Updated Habitat-Based At-Sea Distribution Maps for Harbour and Grey Seals in Scotland

February 2025

Scottish Government
Riaghaltas na h-Alba

Updated habitat-based at-sea distribution maps for harbour and grey seals in Scotland

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Suggested citation:

Carter, M. I. D, Bivins, M., Duck, C. D., Hastie, G. D., Morris, C. D., Moss, S. E. W., Thompson, D., Thompson, P. M., Vincent, C., Russell, D. J. F. (2025) Updated habitat-based at-sea distribution maps for harbour and grey seals in Scotland. Sea Mammal Research Unit, University of St Andrews, Commissioned Report to Scottish Government.

At time of publishing, a manuscript (Carter et al.) is in preparation that will feature this work. Please check the Marine Scotland data portal and search "Updated habitat-based at-sea distribution maps for harbour and grey seals in Scotland ". A link to the publication will be available on the dataset landing page once published. It is recommended to cite the peer-reviewed paper where possible.

This work was funded as part of the Scottish Government's Scottish Marine Energy Research programme (ScotMER), with additional funding from NatureScot, the Department for Energy Security and Net Zero (DESNZ), the INSITE EcoSTAR project (Natural Environment Research Council; NE/T010614/1), and NERC National Capability – National Public Good funding (NE/R015007/1). Data used in this analysis have been funded by a number of different organisations; for a comprehensive list of funders please see the Acknowledgements section.

While every effort has been made to make this publication accessible to all, some sections may remain inaccessible due to the nature of the content. If you are unable to access any content you require, please contact ScotMER@gov.scot

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List of Acronyms

- AR1: First-order Autoregressive (correlation structure)
- ARGOS: Advanced Research and Global Observation Satellite
- DESNZ: Department for Energy Security and Net Zero
- ECOPredS: Ecological Consequences of Orca Predation on Seals
- EcoSTAR: Ecosystem-level importance of STructures as Artificial Reefs
- EMODnet: European Marine Observation and Data Network
- GAMM: Generalized Additive Mixed Model
- GIS: Geographic Information Service
- GPS: Global Positioning System
- GRASS-GIS: Geographic Resources Analysis Support System
- GSM: Global System for Mobile Communications
- GUI: Graphical User Interface
- INSITE: Influence of man-made Structures In The Ecosystem
- LCL: Lower Confidence Limit
- MD-LOT: Marine Directorate – Licensing Operations Team (Scottish Government)
- NERC: Natural Environment Research Council
- ODaT: Ocean Data Tool
- OFB: l'Office Français de la Biodiversité
- PEA: Potential Energy Anomaly
- SAC: Special Area of Conservation
- SCOS: Special Committee on Seals
- ScotMER: Scottish Marine Energy Research programme
- SMRU: Sea Mammal Research Unit
- SST: Sea Surface Temperature
- UCC: University College Cork
- UCL: Upper Confidence Limit

Executive Summary

Scotland is a globally important population centre for both harbour (*Phoca vitulina*) and grey seals (*Halichoerus grypus*). Up-to-date estimates of at-sea distribution are an important resource for marine spatial planning, particularly given the projected scale of decommissioning of oil and gas infrastructure and construction of offshore wind farms in Scottish waters in coming years. Previous distribution estimates were limited by a lack of tracking data for both species in Shetland, and estimates for Shetland were therefore made based on modelled habitat preference relationships of seals tagged in Orkney and the north coast of mainland Scotland. To address this knowledge gap, GPS satellite telemetry devices were deployed on harbour and grey seals in Shetland in 2022, funded by the Scottish Government Marine Directorate, NatureScot and the Department for Energy Security and Net Zero (DESNZ). The Scottish Government Marine Directorate funded the incorporation of these new harbour seal tracking data (Fig. 3), and recent haulout counts to update at-sea density estimates for harbour seals. Here we present updated at-sea distribution maps for both harbour and grey seals hauling out in Scotland, taking advantage of various improvements to the existing methods (Carter et al., 2022) funded by NERC INSITE II project EcoSTAR (with support from NERC National Capability - National Public Good funding). These updated maps are generated using regional habitat preference relationships derived from the new tracking data, in combination with previously used tracking data and the most recent available estimates of seal abundance (haulout counts). The downloadable content associated with this report is a series of Geographic Information Service (GIS) data layers with relative (percentage of at-sea population) and absolute (number of animals) estimates of harbour and grey seal at-sea density on a 5 km by 5 km grid for seals hauling out in Scotland.

1. Introduction

1.1. General Background

Scotland hosts approximately 85% and 80% of the UK's harbour and grey seals, respectively (SCOS, 2022), making it an important population centre for both species. Regular monitoring of population trajectories has revealed complex regional dynamics. Grey seal numbers are generally stable or increasing throughout Scotland (Russell et al., 2022). However, harbour seal numbers are increasing in West Scotland and the Western Isles, while catastrophic declines have been experienced in the last two decades in Orkney and East Scotland (Russell et al., 2022). Harbour seal numbers in Shetland appear to be stable, despite having experienced a decline of > 30% since the early 2000s (Russell et al., 2022) (Fig. 1). However, this trend is not equal across the two Special Areas of Conservation (SACs) designated for harbour seals in Shetland; numbers are stable in the Yell Sound Coast SAC, but severely depleted and continuing to decline at ~22% per annum in the Mousa SAC (Russell et al., 2022) (Fig. 1). Indeed, the most recent count of harbour seals hauled out during the annual moult in 2019 recorded just seven individuals in the Mousa SAC; a decline of > 95% since 1991 (Russell et al., 2022).

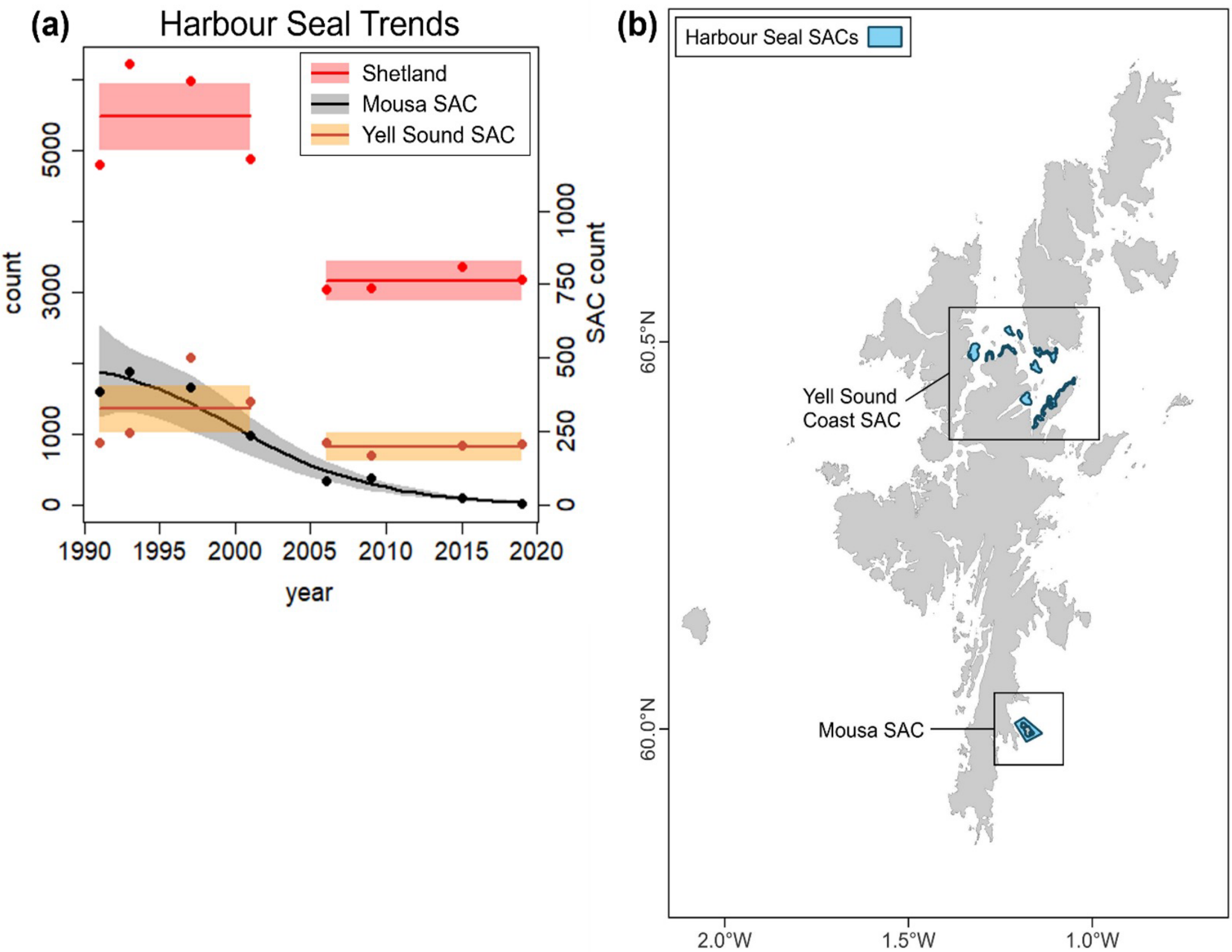

Figure 1: Trends in harbour seal abundance in Shetland during the annual moult. Lines, shaded areas and points (a) represent harbour seal population trends, 95% confidence intervals and counts for Shetland as a whole (red), as well as Mousa (grey) and Yell Sound Coast (orange) SACs. Figure taken from Russell et al. (2022). Map (b) shows the location of the SACs designated for harbour seals within Shetland.

Many key questions related to the ecology and conservation of seals require information on movements and behaviour at sea. Such information is provided by high resolution animal-borne tracking data, which are essential for mapping seal distribution (Russell & Carter, 2020). Through various funding streams over the last two decades, SMRU and collaborators have assembled an unprecedented GPS tracking dataset of grey and harbour seals covering most key centres of abundance in Northwest Europe. Satellite tracking devices (i.e., GPS tags) are glued to fur on the back of the seal's neck. Devices collect and transmit location, dive and haulout information before falling off by the end of the annual moult. Tag deployments can last up to a maximum of 12 months, but there is a trade-off between tag longevity and data resolution.

GPS tracking data have been used to produce and update at-sea distribution maps for harbour and grey seals in recent years (Carter et al., 2022; Jones et al., 2015; Russell et al., 2017). Robust distribution estimates are key tools for the management and conservation of seal populations and are frequently used in marine spatial planning. Offshore energy structures can have complex effects on seal behaviour, ranging from avoidance during construction (Russell et al., 2016; Whyte et al., 2020) to providing novel foraging habitat as artificial reefs once established (Russell et al., 2014). Quantifying seal abundance at sea is therefore increasingly important given the scale of marine construction activity projected for offshore renewable energy installations, and the decommissioning and removal of oil and gas infrastructure. Distribution estimates are essential to understanding the potential magnitude of impacts of offshore activities and informing the consenting process for any future developments. Historically, these maps were generated based on a track smoothing approach applied to the tracking data ("usage maps" (Jones et al., 2015)), and more recently using regional habitat preference models (Carter et al., 2022).

1.2. Habitat Preference

Habitat preference models can be used to estimate the environmental drivers of distribution for a population of animals by relating observations of species presence/absence to metrics of habitat composition (Manly et al., 2002). The modelled relationship can then be used to predict the distribution of a population despite incomplete or non-uniform survey effort (i.e., predicting distribution emanating from haulout sites that no tagged seal has visited). In the case of tracking data, species observations are presence only data (there are no true absence data), thus a use-availability framework is often used to quantify habitat preference. In this approach, rather than presence versus absence, information on where tracked individuals *did go* (i.e., used points: tracking data) is compared to information on where the individuals *could have gone* (i.e., control points: a random sample of locations generated within the available habitat that is accessible to the individual) (Matthiopoulos, 2003). Preference for a particular habitat type is inferred when its use is disproportionate to its availability (Johnson, 1980).

1.3. Overview of Previous Work

In Carter et al. (2022), a regional habitat preference modelling framework was used to generate predicted at-sea distribution maps for harbour and grey seals hauling out in the UK and Ireland. In brief, tracking data from GPS satellite telemetry tags deployed on harbour and grey seals were modelled alongside control points randomly sampled within an area deemed to be accessible to each individual. The accessible area was determined for each species based on the maximum distance from the haulout (accounting for land barriers) recorded for any individual, as a measure of the maximum foraging trip range. Environmental data were then extracted for both used and control points, and modelled in generalized additive mixed models (GAMMs) to quantify habitat preference. At-sea distribution was then predicted for each known haulout around the coast, weighted by the number of animals counted at each haulout on the most recent haulout survey, conducted during the annual harbour seal moult in August (Fig. 2). Importantly, Carter et al. (2022) showed that habitat preference varies regionally, thus discrete models were fitted to data from different regions, and predictions were then combined into one map per species, representing the at-sea distribution of all seals hauling out in the UK and Ireland.

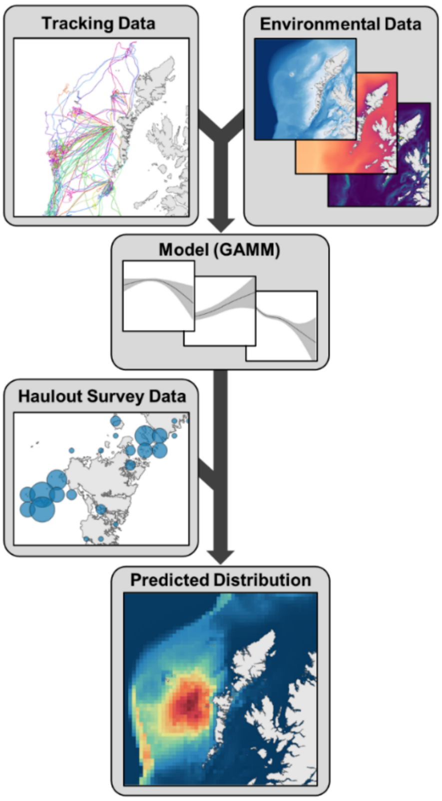

Figure 2: Schematic representation of methods relating to seal distribution estimation. Environmental data are extracted for seal tracking locations and control points and modelled in regional generalized additive mixed models (GAMMs). Model predictions are weighted by the most recent counts of haulouts to generate at-sea distribution estimates. Regional distribution estimates are then combined into one distribution map per species representing the at-sea distribution of all seals from haulouts in Scotland. Figure taken from Carter et al. (2022).

In Carter et al. (2022) tracking data were combined from tags deployed by SMRU, the University of Aberdeen and University College Cork (UCC). However, no recent high resolution (GPS) tracking data were available for either species around Shetland. Thus, the distribution of seals hauling out in Shetland was predicted based on the modelled habitat preference of tracked individuals hauling out in Orkney and the north coast of mainland Scotland (Carter et al., 2022). While a strength of the modelling approach described above is the ability to predict distribution for haulout sites that no tagged animals have visited based on the habitat preference of seals using haulouts elsewhere, the robustness of such predictions is likely compromised when predicting distribution for regions where tracking data are completely lacking. Shetland was therefore highlighted as an important data gap, and a priority for future tag deployments (Carter et al., 2022; Russell & Carter, 2020). Here we present updated distribution maps combining existing tracking data with data from tags deployed on grey and harbour seals in Shetland in 2022, and updated haulout counts.

2. Methods

2.1. Overview of Tracking Data

2.1.1. Deployments Under Current Project

Under the current project, 29 Fastloc® GPS-GSM satellite telemetry devices (SMRU Instrumentation) were deployed on harbour seals in Shetland. The devices collect high resolution location information (accurate to < 70 m (Dujon et al., 2014)), as well as dive and haulout data, and transmit the data via Global System for Mobile Communications (GSM) mobile phone networks (McConnell et al., 2004). The original plan was to deploy all tags in early 2022, but persistent unworkable weather conditions coinciding with a lack of workable tides during daylight hours hampered fieldwork. As a result, the tags were deployed across Spring (n = 5) and Autumn (n = 25) 2022. Tags were deployed in two key areas of interest – Southeast Shetland and Yell Sound – representing the two harbour seal SACs (Fig. 1). Moreover, historic data from low resolution ARGOS tags deployed in 2003-2004 suggested little overlap in distribution of individuals hauling out in these two areas. Therefore, for accurate distribution estimates it was preferable to have tracking data from both centres of abundance. Given that very few harbour seals are now present in the Mousa SAC (Fig. 1), tagging was focussed more generally in the surrounding area of Southeast Shetland. Three of the tags did not transmit sufficient data to be of use for habitat preference modelling. The remaining 26 tags transmitted an average of 95 locations per day (one every 15 min) and lasted an average of 108 days. Figure 3 shows the tracks of seals tagged in Southeast Shetland (n = 15) and Yell Sound (n = 11). For plots by individual, see Appendices Section 8.1, Figures A1-A2. In addition to the harbour seal tags, nine GPS-GSM tags were deployed on grey seals in Shetland in Summer 2022, funded by NatureScot and DESNZ. All capture, handling and other licenced procedures were carried out under UK Home Office project licence PF84B63DE under the Animals (Scientific Procedures) Act 1986 with specific licences from the Scottish Government Marine Directorate (MD-LOT).

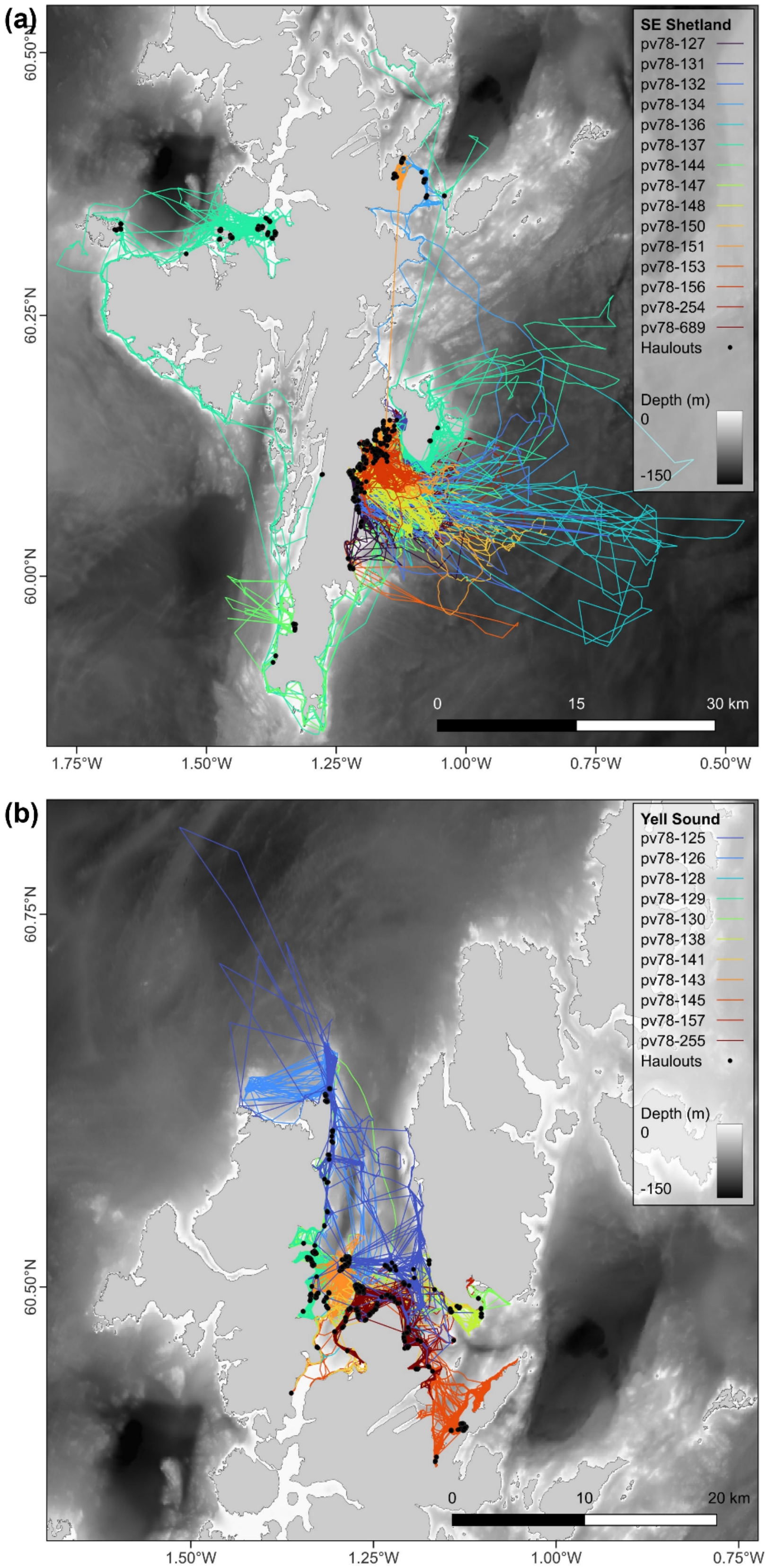

Figure 3: Tracks of 26 harbour seals tagged in Shetland. Maps show seals tagged in (a) Southeast Shetland (n = 15), and (b) Yell Sound (n = 9). Black dots show haulout locations. For plots by individual, see Appendices Section 8.1, Figures A1-A2.

2.1.2. Existing Data

Data from the tags deployed on harbour and grey seals in Shetland in 2022 were combined with existing data from GPS-GSM tags deployed in Scotland and further afield. Models were fitted to discrete habitat preference regions (see Carter et al. (2022)) which were based on regional differences in movement patterns, habitat composition and diet, and do not align with national boundaries. As such, the tracking data used to fit the models required to predict distribution from haulouts in Scotland were from seals hauling out in Scotland and adjacent areas (Celtic and Irish Seas, and down the east coast of the UK to Flamborough Head). The movements of seals between regions allowed the use of data from seals tagged across the UK, Ireland, and France. In total, data from 222 harbour and 169 grey seals were used in this analysis. Data were provided by SMRU (UK), University of Aberdeen (Moray Firth), University College Cork (Ireland) and Université de La Rochelle (France). In contrast to Carter et al. (2022), Shetland was modelled as a sperate region to North Scotland and Orkney. A map of seal trips to and from haulouts in Scotland, colour coded by habitat preference region, is shown in Figure 4.

2.2. Habitat Preference Modelling

Methods for tracking data processing and habitat preference modelling broadly followed those of Carter et al. (2022), with a number of key differences which are outlined in the Discussion (Section 4.1). A comprehensive overview of methods relating to tracking data treatment and statistical analysis in habitat preference models is given in Appendices Section 8.2.

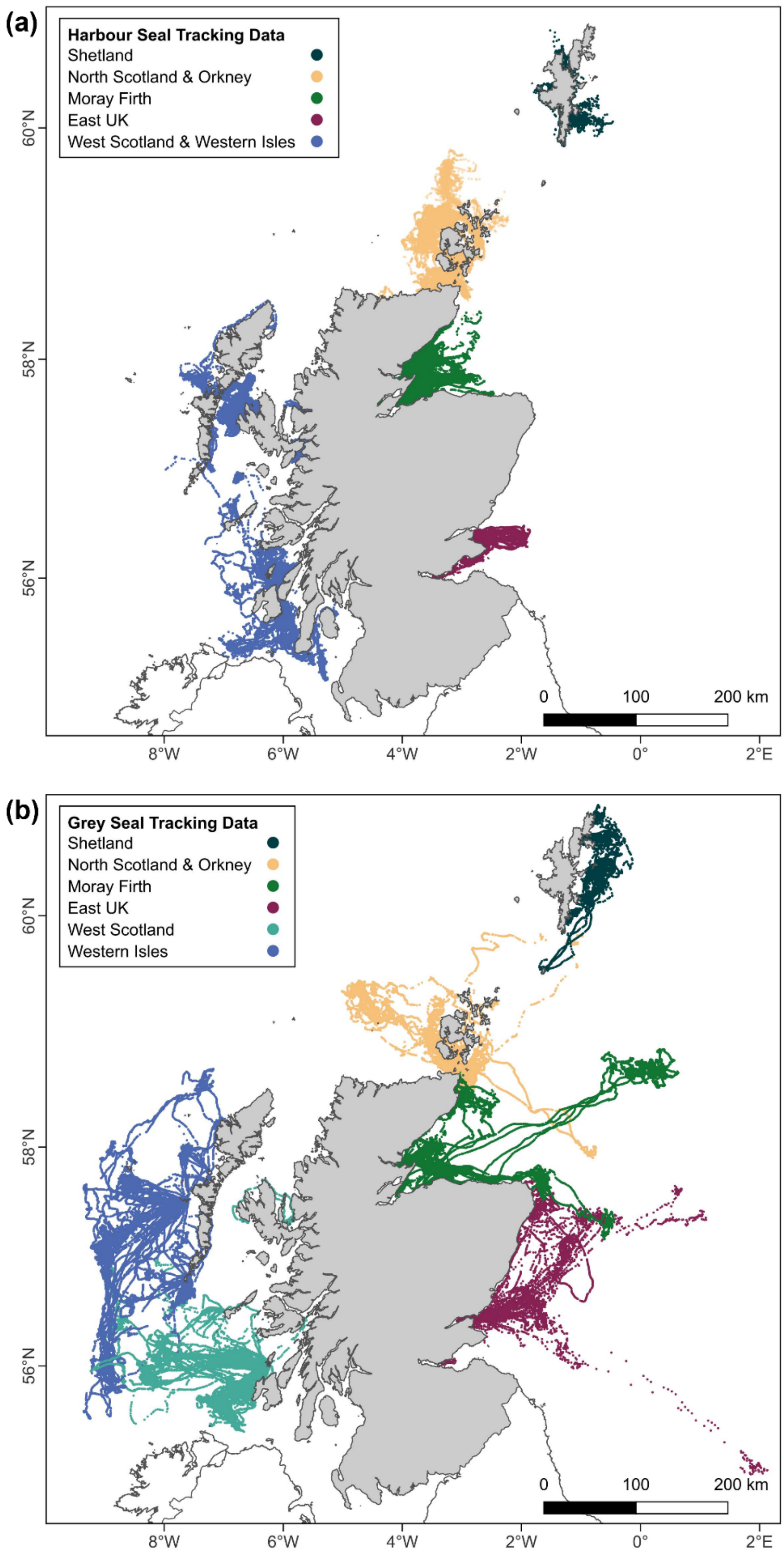
(a)
Harbour Seal Tracking Data
Shetland
North Scotland & Orkney
Moray Firth
East UK
West Scotland & Western Isles
60°N
58°N
56°N
0
100
200 km
8°W
6°W
4°W
2°W
0°
2°E
(b)
Grey Seal Tracking Data
Shetland
North Scotland & Orkney
Moray Firth
East UK
West Scotland
Western Isles
60°N
58°N
56°N
0
100
200 km
8°W
6°W
4°W
2°W
0°
2°E

Figure 4: Tracking data for seals hauling out in Scotland. Data are coloured by habitat preference region. Only trips beginning and ending at haulouts in Scotland are shown. Please note that data shown are raw locations and not at a consistent temporal resolution.

3. Results

3.1. Overview of Downloadable Output

The following files are available for download via the Marine Scotland data portal. Please refer to the associated Seal density estimates README file for advice on interpretation and use of the data.

- Harbour_seal_absolute_density_SCOTLAND_202403.tiff
  - A raster of harbour seal distribution from haulouts in Scotland, presented in the absolute scale (number of animals) per 5km pixel
- Harbour_seal_relative_density_SCOTLAND_202403.tiff
  - A raster of harbour seal distribution from haulouts in Scotland, presented in the relative scale (percentage of at-sea population) per 5km pixel.
- Grey_seal_absolute_density_SCOTLAND_202403.tiff
  - A raster of grey seal distribution from haulouts in Scotland, presented in the absolute scale (number of animals) per 5km pixel.
- Grey_seal_relative_density_SCOTLAND_202403.tiff
  - A raster of grey seal distribution from haulouts in Scotland, presented in the absolute scale (number of animals) per 5km pixel.
- Seal_density_estimates_README_202403.txt

Each of these GeoTiff files contains three GIS raster layers in a Universal Transverse Mercator 30°N World Geodetic System 1984 projection (EPSG: 32630): “mean”, “LCL” and “UCL”. Values are given on a regular 5 km by 5 km grid. Mean values reflect the population mean estimate, while LCL and UCL represent the cell-wise 95% lower and upper confidence limits around the mean, respectively. Briefly, these confidence intervals essentially represent the uncertainty in the modelled distribution, and do not incorporate variability in the haulout abundance. The readme file contains information on usage and limitations of the distribution estimates.

Mean values may be summed across an area of interest (e.g., to estimate the number of animals within a wind farm development zone), but confidence intervals are provided on a cell-by-cell basis and must not be summed across an area (see Discussion Section 4.2.2).

Harbour and grey seal distribution maps are shown in Figures 5 and 6 below. Here we show absolute density (number of animals per grid cell) for ease of interpretation but provide GIS layers for both absolute and relative density (percentage of at-sea population per grid cell). It is important to note that the conversion process from relative to absolute density involves use of population scalars derived from telemetry data, and these are subject to a number of caveats (see Discussion Section 4.2.1 and Carter et al. (2022) for further details). As such, relative density estimates should be used where possible.

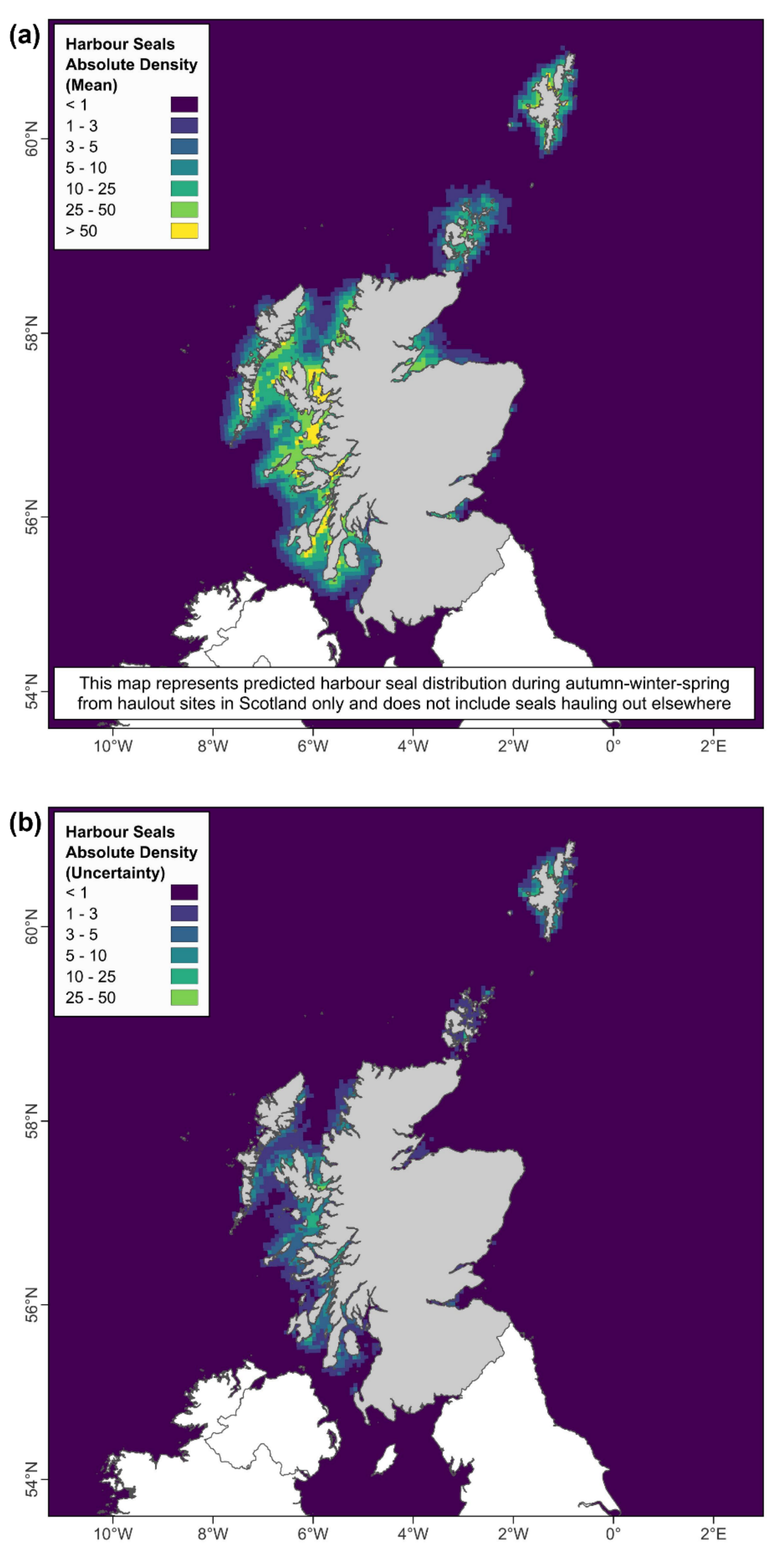

Figure 5: Harbour seal distribution estimates. Maps show (a) mean number of harbour seals estimated to be present in each 5 km by 5 km grid cell at any one time, and (b) cell-wise

uncertainty (difference between upper and lower 95% confidence intervals around the mean prediction).

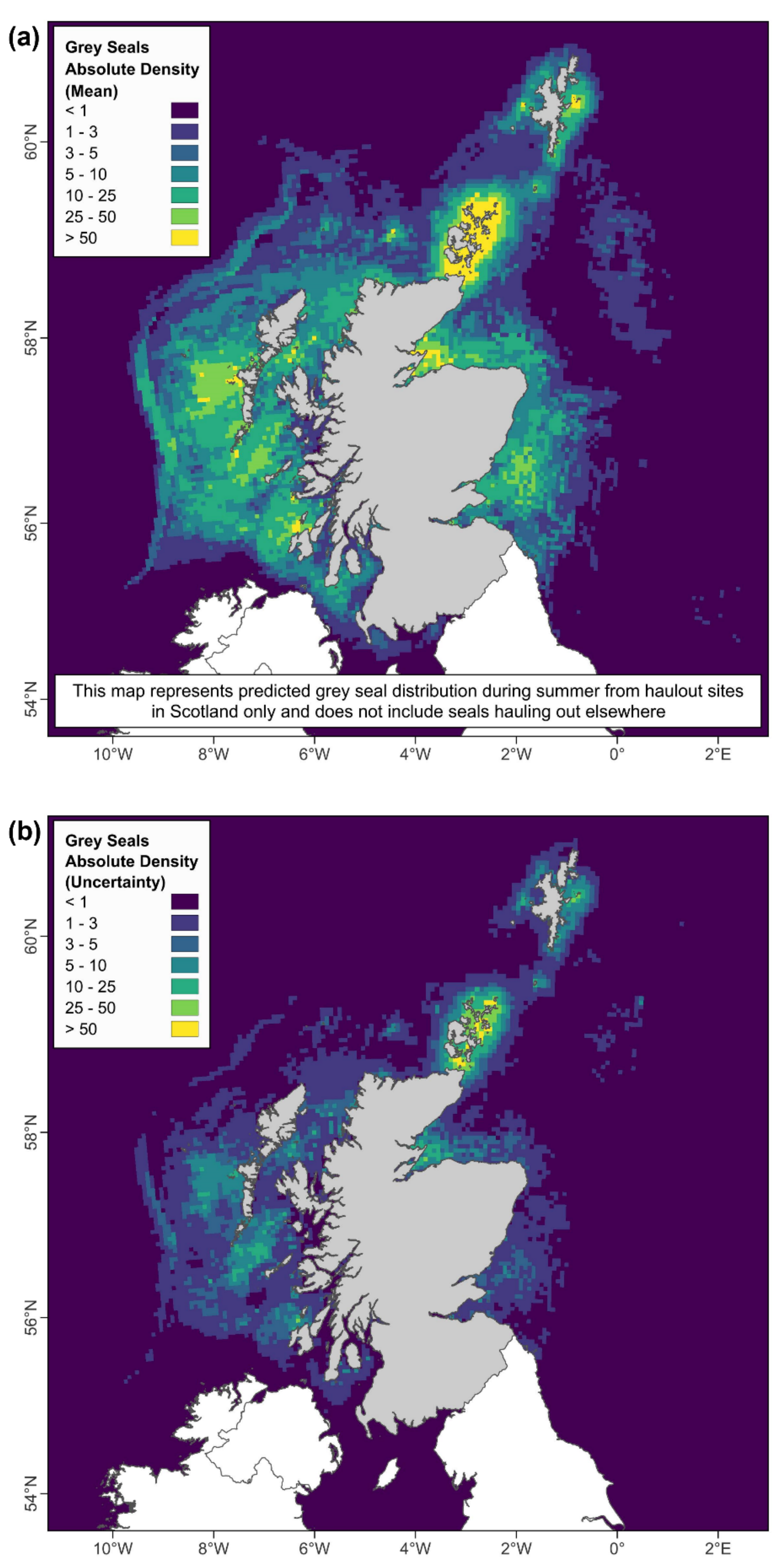

Figure 6: Grey seal distribution estimates. Maps show (a) mean number of grey seals estimated to be present in each 5 km by 5 km grid cell at any one time, and (b) cell-wise

uncertainty (difference between upper and lower 95% confidence intervals around the mean prediction).

3.2. Comparison to Previous Maps

With the inclusion of tracking data from Shetland, predictions for this region are now based on modelled habitat preference relationships of seals hauling out in Shetland, and not those hauling out in Orkney and the north coast of mainland Scotland, as in Carter et al. (2022). Additionally, the latest available count data at the time of analysis for Carter et al. (2022) were from 2015. These have now been updated to counts from 2019. The current analysis has also benefitted from some improvements to the methods for habitat preference modelling (detailed in Discussion Section 4.1). The resulting distributions from the current analysis show a much more coastal distribution for harbour seals in Shetland, with higher density cells adjacent to major haulouts compared to those of previous estimates (Fig. 7). This is consistent with dominant patterns observed in the tracking data. Although a small number of foraging trips were recorded for two individuals extending beyond 20 km from shore (n = 6; 0.3% of all trips), 95% of all harbour seal location data were within 3 km of the coast (mean = 0.6 km).

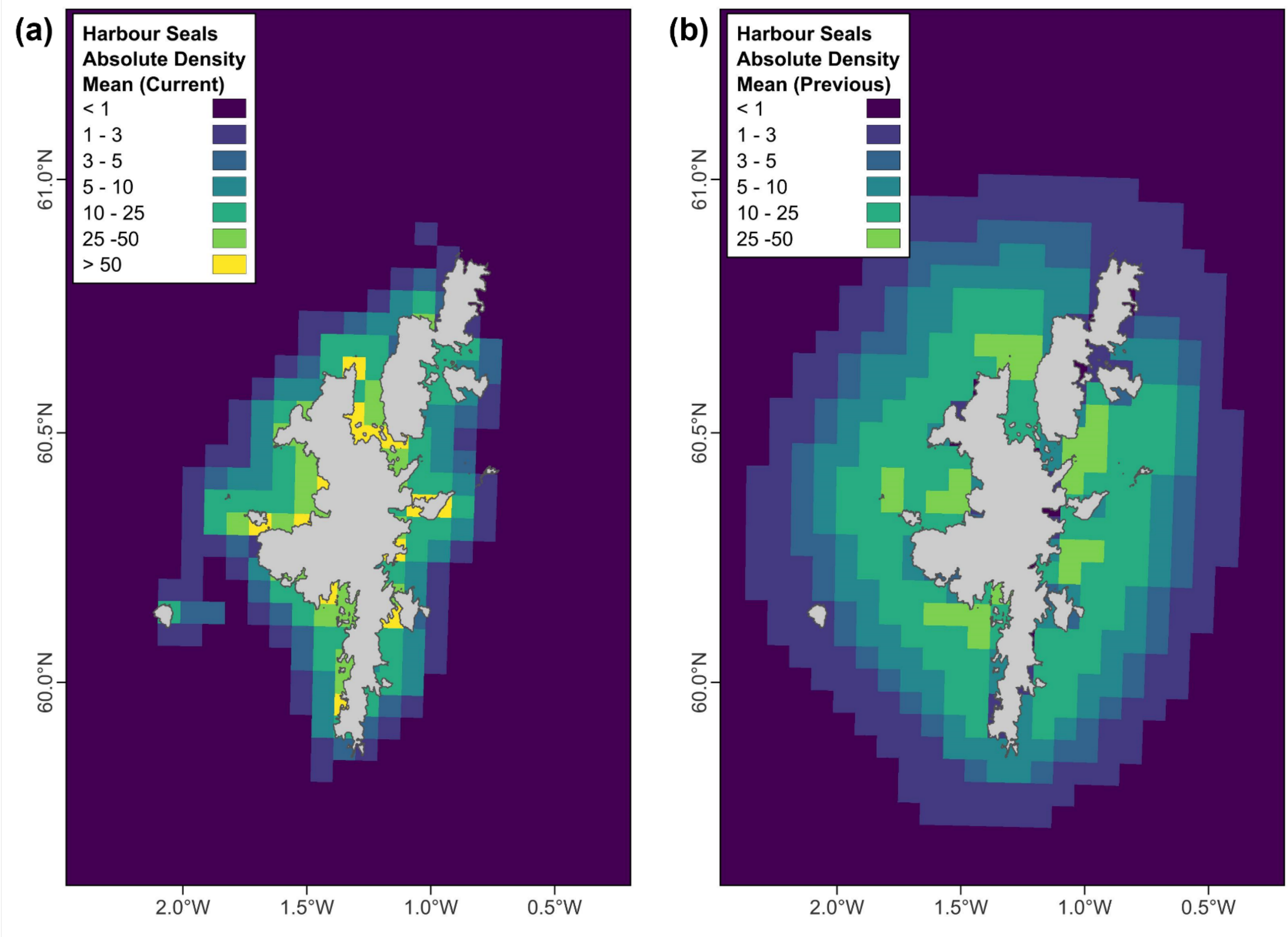

Figure 7: Comparison of predictions for Shetland harbour seal distribution. Maps show (a) current estimate versus (b) previous estimate from Carter et al. (2022). Estimates in Carter et al. (2022) were based on habitat preference relationships for seals in Orkney and the north coast of mainland Scotland with count data from 2015. The current estimate reflects a more coastal distribution consistent with patterns observed in tracking data from tags deployed in Shetland. However, it should be noted that count data for the current estimate were from 2019, and the distribution and total abundance of seals in the count data differed between the two predictions.

4. Discussion

4.1. Summary of Differences to Previous Work

4.1.1. Overview

Table 1: Overview of differences in methods between previous and current approaches. Previous approach refers to Carter et al. (2022). More detail regarding the rationale for, and implications of, differences is given in the sections below (linked in the Category column).

Category	Previous	Current	Rationale
Tracking Data	No data from Shetland	Data from Shetland	Address important knowledge gap in seal distribution
Tracking Data	Data from UK & Ireland	Data from UK, Ireland & France	Improved sample size for grey seal models due to individuals tagged elsewhere making trips within the study area
Tracking Data	Accessible area based on all tracking data	Accessible area defined per region	Better representation of regional environment accessible to seals
Haulout Count Data	Latest available (up to 2018)	Latest available (up to 2023)	Updated abundance estimates
Environmental Covariates	Static & Dynamic	Static only	Provide a more time-independent estimate of distribution
Statistical Modelling	Model selection	No model selection	Focus on best predicted distribution (not ecological inference)
Statistical Modelling	Residual autocorrelation reduced by thinning data	Residual autocorrelation reduced by modelling it	Improved method for handling residual autocorrelation and avoiding underestimation of model uncertainty

4.1.2. Tracking Data

The distribution estimates provided here benefit from an enhanced tracking dataset compared to that used in Carter et al. (2022). In addition to the GPS tracking data from SMRU, UCC and University of Aberdeen used in Carter et al. (2022), the dataset here was augmented with data from grey seals tagged in France by Université de La Rochelle. Furthermore, the deployment by SMRU of tags on harbour and grey seals in Shetland in 2022 has provided a valuable resource to improve distribution estimates for that area. The distribution estimates provided here therefore benefit from a larger sample size of tracking data with better spatial coverage than those presented in Carter et al. (2022). As such, the analysis should give a better approximation of the population-level mean habitat preference relationships, and thus more robust at-sea distributions.

Tracking data were assigned to different habitat preference regions based on the location of the haulout sites used before and after a trip (Fig. 4). Trips starting and ending in different regions were excluded. The region designations followed those of Carter et al. (2022), with two exceptions: (i) Shetland was modelled separately from Orkney and the north coast of mainland Scotland for both species, and (ii) the Western Isles and West Scotland regions were combined for harbour seals in this work because previous work showed little difference in habitat preference between the two (Carter et al., 2022), and combining them allowed for a greater sample size and increased predictive power.

Seal location data were modelled alongside an availability sample; control points randomly spaced within an area deemed accessible to each seal on each foraging trip. In previous work, the accessible area was determined per species based on the maximum swimming distance (i.e., avoiding land) to haulout recorded for any seal in the dataset (Carter et al., 2022). However, this approach does not account for regional differences in scale of movement, which can range from tens to hundreds of kilometres from the haulout (Carter et al., 2022). Such differences may be related to complex regional drivers such as genetics (Carroll et al., 2020), or fear of predation (Moxley et al., 2020) (as is likely relevant for harbour seals in Shetland; see below). With insight from the new Shetland tracking data, it was deemed more appropriate to define the accessible area radius on a species-region basis for this work. Therefore, for each seal trip, control points were placed within an area out to the maximum swimming distance recorded by any seal of that species in that region. The implications of this are that fine-scale distribution patterns are likely to be more accurately represented in regions where seals do not travel far from the haulout site (e.g., Shetland).

The distribution estimates for harbour seals in Shetland reflect a tight coastal distribution compared to those of Carter et al. (2022) (Fig. 7). This provides a better alignment with patterns seen in tracking data collected under this project; seal tracks often traced the coastline of Shetland, and the vast majority of locations (95%) were within 3 km of the nearest land (Figs. 3). This coastal distribution is potentially due to a landscape of fear effect attributable to the presence of killer whales (*Orcinus orca*), with killer whales observed predating seals year-round in Shetland. This further demonstrates the importance of using region-specific tracking data and habitat preference relationships for distribution estimates, since such behaviour was not as frequently observed in tracking data from harbour seals in Orkney and the north coast of mainland Scotland, where predation pressure by killer whales may be less persistent. The impact of killer whale predation on seals is the focus of ongoing PhD research in the Ecological Consequences of Orca Predation on Seals (ECOPredS) project.

4.1.3. Haulout Count Data

Haulout counts used to scale estimates of at-sea distribution have been updated since Carter et al. (2022) due to the availability of more recent survey data. Given that seal population trajectories can vary regionally through time (SCOS, 2022), updating the count data is important to give a more accurate representation of current seal distribution. A summary of these updates is shown in Table 2 below. A map of survey coverage by year used in the current analysis is shown in Appendices Section 8.3 Figure A4. As in Carter et al. (2022), no August survey data were available for the archipelago of St Kilda, thus predictions do not include seals hauled out there.

Table 2: Comparison of count data used in previous and current versions.

	Previous Count Year	**Current Count Year**
Shetland	2015	2019
Orkney	2016	2019
North Coast of Scotland	2016	2016
Northern Moray Firth	2008 & 2011	2019
Inner Moray Firth	2018	2022
Southern Moray Firth	2016	2021
Aberdeenshire & Angus	2016	2021
Eden Estuary	2018	2022
Forth & Berwickshire	2016 & 2018	2022
Central & Southern West Scotland	2018	2018
Northern West Scotland & Western Isles	2011 & 2017	2011 & 2017
Offshore Islands, Scotland	2014	2023

4.1.4. Environmental Covariates

In Carter et al. (2022), a range of dynamic (temporally varying) and static environmental variables were used as potential explanatory covariates in the habitat preference models. Dynamic covariates comprised seasonal means of sea surface temperature (SST), water column stratification and frontal intensity. Environmental data were extracted for the years coinciding with the tracking data, and predictions were made for a focal year of 2018, corresponding to the most recent available count data (Carter et al., 2022). One disadvantage of this approach is that predictions are always only relevant to the focal year and may be strongly influenced by variation in these dynamic covariates.

To address this issue, the current approach fits the models with only static covariates, including static representations of dynamic processes. Thus, covariates included distance to haulout, distance to coast, seabed substrate type, seabed geomorphology and, for grey seals, summer mean potential energy anomaly (PEA; a metric of water column stratification). The PEA data were static in that they represent stratification conditions in a "typical" year (Jones, 2024). For more information on these covariates, see Appendices Section 8.2.2. This approach eliminates the possibility that predictions will be made outside of the covariate space in which the models were fitted. Predictions can also be more easily updated in the future when new count data become available. However, it is important to note that the resulting predictions therefore represent seal distribution in a "typical" year. For some applications where the influence of dynamic processes is of particular interest (e.g., understanding the influence of temporal variation in a particular dynamic oceanographic feature on seal distribution), it will be necessary to use dynamic covariates and generate multiple predictions corresponding to different conditions.

4.1.5. Statistical Modelling

The key aims of the work undertaken by Carter et al. (2022) were to both predict seal distribution, and to understand the key environmental drivers of distribution for grey and harbour seals in different regions. Model selection was undertaken, and non-informative covariates were removed from the model until arriving at a minimal adequate model. In this current work, no model selection was undertaken; non-informative covariates which likely have little to no influence on predicted distributions remained in the model.

Analysis of time-series such as animal tracking data is often affected by the problem of residual serial autocorrelation (Fieberg et al., 2010). If ignored, this can lead to underestimation of model uncertainty (i.e., artificially narrow confidence intervals around the mean) (Fieberg et al., 2010). Having explored the available options for handling this problem, the previous analysis used a time-to-independence approach; effectively thinning the data by removing every n^{th} observation until residual autocorrelation reached acceptable levels (Carter et al. 2022). Whilst this is a legitimate option, it is not without disadvantages. The key disadvantage is that valid data are discarded, often leading to unnecessarily wide confidence intervals, and ultimately dilution of ecological relationships. In the present analysis, a different approach was applied. A first-order autoregressive correlation structure (AR1) was applied to the models, and calibrated such that correlation between time series observations was modelled, rather than removed. The consequences of this difference in data treatment are that modelled uncertainty is reduced in the current approach, and therefore confidence intervals around the mean prediction are likely to be narrower than those of Carter et al. (2022).

4.2. Considerations and Recommendations

4.2.1. Absolute versus Relative Density

Here we provide distribution estimates as both relative density (percentage of at-sea population per grid cell) and absolute density (number of animals per grid cell). For some applications, absolute density is favourable (e.g., estimating the number of animals within an area of interest). However, the conversion process from relative to absolute density involves use of population scalars derived from telemetry data (see Carter et al. (2022)), and uncertainty in these scalars is not propagated through to the confidence intervals around the mean. Confidence intervals therefore only reflect uncertainty in the modelled habitat preference relationships. Another consideration is that density estimates are scaled using the most recent available count data. While relative density estimates are somewhat robust to changes in abundance (provided the distribution of the population remains the same proportionally among haulouts), the absolute density estimates are not. As such, absolute density estimates provided here reflect an approximation of seal distribution in 2023. Here we show maps of absolute density for ease of interpretation but provide GIS layers for both absolute and relative density. Given the caveats listed above, we recommend that relative density estimates be used wherever possible.

4.2.2. Use of Confidence Intervals

Confidence intervals represent the range of values within which, based on the haulout count data and model used, we would expect the true density of seals to be, and the mean is a measure of the centre of this range. Where possible, mean density estimates should be used in conjunction with the confidence intervals. As in Carter et al. (2022), confidence intervals around the mean prediction are generated on a cell-by-cell basis. Thus, although the mean predictions can be summed across an area (e.g., number of animals present within a wind farm development zone), confidence intervals cannot; doing so would lead to inflated uncertainty. Currently, area-based confidence intervals can be generated on a case-by-case basis, but this requires significant extra work. A priority for future work is to produce a graphical user interface (GUI) where users can specify their area of interest and download area-based mean estimates with associated area-based confidence intervals.

4.2.3. Data Limitations

While the distribution estimates presented here benefit from an improved GPS tracking dataset over those of Carter et al. (2022), there remains a key data gap in Scottish waters. Very little recent high resolution tracking data exist for the east coast of Scotland for either species. Data used to fit models for harbour seals in this region were from tags deployed in 2008 (n = 4), 2011 (n= 5) and 2013 (n= 3). Data from grey seals for this region are from 2005 (n = 2), 2008 (n = 9) and 2013 (n = 2), supplemented by individuals tagged between 2014 - 2018 in Orkney (n = 1), the Moray Firth (n = 3) and Southeast England (n = 5) that hauled out there. Predictions for this region should be treated with caution as they likely contain a high degree of unmodelled uncertainty (i.e., uncertainty not incorporated in the confidence intervals). Since the deployment of tags in this region, harbour seal numbers have continued to decline (Russell et al., 2022; Thompson et al., 2019). The vast majority of data for grey seals in east Scotland are from individuals tagged in the Eden Estuary and Firth of Tay, yet large aggregations are now present ~100 km north in Cruden Bay and the Ythan Estuary. Thus, predictions of distribution for seals hauling out in Cruden Bay and the Ythan Estuary are predominantly based on the habitat preference of seals further south, tagged over 15 years ago. Given the current depleted abundance of the harbour seal in this region, a large-scale tag deployment on harbour seals may not be feasible. However, deployment of GPS tags on grey seals should be considered a priority for future work.

4.3. General Conclusion

In conclusion, the seal distribution maps presented here represent an improvement on those of Carter et al. (2022) due to the contribution of new tracking data from tags deployed on harbour and grey seals in Shetland, updated abundance data, and a number of methodological improvements outlined above. The current estimates should therefore be used in favour of those from Carter et al. (2022) for any applications where the distribution of seals from haulouts in Scotland is required.

5. Ethics Statement

All capture, handling and other licenced procedures in the UK were carried out under UK Home Office project licence PF84B63DE (and previous iterations: 60/2589, 60/3303, 60/4009 and 70/7806) under the Animals (Scientific Procedures) Act 1986, with specific licences from the Scottish Government Marine Directorate, the Marine Management Organisation, and Natural Resources Wales. In Ireland the work was conducted under licence from the National Parks and Wildlife Service, with additional licences from the Irish Health Products Regulatory Authority. In France, work was conducted under licence from the Ministère de l'Ensignement Supérieur et de la Recherche, with project-specific approvals from the Ministère de la Transition Ecologique. Appropriate site-specific approvals were obtained, with any associated mitigation measures observed for designated sites.

6. Acknowledgements

The analyses were funded by the Scottish Government Marine Directorate with additional support from NERC (INSITE Phase II NE/T010614/1 EcoSTAR), the Department for Energy Security and Net Zero (DESNZ, facilitated by Hartley Anderson Ltd.) and NERC National Capability - National Public Good funding (NE/R015007/1) which supported DJFR. Telemetry tags and their deployment in the UK were funded by the Scottish Government Marine Directorate through the ScotMER programme, DESNZ (and previous incarnations), NERC, NatureScot, the Met Office, Menter Môn, Marine Current Turbines, Ørsted, The Crown Estate, Highlands & Islands Enterprise, Moray Firth Renewables Limited (MORL), Beatrice Offshore Windfarm Limited (BOWL), Vodafone UK, University of Aberdeen, SMRU, and SMRU Instrumentation Group. Data from seals tagged in Ireland were obtained from University College Cork, funded by Beaufort Marine Award (administered by the Irish Marine Institute), the Irish Research Council and the National Parks and Wildlife Service Ireland. Data from seals tagged in France were provided by Université de La Rochelle, funded by l'Office Français de la Biodiversité (OFB). Fieldwork was supported by OFB, Océanopolis and Zoo de la Flèche. Aerial surveys conducted by SMRU were funded by NERC (NC NPG: NE/R015007/1), NatureScot, the Scottish Government Marine Directorate and Scottish Power. We are grateful to Mark Jessopp (University College Cork) for contributing data and expertise, and the many people involved in tagging and survey work, as well as the support and assistance of landowners and managers at field sites. We thank Dr Sam Jones (Scottish Association for Marine Science) for provision of Potential Energy Anomaly data. We also thank Dr Gavin Simpson (Aarhus University), whose expert knowledge of GAMMs shared on statistics forums and blog posts proved extremely helpful.

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8. Appendices

8.1. Shetland Harbour Seal Tracking Data

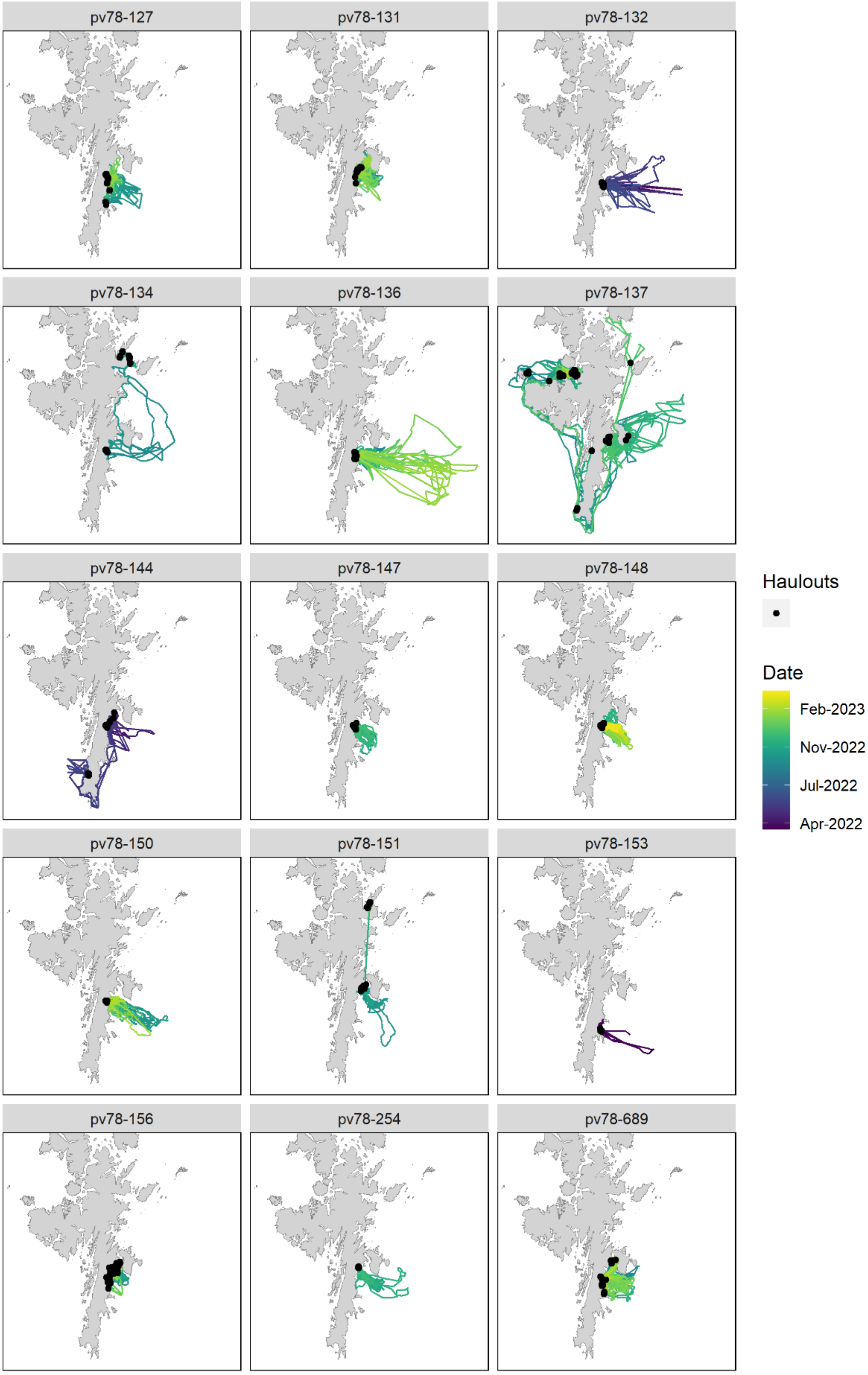

Figure A1: Tracks of fifteen harbour seals tagged in Southeast Shetland, colour coded by date. Black dots show haulouts.

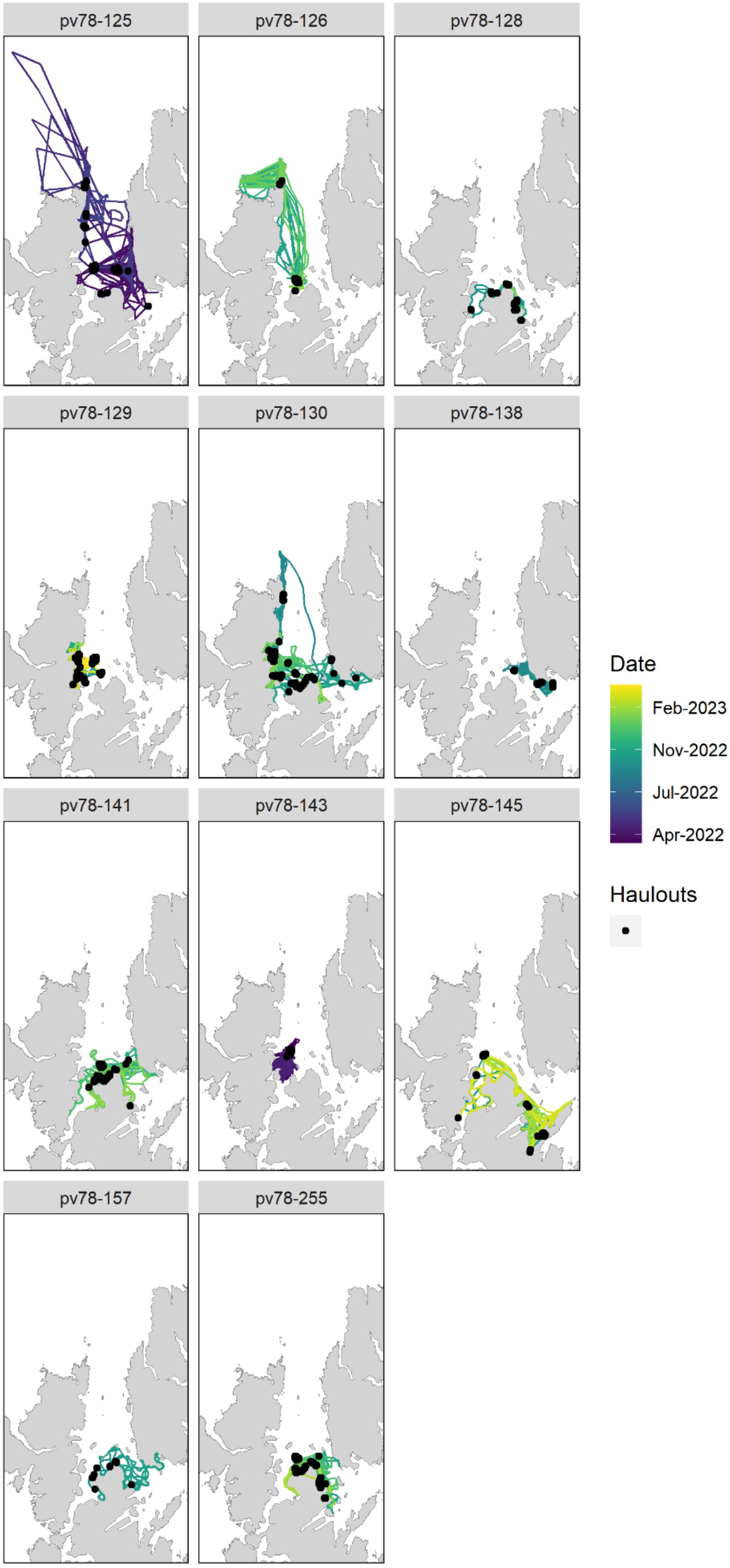

Figure A2: Tracks of eleven harbour seals tagged in Yell Sound, colour coded by date. Black dots show haulouts.

8.2. Habitat Preference Modelling Methods

8.2.1. Data Processing

Tracking data were first cleaned to remove erroneous location fixes and partitioned into trips using start and end haulout locations following the protocol outlined in Carter et al. (2022). Trips were assigned to different habitat preference regions based on the location of the haulout sites used before and after a trip, and trips that started in one region and finished in another were excluded. As per Carter et al. (2022), habitat preference regions were assigned based on regional differences in movement patterns, habitat composition and diet (see Fig. 4, main text).

Data from any trip initiated during the first week after tagging were excluded to remove any potential bias associated with altered behaviour resulting from capture. As per Carter et al. (2022), data were clipped to summer (May – August) for grey seals or autumn-winter-spring (September – May) for harbour seals to remove any locations during breeding and moult seasons. Locations were then interpolated to a constant 30-min time step, and any interpolated location with no observed GPS fix in the surrounding six hours was flagged as unreliable and excluded from the dataset. Each presence (interpolated location) was then matched to 30 control points which were randomly spaced within a trip-specific availability polygon, defined based on the maximum swimming distance (i.e., accounting for land barriers) travelled from a haulout of any individual in that species-region combination. The area beyond the continental shelf break (taken here as the 600 m isobath) was excluded from accessibility polygons since this is unlikely to represent viable habitat for seals (Carter et al., 2022). Environmental covariate values (see Section 8.2.2 below) were then extracted for all presences and control points. The ratio of control points to presences can have a dramatic effect on model inference if the availability sample does not effectively capture the composition of available habitat (Beyer et al., 2010). As per Carter et al. (2022) preliminary models were fitted with ratios between 1:1 and 1:30, and model coefficient values plotted to identify the ratio at which values stabilised. This analysis showed that a ratio of 1:30 was sufficient to adequately capture the available environment in all species-region combinations. For a more detailed account of data preparation protocols and the use-availability design, please see appendices in Carter et al., (2020).

8.2.2. Environmental Covariates

Environmental data from a range of data sources were extracted for every presence and control point, and included as explanatory covariates in the habitat preference models. Covariates were chosen on the basis of biological relevance to seals and/or their prey, or to control for the effects of accessibility on habitat selection. Firstly, distance to haulout (accounting for land barriers) was calculated and included to control for decreasing accessibility with increasing distance (Matthiopoulos, 2003). Distance to coast was also included since visual inspection of tracking data around Shetland revealed seals travelling far from the haulout but remaining very close to the coast. For example, a harbour seal was recorded 76 km from the haulout, but only 300 m from the coast. Coastline data were accessed from the European Environment Agency (EEA) Datahub.

Seabed geomorphology is known to influence the behaviour of some individual seals (Wyles et al., 2022). A dataset of geomorphological features for the Northeast Atlantic was generated from the freely available EMODnet harmonised gridded digital terrain model (DTM) for European sea regions (EMODnet Bathymetry, 2020). The DTM data were processed using the "r.geomorphon" extension for the Geographic Resources Analysis Support System (GRASS GIS) (Neteler & Mitasova, 2007) developed by Jasiewicz & Stepinski (2013), as described in Wyles et al. (2022). Seabed substrate type has also been shown to influence the habitat selection of harbour and grey seals in Scotland (Aarts et al., 2008; Carter et al., 2022), thus substrate type was extracted from the EMODnet Broad-Scale Habitat Map for Europe (EMODnet Seabed Habitats, 2021).

For grey seals, vertical water column stratification during summer has been shown to be an important predictor of habitat use in some regions (Carter et al., 2022). Summer mean potential energy anomaly (PEA) values were extracted from a data product developed under the Ocean Data Tool (ODaT) project (Jones, 2024). This covariate represents the amount of energy required in J/m^3 to result in complete mixing of the water column under "typical" conditions for a given time of year. Thus, areas where the water column is fully mixed would have a PEA value of 0, and high values are associated with areas of strong water column stratification. This covariate was not included for harbour seals as there was little variation in PEA values experienced by the seals during the months coinciding with the tracking data.

As in Carter et al. (2022) "shelf" was included as a binary categorical term for grey seals hauling out in the Western Isles to account for the fact that many foraging trips were concentrated within 20 km of the shelf edge (600 m isobath). Bathymetric depth was included in preliminary models but was found to cause issues of high concurvity (assessed using the "performance" package (Lüdecke et al., 2021) in R (R Core Team, 2023)), and thus was excluded from further analyses. Retaining a covariate with high concurvity may result in over-estimation of model variance and masking of the effects of other covariates. All processing and extraction of environmental covariates was done using the "terra" (Hijmans, 2023) and "sf" (Pebesma & Bivand, 2023) packages in R.

8.2.3. Statistical Modelling Framework

For each species-region combination, control points and presences were modelled as a binary response term (0/1: available/used) as a function of the environmental covariates in a GAMM using the "bam" function in the "mgcv" package (Wood, 2017) in R. A binomial error family was specified with a logit link function. An individual seal identifier was included as a random intercept term using the "re" basis spline, allowing the modelled relationships to be estimated across individuals rather than data points, and ensuring that data-rich individuals did not unduly affect the results. Continuous covariates (distance to haulout, distance to coast and PEA) were modelled with a cubic regression spline with shrinkage, such that uninformative terms can be penalised to zero (Wood, 2017). To avoid over-fitting of smooth functions to the data, the number of knots (*k*) was limited to a maximum of five. Categorical covariates (geomorphology and substrate) were included both individually and in an interaction term.

Preliminary analysis revealed significant serial autocorrelation in model residuals for "used" data points. If ignored, this residual autocorrelation may lead to underestimation of model uncertainty. Examination of the partial autocorrelation function applied to residuals revealed that a first-order autoregressive (AR1) correlation structure would be appropriate. An AR1 structure was therefore applied with each trip treated as a separate time series. Each control point was also treated as a separate time series, such that no dependency was assumed between them, since they were randomly distributed in space. The correlation coefficient value ρ was determined by calculating the autocorrelation value of residuals for "used" points with residuals for "used" points at lag 1 for each trip for each seal. The median value across trips was then calculated for each seal, and the overall median of these seal-specific values was used as ρ in the final model. Model residuals were again examined after fitting to determine if the value of ρ was sufficiently high.

No model selection was undertaken, since the goal here was to find the best model for predicting distribution, rather than making biological inference about habitat selection. Thus, it was deemed better to retain all covariates rather than risk removing a potentially informative covariate, since non-informative terms that remained in the model would have little to no effect on the resulting distribution estimates.

8.2.4. Predicting At-Sea Distribution

As in Carter et al. (2022), predictions of at-sea distribution (mean and associated lower and upper 95% confidence intervals) were generated on a 5 km x 5 km grid encompassing the marine area accessible to seals from all haulouts. Environmental data corresponding to the modelled covariates were first extracted for each cell in the prediction grid. Spatial predictions were then made emanating from each haulout site in Scotland with a non-zero count on the most recent survey (with the exception of the St Kilda archipelago, for which count data were not available; see Appendix Section 8.3 below), using the corresponding species-region model. Predictions were weighted by the relative area of sea in each cell (i.e., a coastal cell with 50% land cover would be weighted as 0.5), estimated using the EEA coastline dataset and the R package "extactextractr" (Baston, 2023). Raw predictions (on the logit scale) were exponentiated, then normalised (Manly et al., 2002). Haulout-specific prediction surfaces were then weighted by the number of individuals counted on the most recent survey, and summed into one multi-region surface per species. The multi-region surfaces were then normalised, such that the sum of values for all cells in the mean layer is 100, representing the percentage of the at-sea population predicted to be present in each cell (i.e., relative density). Cell-wise lower and upper 95% confidence intervals were generated using a posterior simulation approach (Carter et al., 2022; Wood, 2017).

8.3. Count Data

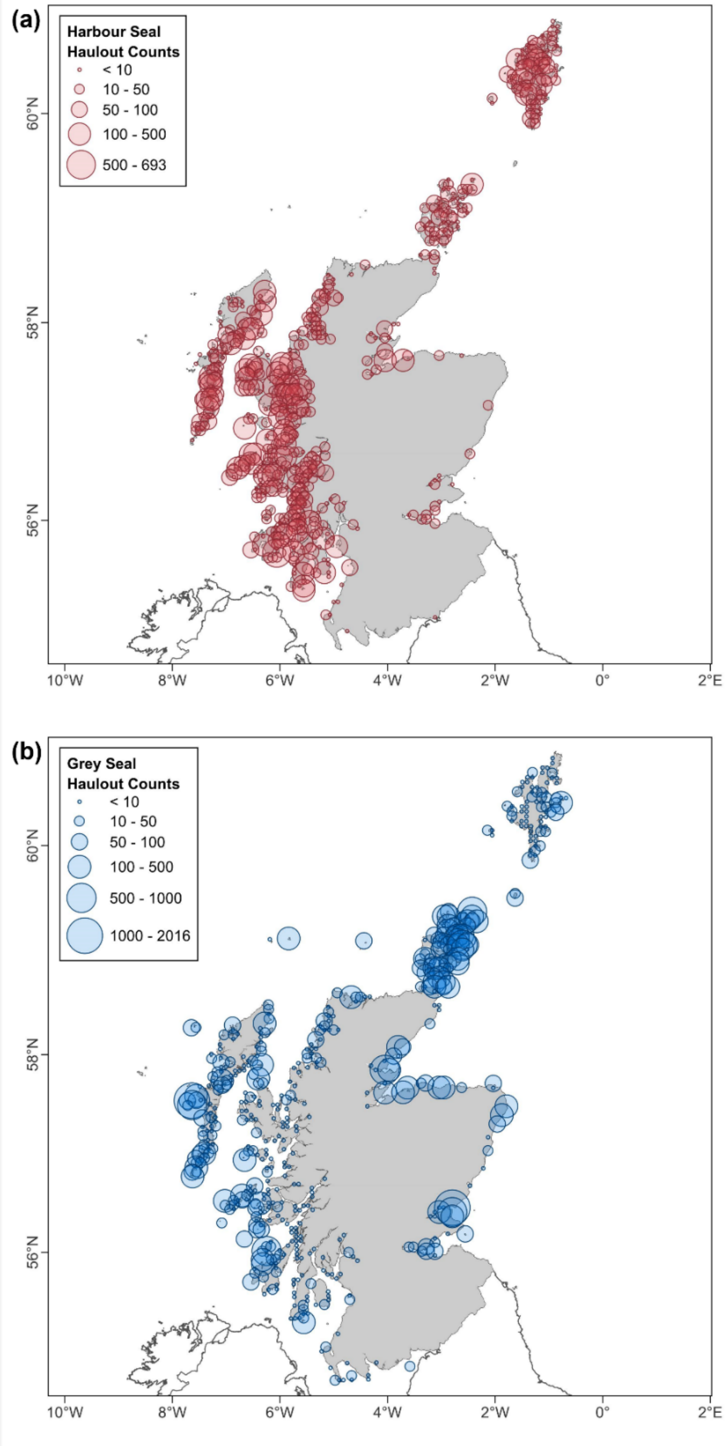

Figure A3: Most recent haulout counts for (a) harbour and (b) grey seals in Scotland. Surveys are conducted during the annual harbour seal moult in August. Survey coverage by year is shown in Figure A4.

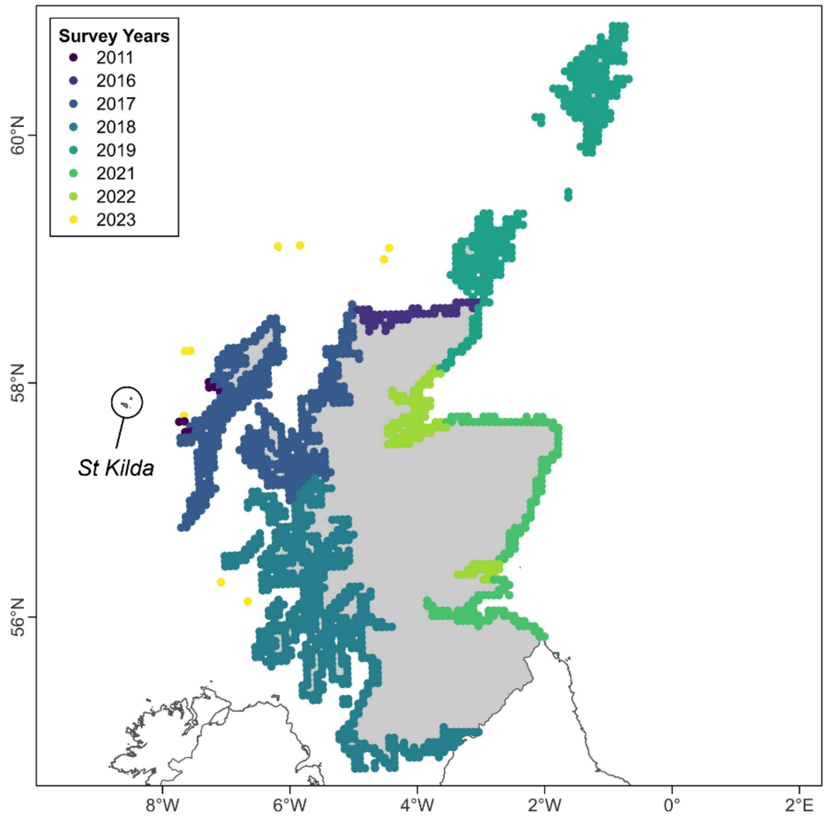

Figure A4: Spatial and temporal coverage of haulout survey data for Scotland. The survey year reflects the most recent available data. Counts are aggregated to 5 km x 5 km grid cells. A survey of northern and central West Scotland, as well as the Western Isles was conducted in 2022, but data were not yet available for this analysis, thus counts from 2017 were used. No count data were available from the St Kilda archipelago; thus predictions do not include seals hauled out there.

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The Scottish Government
St Andrew's House
Edinburgh
EH1 3DG

ISBN: 978-1-83601-985-5 (web only)

Published by The Scottish Government, February 2025

Produced for The Scottish Government by APS Group Scotland, 21 Tennant Street, Edinburgh EH6 5NA
PPDAS1488338 (02/25)