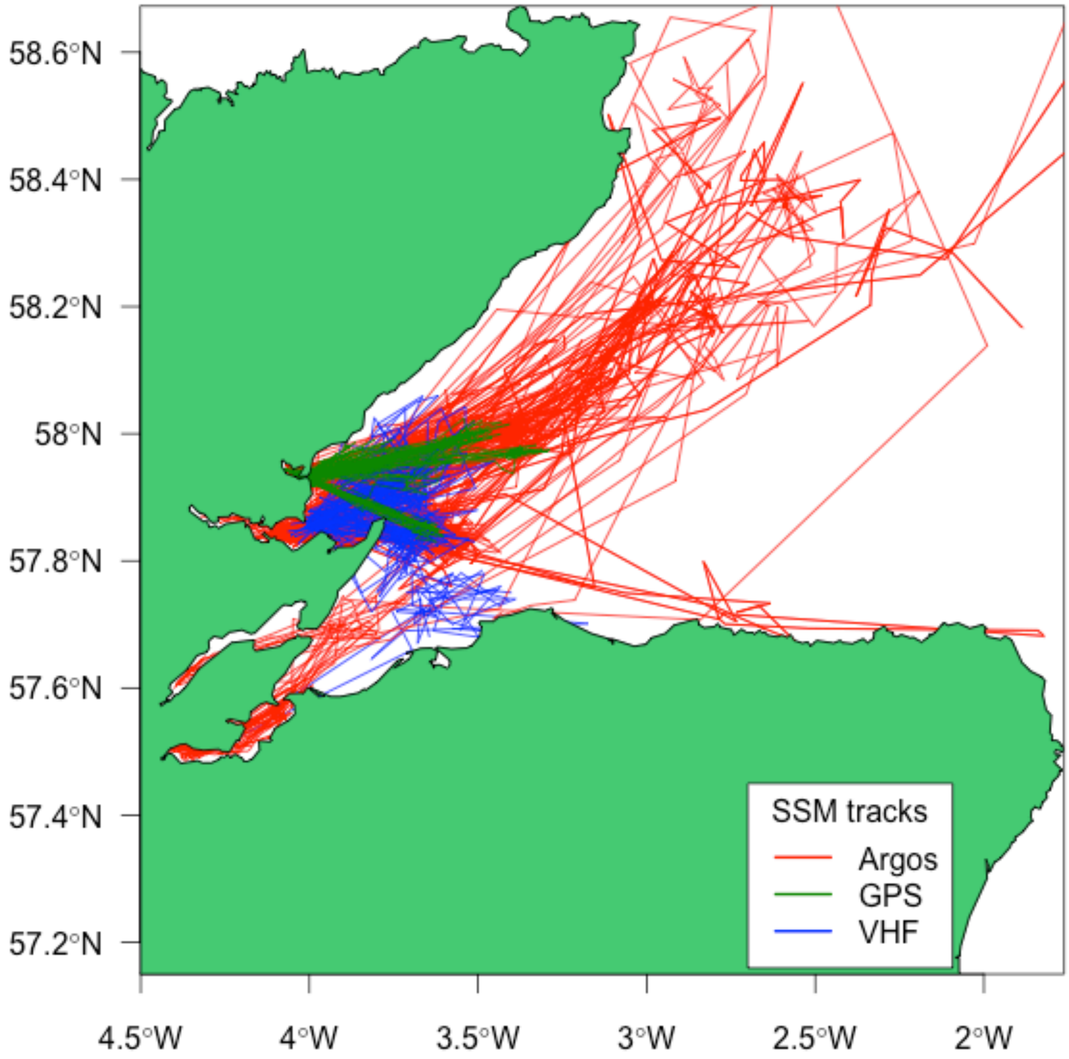
Figure 7



Electronic Supplement 1. Harbour seals tracked in the Moray Firth, Scotland.

Deployment year	Tag ID	Sex	Weight (kg)	Data type	Data start	Data end	# Days
1989	108	F	79	VHF	31/05/1989	29/07/1989	60
1989	100	F	90.5	VHF	01/06/1989	29/07/1989	59
1989	101	F	93.5	VHF	01/06/1989	29/07/1989	59
1989	102	F	89.5	VHF	01/06/1989	29/07/1989	59
1989	103	F	74.5	VHF	01/06/1989	08/07/1989	38
1989	107	F	89.5	VHF	01/06/1989	29/07/1989	59
1989	70	F	59	VHF	30/10/1989	30/11/1989	32
1989	140	M	73	VHF	30/10/1989	06/02/1990	100
1989	131	M	66	VHF	31/10/1989	18/01/1990	80
1989	132	M	77.5	VHF	31/10/1989	06/02/1990	99
1989	133	F	66	VHF	31/10/1989	06/02/1990	99
1991	179	M	55.5	VHF	28/05/1991	05/07/1991	39
1991	180	M	85	VHF	28/05/1991	31/07/1991	65
1991	181	M	58.5	VHF	28/05/1991	29/06/1991	33
1991	183	M	56	VHF	28/05/1991	06/07/1991	40
1991	184	M	81.7	VHF	28/05/1991	27/07/1991	61
1991	185	M	57	VHF	28/05/1991	08/07/1991	42
1991	193	M	55.5	VHF	28/05/1991	06/07/1991	40
1991	194	M	88	VHF	28/05/1991	23/07/1991	57
1991	198	M	88.5	VHF	28/05/1991	17/07/1991	51
1991	199	F	95	VHF	03/06/1991	31/07/1991	59
2004	43861	M	78	SRDL	29/09/2004	16/11/2004	49
2004	43866	M	78	SRDL	29/09/2004	09/12/2004	72
2004	43867	M	77	SRDL	29/09/2004	02/04/2005	186
2004	43864	F	60	SRDL	16/10/2004	13/03/2005	149
2004	43868	M	68	SRDL	16/10/2004	14/03/2005	150
2005	33185	F	71	SRDL	05/03/2005	23/05/2005	80
2005	33257	M	70	SRDL	05/03/2005	06/04/2005	33
2005	33869	F	79	SRDL	05/03/2005	28/07/2005	146
2005	33255	F	80	SRDL	06/03/2005	23/06/2005	110
2005	33843	M	87.5	SRDL	06/03/2005	13/07/2005	130
2007	26629	F	61	SRDL	01/03/2007	13/06/2007	105
2009	44281081	F	81.8	GPS-GSM	14/04/2009	07/06/2009	55
2009	44494740	F	61.2	GPS-GSM	14/04/2009	19/07/2009	97
2009	44671242	F	82	GPS-GSM	14/04/2009	17/07/2009	95
2009	44542657	F	78	GPS-GSM	14/04/2009	26/07/2009	104
2009	44671246	F	80.8	GPS-GSM	14/04/2009	22/08/2009	131

Electronic Supplement 2. Harbour seal tracks connecting daily state-space model (SSM) locations derived from Argos satellite (red), GPS (green), and VHF (blue) telemetry.



Electronic Supplement 3. Map of the standard error of the predictions from the generalised additive model (GAM) of seal occurrence (white cells indicate no data).