Habitat-based predictions of at-sea distribution for grey and harbour seals in the British Isles

Report to BEIS

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1. Executive Summary

The United Kingdom has large populations of both grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*), which are protected under national and international legislation. In recent years, aerial surveys have revealed region-specific changes in population dynamics for both species, ranging from exponential increases (e.g. grey seals in the Southern North Sea) to catastrophic localised declines (e.g. harbour seals in East Scotland and Orkney). Up-to-date information on the at-sea distributions of these species is required to inform environmentally sensitive management strategies and marine spatial planning. Such distributions have been estimated using data from animal-borne telemetry tags which record and transmit tracking data, providing information on at-sea movements and haul-out behaviour. Such tags are glued to the seal's fur and fall off during the annual moult.

The Department for Business, Energy and Industrial Strategy, through their Offshore Energy Strategic Environmental Assessment (OESEA) programme, provided funding for a large-scale deployment of high resolution GPS telemetry tags on grey seals around the UK, and the subsequent analyses to generate up-to-date estimates of at-sea distribution for both seal species. To produce these estimates, a habitat modelling approach was adopted; seal tracking data were matched to a sample of the available habitat to quantify the region-specific species-environment relationships underpinning seal distribution. Spatially resolved abundance data (i.e. haulout counts) were then used to generate predictions for both species emanating from all known haulouts in the British Isles. The resulting predicted distribution maps provide estimates per species, on a 5 km x 5 km grid, of relative at-sea density for seals hauling-out in the British Isles. Three values are given for each grid cell: the mean density prediction from the habitat preference models and associated lower and upper 95% confidence intervals. For each cell, the confidence intervals provide a range of values in which, according to the models, the true seal density is likely encompassed. The mean provides a measure of the centre of this range.

Appendices to this report present some additional analyses, including an example of a potential application of the predicted distribution maps by means of a case study estimating the number of grey and harbour seals using areas of interest, specifically windfarm lease areas and tidal energy development sites in the UK sector. Moreover, analysis of recent tracking data has revealed further evidence that seals use man-made structures for foraging, and potentially navigation, especially in the North Sea where structure density is highest. Lastly, additional analyses reveal movements of female grey seals between foraging grounds in the Hebrides and breeding sites in North Scotland, providing further evidence that regional population dynamics may be affected by foraging conditions elsewhere.

2. Introduction

The United Kingdom (UK) has globally significant populations of both grey and harbour seals, with current numbers estimated at 152,800 individuals (approx. 38% of global population), and 45,800 individuals (approx. 30% of Eastern Atlantic subspecies population) respectively (SCOS 2019). Grey seal numbers have increased steadily over the past 60 years since survey effort began, but the rate of population growth varies among regions (Thomas et al. 2019). For example, pup production in Orkney and the Hebrides has plateaued in recent years, where numbers have potentially reached carrying capacity, while pup production along the east coast continues to grow exponentially (Russell et al. 2019, Thomas et al. 2019). Conversely, current UK harbour seal numbers are comparable to those of two decades ago (Thompson et al. 2019). However, there is marked regional variation in population trends, with some areas experiencing unexplained catastrophic declines (e.g. Orkney, Shetland and East Scotland), while other areas are stable (e.g. Western Isles and West Scotland) or increasing (e.g. Southeast England) (Thompson et al. 2019).

Nationally, seals are protected under the Conservation of Seals Act 1970 (UK), the Marine (Scotland) Act 2010 and the Wildlife (Northern Ireland) Order 1985. They are also listed under Annex II of the EU Habitats Directive (92/43/EEC), requiring member states to designate important habitat as Special Areas of Conservation (SACs), and maintain populations in a “Favourable Conservation Status” (Council of the European Communities 1992). All 16 UK SACs for which seals are a primary feature for designation are coastal sites. Seals overlap, and potentially interact, with anthropogenic activities throughout their UK range. Such activities include fisheries and aquaculture (SCOS 2019), shipping (Chen et al. 2017, Jones et al. 2017a), oil and gas and renewable energy industries (Russell et al. 2014, 2016a, Hastie et al. 2018, Whyte et al. 2020). Understanding, and effectively mitigating, the impacts of anthropogenic stressors on seal populations requires knowledge of at-sea movements on both broad (regional, seasonal movements) and fine (foraging areas, individual trips) spatial and temporal scales. Evidence suggests that, for grey seals, females may not always forage in the same region where they breed (Russell et al. 2013), thus disturbance to offshore foraging habitat may have effects on breeding numbers in adjacent regions. This suggests that effective management may require consideration of both terrestrial and marine habitat, combining SACs with Marine Protected Areas (MPAs).

Over the next decade, the anthropogenic footprint on the marine environment in the UK will undergo dramatic changes, with many oil and gas structures scheduled for decommissioning, and extensive marine renewable energy sites proposed for development. Previous studies funded by BEIS have shown that man-made structures may provide novel foraging habitat for seals (Russell et al. 2014), but that construction and operational noise from marine renewable energy sites may have complex impacts on their behaviour (Hastie et al. 2015, 2018, Russell et al. 2016a, Whyte et al. 2020). The population-level implications of these impacts remain unclear. Understanding the potential for impacts on seal populations from anthropogenic activity in the marine environment is therefore critical to environmentally sensitive marine spatial planning. A key step in this process is estimating seal distribution at-sea and quantifying the number of animals likely to be present in areas of human activity.

Mapping seal distribution at-sea requires tracking data from animal-borne telemetry tags. Currently, the most appropriate technology for this purpose in the UK is a GPS-GSM tag (SMRU Instrumentation, UK), which records data on locations, dives (time-depth), and haul-out events at a high spatial and temporal resolution, and transmits the data via the Global System for Mobile Communications (GSM) phone network (McConnell et al. 2004). Telemetry tags are glued to the seal's fur and fall off during the annual moult. Previously seal tracking data were combined with haulout-specific population estimates to generate at-sea abundance maps (hereafter usage maps) for both grey and harbour seals around the British Isles (UK, Isle of Man and Republic of Ireland) at a spatial resolution of 5 km x 5 km (Jones et al. 2013, 2015; funded by Scottish Government). Data were included from high resolution GPS tags and older, lower resolution, Argos tags. In 2015, BEIS funded a large deployment of GPS tags on grey seals in Southeast England (Russell 2016), and grey seal usage maps for the North Sea were subsequently updated (Jones and Russell 2016). The usage maps for the entire British Isles were updated for both species in 2017 to incorporate the new tracking data and more recent population estimates (Russell et al. 2017). However, with the exception of East Scotland and Southeast England, grey seal usage estimates were still almost entirely informed by old, low resolution (Argos) tracking data (up to 2010). A key limitation of the usage map approach is that predictions are based largely on the spatial distribution of tagged animals, and only a subset of all haulouts used by grey and harbour seals were visited by those individuals. Therefore, an assumption was made that, for the remaining haulouts, usage declines monotonically with distance from the haulout, based on an averaged distance-density relationship from around the whole coast for each species (Jones et al. 2013, Russell et al. 2017). However, this "null usage" prohibits the identification of hotspots of important habitat which are distributed heterogeneously offshore. Specifically, if no tagged individual visited an offshore foraging patch, the density in this area would be overlooked. This is particularly problematic in areas where tracking data are sparse or non-existent, such as Southwest England. Moreover, seals in different regions may exhibit differences in the spatial range of foraging trips (Sharples et al. 2012).

An alternative approach to the usage maps is the generation of predicted distribution estimates using habitat preference models. Such an approach requires tracking data at high spatial and temporal resolutions (i.e. GPS data). As mentioned above, prior to this project such data were lacking for grey seals around much of the UK. Previous studies have used habitat preference models to investigate the environmental drivers of distribution for UK seals in discrete areas of the North Sea (Aarts et al. 2008, Bailey et al. 2014, Jones et al. 2017b) or the whole of the UK North Sea (Grecian et al. 2018), but no study has used this approach to predict the distribution of the entire population of the UK or British Isles. One study used the estimated distributions from the usage maps generated by Jones et al. (2013) to infer species-environment relationships for both grey and harbour seals in the UK (Sadykova et al. 2017). However, the modelled relationships are potentially distorted by the aforementioned limitations associated with the usage maps. Moreover, this study assumed one species-environment relationship for the entire UK population for each species (Sadykova et al. 2017). Given that seals display regional differences in diet (Wilson and

Hammond 2019) and population trajectories (Thomas et al. 2019, Thompson et al. 2019), it is possible that they have regional differences in habitat preference.

To account for potential regional variation in habitat preference, and provide more ecologically informed estimates of seal distribution at-sea, the British Isles were divided into discrete regions (see Section 3.2.3 below). Region-specific use-availability habitat preference models (see Section 3.2.1 below) were used to investigate the environmental drivers of distribution for each species in each region. These modelled regional species-environment relationships were combined with recent spatially resolved population survey data to generate predicted at-sea density maps for both grey and harbour seal populations in the British Isles. A key advantage of the habitat preference approach over the usage maps is the ability to generate ecologically relevant predictions of distribution emanating from haulouts for which there are no associated tracking data.

To undertake this habitat preference analysis, recent GPS tracking data were required for both species. Through previous projects, GPS tags have been deployed on >200 harbour seals throughout their UK range, but prior to the commencement of this project in 2017, GPS tracking datasets for grey seals were restricted to the east coasts of England and Scotland (see Section 3.1.1 below). During this project, 100 GPS telemetry tags were deployed on grey seals at six sites around the UK, considered to be priority areas where recent tracking data were lacking (see Section 3.1.2 below). When combined with existing GPS tracking datasets held by SMRU, University of Aberdeen and University College Cork (UCC), the resulting data (and updated count data) allow us to address the following primary objective: (1) provide up-to-date maps of at-sea distribution (with associated uncertainty) for grey and harbour seal populations in the British Isles based on regional habitat preference models. Appendix 1 includes supplementary material relating to this primary objective. These new data allow us to provide additional information relevant to management in the form of the following secondary objectives: (2) estimate the number of seals using areas of interest: a case study of windfarm lease areas and tidal energy development sites in the UK sector (Appendix 2); (3) update knowledge on how seals use man-made structures at-sea (Appendix 3); and (4) update our understanding of the relationship between where grey seals acquire the prey resources necessary for reproduction and where they breed (Appendix 4). All place names mentioned in this report are shown in Appendix 1, Section A1.1.

3. Methods

3.1 Overview of tracking data

3.1.1 Existing data

Excluding data from tags deployed during this project (detailed below), existing data for adult grey seals, from SMRU, University of Aberdeen and UCC, comprised GPS data from 56 individuals: 16 in Southeast Scotland (2005, 2008, 2013), 21 in Southeast England (2015; Russell (2016)), and 19 in the Republic of Ireland (2009, 2011, 2012, 2019). Argos Satellite Relay Data Loggers (SRDLs) have also been deployed by SMRU on 180 individuals throughout 1991 – 2008 in the UK. While the GPS tags typically record > 50 location estimates per day with high spatial accuracy (< 50 m error), location estimates from Argos SRDLs were far fewer (< 12 per day) (Russell 2015), with spatial error ranging from 50 m to > 2.5 km (Vincent et al. 2002). Argos data were excluded as they were mostly collected over 15 years ago, and the relatively low resolution would be problematic for matching locations to high resolution environmental data. In addition to tag deployments on adult seals, 85 telemetry tags have been deployed on grey seal pups in the UK. However, these data were not deemed to be suitable for population-level inference of habitat preference as pup behaviour changes rapidly throughout the initial months of life at-sea (Carter et al. 2017, 2020), and thus were excluded from this analysis.

Existing data for adult harbour seals from SMRU, University of Aberdeen and UCC comprise GPS data from 288 individuals: 54 in Southeast England (2006, 2012, 2016), 16 in Southeast Scotland (2008, 2011, 2013), 66 in Moray Firth (2009, 2013, 2014, 2015, 2017), 42 in Orkney & North Coast (2011, 2012, 2014, 2016, 2017), 48 in West Scotland (2011, 2012, 2014, 2017), four in the Western Isles (2006), 36 in Northern Ireland (2006, 2008, 2010), five in the English Channel (2009), and 17 in the Republic of Ireland (2006, 2007). Argos SRDLs have been deployed on 139 adults throughout 2001 – 2007 in the UK. As with grey seals, data from Argos tags were excluded for this project.

3.1.2 Deployments under current project

Under this current project (including additional funding: OESEA-17-85), funding was available for the deployment of 67 GPS-GSM tags on grey seals. Tags were allocated to regions of the UK based on: (i) proportion of the UK grey seal population using that area; (ii) age and quantity of existing tracking data available (see Section 3.1.1 above); (iii) priorities for marine spatial planning. The specific haulout sites considered for deployment were based on fieldwork logistics. The aim was to deploy the tags as follows: Orkney (*n*=11), Monach Isles (Western Isles, *n*=12), Islay (West Scotland, *n*=12), Dee Estuary (North Wales, *n*=12), Bardsey Island (Northwest Wales, *n*=10 (OESEA-17-85)), and Ramsey and Skomer Islands (Southwest Wales, *n*=10 (OESEA-17-85)). Both Ramsey and Skomer are important seabird colonies, and to minimise any disturbance to breeding birds, fieldwork was both temporally and spatially restricted; fieldwork was prohibited from the start of May, and certain beaches and caves were off-limits. Within these limitations, fieldwork was undertaken as late as possible to maximise the number of seals that had finished the moult. Although ten tags were originally planned for deployment, an unexpectedly high proportion of individuals were still moulting, and bad weather meant that fieldwork was curtailed after the deployment of seven tags. Tracks from all tags deployed on grey seals during this project are shown in Fig. 1.

The first four deployments (Orkney, Monach Isles, Islay and Dee Estuary) were planned for 2017. In 2017, of the tags planned for deployment at each site, five (four for Orkney) were upgraded (funded by the UK Met Office) to include Argos transmission (GPS-GSM-Argos) to provide real-time water column temperature data for use in weather forecasting models. Unfortunately, a high proportion of the tags deployed in 2017 did not transmit data that were suitable for habitat preference analysis (Appendix 1, Section A1.2), although the data were suitable for some other research questions (see Carter and Russell (2018) for more details). These issues were only identifiable at the end of the 2017 field season. As a result of these issues, and the recovery of previously deployed tags which could be refurbished and redeployed, 36 additional tags were made available to this project (at no cost to BEIS). Three of these tags were deployed at the final site (Dee Estuary) in 2017, seven were deployed in Orkney in 2018, ten (seven provided by the University of Aberdeen) in the Moray Firth in 2018, ten in the Monach Isles in 2019 and six in Islay in 2019 (Appendix 1, Section A1.2). Allocation of tags was prioritised based on the results of preliminary habitat preference analysis conducted on the data collected in 2017. The Moray Firth was an additional site and was a priority area lacking in recent grey seal data. This site is the focus of a long-term study of harbour seals by the University of Aberdeen. In total, data from 31 of the 100 tags deployed during this project were not suitable for habitat preference analysis (Appendix 1, Section A1.2).

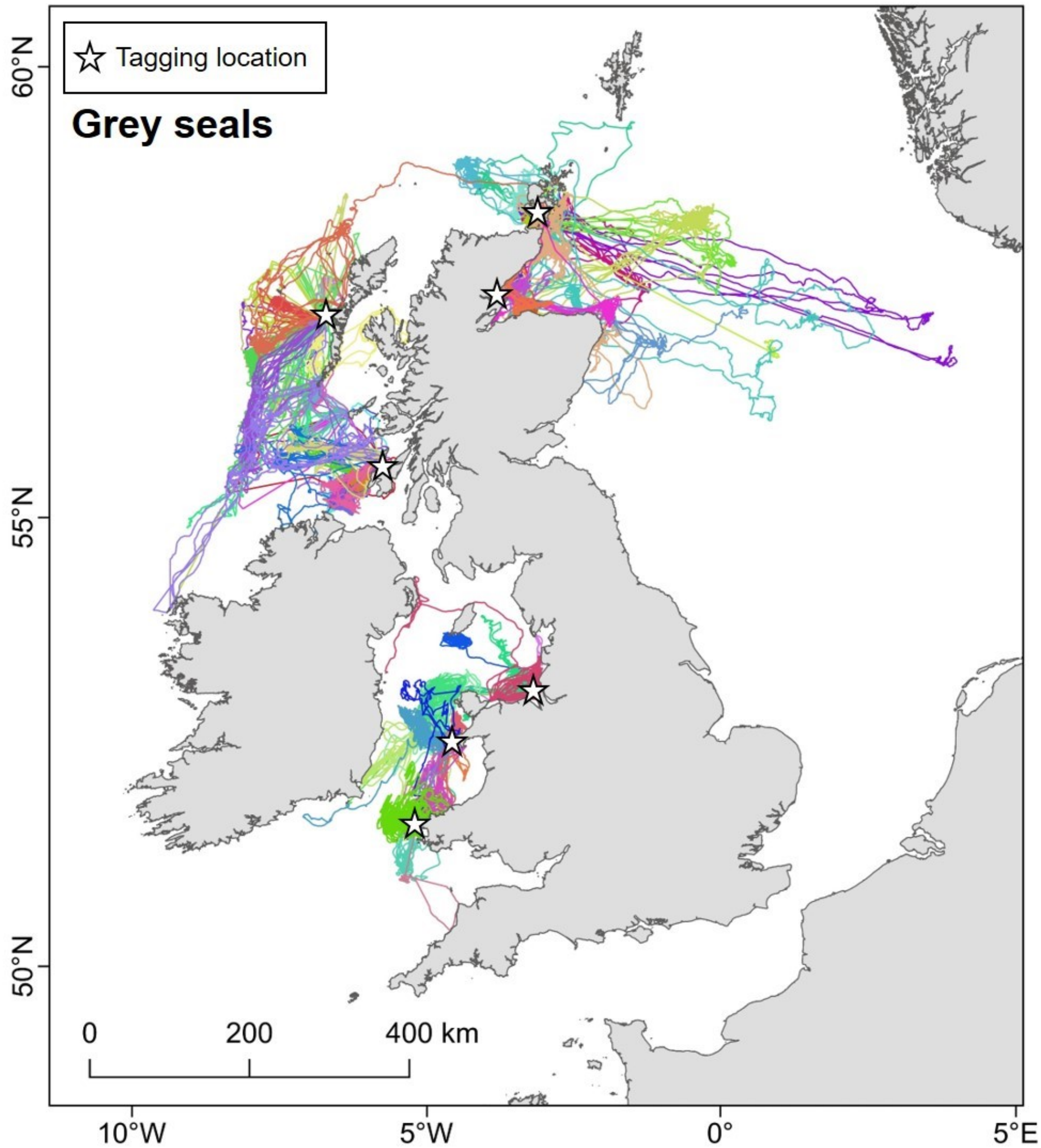


Figure 1: Grey seal GPS tracking data from tags deployed during this project. *Tracks are coloured by individual (n=100). White stars denote deployment locations (clockwise from bottom left); Ramsey & Skomer Islands, Bardsey Island, Dee Estuary, Islay & Oronsay (West Scotland), the Monach Isles (Western Isles), Orkney & Pentland Firth (North Scotland & Northern Isles), Dornoch Firth (Moray Firth).*

3.1.3 *Sample sizes for habitat preference analysis*

After data cleaning (see Appendix 1, Section A1.5.2), GPS data were available for 114 (45M, 69F) grey and 239 (107M, 132F) harbour seals. Sample sizes and tag deployment details for each regional habitat preference model are shown in Appendix 1, Section 1.3 (grey seals) and Section 1.4 (harbour seals). Maps of tracks for all individuals included in habitat preference analysis are shown below in Fig. 2.

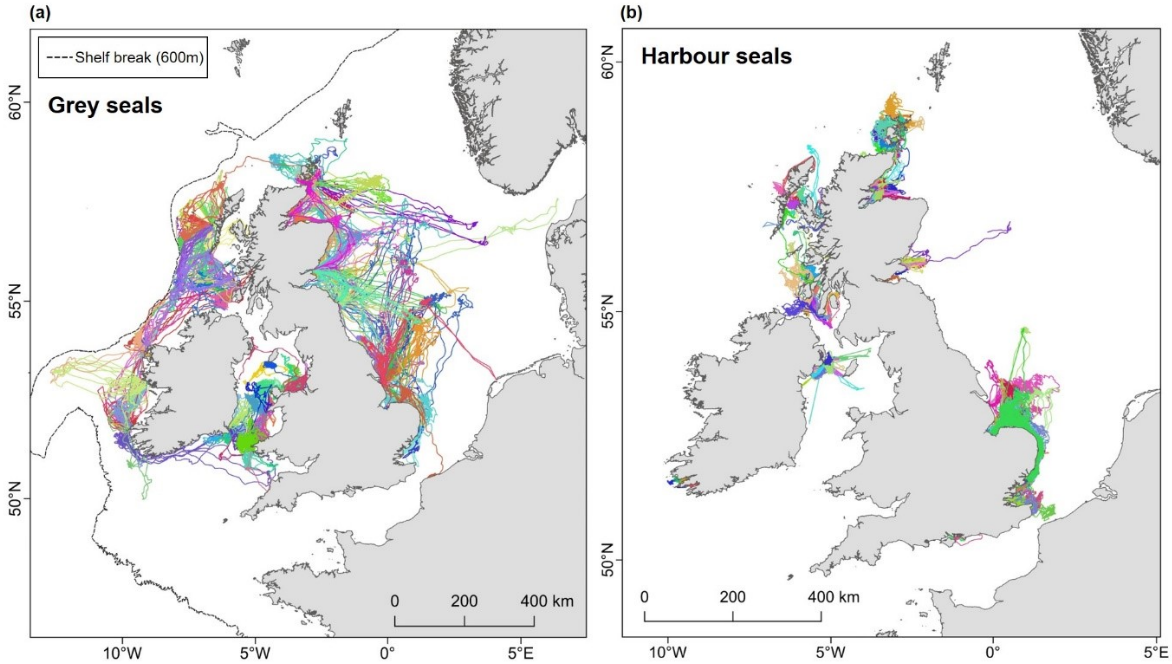


Figure 2: GPS tracking data for (a) grey and (b) harbour seals available for habitat preference models*. Data were combined from SMRU, University of Aberdeen and University College Cork. Tracks are shown before cleaning, coloured by individual (grey seals = 114; harbour seals = 239).*

3.2 Habitat preference

3.2.1 *What are habitat preference models?*

Habitat preference modelling involves determining the environmental drivers of distribution for a population by relating spatially resolved abundance data to metrics of habitat composition. This modelled species-environment relationship (resource selection function (RSF); Boyce and McDonald (1999)) can then be used to predict the distribution of a population, despite incomplete or non-uniform spatial survey effort. This approach was originally developed on terrestrial species, and is most commonly used with census or transect survey data (Manly et al. 2002), but can be applied to marine species (e.g. cetacean surveys (Hammond et al. 2013)). Adaptations to the modelling framework can be implemented to apply this approach to presence-only data (e.g. animal-borne tracking data). Briefly, in this adapted approach (use-availability habitat preference models), to infer "preference" for a particular type of habitat, the areas where individuals go (presences; tracking data) must be modelled alongside areas where they *could* go (control points; a random sample of available habitat accessible to the individual) (Matthiopoulos 2003). Preference for a particular type of habitat is then inferred where its use is disproportionate to its availability (Johnson 1980).

In this current analysis, recent GPS tracking data for grey and harbour seals were used to provide insight into the regional environmental drivers of at-sea distribution. Seal tracking data, and a sample of random control points in the area accessible to tracked seals, are matched to a suite of static and seasonal environmental covariates (e.g. water depth, seabed topography, winter sea surface temperature (SST); see Section 3.2.2 below) to quantify habitat use in the context of what is available to the tracked seals. The maximum foraging range of tracked seals was used to define the accessible area during each trip conducted by a tracked seal (see Appendix 1, Section A1.6.1 for more detail). In this analysis, regional habitat preference was modelled using binomial generalized additive mixed models (GAMMs) in the "mgcv" package (Wood 2015) in R (R Core Team 2020). For technical information on instrumentation protocol, tracking data handling, the use-availability design, model formulation, model selection and model validation, see Appendix 1, Section A1.5-A1.6.

3.2.2 Environmental covariates

Environmental data from a range of static and seasonal covariates were extracted for each seal location estimate (presence) and control point (availability sample) and included as explanatory covariates in a maximal model. 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. The data source and/or calculation method for each covariate is given in

Table 1 below. Environmental datasets were imported into R as georeferenced raster layers. Although the spatial resolution varied among rasters (~1 m to ~1.5 km; Table 1), values were extracted from the raster cell directly underlying each seal location or control point. Firstly, distance to haulout was included to control for decreasing accessibility with increasing distance (Matthiopoulos 2003). Bathymetric depth was included as it is also potentially a key factor limiting habitat suitability for benthic or demersal air-breathing predators (Boyd 1997). Seabed gradient (slope) and heterogeneity (rugosity) were included as they are important predictors of foraging habitat for some marine predators (Hastie et al. 2004, Bailey and Thompson 2009); seabed topography may concentrate prey in steep areas of upwelling. Slope and rugosity were highly correlated in all regions, and thus to aid interpretation of the ecological relationships, only the variable that provided the best model fit was selected in each region (see Appendix 1, Section A1.7 for details). Previous studies have demonstrated the importance of sandeels (*Ammodytes spp.*), particularly lesser sandeels (*A. marinus*) in the diet of seals, especially in the North Sea (Wilson and Hammond 2019). Carroll et al. (2017) found an inverse relationship between lagged (1 yr) mean winter sea surface temperature (SST) and lesser sandeel spawning stock biomass in the North Sea, suggesting that adult sandeels should be more abundant in areas that experienced lower SST during the previous winter. Lagged (1 yr) mean winter SST was therefore included as a potential explanatory covariate. This covariate will vary spatially and temporally between tracking data years.

The shelf seas around the British Isles have a variety of seasonal tidal mixing regimes (Hill et al. 2008), providing water column conditions (i.e. vertical structure) which may be spatially and temporally predictable, and may help seals to navigate and identify foraging areas. Vertically stratified waters, where warm surface water sits on top of colder denser water, may represent different foraging opportunities to mixed waters, where the temperature of the water column is homogeneous. Furthermore, the boundaries (frontal zones) where stratified and mixed water masses meet may host increased biomass and productivity (Fogg et al. 1985, Woodson and Litvin 2015). To investigate the significance of these features for seals, seasonal mean stratification (SST – SBT (sea bottom temperature)) was included as a covariate, alongside horizontal heterogeneity in stratification (Δ stratification; maximum range of stratification values in the 8 surrounding pixels (~1.5 km x 1.5 km)). Areas with strong heterogeneity in stratification indicate where mixed and stratified waters meet.

Seabed substrate type may be related to the foraging preferences of seals, either due to a relationship with the distribution of their favoured prey species, or with prey catchability (McConnell et al. 1992, Aarts et al. 2008, Jones et al. 2017b). Seabed substrate type was extracted from the EMODnet Broad-Scale Seabed Habitat Map for Europe (EMODnet Seabed Habitats Consortium 2016). The substrate data comprised seven factor levels which were combined into groups to improve model parsimony (see Appendix 1, Section A1.7). Grey seals from haulout sites in some regions (WIRL and WISL; see Section 3.2.3 below) made frequent trips to areas along the shelf edge. Thus an additional covariate, “shelf”, was included in the maximal models for grey seals in these regions to account for differences in habitat preference in areas on-shelf vs at the shelf edge, where prey selection and habitat composition is likely to be different. Areas were classified as on-shelf / shelf edge based on distance to the 600 m isobath (Fig. 2a) whereby a distance ≤20 km is classed as shelf edge, and >20 km is classed as on-shelf. The shelf break was taken as the 600 m isobath as no seal in the tracking dataset crossed this line (Fig. 2). The 20 km threshold was chosen as visual inspection of the tracks indicated that putative area-restricted search (ARS) behaviour was concentrated within this area. This “shelf” term was included in a full model as a factorial covariate, interacting with all other covariates (except distance to haulout). For each regional model, covariates were dropped in stepwise backwards model selection based on model Akaike Information Criterion (AIC) score until arriving at a minimal adequate model (see Appendix 1, Section A1.6.3 for details).

Table 1: Candidate environmental covariates for habitat preference models. *Res. indicates the spatial resolution in the horizontal (x-y) plane. *Seasonal mean variables were calculated for summer (May-Aug) for grey seals and for autumn (Sep-Dec), winter (Jan-Mar) and spring (Apr-May) for harbour seals. ‡Shelf was included in regions where seals showed evidence of foraging at the shelf edge. †Slope and rugosity were correlated in all regions, so were not modelled together (see Appendix 1, Section A1.7).*

Covariate	Unit	Res.	Description	Data source / calculation method
Distance to haulout	km	1 m	Minimum geodesic distance to pre / post haulout location	Calculated with R package "gdsitance" (van Etten 2015)
Depth	m	500 m	Bathymetric depth	Extracted from harmonised European Marine Observation and Data Network (EMODnet) Digital Terrain Model for European Waters http://www.emodnet-bathymetry.eu
Shelf‡	Y/N	1 m	Binary descriptor of if the location is ≤20 km from shelf break (600 m isobath)	Calculated with R package "gdsitance" (van Etten 2015)
Substrate	-	~150 m	Seabed substrate classification	EMODnet broad-scale seabed habitat map for Europe (EUSeaMap) http://www.emodnet.eu/seabed-habitats
SST (winter mean lag 1 yr)	°C	~1.5 km	Sea surface temperature for winter months (Jan-Mar) for the year preceding tracking data	Averaged from daily mean predictions, extracted from Met Office NW Shelf models: http://marine.copernicus.eu
Stratification*	°C	~1.5 km	SST-SBT (sea surface temperature – sea bottom temperature)	Averaged from daily mean predictions, extracted from Met Office NW Shelf models: http://marine.copernicus.eu
Δ Stratification*	°C	~1.5 km	Maximum difference in stratification values of 8 surrounding pixels	Calculated from stratification data using "terrain" function in R package "raster" (Hijmans 2016)
Slope†	°	500 m	Seabed gradient	Calculated from bathymetry data using "terrain" function in R package "raster" (Hijmans 2016)
Rugosity†	m	500 m	Seabed topographic heterogeneity	Calculated from bathymetry data using "terrain" function in R package "raster" (Hijmans 2016)

3.2.3 Regional designations

Predicted at-sea density maps for grey and harbour seals were developed based on region-specific models of habitat preference. Regional boundaries (Fig. 3; Table 2) were broadly based on the Seal Management Units (SMUs) used in UK seal conservation and management (SCOS 2019), but with some alterations to improve the predictive power of the models. For example, no GPS tracking data exist for either species in the Shetland SMU, thus it was necessary to use data from tags deployed in the North Coast and Orkney SMU to build a regional habitat preference model which could be used to predict distributions for seals hauling out in Orkney and Shetland. Grey seal tracking data revealed contrasting distributions and behavioural patterns of individuals hauling-out in North Wales and the Isle of Man to those hauling-out in West Wales and Southeast Ireland. Therefore, data from these two areas were modelled separately. Habitat preference regions were therefore defined based on a mixture of insights from tracking data, the spatial distribution of haulouts (Fig. 4), and the heterogeneity of habitat. Each habitat preference region is assigned a four-letter code (see Table 2 and Fig. 3 below) which is used throughout this report.

Table 2: Habitat preference regional designations. *Each region is assigned a four-letter code, used throughout this report. For graphical representation of the regions, see Figure 3. Place names mentioned in the descriptions are shown on the map in Appendix 1, Section A1.1.*

Region	Code	Description
West Scotland & Ireland North	WSIN	Encompassing the west coast of Scotland, including the Inner Hebrides, south to the Mull of Kintyre, as well as the northern coast of Northern Ireland and Rep. Ireland, from Torr Head west to Lough Swilly
Western Isles	WISL	Encompassing the Outer Hebrides, Flannan Islands and North Rona
North Coast & Northern Isles	NCNI	Encompassing the north coast of Scotland, as well as Orkney and Shetland
Moray Firth	MRYF	Encompassing the Moray Firth, from John o' Groats to Fraserburgh
East Coast	ECST	Encompassing the east coast of Scotland and England, from Fraserburgh south to Flamborough Head
Southeast England	SEEN	From Flamborough Head south to Beachy Head, encompassing The Wash and Thames Estuary
English Channel	ECHL	From Beachy Head west to Prawle Point
Celtic Sea & Irish Sea South	CISS	Encompassing Southwest England, the Bristol Channel, West Wales and the southeast coast of Rep. Ireland from Dublin Bay to Cork
Irish Sea North	IRSN	Encompassing the coast of North Wales, Northwest England and Southwest Scotland up to the Mull of Kintyre, as well as the west coast of Northern Ireland and Northeast Rep. Ireland, from Torr Head south to Dublin Bay
Western Ireland	WIRL	Encompassing the western half of Rep. Ireland from Lough Swilly round to Cork

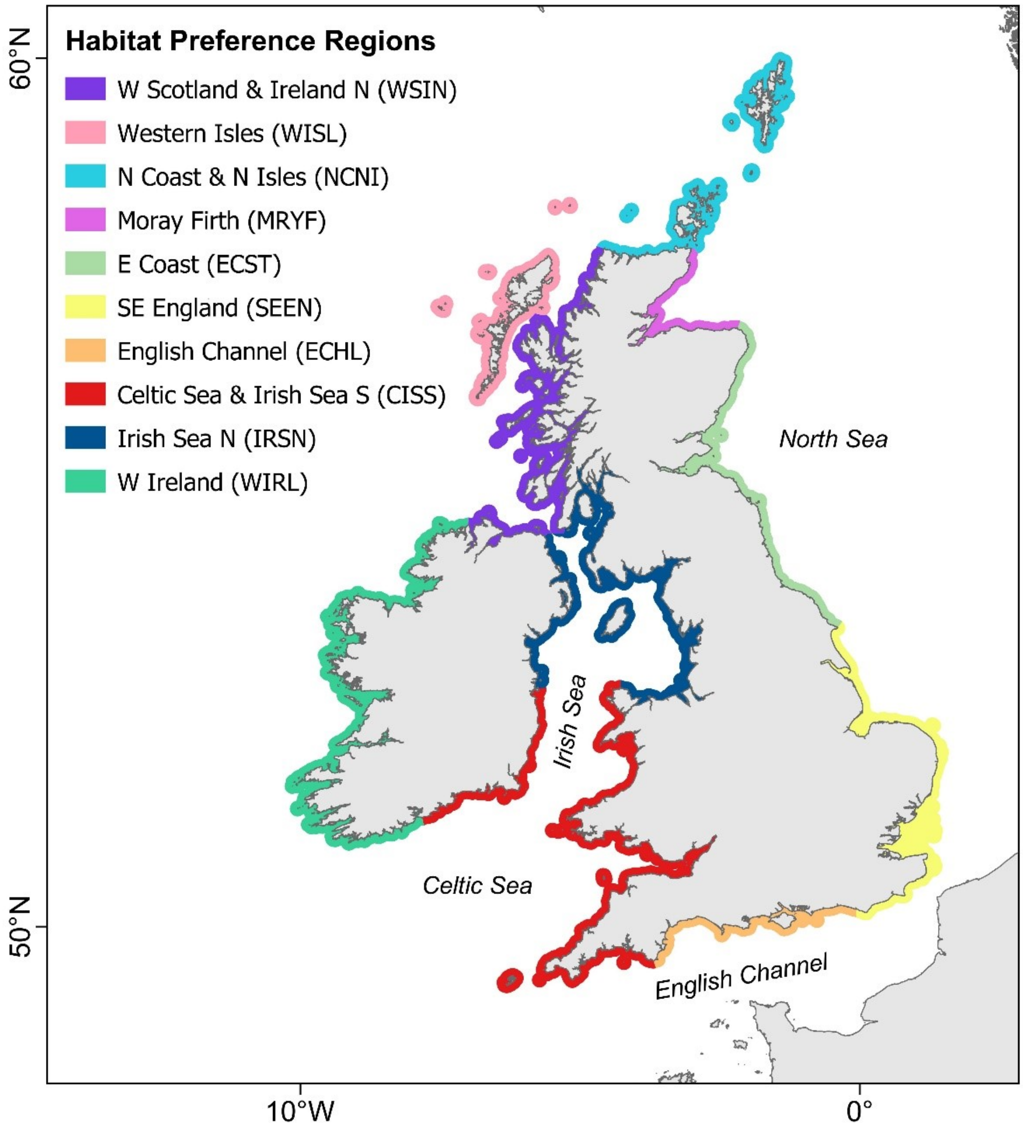


Figure 3: Regional designations for habitat preference models. *Haul-out sites were grouped into regional designations based on the movement patterns of seals using these haul-out sites, differences in habitat composition, and the availability of tracking data. Each region is assigned a four-letter code, used throughout this report.*

3.2.4 Predicting at-sea distribution

a. Prediction grid

A prediction grid was generated on a 5 km x 5 km cell resolution encompassing the area accessible to seals from all haulouts in the British Isles (see Appendix 1, Section A1.6.1). Environmental data were extracted for each of the covariates listed above in Table 1 for the centroid of each cell in the prediction grid. Non-static covariates (SST, stratification, Δ stratification) were extracted for data from 2018. Where seasonal covariates (i.e. stratification and Δ stratification for harbour seals) were retained in the minimal adequate models, the predictions were made using mean values for spring (April – May), as the majority of tracking data used to inform the models were from this period. For some coastal cells, the centroid fell on land, and therefore no environmental data were available. For these cells, covariate values were derived by taking the mean (or mode in the case of factorial covariates) of all environmental data values within the 5 km x 5 km cell boundaries (instead of at the centroid) (see Appendix 1, Section A1.8 for graphical explanation). This was possible as the resolution of environmental covariates was much finer than 5 km; for example, for any 5 km x 5 km cell in the prediction grid, there would be 100 cells in the bathymetry raster (resolution = 500 m). Coastal cells in the prediction grid pose a further problem relating to seal density estimates; seal density would be over-estimated if predictions were not corrected for the proportion of sea (versus land) in that cell. For example, if a coastal cell is 95% land, but treated as 100% sea, predictions for this cell may over-estimate seal abundance by 95%, assuming that seal density is evenly distributed throughout the cell. Thus, for each cell in the prediction grid, the proportion of the cell that included sea at mean spring high water was estimated (see Appendix 1, Section A1.8).

b. Survey data

Survey data comprise counts of seals on land from aerial and ground survey platforms conducted during the annual harbour seal moult in August (Figs. 4-5). For a detailed description of survey methods, see Thompson et al. (2019). Counts are aggregated to 5 km x 5 km grid cells (hereafter haulout cells; see Fig. 5). Data are included from multiple sources: UK aerial surveys (conducted by SMRU (Northern Ireland, Scotland, Southeast England) and ZSL (Thames Estuary)); Republic of Ireland aerial surveys (conducted by SMRU: Cronin et al. (2004), Duck and Morris (2013a, b), Morris and Duck (2019)); and UK ground counts (Westcott (2009, 2002, 2008), Westcott and Stringell (2004), Leeney et al. (2010), Sayer (2010, 2011, 2012a, b), Sayer et al. (2012), Bond (2018), Büche and Stubbings (2019)), unpublished data (see Acknowledgments)). For survey funding information, see Acknowledgements.

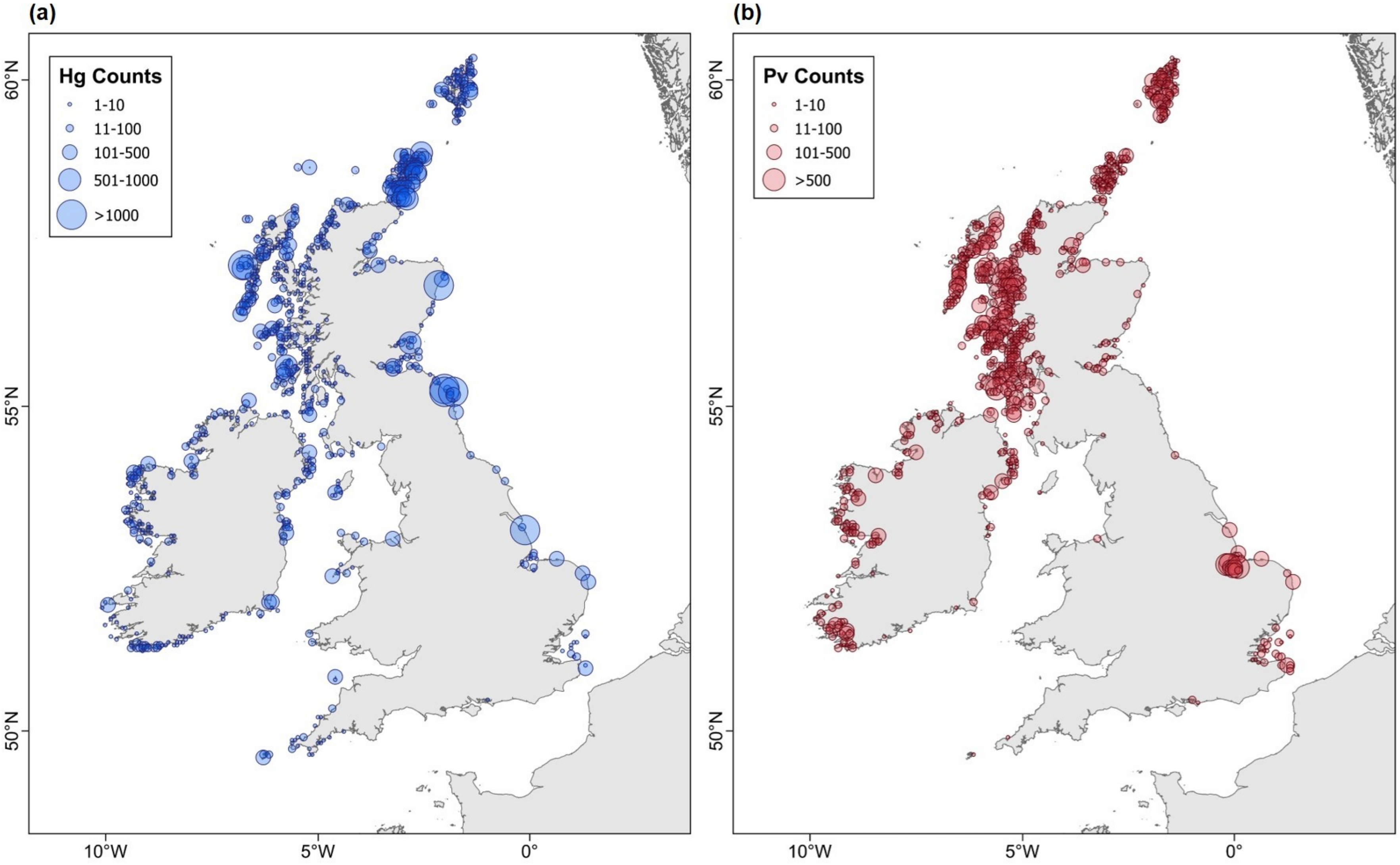


Figure 4: Most recent available count data for (a) grey and (b) harbour seals per 5 km x 5 km haulout cell used in the distribution analysis. *Surveys are conducted during the harbour seal moult (August). Areas that were surveyed but recorded no seals are not shown. For spatial and temporal survey coverage see Fig. 5.*

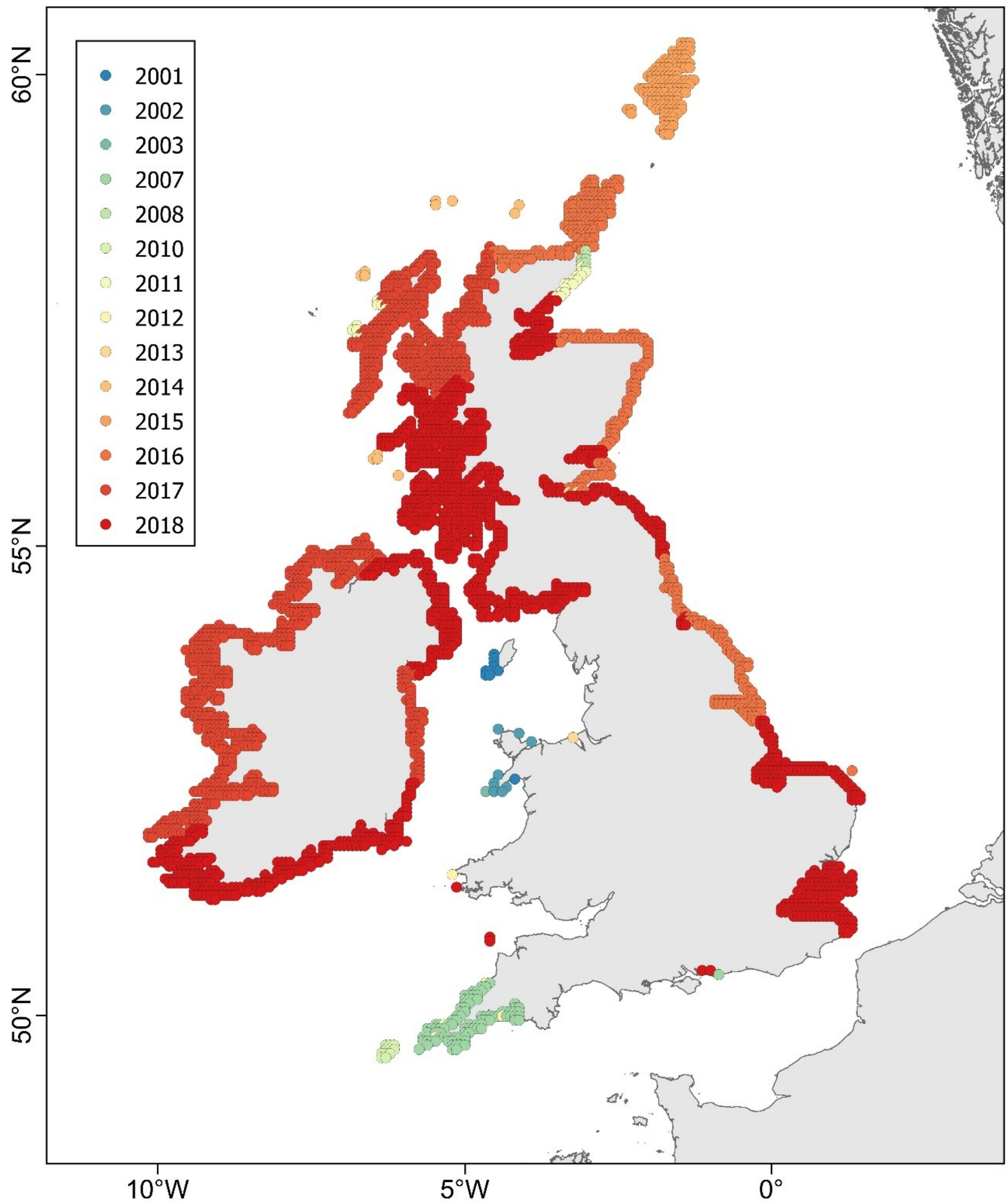


Figure 5: Date distribution of most recent survey data available for use in the analysis. *Surveys are conducted during the harbour seal moult (August), and both grey and harbour seals are recorded on the same surveys. Note that areas of coast that do not show survey data have not been surveyed because they are either associated with areas where seals are sparse and rarely haul-out, or with distant offshore islands (e.g. St Kilda, Fair Isle). For this analysis, cells which have not been surveyed were assumed not to contain any haulout sites.*

c. *Mean predicted distribution estimates*

For each species, spatial predictions of relative density emanating from each haulout cell with a non-zero count in the most recent survey (Figs. 4-5) were generated using the corresponding region-specific habitat preference model. The values given in the resulting maps are percentage of the at-sea population of each species estimated to be present in each 5 km x 5 km cell in the prediction grid. To generate these values, for each haulout cell, the raw at-sea predictions (which were on the logit scale) were exponentiated and then normalised (Manly et al. 2002, Beyer et al. 2010) (after any adjustment for the proportion of sea in coastal cells). Haulout-specific prediction surfaces were then weighted by the number of individuals counted in the most recent survey of that haulout cell. These haulout-specific predictions were then combined to create a multi-region surface. Cells in the multi-region surface were normalised, such that the value of each cell represents the percentage of the at-sea population for the British Isles (i.e. excluding hauled-out animals) of grey or harbour seals expected to be in the water in that cell at any given time (Russell et al. 2017) (i.e. cells in each species' predicted mean density surface sum to 100%). Thus, the predicted distribution maps represent relative seal density at-sea (relative to population size) in 2018. Note that the maps provided here show the mean with associated upper and lower 95% confidence intervals per cell. Calculation of confidence intervals is detailed below (Section 3.2.5). Estimates represent overall habitat preference, and thus do not distinguish between types of habitat use (e.g. foraging or travelling behaviour).

There was significant serial autocorrelation in model residuals which may lead to underestimation of model variance (Fieberg et al. 2010). To mitigate these effects, the data were thinned before fitting the final model for mean and uncertainty (see below) estimates using a "time to independence" approach (Swihart and Slade 1985). This constitutes sub-sampling the data to every n^{th} presence and associated control points. Models were then fitted with the subsampled datasets before examining the autocorrelation of model residuals for presences for each individual (Venables and Ripley 2002). At the value of n where all individuals returned autocorrelation values within the approximate 95% confidence limits for an independent time series, it was assumed that the residuals were statistically independent (Venables and Ripley 2002), and the resulting model was used to generate the predicted distributions. The value of n varied among regions for each species (grey seals: min = 12, max = 50; harbour seals: min = 5, max = 55).

Although previous seal distribution maps (usage maps (Jones et al. 2013, 2015, Jones and Russell 2016, Russell et al. 2017)) have presented *absolute* density (i.e. number of animals) rather than *relative* density (i.e. percentage of at-sea population), providing such estimates requires knowledge of two scaling factors to estimate the total size of the at-sea population:

(1) the proportion of the overall population hauled-out, and thus available to count during the survey window (within 2 h either side of low tide in August), and (2) the proportion of time seals spend at-sea on average during the main foraging season. Predicted distribution is given as relative density in this report because there are caveats currently associated with these scalars that prohibit accurate estimation of absolute density; the first scalar is currently under review for grey seals (Russell et al. 2016b). An example using absolute estimates of seal density (and discussion of associated caveats) is presented in Appendix 2.

3.2.5 Uncertainty in distribution estimates

Lower and upper 95% confidence intervals presented in this report represent the range of values *per cell* within which, based on the habitat preference models, the true seal density value is likely to be. Therefore, uncertainty estimates should be treated as cell-specific and should not be summed across an area; doing so would generate exaggerated confidence intervals. Lower and upper 95% Bayesian credible intervals (i.e. confidence intervals) were generated for each cell in the prediction grid using a posterior simulation approach (Wood 2006, Augustin et al. 2013). This approach takes advantage of the fact that fitting a GAMM in using the “mgcv” package (Wood 2015) is an empirical Bayes procedure, providing a posterior distribution for the model coefficients. For each cell, 1,000 realisations were generated from this (approximately multivariate-normal) posterior distribution. For each of the 1,000 realisations, predictions were generated on the scale of the linear predictor, which were then exponentiated, multiplied by the proportion of each cell that contained sea, and normalised, as with the mean estimates (see Section 3.2.4c above). The result was 1,000 possible predicted distribution surfaces. The 2.5% and 97.5% quantiles per cell of these surfaces were then taken as the cell-wise lower and upper confidence intervals, and predicted relative density surfaces for upper and lower confidence intervals were generated.

4. Results

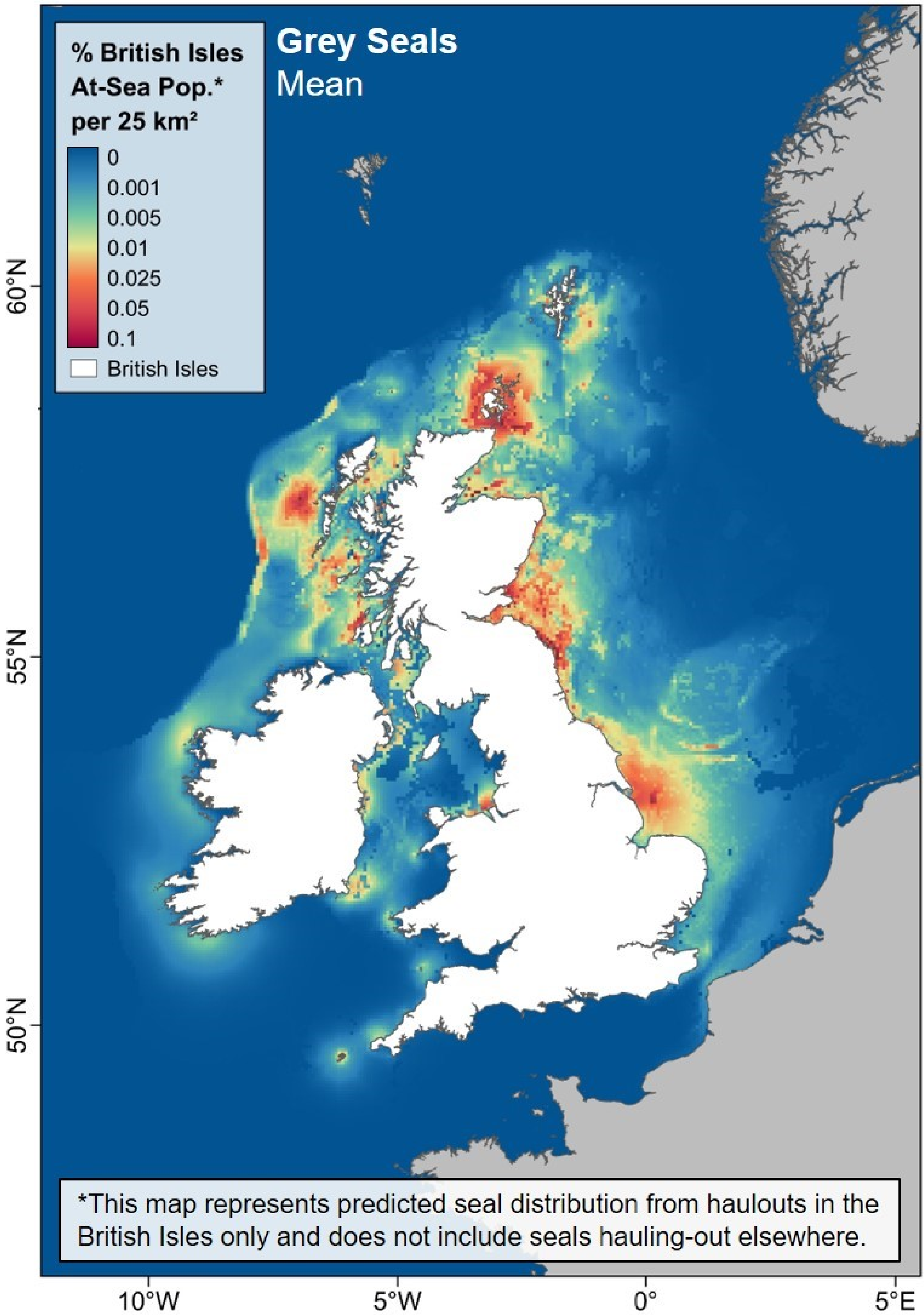
4.1 Overview of downloadable output

Maps showing the mean (and associated cell-wise 95% confidence intervals) predicted relative density at-sea for seals hauling-out in the British Isles are given in Fig. 6 for grey seals and Fig. 7 for harbour seals. The following shapefiles (in a Universal Transverse Mercator 30°N World Geodetic System 1984 projection; UTM30NWGS84) are available for download (https://doi.org/10.17630/dcebb865-3177-4498-ac9d-13a0f10b74e1), corresponding to each figure:

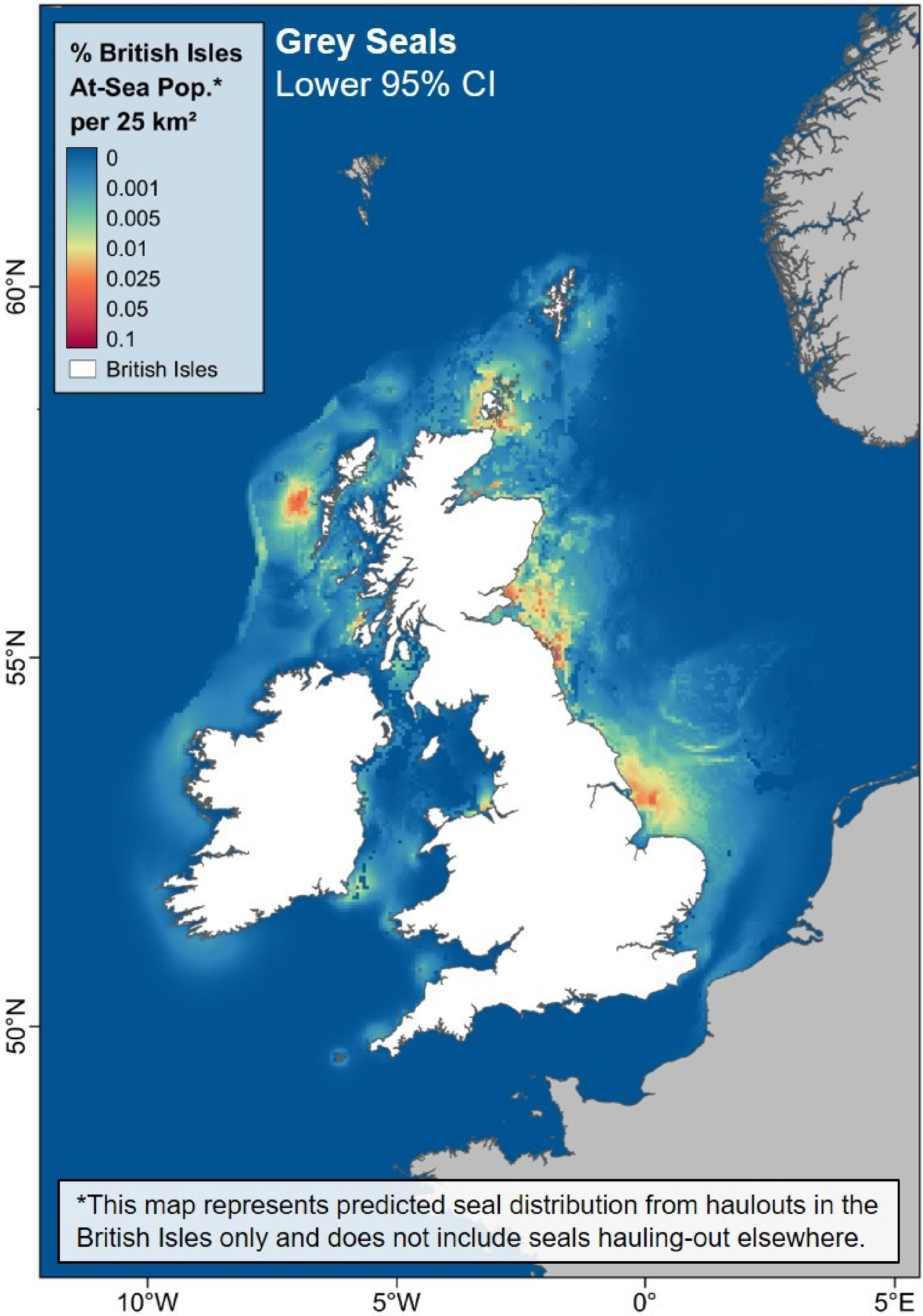
- Fig. 6a: "Hg_Sea_Mean.shp"
- Fig. 6b: "Hg_Sea_LowerCI.shp"
- Fig. 6c: "Hg_Sea_UpperCI.shp"
- Fig. 7a: "Pv_Sea_Mean.shp"
- Fig. 7b: "Pv_Sea_LowerCI.shp"
- Fig. 7c: "Pv_Sea_UpperCI.shp"

4.2 Grey seal at-sea distribution maps

(a) Mean



(b) Lower 95% confidence interval



(c) Upper 95% confidence interval

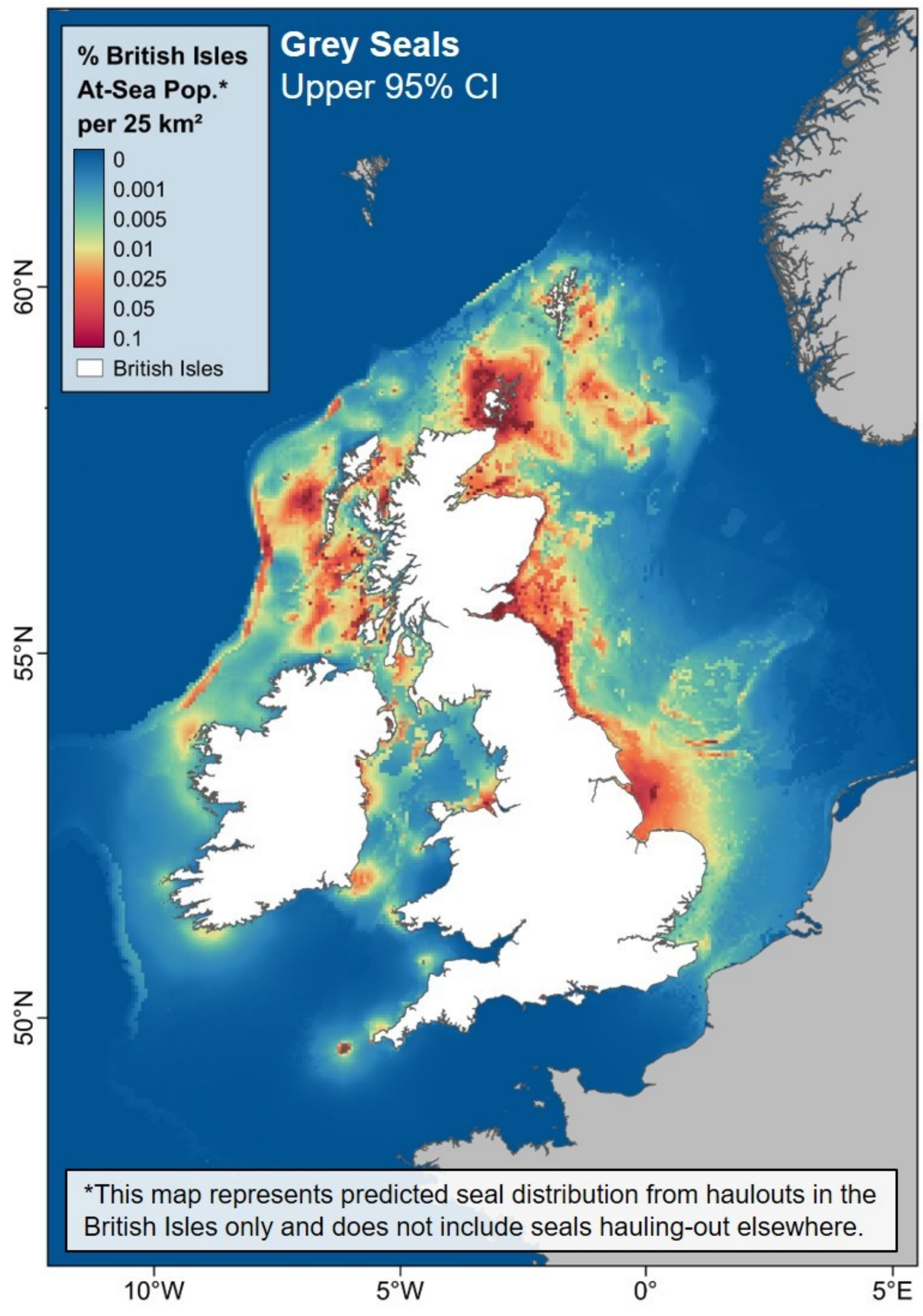
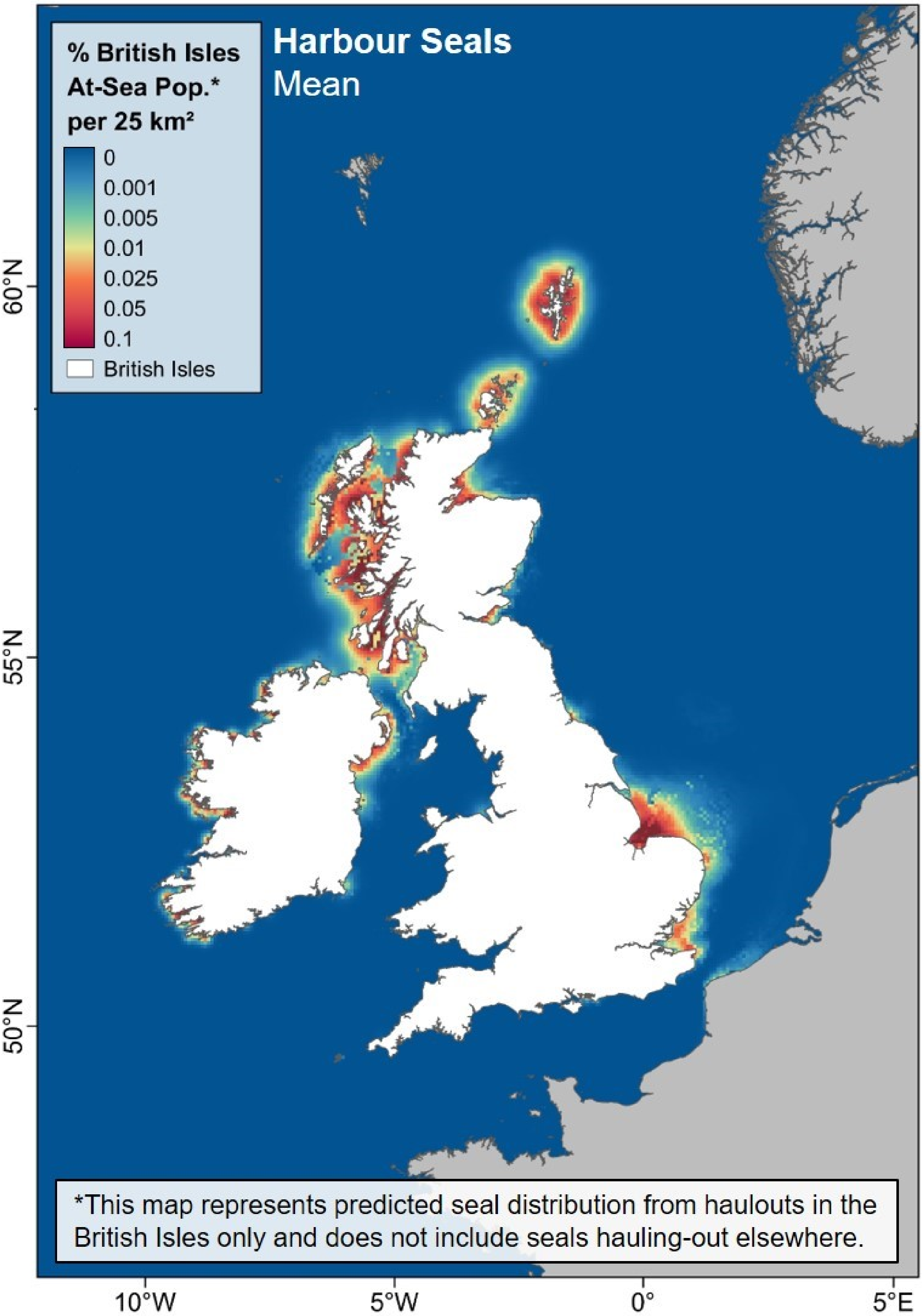


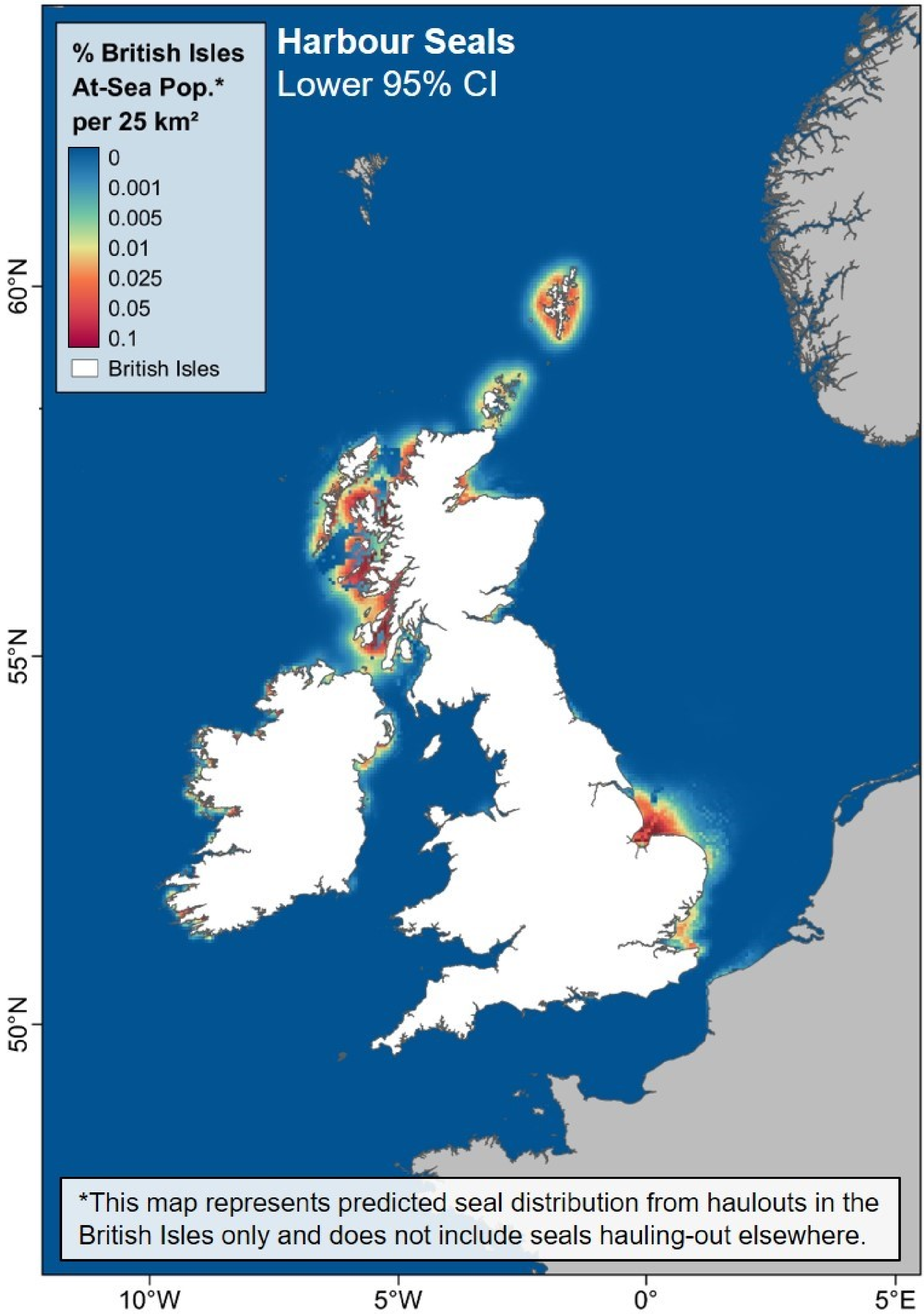
Figure 6: At-sea distribution of grey seals from haulouts in the British Isles in 2018. *Maps show (a) mean percentage of at-sea population estimated to be present in each 5 km x 5 km grid cell at any one time, and the cell-wise (b) lower 95% and (c) upper 95% confidence intervals.*

4.3 Harbour seal at-sea distribution maps

(a) Mean



(b) Lower 95% confidence interval



(c) Upper 95% confidence interval

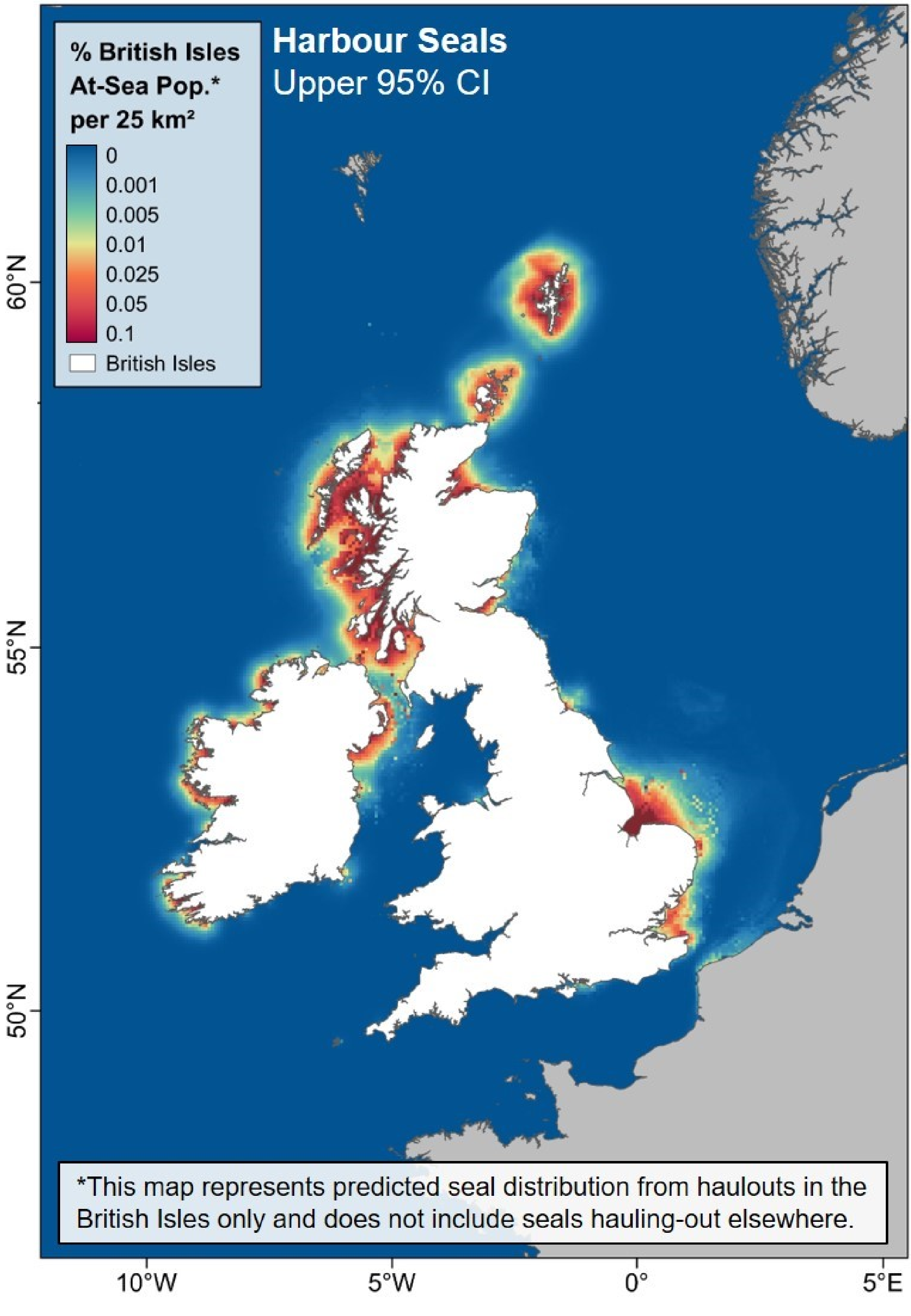


Figure 7: At-sea distribution of harbour seals from haulouts in the British Isles in 2018. *Maps show (a) mean percentage of at-sea population estimated to be present in each 5 km x 5 km grid cell at any one time, and the cell-wise (b) lower 95% and (c) upper 95% confidence intervals.*

5. Discussion

5.1 Seal distribution maps

In this report high resolution GPS tracking data were combined with survey data (aerial and ground counts) in a use-availability habitat preference modelling framework to generate estimates of predicted at-sea density for grey and harbour seals in the British Isles. Importantly, the analysis allowed for discrete species-environment relationships in different regions of the British Isles. The primary output of this project is a series of maps (Figs. 6-7), and associated shapefiles, providing the relative density of grey and harbour seals (percentage of the at-sea population estimated to be present at any one time) on a 5 km x 5 km grid. Three maps are provided for each species: the mean estimate and associated lower and upper 95% confidence intervals. The maps, and important considerations for interpretation and future work are discussed below.

The maps reveal large areas of relatively high at-sea density for grey seals in Southeast England, East Scotland and Northeast England, Orkney and the Western Isles (Fig. 6). Besides these areas of important habitat adjacent to large haulout sites, the maps identify important offshore areas. As a notable difference to previous distribution estimates (usage maps), these maps indicate a relatively high density of grey seals along the shelf edge to the west of the Western Isles. This is supported by the tracking data, with nine individuals (60%) in WISL performing repeated trips to the shelf edge. On the east coast, hotspots of density are patchily distributed out to ~100 km from the coast. In Southeast England, hotspots are evident along the western and southern fringes of the Dogger Bank, which appears to be an important feature in the region, potentially influencing seal foraging distribution. Eight individuals (42%) in SEEN used this area. In comparison to grey seals, important areas for harbour seals were much more tightly concentrated around the coastline adjacent to haulouts (Fig. 7). Core areas for harbour seals include the Inner Hebrides, particularly waters to the south and east of Islay, south and east of Tiree, north and east of Skye, as well as Orkney, Shetland, the inner Moray Firth, the Firth of Forth, The Wash and the Thames Estuary. All place names mentioned are shown on the map in Appendix 1, Section A1.1.

5.2 Presentation of density index

The predicted distribution maps presented here provide a relative index of seal density at-sea (i.e. percentage of at-sea population present in each 5 km x 5 km grid cell at any one time). Previous seal distribution maps (usage maps (Jones et al. 2013, 2015, Jones and Russell 2016, Russell et al. 2017)) have provided estimates of seal distribution as absolute density (i.e. number of seals per cell). Whilst the relative density estimates presented here are perhaps less readily usable in an applied context, they have the advantage that they are independent of scalars relating to the proportion of the population available for counting during August surveys, and the proportion of time individuals spend at-sea during the main foraging season. These relative density estimates can be readily converted to absolute density estimates as more accurate scaling factors become available. As mentioned above (Section 3.2.4c), the population scalar for grey seals is currently under review (Russell et al. 2016b), thus the absolute density values given in the case study (Appendix 2) should be treated as rough estimates. Relative density provides an index that is robust to any future changes in population scaling methodology. These estimates would be sensitive to any regional change in population size, but estimates can be updated with new count data in the future. Furthermore, relative at-sea density estimates for seals hauling-out at specific sites, such as SACs, can be generated even when count data are out-dated.

5.3 Count data

In addition to recent tracking data, accurately estimating seal density at-sea requires recent spatially resolved abundance data. This is especially critical in areas with strong changes in abundance through time, such as ECST and NCNI where harbour seals are in steep decline, and SEEN where grey seal numbers are increasing exponentially. In this project, the most recent available count data were used for each haulout cell surveyed around the British Isles (Fig. 5). In the UK, the majority of haulouts in Scotland and Southeast England (including all SACs where seals are a primary qualifying feature) are covered by aerial surveys with a maximum gap of five years. Elsewhere, for example in Wales and Southwest England, aerial surveys are not feasible due to the high proportion of individuals hauling-out in caves and secluded coves, thus ground and boat-based counts are compiled where available (see

Section 3.2.4b), and counts are therefore less systematic. Although this approach involves some spatial inconsistencies in survey effort, the vast majority of count data included (94.4%) were from the past five years (Fig. 5). Previously, abundance estimates for the usage maps were derived by taking the mean of previous counts, or extrapolating from a temporal trend fitted to the data (Jones et al. 2013, 2015, Jones and Russell 2016, Russell et al. 2017). In this habitat preference approach, the use of most recent count was deemed favourable, as recent evidence suggests that extrapolating from simple temporal trends may not accurately capture harbour seal population dynamics (Thompson et al. 2019), and many older (pre 2008) counts for grey seals during August surveys were opportunistic, rather than systematic. However, one limitation of this approach is that it is potentially more susceptible to anomalies in the count data. For example, a haulout that normally has large numbers of seals, but had no seals on the most recent survey because of some unknown factor, such as localised disturbance, may impact the density estimates.

5.4 Modelled uncertainty

Upper and lower 95% confidence intervals presented in this report represent the range of values in which, based on the habitat preference model, the true seal density is likely to be encompassed. These confidence intervals capture uncertainty in the habitat preference relationship across all individuals. Although individual seal was included as a blocking factor in the models (see Appendix 1, Section A1.6.2) to ensure that the preference relationship was not unduly dominated by data-rich individuals, restrictions associated with the analytical framework and the scale of the modelling exercise meant that it was not possible to explicitly model uncertainty relating to individual variation in habitat preference. Regions in which cells generally show wide confidence intervals indicate high uncertainty in the mean prediction as a result of insufficient sample size of tagged seals, that the tagged individuals represent multiple foraging strategies (and thus habitat preferences), and/or that key environmental drivers of distribution have not been included in the model (either due to lack of knowledge of those drivers or lack of appropriate environmental data). Results indicate that NCNI is a low confidence region for both species, while WISL, ECST, CISS and WIRL are low confidence for harbour seals. These areas would therefore benefit from future tag deployments.

5.5 Methodological considerations

Despite the advantages of the habitat preference approach, there are some associated caveats which should be carefully considered when interpreting the predicted distribution maps. One element of uncertainty that is not captured by the models (and thus not encompassed in the lower and upper confidence intervals) is how representative the tracking data are of the regional habitat preference, which is contingent on both the spatial and temporal stability of preference. In this project, marked regional differences in preference were encountered, suggesting that spatial stability is violated at large scales. This is particularly problematic in the case of Shetland. Ideally, Shetland should be modelled as a discrete region. However, a lack of GPS tracking data for both species in Shetland meant that this area was grouped into one region with Orkney and the North Coast (NCNI), and thus the distribution estimates were based on a preference relationship for seals hauling-out elsewhere within the region (predominantly Orkney). A study comparing the diet of both seal species around the UK revealed differences in prey composition for both species between Orkney and Shetland (Wilson and Hammond 2019), which may be indicative of differences in habitat preference. Similarly, in the CISS region, the grey seal predictions for Cornwall and the Isles of Scilly are based on a habitat preference relationship for individuals tagged in Southwest Wales and Southeast Ireland. These tagged seals did not visit haulouts in Southwest England, and the predictions for this area therefore carry a high degree of unmodelled uncertainty. Moreover, no tracking data exist for harbour seals in the CISS region, thus predictions were based on the modelled relationship for the adjacent IRSN region. Given that CISS does not host a large population of harbour seals (~0.1% of British Isles population), this is unlikely to have a profound effect on the overall distribution estimates, but nevertheless, users should treat the estimates for this region with an extra degree of caution.

A similar extrapolation was necessary in the ECST region, where the majority of grey seal data are from tag deployments in the Eden Estuary and Firth of Tay, yet the largest haulout aggregations in the region are ~100 km further north in the Ythan Estuary, and ~100 km further south at the Farne Islands. However, in general, the assumption of spatial stability is less problematic for grey than for harbour seals; as grey seals are wide-ranging, there is considerable overlap in distributions emanating from different haulouts in the region.

Indeed, individuals tagged in the Eden and Firth of Tay did visit the Farne Islands, as did individuals tagged at Donna Nook and Blakeney Point in SEEN. However, for harbour seals, distributions can be much more discrete between haulouts. For example, in the WSIN region, individuals tagged at Dunvegan on the north coast of Skye showed no overlap in distribution with those tagged at Kyle Rhea, on the opposite side of the island. Similarly, nine harbour seals tagged in the Eden Estuary in ECST foraged largely to the east of St Andrews Bay, with three undertaking repeated trips to Wee Bankie, a known historical sandeel fishing ground. However, two seals tagged in the Firth of Forth (30 km to the south of the Eden Estuary) remained within the Forth and did not visit Wee Bankie. Such variation in habitat preference among haulouts in a region, or among individuals at a haulout, may complicate identification of an ecologically relevant regional mean species-environment relationship. In both these cases, the habitat preference relationship is potentially conflated by combining preferences of two distinct foraging strategies. This is most likely in areas of high tidal flow which are associated with localised preferences (e.g. Kyle Rhea (WSIN) (Hastie et al. 2016) and the Pentland Firth (NCNI)). To some extent multiple habitat preferences within a region will be reflected in wide confidence intervals, but to what degree is dependent on the habitat preference composition of the tagged seals. Further tagging is required across such regions to investigate and quantify within-region variation in habitat preference.

In addition to the above considerations on the spatial stability of predictions, there are certain considerations associated with temporal stability. The predictions given here are for a specific timeframe: 2018 (grey seals: summer; harbour seals: spring). Distribution estimates may vary for different prediction years, and for different seasons. Summer and spring were chosen for grey and harbour seals respectively, since the majority of tracking data fall in these seasons. Tracking data from the breeding season were excluded, as the behaviour of breeding animals is not representative of the key foraging season (Appendix 1, Section A1.5.2). Further tracking data and analyses would be required to determine the stability of habitat preference among seasons. Furthermore, tracking data used in the models are collected from multiple years (2005-2019; Appendix 1, Tables A1.2-A1.3). Thus, there is an implicit assumption of temporal stability in patterns of seal space use across years. In areas where population trajectories have changed throughout the tracking data time-span, this assumption may not hold true. The recent large-scale deployments on both species mean that any temporal changes in habitat preference are only a potential issue for ECST and SEEN, where tracking data pre-date large population changes (Russell et al. 2019). Indeed, changes in grey seal movement patterns through time have been observed in ECST during a time of population change (Russell 2015), and there have been further changes in the population size of both species since the majority of the tagging data were collected (Russell et al. 2019, Thompson et al. 2019) (Appendix 1, Section A1.3-A1.4). Although both grey and harbour seals have been tracked in the southern North Sea more recently (in 2015 and 2016, respectively), the rapidly changing population of both species (Thompson et al. 2019), and potential role of grey seal competition in the stabilisation of harbour seal trends, suggest that there may be rapid changes in at-sea distribution in this region.

Lastly, different environmental drivers of distribution may be associated with different behavioural modes (i.e. foraging versus travelling). The distribution estimates provided here are based on overall habitat preference, with the implicit assumption that foraging, and all other activities have the same habitat preference relationship. In reality, this may not be the case, and activity-specific preference relationships may impact the accuracy of the mean estimate, and therefore the predicted distribution maps. Moreover, the degree to which preference relationships for foraging and travelling differ will vary by region in a species-specific manner. For example, harbour seals typically exhibit discrete travelling and foraging-type movements in ECST, but not in WSIN. For grey seals, foraging and travelling behaviours are likely to be more spatially discrete, particularly for individuals hauling-out in WISL and ECST. In areas where haulout availability is tidal (e.g. The Wash), seals often spend protracted amounts of time in the water adjacent to the haulout. It is not clear whether this behaviour represents foraging or resting, but it may give rise to a bimodal preference relationship. This dichotomy between nearshore and offshore preference can be captured to some extent by the inclusion of the "distance to haulout" covariate. Nevertheless, in order to understand the environmental drivers of foraging behaviour, and identify critical foraging habitat, it would be necessary to perform habitat preference analysis specifically on foraging locations, which would first have to be identified from the tracking data using behavioural models (Russell et al. 2015). This is particularly important in the context of marine spatial planning, as disturbance or alteration to habitat will likely have different impacts depending on if they are in foraging or travelling areas.

5.6 Conclusions

This report presents the most comprehensive and up-to-date estimates of the at-sea distribution of grey and harbour seals hauling-out in the British Isles. As such, density contributed by seals hauling-out on the continent is not considered. Interpretation of these maps should be with consideration of the caveats discussed above, and confidence intervals should be utilised whenever possible. To improve the accuracy and robustness of the estimates, additional tagging should be focussed in Shetland, East Coast and Southeast England. Future analyses should focus on modelling the at-sea foraging distribution.

6. Ethics Statement

All licensed work in the UK was conducted under UK Home Office licence 70/7806 (and previous versions). All work was also conducted under licences issued by Marine Scotland (Research 01/2017/0 & 01/2018/0), Natural Resources Wales Licence (75896a:OTH:SA:2017), the Marine Management Organisation (L/2016/00315) and the National Parks and Wildlife Service, Republic of Ireland (C16/2006, C8/2007, C35/2008, C0019/2011, CO14/2012, C04/2013, C023/2013, C016/2014, 02/2019, C70/2019). Additional permissions for work on designated sites were obtained. Tagging on Ramsey RSPB reserve was approved by the RSPB's Ethics Advisory Committee (EAC2018-01). This work (including use of data from the Republic of Ireland) was approved by the University of St Andrews Ethics Committee.

7. Acknowledgements

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8. References

Aarts, G. et al. 2008. Estimating space-use and habitat preference from wildlife telemetry data. - Ecography 31: 140–160.

Augustin, N. H. et al. 2013. Space-time modelling of blue ling for fisheries stock management. - Environmetrics 24: 109–119.

Bailey, H. and Thompson, P. M. 2009. Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. - Mar. Ecol. Prog. Ser. 378: 279–287.

Bailey, H. et al. 2014. Modelling harbour seal habitat by combining data from multiple tracking systems. - J. Exp. Mar. Bio. Ecol. 450: 30–39.

Beyer, H. L. et al. 2010. The interpretation of habitat preference metrics under use-availability designs. - Philos. Trans. R. Soc. B Biol. Sci. 365: 2245–2254.

Bond, I. 2018. Tees Seals Research Programme, Monitoring Report No. 27. (1989–2018). Unpublished report to the Industry Nature Conservation Association.

Boyce, M. S. and McDonald, L. L. 1999. Relating populations to habitat using resource selection functions. - Trends Ecol. Evol. 14: 268–272.

Boyce, M. S. et al. 2002. Evaluating resource selection functions. - Ecol. Modell. 157: 281–300.

Boyd, I. L. 1997. The behavioural and physiological ecology of diving. - Trends Ecol. Evol. 12: 213–217.

Brasseur, S. M. J. M. et al. 2015. Rapid recovery of Dutch gray seal colonies fueled by immigration. - Mar. Mammal Sci. 31: 405–426.

Büche, B. and Stubbings, E. 2019. Grey Seal Breeding Census Skomer Island, 2018. The Wildlife Trust of South and West Wales. NRW Evidence Report 352.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed.). - Springer-Verlag.

Carroll, M. J. et al. 2017. Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality. - Aquat. Conserv. Mar. Freshw. Ecosyst. 27: 1164–1175.

Carter, M. I. D. and Russell, D. J. F. 2018. Seal habitat preference and distribution on the west and north UK coasts. Sea Mammal Research Unit, University of St Andrews, Interim Report to BEIS, OESEA-16-76/OESEA-17-78.

Carter, M. I. D. et al. 2017. Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behaviour in a marine top predator. - Sci. Rep. 7: 15505.

Carter, M. I. D. et al. 2020. From pup to predator: generalized hidden Markov models reveal rapid development of movement strategies in a naïve long-lived vertebrate. - Oikos 129: 630–642.

Caudron, A. K. et al. 2001. Comparative activity budget among grey seal (*Halichoerus grypus*) breeding colonies - the importance of marginal populations. - Mammalia 65: 373–382.

Chen, F. et al. 2017. Shipping noise in a dynamic sea: a case study of grey seals in the Celtic Sea. - Mar. Pollut. Bull. 114: 372–383.

Council of the European Communities 1992. Council Directive 92/43/EEC of 21 May 1992: on the conservation of natural habitats and of wild fauna and flora. - Official Journal of the European Communities: 1–9, 17.

Cronin, M. et al. 2004. Harbour seal population assessment in the Republic of Ireland: August 2003. Irish Wildlife Manuals No. 11. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland. - National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland

Duck, C. and Morris, C. 2013a. An aerial survey of harbour seals in Ireland: Part 2: Galway Bay to Carlingford Lough: August-September 2012. Unpublished report to the National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, Ireland.

Duck, C. and Morris, C. 2013b. An aerial survey of harbour seals in Ireland: Part 1: Lough Foyle to Galway Bay. August 2011. Unpublished report to the National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, Ireland.

EMODnet Seabed Habitats Consortium 2016. EMODnet European Seabed Habitat Maps.

Fieberg, J. et al. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? - Philos. Trans. R. Soc. B Biol. Sci. 365: 2233–2244.

Fogg, G. E. et al. 1985. Biological studies in the vicinity of a shallow-sea tidal mixing front VII. The frontal ecosystems. - Philos. Trans. R. Soc. London. B, Biol. Sci. 310: 555–571.

Fox, J. and Weisberg, S. 2011. An R companion to applied regression (2nd ed.). - Sage.

Grecian, W. J. et al. 2018. Man-made structures and Apex Predators: Spatial interactions and overlap (MAPS). Report to INSITE.

Hammond, P. S. et al. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. - Biol. Conserv. 164: 107–122.

Hastie, G. D. et al. 2004. Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to foraging. - Mar. Biol. 144: 397–403.

Hastie, G. D. et al. 2015. Sound exposure in harbour seals during the installation of an offshore wind farm: predictions of auditory damage. - J. Appl. Ecol. 52: 631–640.

Hastie, G. D. et al. 2016. Dynamic habitat corridors for marine predators; intensive use of a coastal channel by harbour seals is modulated by tidal currents. - Behav. Ecol. Sociobiol. 70: 2161–2174.

Hastie, G. D. et al. 2018. Harbour seals avoid tidal turbine noise: implications for collision risk. - J. Appl. Ecol. 55: 684–693.

Hijmans, R. J. 2016. raster: geographic data analysis and modelling. R package version 2.5-8.: https://CRAN.R-project.org/package=raster.

Hill, A. E. et al. 2008. Thermohaline circulation of shallow tidal seas. - Geophys. Res. Lett. 35: 5–9.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. - Ecology 61: 65–71.

Jones, E. L. and Russell, D. J. F. 2016. Updated grey seal (*Halichoerus grypus*) usage maps in the North Sea. Sea Mammal Research Unit, University of St Andrews, Report to DECC, OESEA-15-65.

Jones, E. et al. 2013. Grey and harbour seal usage maps. Report to Scottish Government MR5. Sea Mammal Research Unit, University of St Andrews. - Sea Mammal Research Unit Report to Scottish Government 5

Jones, E. L. et al. 2015. Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. - Mar. Ecol. Prog. Ser. 534: 235–249.

Jones, E. L. et al. 2017a. Seals and shipping: quantifying population risk and individual exposure to vessel noise. - J. Appl. Ecol. 54: 1930–1940.

Jones, E. L. et al. 2017b. Fine-scale harbour seal usage for informed marine spatial planning. - Sci. Rep. 7: 11581.

Langley, I. et al. 2020. Site use and connectivity of female grey seals (*Halichoerus grypus*) around Wales. - Mar. Biol. 167: 86.

Leeney, R. H. et al. 2010. Abundance, distribution and haul-out behaviour of grey seals (*Halichoerus grypus*) in Cornwall and the Isles of Scilly, UK. - J. Mar. Biol. Assoc. United Kingdom 90: 1033–1040.

Lonergan, M. et al. 2013. Rescaling of aerial survey data with information from small numbers of telemetry tags to estimate the size of a declining harbour seal population. - Aquat. Conserv. Mar. Freshw. Ecosyst. 23: 135–144.

Manly, B. F. J. et al. 2002. Resource selection by animals: statistical design and analysis for field studies (2nd ed.). - Kluwer Academic Publishers.

Matthiopoulos, J. 2003. The use of space by animals as a function of accessibility and preference. - Ecol. Modell. 159: 239–268.

McConnell, B. J. et al. 1992. Satellite tracking of grey seals (*Halichoerus grypus*). - J. Zool. 226: 271–282.

McConnell, B. J. et al. 2004. Phoning home - a new GSM mobile phone telemetry system to collect mark-recapture data. - Mar. Mammal Sci. 20: 274–283.

Morris, C. D. and Duck, C. D. 2019. Aerial thermal-imaging survey of seals in Ireland, 2017 to 2018. Irish Wildlife Manuals, No. 111. National Parks and Wildlife Service, Department of Culture, Heritage and the Gaeltacht, Ireland.

Pomeroy, P. P. et al. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. - Ethology 106: 899–919.

R Core Team 2020. R: a language and environment for statistical computing, Version 3.6.3.

Russell, D. J. F. 2015. Changes in at-sea foraging trips of harbour seals and grey seals in south-east Scotland. Sea Mammal Research Unit Report to Scottish Government, no. CSD 5.

Russell, D. J. F. 2016. Movements of grey seal that haul out on the UK coast of the southern North Sea. Sea Mammal Research Unit Report to DECC.

Russell, D. J. F. et al. 2013. Uncovering the links between foraging and breeding regions in a highly mobile mammal. - J. Appl. Ecol. 50: 499–509.

Russell, D. J. F. et al. 2014. Marine mammals trace anthropogenic structures at sea. - Curr. Biol. 24: R638–R639.

Russell, D. J. F. et al. 2015. Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals. - Oikos 124: 1462–1472.

Russell, D. J. F. et al. 2016a. Avoidance of windfarms by harbour seals is limited to pile driving activities. - J. Appl. Ecol. 53: 1642–1652.

Russell, D. J. F. et al. 2016b. Independent estimates of grey seal population size: 2008 and 2014. SCOS Briefing paper 16/3, Sea Mammal Research Unit, University of St Andrews.

Russell, D. J. F. et al. 2017. Updated seal usage maps: the estimated at-sea distribution of grey and harbour seals. Scottish Marine and Freshwater Science Report Vol 8 No 25. 8

Russell, D. J. F. et al. 2019. Monitoring long-term changes in UK grey seal pup production. - Aquat. Conserv. Mar. Freshw. Ecosyst. 29: 24–39.

Sadykova, D. et al. 2017. Bayesian joint models with INLA exploring marine mobile predator–prey and competitor species habitat overlap. - Ecol. Evol. 7: 5212–5226.

Sayer, S. 2010. Looe Island Seal Photo Identification Project (LISPIP) 2008/9/10: Aug 2010. A collaborative project between the Looe VMCA Marine Volunteers, Cornwall Wildlife Trust and Cornwall Seal Group. Unpublished report.

Sayer, S. 2011. Carracks to St Agnes Seal Photo Identification Project (CASPIP): July 30th (Aug) 2011. A collaborative project between British Divers Marine Life Rescue and Cornwall Seal Group. Unpublished report.

Sayer, S. 2012a. Polzeath Seal Photo Identification Project (POLPIP7), September 2012. A collaborative project between Cornwall Wildlife Trust, Polzeath Voluntary Marine Conservation Area, Cornish Sea Tours and Cornwall Seal Group. Unpublished report.

Sayer, S. 2012b. Marine Discovery Seal Photo Identification Project (MARPIP1), December 2012. A collaborative project between Marine Discovery and Cornwall Seal Group. Unpublished report.

Sayer, S. et al. 2012. Monitoring Grey Seals (*Halichoerus grypus*) in the Isles of Scilly during the 2010 Pupping Season (August to December 2010). Natural England Commissioned Reports, Number 103.

SCOS 2019. Scientific advice on matters related to the management of seal populations. Main Advice Report.

Sharples, R. J. et al. 2012. Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. - PLoS One 7: e37216; 10.1371/journal.pone.0037216.

Swihart, R. K. and Slade, N. A. 1985. Testing for independence of observations in animal movements. - Ecology 66: 1176–1184.

Thomas, L. et al. 2019. Modelling the population size and dynamics of the British grey seal. - Aquat. Conserv. Mar. Freshw. Ecosyst. 29: 6–23.

Thompson, D. et al. 2019. The status of harbour seals (*Phoca vitulina*) in the UK. - Aquat. Conserv. Mar. Freshw. Ecosyst. 29: 40–60.

van Etten, J. 2015. gdistance: distances and routes on geographical grids. R Package version 1.1-9.: https://CRAN.R-project.org/package=gdistance.

Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S (J Chambers, W Eddy, W Härdle, S Sheather, and L Tierney, Eds.). - Springer Science+Business Media.

Vincent, C. et al. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. - Mar. Mammal Sci. 18: 156–166.

Westcott, S. 2002. The Distribution of Grey Seals (*Halichoerus grypus*) and Census of Pup Production in North Wales 2001. CCW Contract Science Report No 499.

Westcott, S. 2008. Procedural Guidelines for Studying Grey Seals in Southwest England, 2006. Natural England Research Report NERR017.

Westcott, S. 2009. The Status of Grey Seals (*Halichoerus grypus*) at Lundy, 2008-2009. Report for Lundy MCZ.

Westcott, S. and Stringell, T. 2004. Grey Seal Distribution and Abundance in North Wales, 2002-2003. Bangor, CCW Marine Monitoring Report No 13.

Whyte, K. F. et al. 2020. Estimating the impacts of pile driving sounds on seals: pitfalls and possibilities. - J. Acoust. Soc. Am. 147: 3948–3958.

Wiens, T. S. et al. 2008. Three way k-fold cross-validation of resource selection functions. - Ecol. Modell. 212: 244–255.

Wilson, L. and Hammond, P. S. 2019. The diet of habour and grey seals around Britain: examining the role of prey as a potential cause of harbour seal declines. - Aquat. Conserv. Mar. Freshw. Ecosyst. 29: 71–85.

Wood, S. N. 2006. Generalized additive models: an introduction with R. - Chapman & Hall/CRC Press.

Wood, S. N. 2015. “mgcv”: mixed GAM computation vehicle with automatic smoothness estimation. R package version 1.8-31.: https://CRAN.R-project.org/package=mgcv.

Woodson, C. B. and Litvin, S. Y. 2015. Ocean fronts drive marine fishery production and biogeochemical cycling. - Proc. Natl. Acad. Sci. U. S. A. 112: 1710–1715.

Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. - Methods Ecol. Evol. 1: 3–14.

9. Appendices

9.1 Appendix 1: Supplementary material for main report

A1.1 Place names

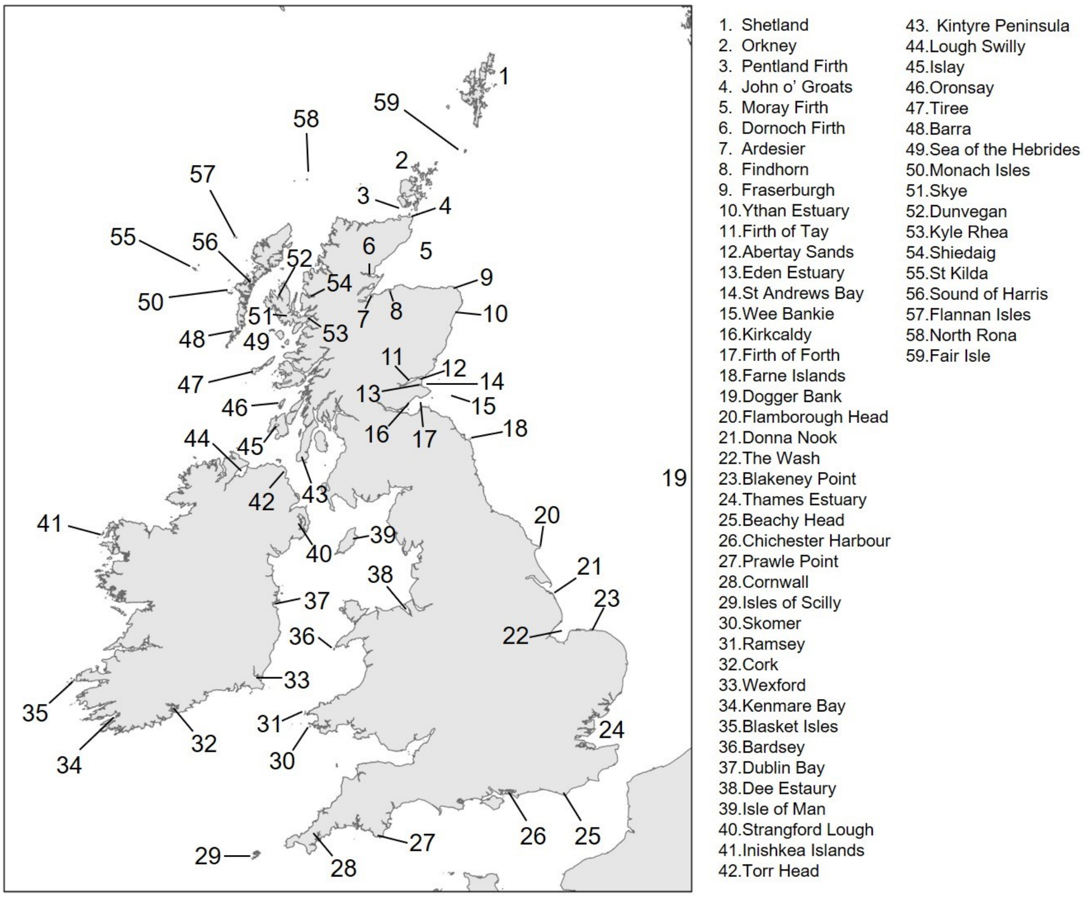

Figure A1.1: Place names mentioned throughout the text are shown on the map.

A1.2 Grey seal tag deployments during this project

Table A1.1: Tag deployments on grey seals during this project (n=100). *Tag duration is given in days. Seal IDs marked * denote deployments where little or no GPS data were transmitted (n=31). For explanation of habitat preference (HP) regions see Fig. 3 / Table 2 in main document.*

Seal ID	Year	Tag	Sex	Deployment Site	HP Region	On date	End date	Duration
hg53-503-17	2017	GPS-GSM	M	Orkney/Pentland	NCNI	30/05/2017	24/09/2017	117
hg53-504-17	2017	GPS-GSM	M	Orkney/Pentland	NCNI	30/05/2017	29/09/2017	122
hg53-570-17*	2017	GPS-GSM	M	Orkney/Pentland	NCNI	29/05/2017	-	-
hg53-572-17	2017	GPS-GSM	F	Orkney/Pentland	NCNI	21/05/2017	26/11/2017	189
hg53-573-17*	2017	GPS-GSM	M	Orkney/Pentland	NCNI	30/05/2017	-	-
hg53-580-17	2017	GPS-GSM	F	Orkney/Pentland	NCNI	23/05/2017	13/11/2017	174
hg53-585-17	2017	GPS-GSM	F	Orkney/Pentland	NCNI	26/05/2017	29/10/2017	156
hg53-M542-17*	2017	GPS-GSM-Argos	M	Orkney/Pentland	NCNI	29/05/2017	-	-
hg53-M543-17*	2017	GPS-GSM-Argos	F	Orkney/Pentland	NCNI	27/05/2017	24/09/2017	120
hg53-M545-17*	2017	GPS-GSM-Argos	F	Orkney/Pentland	NCNI	25/05/2017	22/06/2017	28
hg53-M546-17*	2017	GPS-GSM-Argos	F	Orkney/Pentland	NCNI	24/05/2017	07/08/2017	75
hg54-571-17	2017	GPS-GSM	F	Islay/Oronsay	WSIN	11/06/2017	24/11/2017	166
hg54-574-17	2017	GPS-GSM	M	Islay/Oronsay	WSIN	12/06/2017	07/10/2017	117
hg54-577-17	2017	GPS-GSM	F	Islay/Oronsay	WSIN	13/06/2017	05/10/2017	114
hg54-578-17	2017	GPS-GSM	M	Islay/Oronsay	WSIN	12/06/2017	08/10/2017	118
hg54-579-17	2017	GPS-GSM	F	Islay/Oronsay	WSIN	11/06/2017	30/11/2017	172
hg54-586-17	2017	GPS-GSM	F	Islay/Oronsay	WSIN	12/06/2017	12/07/2017	30
hg54-589-17	2017	GPS-GSM	M	Islay/Oronsay	WSIN	14/06/2017	20/08/2017	67
hg54-M544-17*	2017	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	11/06/2017	22/11/2017	164
hg54-M559-17*	2017	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	13/06/2017	27/07/2017	44
hg54-M564-17*	2017	GPS-GSM-Argos	M	Islay/Oronsay	WSIN	12/06/2017	06/07/2017	24
hg54-M565-17*	2017	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	11/06/2017	22/09/2017	103
hg54-M566-17*	2017	GPS-GSM-Argos	M	Islay/Oronsay	WSIN	13/06/2017	21/10/2017	130
hg55-575-17	2017	GPS-GSM	F	Monach Isles	WISL	22/06/2017	19/10/2017	119
hg55-581-17*	2017	GPS-GSM	M	Monach Isles	WISL	22/06/2017	06/09/2017	76
hg55-582-17*	2017	GPS-GSM	F	Monach Isles	WISL	21/06/2017	02/07/2017	11
hg55-583-17*	2017	GPS-GSM	M	Monach Isles	WISL	22/06/2017	07/07/2017	15
hg55-584-17	2017	GPS-GSM	F	Monach Isles	WISL	20/06/2017	05/11/2017	138
hg55-587-17	2017	GPS-GSM	F	Monach Isles	WISL	22/06/2017	12/10/2017	112
hg55-588-17	2017	GPS-GSM	M	Monach Isles	WISL	20/06/2017	30/10/2017	132
hg55-M555-17*	2017	GPS-GSM-Argos	F	Monach Isles	WISL	20/06/2017	14/11/2017	147
hg55-M556-17*	2017	GPS-GSM-Argos	F	Monach Isles	WISL	19/06/2017	19/11/2017	153
hg55-M558-17*	2017	GPS-GSM-Argos	M	Monach Isles	WISL	21/06/2017	16/09/2017	87
hg55-M560-17*	2017	GPS-GSM-Argos	M	Monach Isles	WISL	20/06/2017	04/08/2017	45
hg55-M567-17*	2017	GPS-GSM-Argos	M	Monach Isles	WISL	20/06/2017	05/09/2017	77
hg56-576-17	2017	GPS-GSM	F	Dee Estuary	IRSN	03/07/2017	24/08/2017	52
hg56-625-17	2017	GPS-GSM	F	Dee Estuary	IRSN	04/07/2017	07/08/2017	34
hg56-626-17	2017	GPS-GSM	F	Dee Estuary	IRSN	03/07/2017	25/08/2017	53
hg56-627-17	2017	GPS-GSM	F	Dee Estuary	IRSN	03/07/2017	19/08/2017	47
hg56-628-17	2017	GPS-GSM	M	Dee Estuary	IRSN	04/07/2017	03/08/2017	30

Seal ID	Year	Tag	Sex	Deployment Site	HP Region	On date	End date	Duration
hg56-629-17*	2017	GPS-GSM	F	Dee Estuary	IRSN	03/07/2017	06/07/2017	3
hg56-630-17	2017	GPS-GSM	F	Dee Estuary	IRSN	04/07/2017	27/07/2017	23
hg56-632-17*	2017	GPS-GSM	M	Dee Estuary	IRSN	03/07/2017	08/07/2017	5
hg56-750-13	2017	GPS-GSM	M	Dee Estuary	IRSN	04/07/2017	22/10/2017	110
hg56-752-13	2017	GPS-GSM	M	Dee Estuary	IRSN	04/07/2017	21/09/2017	79
hg56-M557-17	2017	GPS-GSM-Argos	F	Dee Estuary	IRSN	04/07/2017	18/11/2017	137
hg56-M562-17*	2017	GPS-GSM-Argos	M	Dee Estuary	IRSN	27/06/2017	21/07/2017	24
hg56-M563-17*	2017	GPS-GSM-Argos	F	Dee Estuary	IRSN	30/06/2017	30/09/2017	92
hg56-M568-17*	2017	GPS-GSM-Argos	M	Dee Estuary	IRSN	28/06/2017	27/09/2017	91
hg56-M569-17*	2017	GPS-GSM-Argos	M	Dee Estuary	IRSN	30/06/2017	09/08/2017	40
hg59-439-BAT-18	2018	GPS-GSM	F	Orkney/Pentland	NCNI	26/04/2018	01/10/2018	158
hg59-460-BAT-18	2018	GPS-GSM	M	Orkney/Pentland	NCNI	24/04/2018	27/10/2018	186
hg59-464-BAT-18	2018	GPS-GSM	F	Orkney/Pentland	NCNI	28/04/2018	01/09/2018	126
hg59-477-BAT-18	2018	GPS-GSM	M	Orkney/Pentland	NCNI	29/04/2018	25/10/2018	179
hg59-478-BAT-18*	2018	GPS-GSM	F	Orkney/Pentland	NCNI	27/04/2018	-	-
hg59-479-BAT-18*	2018	GPS-GSM	M	Orkney/Pentland	NCNI	29/04/2018	-	-
hg59-M787-18	2018	GPS-GSM-Argos	M	Orkney/Pentland	NCNI	27/04/2018	15/08/2018	110
hg60-438BAT-18	2018	GPS-GSM	M	Findhorn	MRYF	09/05/2018	16/11/2018	191
hg60-792-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	28/05/2018	12/12/2018	198
hg60-793-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	29/05/2018	09/11/2018	164
hg60-794-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	28/05/2018	01/10/2018	126
hg60-803-18	2018	GPS-GSM	M	Dornoch Firth	MRYF	29/05/2018	26/10/2018	150
hg60-805-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	28/05/2018	08/10/2018	133
hg60-806-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	29/05/2018	04/08/2018	67
hg60-807-18	2018	GPS-GSM	F	Dornoch Firth	MRYF	28/05/2018	05/09/2018	100
hg60-M786-18	2018	GPS-GSM-Argos	F	Ardersier	MRYF	09/05/2018	05/06/2018	27
hg60-M820-18	2018	GPS-GSM-Argos	F	Dornoch Firth	MRYF	28/05/2018	31/10/2018	156
hg61-738-18	2018	GPS-GSM	M	Bardsey	CISS	18/05/2018	14/01/2019	241
hg61-795-18	2018	GPS-GSM	F	Bardsey	CISS	17/05/2018	29/05/2018	12
hg61-809-18	2018	GPS-GSM	F	Bardsey	CISS	17/05/2018	06/10/2018	142
hg61-811-18	2018	GPS-GSM	M	Bardsey	CISS	18/05/2018	19/08/2018	93
hg61-812-18	2018	GPS-GSM	F	Bardsey	CISS	16/05/2018	18/07/2018	63
hg61-813-18	2018	GPS-GSM	F	Bardsey	CISS	17/05/2018	01/06/2018	15
hg61-M818-18	2018	GPS-GSM-Argos	M	Bardsey	CISS	16/05/2018	30/08/2018	106
hg61-M819-18*	2018	GPS-GSM-Argos	M	Bardsey	CISS	16/05/2018	-	-
hg61-M821-18	2018	GPS-GSM-Argos	F	Bardsey	CISS	15/05/2018	20/10/2018	158
hg61-M823-18	2018	GPS-GSM-Argos	F	Bardsey	CISS	15/05/2018	13/08/2018	90
hg62-698-18*	2019	GPS-GSM	M	Skomer	CISS	16/04/2019	-	-
hg62-788-18*	2019	GPS-GSM	M	Ramsey	CISS	18/04/2019	-	-
hg62-791-18	2019	GPS-GSM	M	Skomer	CISS	16/04/2019	10/08/2019	116
hg62-796-18	2019	GPS-GSM	M	Ramsey	CISS	17/04/2019	09/08/2019	114
hg62-992-19	2019	GPS-GSM	M	Ramsey	CISS	19/04/2019	15/09/2019	149
hg62-M000-19	2019	GPS-GSM-Argos	F	Ramsey	CISS	18/04/2019	12/08/2019	116
hg62-M026-19	2019	GPS-GSM-Argos	F	Ramsey	CISS	22/04/2019	16/09/2019	147
hg64-357-BAT-15	2019	GPS-GSM	M	Monach Isles	WISL	21/05/2019	20/08/2019	91
hg64-925-BAT-15	2019	GPS-GSM	M	Monach Isles	WISL	21/05/2019	23/06/2019	33
hg64-994-19	2019	GPS-GSM	M	Monach Isles	WISL	20/05/2019	19/12/2019	213

Seal ID	Year	Tag	Sex	Deployment Site	HP Region	On date	End date	Duration
hg64-M018-19	2019	GPS-GSM-Argos	F	Monach Isles	WISL	20/05/2019	04/11/2019	168
hg64-M019-19	2019	GPS-GSM-Argos	F	Monach Isles	WISL	22/05/2019	10/12/2019	202
hg64-M020-18	2019	GPS-GSM-Argos	F	Monach Isles	WISL	21/05/2019	20/10/2019	152
hg64-M021-19	2019	GPS-GSM-Argos	F	Monach Isles	WISL	20/05/2019	29/09/2019	132
hg64-M028-19	2019	GPS-GSM-Argos	F	Monach Isles	WISL	23/05/2019	10/11/2019	171
hg64-M561-18*	2019	GPS-GSM-Argos	M	Monach Isles	WISL	23/05/2019	-	-
hg64-M999-19	2019	GPS-GSM-Argos	M	Monach Isles	WISL	22/05/2019	16/09/2019	117
hg65-363-BAT-15	2019	GPS-GSM	F	Islay/Oronsay	WSIN	07/05/2019	28/07/2019	82
hg65-M027-19	2019	GPS-GSM-Argos	M	Islay/Oronsay	WSIN	07/05/2019	06/12/2019	213
hg65-M029-19	2019	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	06/05/2019	03/08/2019	89
hg65-M822-18	2019	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	07/05/2019	25/09/2019	141
hg65-M996-19	2019	GPS-GSM-Argos	M	Islay/Oronsay	WSIN	06/05/2019	05/10/2019	152
hg65-M998-19	2019	GPS-GSM-Argos	F	Islay/Oronsay	WSIN	05/05/2019	20/11/2019	199

A1.3 Grey seal tracking data

Table A1.2: Grey seal GPS tag deployments used for regional habitat preference models. *Sample sizes shown are after data cleaning. Some seals performed return trips in multiple regions and so were used in multiple models. The total number of tracks (i.e. a seal that performed trips in two different regions counts as two tracks) and the number of unique individuals in the dataset is shown. For habitat preference (HP) regional designations see Fig. 3 / Table 2 in main document. UCC = University College Cork, UofA = University of Aberdeen.*

HP Region	Deployment	Deployment Location	Data Provider	M	F	Year
WSIN	gp14	Blasket Isles	UCC	-	1	2009
	hg54	Islay / Oronsay	SMRU	3	2	2017
	hg55	Monach Isles	SMRU	1	-	2017
	hg64	Monach Isles	SMRU	1	1	2019
	hg65	Islay / Oronsay	SMRU	2	4	2019
WISL	gp14	Blasket Isles	UCC	-	1	2009
	hg54	Islay / Oronsay	SMRU	1	-	2017
	hg55	Monach Isles	SMRU	-	3	2017
	hg64	Monach Isles	SMRU	4	5	2019
	hg65	Islay / Oronsay	SMRU	-	1	2019
NCNI	pv14	Abertay Sands	SMRU	1	-	2005
	hg53	Orkney & Pentland	SMRU	2	3	2017
	hg59	Orkney & Pentland	SMRU	3	2	2018
	hg60	Moray Firth	SMRU/UofA	1	-	2018
MRYF	hg60	Moray Firth	SMRU/UofA	2	8	2018
ECST	pv14	Abertay Sands	SMRU	1	1	2005
	gp13	Abertay Sands	SMRU	4	5	2008
	ab09g	Abertay Sands	SMRU	1	2	2013
	hg48	Donna Nook / Blakeney Point	SMRU	3	2	2015
	hg60	Moray Firth	SMRU/UofA	1	2	2018
SEEN	hg48	Donna Nook / Blakeney Point	SMRU	7	12	2015
ECHL	-	-	-	-	-	-
CISS	gp17	Blasket Isles	UCC	1	-	2012
	gp18	Wexford	UCC	1	-	2013
	gp19	Wexford	UCC	1	3	2014
	hg56	Dee Estuary	SMRU	1	1	2017
	hg61	Bardsey	SMRU	3	5	2018
	hg62	Ramsey / Skomer	SMRU	1	2	2019
IRSN	gp18	Wexford	UCC	1	-	2013
	gp19	Wexford	UCC	1	-	2014
	hg56	Dee Estuary	SMRU	2	5	2017
WIRL	gp14	Blasket Isles	UCC	-	5	2009
	gp16	Blasket Isles	UCC	1	-	2011
	gp17	Blasket Isles	UCC	2	-	2012
	gp21	Inishkea Islands	UCC	1	1	2019
			Total Tracks	M: 54	F: 77	**Total: 131**
			Total Indiv.	M: 45	F: 69	**Total: 114**

A1.4 Harbour seal tracking data

Table A1.3: Harbour seal GPS tag deployments used for regional habitat preference models. *The total number of unique individuals in the dataset is given at the bottom of the table. For habitat preference (HP) regional designations see Fig. 3 / Table 2 in main document. UCC = University College Cork, UofA = University of Aberdeen, ZSL = Zoological Society of London.*

HP Region	Deployment	Deployment Location	Data Provider	M	F	Year
WSIN	pl04	Shieldaig	SMRU	-	1	2011
	pv41	Islay	SMRU	7	7	2011/2012
	pv43	Skye	SMRU	4	3	2012
	pv55	Islay	SMRU	-	7	2014
	vf02	Skye	SMRU	-	6	2017
WISL	pv18g	Sound of Harris	SMRU	-	1	2006
	pv19g	Sound of Harris / Barra	SMRU	2	1	2006
	pv55	Islay	SMRU	-	1	2017
NCNI	pv24	Pentland Firth	SMRU	8	4	2011
	pv47	Orkney	SMRU	5	-	2012
	pv57	Orkney	SMRU	-	3	2014
	pv59	Moray Firth	SMRU/UofA	-	1	2015
	vf01	Orkney	SMRU	3	6	2016
	pv64	Moray Firth	SMRU/UofA	-	1	2017
	vf03	Orkney	SMRU	-	7	2017
MRYF	pv27	Moray Firth	SMRU/UofA	-	5	2009
	pv58	Moray Firth	SMRU/UofA	6	5	2013/2014
	pv59	Moray Firth	SMRU/UofA	6	6	2015
	vf01	Orkney	SMRU	-	1	2016
	pv64	Moray Firth	SMRU/UofA	11	19	2017
ECST	pv23	Eden Estuary	SMRU	2	2	2008
	pv24e	Eden Estuary	SMRU	4	1	2011
	pv50	Kirkcaldy	SMRU	1	1	2013
SEEN	pv20g	Thames	SMRU	1	-	2006
	pv40	Thames	SMRU/ZSL	5	4	2012
	pv42	The Wash	SMRU	8	10	2012
	pv63	The Wash	SMRU	5	14	2016
ECHL	pv26	Chichester Harbour	SMRU	4	-	2009
CISS	-	-	-	-	-	-
IRSN	gp4	Strangford Lough	SMRU	3	5	2006
	gp9	Strangford Lough	SMRU	3	4	2008
	pv33	Strangford Lough	SMRU	8	4	2010
	pv41	Islay	SMRU	2	-	2011/2012
WIRL	gp12	Kenmare Bay	UCC	3	2	2007
	gp5	Kenmare Bay	UCC	3	-	2006
	gp7	Kenmare Bay	UCC	3	-	2006
			Total Indiv	M: 107	F: 132	**Total: 239**

A1.5 Tracking data handling

A1.5.1 Instrumentation

Animal-borne GPS telemetry tags were deployed on grey and harbour seals by SMRU, the University of Aberdeen and UCC between 2006 and 2019. Seals were caught on, or close to, haulout sites using either seine, pop-up, tangle or hand nets. All seals were instrumented with either Fastloc® GPS phone tags (GPS-GSM) or Fastloc® GPS Argos phone tags (GPS-GSM-Argos) (SMRU Instrumentation, UK). A tag was glued to cleaned, dried fur at the base of the skull using RS Quick-Set Epoxy Adhesive (RS Components Ltd., UK), or Loctite® 422™ cyanoacrylate adhesive (Henkel, UK). All capture, handling and other procedures were carried out under appropriate licenses, with permissions concerning designated areas and landowners (see Section 6 in the main report). Tags were deployed outside of the breeding and moulting season for each species.

A1.5.2 Data cleaning

Erroneous location estimates were identified and excluded using residual error threshold and number of satellites (Russell et al. 2015). Data from the first week post-capture were removed to minimise the possibility of including anomalous behaviour as a result of capture. Although some tags transmitted through the breeding seasons (grey seals: September – January, harbour seals: June – July), the breeding status of each animal was unknown. The behaviour of breeding animals during this time is not representative of the key foraging season, thus data during this period were omitted.

A1.5.3 Identification of trips

Following Russell et al. (2015), a seal's location during a haul-out event was taken as the latitude and longitude (or mean if multiple locations) associated with the highest number of satellite fixes during the time hauled-out. If no location estimates were available from a haul-out event, the haul-out location was derived using linear interpolation between pre- and post- haul-out location fixes. The location data were then restricted to discrete trips (at-sea locations between haul-out events). Location data were then regularised to a 2 h time interval using linear interpolation. Regularised location fixes were flagged as unreliable if there was a gap >6 h between the observed locations surrounding an interpolated location. If there was no reliable estimated location fix during a haulout at the start and end of a trip, then the trip was excluded from the analysis. The habitat preference region of each haul-out was classified based on designations shown in Fig. 3 in the main document. Trips were only included in the analysis if they originated and terminated at haulout sites in the same habitat preference region (grey seals: 93% of locations; harbour seals: 99.5% of locations). Finally, location data during the haul-out interval were excluded, leaving only at-sea locations.

A1.6 Habitat preference modelling

A1.6.1 Use-availability design

Use-availability habitat preference models (Aarts et al. 2008, Beyer et al. 2010) were used to quantify the environmental drivers of distribution for grey and harbour seals in each region. This framework is based on the concept that the location of an animal is a product of both where it *can* go (accessibility) and where it *chooses* to go (preference; Matthiopoulos (2003)). Under this framework, accessibility polygons were generated per species for each haulout site used, with a radius based on the maximum geodesic distance (shortest path at sea without crossing land) travelled from a haulout by any seal in the cleaned tracking dataset (Russell et al. 2016a) (grey seals: 448 km, harbour seals: 273 km). Where a seal left a haulout and returned to a different haulout in the same habitat preference region (non-return trips), the area where both haulout-specific accessibility polygons overlapped was used (Fig. A1.2). Non-return trips that started and finished in different habitat preference regions were excluded. The accessibility polygons were clipped to remove any area beyond the shelf edge (600 m isobath; Fig. 2a in the main document). There was no evidence of seals using the area beyond the shelf edge in the tracking dataset, and it is therefore unlikely to represent accessible foraging habitat. For each regularised seal location, a random sample of control points was generated within the corresponding accessibility polygon (Fig. A1.2). These control points are a representation of the available habitat that is accessible to the tagged seal (Aarts et al. 2008, Beyer et al. 2010).

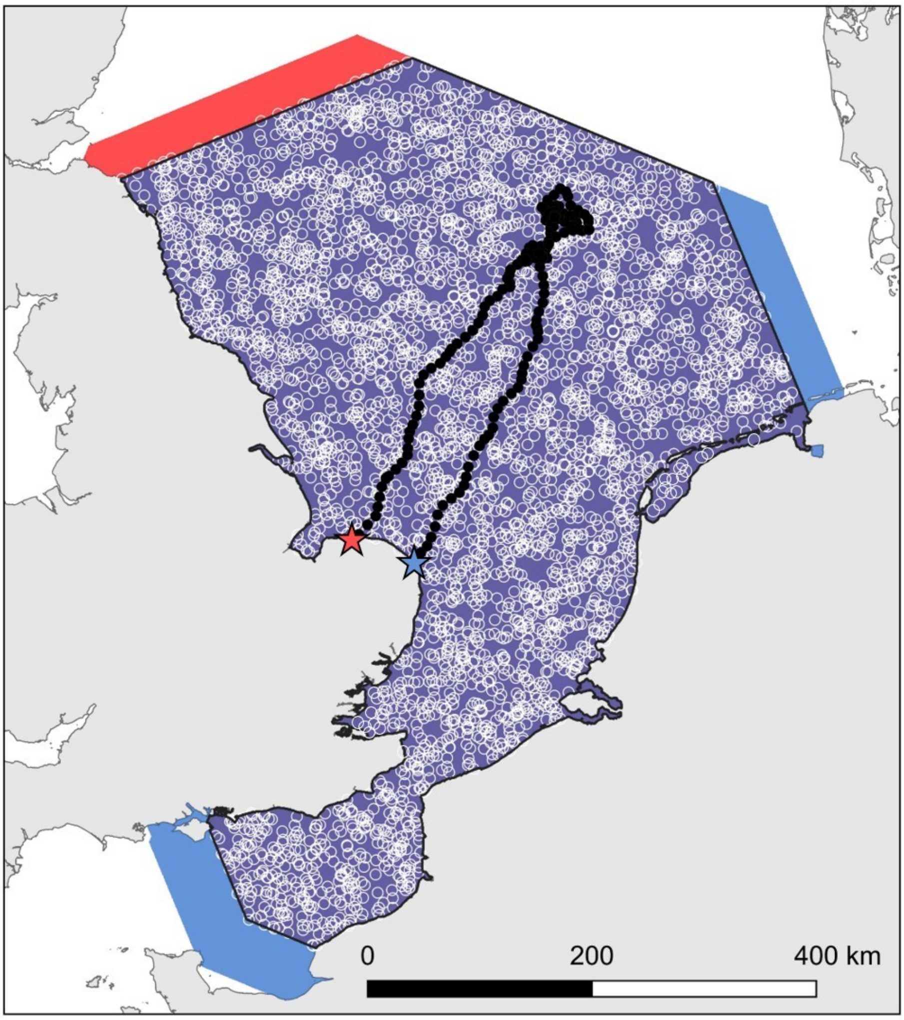

Figure A1.2: Example accessibility polygon. *Accessibility polygons were generated for each haulout, with a radius equal to the maximum distance travelled by any seal in the cleaned tracking dataset (grey seals = 448 km; harbour seals = 273 km). In this example of a grey seal trip, the start and end haulout sites are shown with a blue and red star, respectively. 30 randomly spaced control points (white open circles) are generated for each seal location (black closed circles) within the area where both accessibility polygons (blue and red for the start and end haulouts, respectively) overlap (purple area).*

A1.6.2 Model formulation

Control points were modelled alongside the regularised seal location estimates (presences) in a binomial process (0/1) as a function of categorical and continuous environmental covariates (Table 1 in the main document) in a generalized additive mixed model (GAMM) using the package "mgcv" (Wood 2015) in R. The ratio of control points to presences can have a profound effect on model inference (Beyer et al. 2010). The appropriate ratio was determined for each species in each regional model by fitting the model with a range of ratios (between 1:1 and 30:1) and visually inspecting model coefficient values, identifying the point at which values stabilised (Beyer et al. 2010). GAMMs were fitted with a binomial response and logit-link function. Control points were weighted in the models such that each set contributed the same as one presence. Individual seal was included as a blocking factor (random intercept) to account for differences in the number of observations (i.e. tag duration) among individuals using the “re” basis spline in “mgcv” (Wood 2015). Each continuous covariate was fitted as a smoothed term with shrinkage, such that uninformative terms can be penalised to zero, effectively making them linear (Wood 2015). To avoid over-fitting of smooth functions to the data, the number of knots (*k*) was determined for each smooth by trialling different values (*k* = 2:10) and selecting the value that minimised the model Akaike Information Criterion (AIC) score whilst still returning a relationship that was biologically interpretable.

A1.6.3 Model selection and validation

To ensure that the most parsimonious model was used for predictions in each region, backwards model selection was performed in two stages. In Stage One, models were simplified by dropping one covariate at a time from the maximal model (containing all covariates), and assessing the model’s AIC score until arriving at a minimal adequate model (threshold for covariate exclusion ΔAIC<2 (Burnham and Anderson 2002)). In Stage Two, candidate models from the final round of Stage One were submitted to a further level of model selection based on model predictive performance using three-fold cross validation. This second stage provides a more conservative model selection process to guard against overfitting (i.e. the risk of retaining covariates that explain a very small amount of variance) as a result of the residual temporal autocorrelation found in preliminary analyses (Aarts et al. 2008, Fieberg et al. 2010). In this process, individuals were assigned to one of three folds; models were trained on two of the folds, and predictions were made for the remaining fold (Wiens et al. 2008). Models were assigned a resource selection function (RSF) score based on the coefficient of the Spearman rank correlation between binned predicted probabilities and the observed area-adjusted frequency of presences in the data (Boyce et al. 2002, Wiens et al. 2008). Where the model with the highest RSF score differed from the best model identified in Stage One (i.e. a further covariate could be removed), further rounds of model selection by cross validation were conducted until arriving at a minimal adequate model. The minimal adequate model from Stage Two was then used to generate predicted at-sea distribution maps.

A1.7 Environmental covariates

Modelling correlated variables together may lead to artificial inflation of the variance of the regression coefficient, making it more difficult to detect significant relationships. Variance Inflation Factors (VIFs) were calculated for pair-wise relationships between all covariates using the “car” package in R (Fox and Weisberg 2011), and correlated variables (VIF > 10) were not modelled together (Zuur et al. 2010). In all models, slope and rugosity were correlated. Models were therefore fitted with either slope or rugosity in turn, and the covariate that returned the lowest model AIC score was chosen for the full model to undergo model selection (see A1.6.3 above).

Seabed substrate comprised seven factor levels (see Fig. A1.3 below). To reduce the number of factor levels, and improve model parsimony, we tested if any of the substrate types could be grouped by systematically combining factor levels in all possible pairwise combinations and fitting a full model (with all other candidate covariates). Model AIC scores were then compared between models with different combinations of factor levels, and the combination of substrate types that returned the lowest AIC score was selected. This process was then repeated until no further combination reduced the AIC score. Under this process, for example, if a model with “mud to muddy sand” and “sandy mud to muddy sand” grouped into one factor level achieved a lower AIC score than having both factor levels separate, then the former was preferred. This process was performed for each species in each habitat preference region (except WIRL where there was a lack of adequate substrate data).

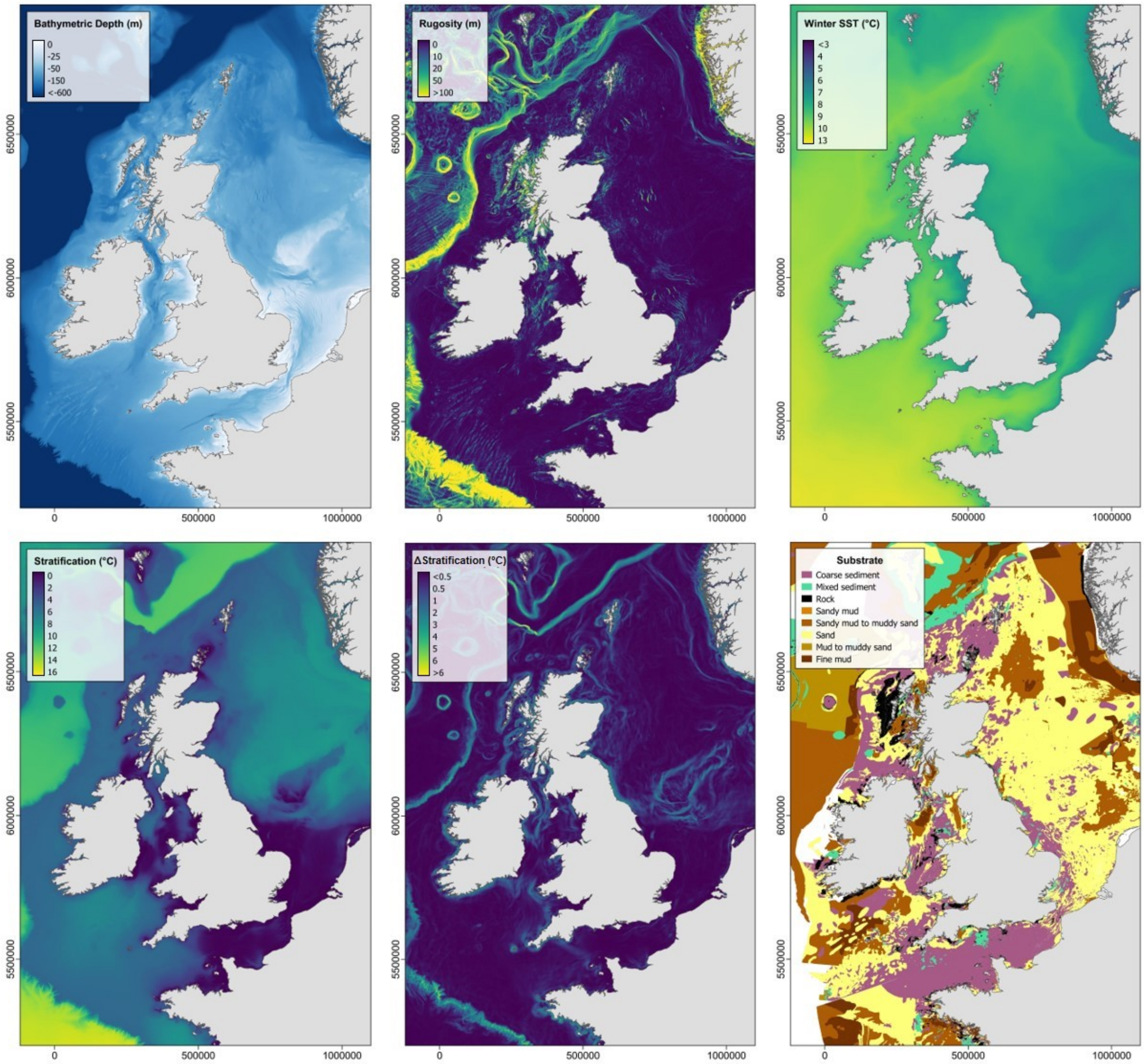

Figure A1.3: Maps of environmental covariates used in habitat preference models.
Dynamic covariates (SST, stratification, Δ stratification) are shown for 2018. Slope is not shown as this was collinear with rugosity in all regions.

A1.8 Coastal cells

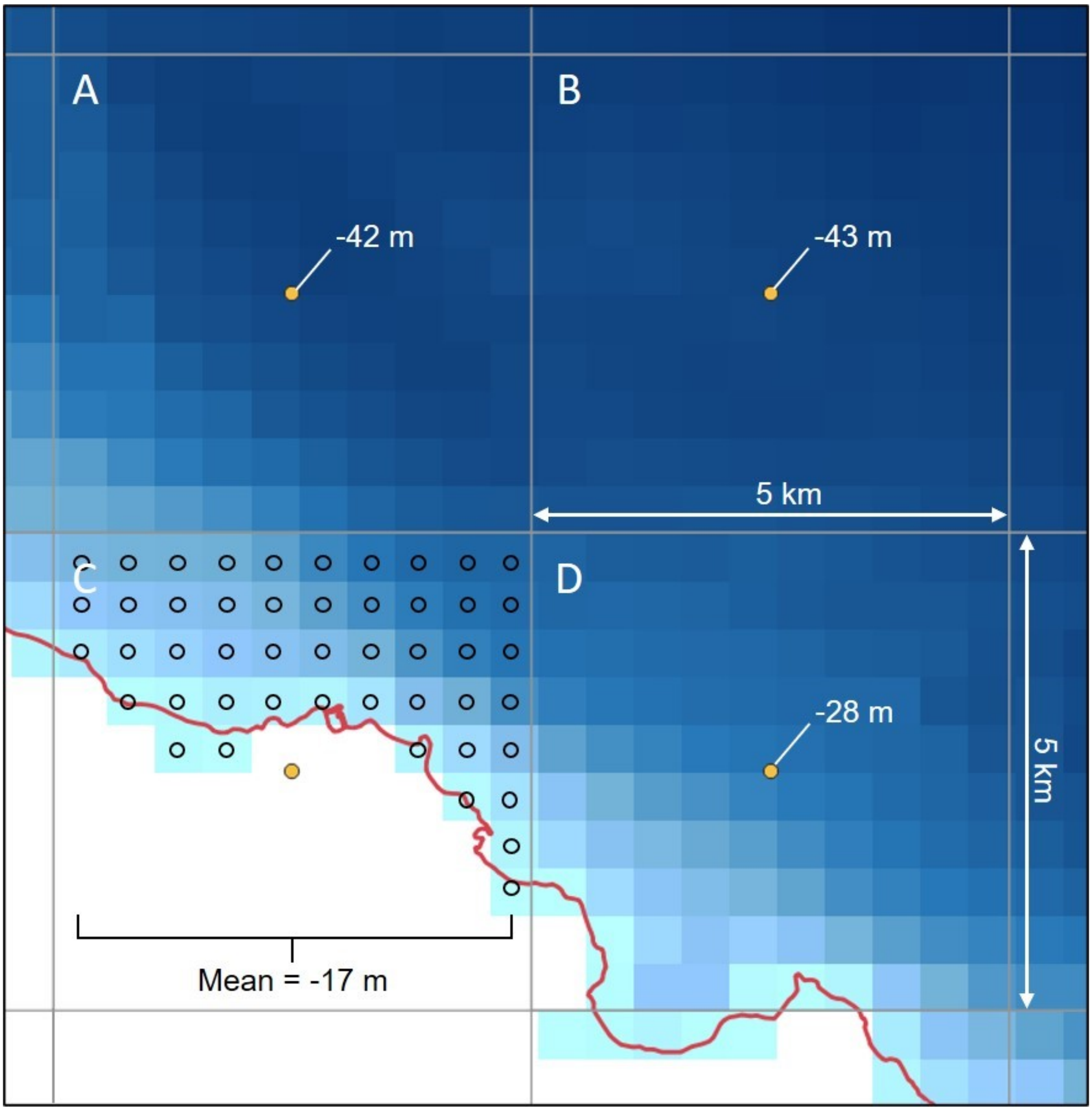

Figure A1.4: Example extraction of environmental data for coastal cells in the prediction grid. *The graphic shows sampling of an environmental covariate for the prediction grid. White areas denote land where no environmental data exist; the red line indicates the coastline. In this example the covariate (bathymetric depth) is on a 500 m resolution, thus there are 100 pixels in the bathymetry raster per 5 km x 5 km cell in the prediction grid. Environmental data were extracted from the pixel underlying the centroid of each cell in the 5 km x 5 km prediction grid (grey lines indicate cell boundaries; gold dots indicate the centroids). However, in some coastal cells (e.g. cell C), the centroid fell on land, and thus no data value existed. In this instance, to avoid gaps in the seal distribution estimates, the environmental data value was derived by taking the mean of all environmental data values that fell within the 5 km x 5 km prediction gird cell boundaries (black open circles).*

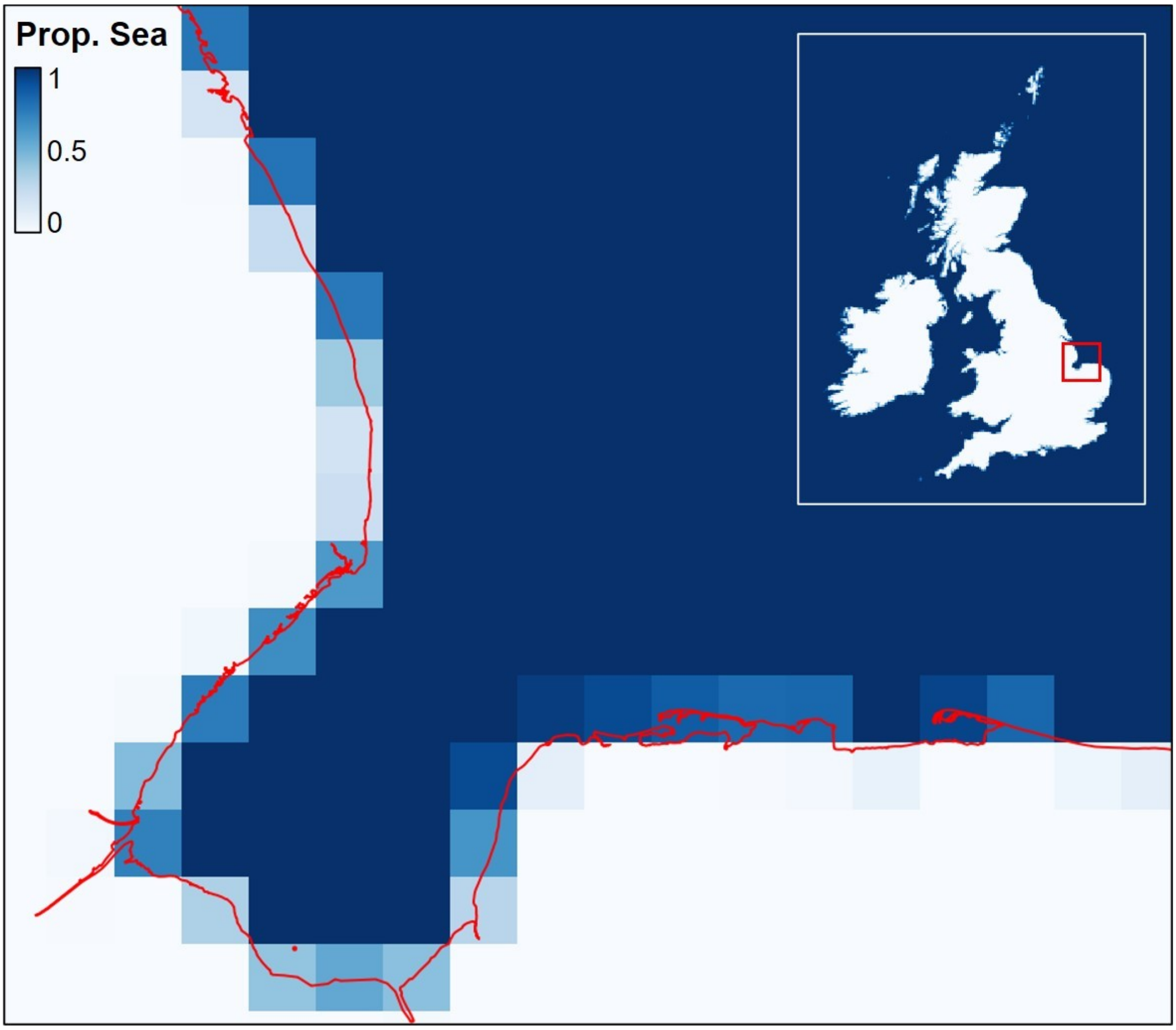

Figure A1.5: Example estimation of proportion of sea in each prediction cell. *The proportion of each 5 km x 5 km cell in the prediction grid that comprised sea was estimated for the entire study area (inset map), and seal abundance predictions were multiplied by this value to ensure that coastal predictions were not over-estimated. The colour scale indicates the proportion per cell, ranging from white (0; 100% land) to dark blue (1; 100% sea). The coastline (at mean spring high water) is shown in red.*

9.2 Appendix 2: Number of seals present in areas of interest: wind and tidal energy case study

A2.1 Methods

For some applications (i.e. estimating the number of seals present in areas of interest), it is necessary to estimate the number of individuals present in a cell at any given time (i.e. *absolute* rather than *relative* density). Absolute density estimates were generated by scaling from percentage of at-sea population to number of individuals using the two population scalars outlined in Section 3.2.4c of the main report. In light of the caveats mentioned in Section 3.2.4c relating to concerns about the accuracy of these scalars, the results of this analysis are to be taken as rough estimates, rather than definitive. For grey seals, the total population size for the British Isles was estimated using the scalar from Russell et al. (2016b). This scalar assumes that 23.9% of the total population are available to count during the August surveys, as estimated from analysis of tracking data (Russell et al. 2016b). During the main foraging season, grey seals are estimated to spend 77% of their time at-sea on average (Russell et al. 2015), thus the total at-sea population size for the British Isles is estimated to be ~150,700 individuals. For harbour seals, the total population size for the British Isles was estimated using the scalar from Lonergan et al. (2013). This scalar assumes that the percentage of the total population hauled-out during the August surveys is 72% (Lonergan et al. 2013). During spring, harbour seals are estimated to spend 83.4% of their time at sea on average (Russell et al. 2015). Thus, the total size of the at-sea population of the British Isles was estimated to be ~42,800 individuals.

Polygons for windfarm lease areas and tidal energy development sites in the UK sector (Fig. A2.1) were overlaid onto the absolute density maps, and the number of animals estimated to be within cells 50% or more inside the polygon boundaries was summed for each species. A series of buffers were then generated around each polygon with radii of 5 and 25 km for windfarms, 2.5 km for tidal energy sites, from the polygon edges, and the number of individuals within each buffer was estimated (Fig. A2.2). Cancelled and decommissioned sites were not included.

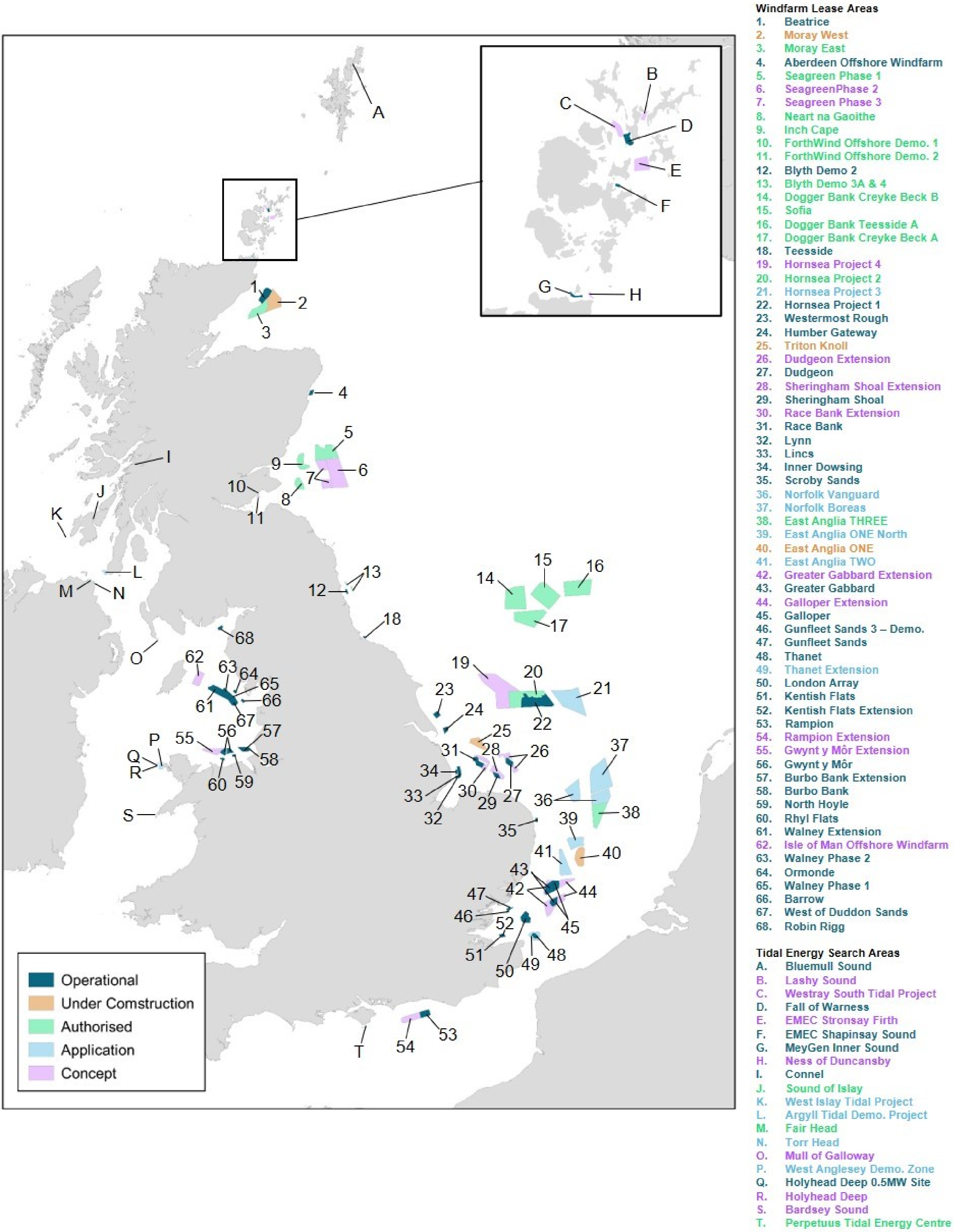

Figure A2.1: Windfarm lease areas and tidal energy development sites in the UK sector. *Status designations are given as of 21/02/2020. Cancelled and decommissioned sites are not shown.*

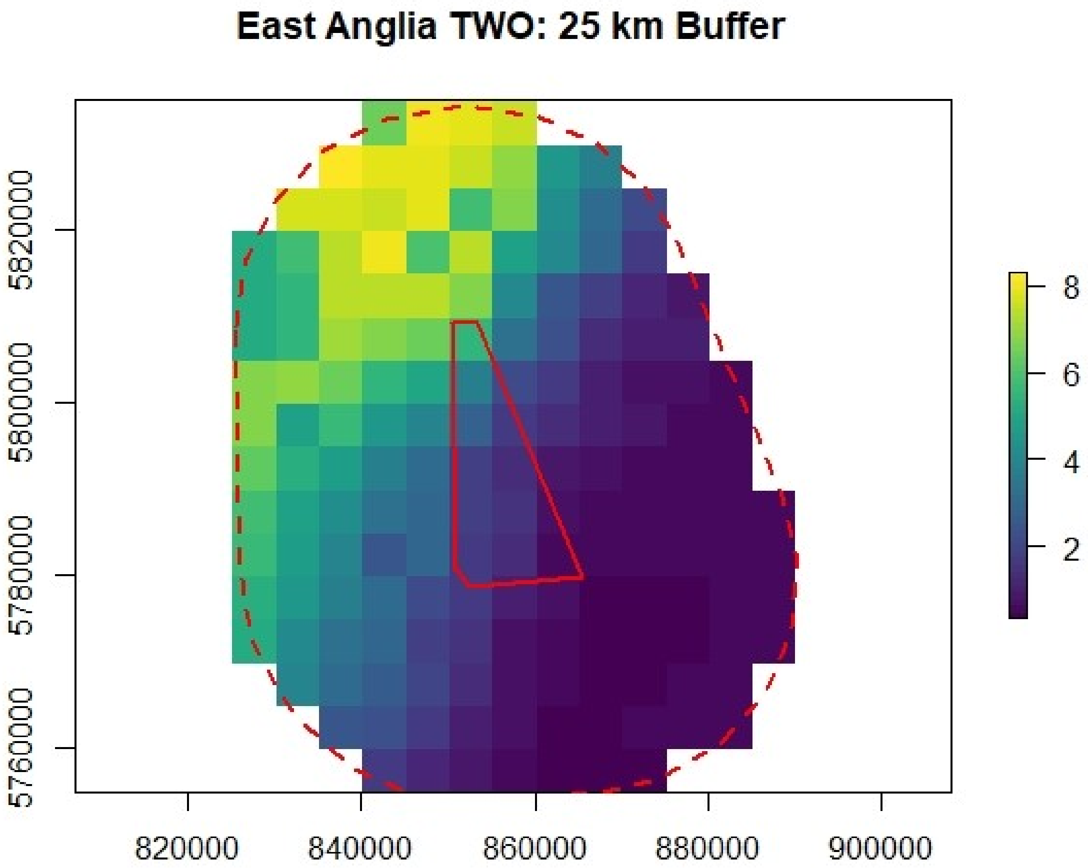

Figure A2.2: Example estimation of number of seals present within a buffer surrounding marine renewable energy sites. *The colour scale indicates the approximate number of individual grey seals estimated to be within each 5 km x 5 km grid cell at any time. X axis indicates eastings (m) and y axis indicates northings (m). Cell values are summed from the seal distribution layer within the buffer radius (dashed red line) of the lease area polygon (solid red line). Only cells that are >50% inside the buffer are counted.*

A2.2 Results

A2.2.1 Windfarm lease areas

Overall, approximately 8% of the British Isles at-sea population of grey seals was estimated to be present within 5 km of a windfarm lease area at any one time. For harbour seals, approximately 3% of the British Isles at-sea population was estimated to be within 5 km of a windfarm lease area at any one time. The numbers of individual harbour seals estimated to be present were much lower compared to grey seals (Table A2.1). There were large differences in seal density among sites for both species (Table A2.1). Windfarms in Southeast England, particularly in the vicinity of The Wash and surrounding coastline recorded high numbers of both species. Large aggregations of grey seals are present at

Donna Nook and Blakeney Point (see Fig. 4a in the main report), while The Wash has large aggregations of harbour seals (Fig. 4b). The waters adjacent to these haulouts are areas of high predicted seal density (Figs. 6-7 in the main report). Windfarms off the east coast of Scotland and Northeast England also recorded relatively high numbers of grey seals. Grey seal density in this area is estimated to be patchy (Fig. 6), but some windfarms overlap with hotspots which extend out to ~100 km from the coast. Windfarms off the north coast of Wales also recorded relatively high numbers of grey seals (Table A2.1), where lease areas overlap with high density areas for seals hauling-out at the Dee Estuary (Fig. 6; Fig. A2.1). Windfarms in the English Channel and the northern part of the Irish Sea recorded the lowest numbers for both species (Table A2.1). For harbour seals, windfarms with particularly high numbers of individuals estimated to be present generally occurred in waters adjacent to large haulouts. For example, in addition to The Wash, relatively high numbers were recorded in the Thames Estuary and the Firth of Forth, where lease areas are close to the coast (Table A2.1).

Table A2.1: Approximate number of seals estimated to be present within a 5 km and 25 km buffer of windfarm lease areas in the UK sector. *Construction status is given as reported at* https://www.4coffshore.com/windfarms/united-kingdom/, date accessed 21/02/2020. *For a map showing the location of windfarm lease areas see Figure A2.1.*

		Grey Seals		Harbour Seals	
Windfarm Lease Area	**Status**	**5 km**	**25 km**	**5 km**	**25 km**
Aberdeen Offshore Windfarm	Operational	232	1031	15	28
Barrow	Operational	6	115	0	0
Beatrice	Operational	164	1463	2	21
Blyth Offshore Demo. 2	Operational	120	1068	0	2
Blyth Offshore Demo. 3A & 4	Authorised	183	1534	0	2
Burbo Bank	Operational	226	1031	2	14
Burbo Bank Extension	Operational	445	1163	3	14
Dogger Bank – Creyke Beck A	Authorised	138	759	1	5
Dogger Bank – Creyke Beck B	Authorised	216	895	0	2
Dogger Bank – Teesside A	Authorised	107	473	0	0
Dudgeon	Operational	180	2011	21	336
Dudgeon Extension	Concept	479	2942	55	506
East Anglia ONE	Construction	25	280	0	4
East Anglia ONE North	Application	75	487	1	32
East Anglia Hub - TWO	Application	53	369	0	5
East Anglia Hub - THREE	Authorised	94	577	2	47
ForthWind Offshore Demo. 1	Authorised	218	1411	49	274
ForthWind Offshore Demo. 2	Concept	228	1450	48	290

		Grey Seals		Harbour Seals	
Windfarm Lease Area	**Status**	**5 km**	**25 km**	**5 km**	**25 km**
Galloper	Operational	53	436	1	27
Galloper Extension	Concept	37	324	0	6
Greater Gabbard	Operational	68	459	1	43
Greater Gabbard Extension	Concept	102	611	2	72
Gunfleet Sands	Operational	29	342	57	432
Gunfleet Sands 3 – Demo.	Operational	15	287	39	422
Gwynt y Môr	Operational	67	1144	1	14
Gwynt y Môr Extension	Concept	73	931	0	8
Hornsea Project 2	Authorised	608	2472	2	19
Hornsea Project 3	Application	370	1258	1	5
Hornsea Project 4	Concept	814	3236	2	21
Humber Gateway	Operational	431	3979	29	317
Inch Cape	Authorised	538	4168	2	53
Inner Dowsing	Operational	119	1718	177	2240
Isle of Man Offshore Wind Farm	Concept	40	179	0	0
Kentish Flats	Operational	21	245	40	427
Kentish Flats Extension	Operational	36	252	61	426
Lincs	Operational	293	2434	369	2748
London Array	Operational	80	587	28	455
Lynn	Operational	145	1469	294	2577
Moray East	Construction	318	2029	3	24
Moray West	Authorised	280	2402	7	74
Neart na Gaoithe	Authorised	476	4441	0	19
Norfolk Boreas	Application	141	556	3	14
Norfolk Vanguard	Application	209	886	7	57
North Hoyle	Operational	64	1084	1	14
Ormonde	Operational	5	76	0	0
Race Bank	Operational	354	3790	134	1610
Race Bank Extension	Concept	594	4356	212	1772
Rampion	Operational	0	5	0	0
Rampion Extension	Concept	0	5	0	15
Rhyl Flats	Operational	85	728	1	9
Robin Rigg	Operational	19	113	0	0
Scroby Sands	Operational	48	492	60	216
Seagreen Phase One	Authorised	801	3795	1	8
Seagreen Phase Two	Concept	1111	4898	0	2
Seagreen Phase Three	Concept	1073	5160	0	4
Sheringham Shoal	Operational	188	2020	74	970
Sheringham Shoal Extension	Concept	386	2547	135	1113
Sofia	Authorised	138	650	0	1
Teesside	Operational	64	655	37	81
Thanet	Operational	69	424	11	188
Thanet Extension	Application	97	473	15	240
Triton Knoll	Construction	879	5125	79	667
Walney Enxtension	Operational	30	181	0	0

		Grey Seals		Harbour Seals	
Windfarm Lease Area	**Status**	**5 km**	**25 km**	**5 km**	**25 km**
Walney Phase 1	Operational	9	109	0	0
Walney Phase 2	Operational	11	113	0	0
West of Duddon Sands	Operational	17	156	0	0
Westermost Rough	Operational	424	2980	6	83

A2.2.2 Tidal energy development sites

Overall, approximately 0.5% of the British Isles at-sea population of grey seals, and approximately 0.4% of the harbour seal at-sea population, was estimated to be present within a potential 2.5 km of a tidal energy development site at any one time. The numbers of individual harbour seals estimated to be present were much lower compared to grey seals (Table A2.2). For both species, sites with the highest numbers were in Orkney, where there is a relatively high concentration of development sites (Fig. A2.1 inset map) close to haulouts (Fig. 4 in the main report). For harbour seals, a relatively high number of individuals was estimated to be present in the vicinity of the Argyll Tidal Demonstration Project, which is proposed for development close to the Mull of Kintyre. This area has a high at-sea density of harbour seals from haulouts on the Kintyre Peninsula (Fig. 7).

Table A2.2: Approximate number of seals estimated to be present within a 2.5 km buffer of tidal energy development sites in the UK sector. *Cancelled and decommissioned sites are excluded. For a map of tidal energy development sites see Figure A2.1.*

Tidal Energy Development Site	Status	Grey seals	Harbour seals
Argyll Tidal Demo. Project	Application	20	30
Bardsey Sound	Concept	2	0
Bluemull Sound	Operational	0	2
Connel	Operational	3	5
EMEC Shapinsay Sound	Operational	59	4
EMEC Stronsay Firth	Concept	170	21
Fair Head	Authorised	14	12
Fall of Warness	Operational	133	37
Holyhead Deep	Concept	4	0
Holyhead Deep 0.5MW Site	Operational	2	0
Lashy Sound	Concept	100	10
MeyGen Inner Sound	Operational	72	11
Mull of Galloway	Concept	23	1
Ness of Duncansby	Concept	79	7
Perpetuus Tidal Energy Centre	Authorised	0	0

Sound of Islay	Authorised	3	7
Torr Head	Application	12	8
West Anglesey Demo. Zone	Application	7	0
West Islay Tidal Project	Application	47	5
Westray South Tidal Project	Concept	91	28

A2.3 Discussion

In this case study, the approximate number of individual grey and harbour seals present at any given time within the vicinity of marine renewable energy developments was estimated. A key finding is that approximately 8% of the grey seal at-sea population of the British Isles is estimated to be within 5 km of a windfarm lease area (where windfarms are either currently operational, under construction, or proposed for construction) at any one time. This suggests that a high proportion of grey seals are likely to encounter windfarms in the future. The analysis revealed that a number of lease area sites may be particularly important for seals. For both species, windfarms in Southeast England recorded the highest numbers. In this area, there is a relatively high density of windfarm lease areas close to shore in waters adjacent to large haulout aggregations which are primary designating features for the Humber Estuary SAC (grey seals) and The Wash and North Norfolk Coast SAC (harbour seals). For grey seals, relatively high numbers were also estimated to be present at windfarms off the east coast of Scotland to the east of the Firth of Forth. These areas are estimated to have high at-sea density of seals hauling-out in Southeast Scotland and Northeast England, including the Isle of May SAC and the Berwickshire and North Northumberland Coast SAC, for which grey seals are a primary feature for designation. Windfarm lease areas in the Firth of Forth recorded relatively high numbers of harbour seals. Although the estimated number of individuals is lower than at sites in the Southern North Sea, the population of harbour seals in this region has experienced a dramatic decline in recent years, and thus is of significant conservation concern (Thompson et al. 2019). Given the scale of overlap between seal distributions and windfarm developments in the UK sector, further research into the positive and negative implications of such developments for both species is required to understand the potential population-level consequences.

The analysis revealed that, overall, the numbers of seals estimated to be present in tidal energy sites was relatively low. However, for grey seals, sites in Orkney overlapped with areas of relatively high at-sea density for grey seals hauling-out in the Faray and Holm of

Faray SAC, and of harbour seals hauling-out in the Sanday SAC, for which grey and harbour seals are primary features for designation respectively. Although the numbers of harbour seals are an order of magnitude lower than for grey seals, the Orkney harbour seal population has experienced a steep decline in recent years (Thompson et al. 2019), thus concerns of negative impacts such as collision and displacement may be higher in this region. Furthermore, although the long-term nature of risk from operating tidal turbines is not effectively captured by instantaneous estimates of seal numbers (i.e. different individuals could enter the area at various points within a given timeframe), these estimates of predicted abundance may prove useful in quantifying the magnitude of potential collision risks and displacement.

The approach to estimating numbers of seals within areas of interest is subject to several caveats and limitations, and therefore should be taken as an approximate estimate of seal abundance. Importantly, these numbers do not account for various sources of uncertainty. Firstly, the estimates are based on mean predictions, both in terms of relative density and of the size of the at-sea population. This is because upper and lower confidence intervals for the density maps are calculated in a cell-wise manner, and therefore cannot be summed across an area in the same way as the mean estimate. Secondly, the population scalars used to estimate absolute density are under review. Furthermore, given that the resolution of seal abundance estimates from habitat preference maps was 5 km, it was not possible to estimate numbers at a finer scale than a 2.5 km buffer. The figures given here should therefore serve as a rough estimate to indicate the magnitude of overlap between seals and marine renewable energy development areas, and should not be used to infer impacts. More fine-scale estimates with associated area-wide confidence intervals are possible, but would require further work that was beyond the scope of this case study.

9.3 Appendix 3: Seal use of man-made structures

A3.1 Methods

The foraging range of both grey and harbour seals overlaps with many man-made structures, including windfarms, pipelines and fixed (oil and gas) platforms. Overlap with such structures is particularly high in the North Sea. There is evidence from seal tracking data that individuals may interact with such structures for foraging (Russell et al. 2014). Here, the tracks of grey and harbour were examined for evidence of interactions with structures, consisting of prolonged periods spent within 250 m of a structure, or behaviour that appeared consistent with foraging (area-restricted search). A seal-structure interaction was assumed where there was evidence of a disproportionate overlap of area-restricted search with a structure, or where the seal track closely followed a pipeline.

A3.2 Results

A3.2.1 Grey seals

Of the 114 grey seals for which there are high resolution tracking data, 12 (10.5%) showed evidence of association with man-made structures that consisted of either repeated visits to a specific structure, or prolonged activity at a structure on one or more trips. All but one of these interactions occurred in the North Sea, with one individual in North Wales visiting a windfarm. The most common structure type visited was pipelines (ten individuals), followed by platforms (five individuals) and windfarms (one individual). One individual from Orkney transited past a particular platform in the North Sea with a high degree of repeatability, passing the structure en-route to and from foraging grounds on three discrete trips (Fig. A3.1).

A3.2.2 Harbour seals

Of the 239 individuals for which there are high resolution tracking data, 20 (8.4%) showed evidence of association with man-made structures that consisted of either repeated visits to a specific structure, or prolonged activity at a structure on one or more trips (for description of trips see Appendix 1, Section A1.5.3). All but one of these interactions occurred in the Southern North Sea, where 19 of 47 individuals tagged in the region (40.4%) showed evidence of association with man-made structures. The other interaction was by an individual tagged in East Scotland. The most common structure type visited was pipelines (ten individuals), followed by windfarms (nine individuals), and platforms (five individuals).

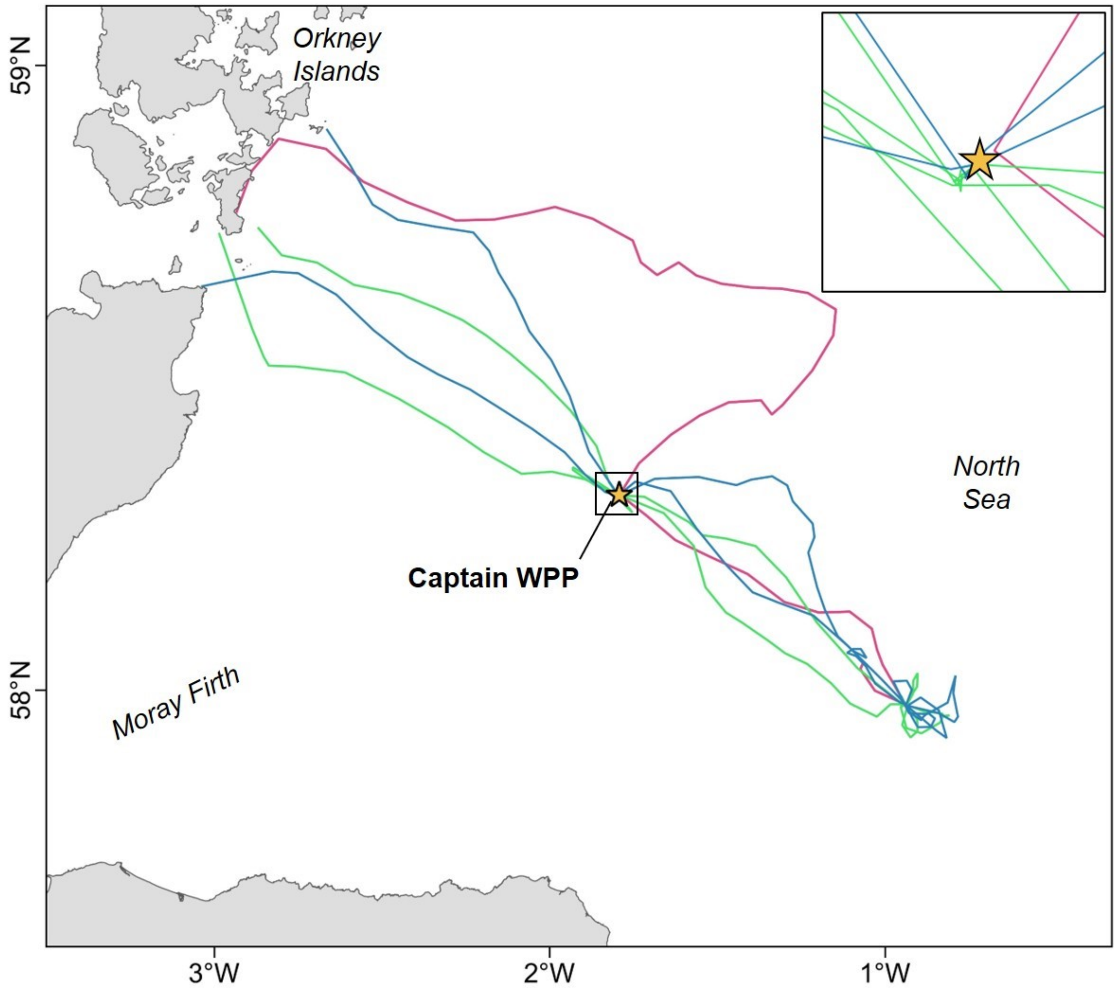

Figure A3.1: Example of seal interactions with a man-made structure*. A grey seal tagged in Orkney transited past the Captain Wellhead Protection Platform (WPP) (gold star) en-route to and from foraging grounds in the North Sea on three discrete foraging trips (coloured tracks). There was evidence of area-restricted search at the platform on only one of these trips (green track, inset map), suggesting that the seal may have used it for opportunistic foraging, and/or as a navigational aid.*

A3.3 Discussion

Building on the results of Russell et al. (2014), data collected during this project has provided further evidence that some seals use man-made structures (e.g. windfarm turbines, oil and gas platforms and pipelines). The majority of interactions recorded from new grey seal data collected during this project occurred in the North Sea, by individuals hauling-out in Orkney. Likely ARS behaviour associated with foraging was identified at a windfarm in North Wales, along with evidence that seals may use certain structures as way markers or navigation aids. One seal repeatedly transited past a particular fixed platform in the North Sea, passing the structure en-route to and from foraging grounds on three discrete trips (Fig. A3.1). There was evidence of ARS at the platform on only one of these trips, suggesting that the seal may have used it for opportunistic foraging, or as a navigational aid. Importantly, shipwrecks were not considered in this analysis due to the complexities of obtaining information on how much, if any, of the structure is in-tact and exposed on the seabed. However, there are thousands of wrecks within the seals' foraging range which may act as artificial reefs, meaning that seal use of man-made structures may be much more prevalent. The percentage of tagged seals demonstrating associations with structures reported here should not be taken as population level estimates, as tagging effort is not proportional to population sizes in these areas.

The landscape of man-made structures in UK waters (particularly the North Sea) is entering a period of dramatic change, with hundreds of oil and gas platforms scheduled for decommissioning in coming years, and rapid expansion of the marine renewable sector, particularly wind. Current decommissioning policy requires the removal of most structures once their serviceable lifespan is complete. However, these structures may act as artificial reefs providing habitat for fish. Moreover, due to exclusion zones for fisheries and shipping traffic they may function as de-facto MPAs. Given the evidence that man-made structures may provide foraging opportunities for seals (Russell et al. 2014), urgent research is needed to determine their ecosystem-level importance as artificial reefs, and thus the ecological consequences of their placement and removal (Grecian et al. 2018). For seals, a priority for future research should be to determine if man-made structures have a population-level influence on at-sea distribution and foraging behaviour. Moreover, investigating how structure type, age and placement affects the likelihood of its use by seals will help to inform ecologically sensitive development and decommissioning policies.

9.4 Appendix 4: Breeding status and location of female grey seals

A4.1 Methods

Data from Russell et al. (2013) were updated with findings from tags deployed after that study. Following Russell et al. (2013), for those tags that transmitted data throughout the breeding season, a female grey seal was assumed to have bred if she was recorded as hauled-out for the majority of an 18 day period during the breeding season, and spent < 10% of the this time diving. This is likely a conservative estimate of breeding, as in some colonies lactating females can spend up to 60% of their time in the water (Caudron et al. 2001). Where possible, sightings of tagged females at breeding colonies, and their breeding status (presence/absence of a dependent pup), were recorded. Foraging and breeding regions were assigned based on those used in Russell et al. (2013): Hebrides; Northern Scotland (including Orkney, Shetland and the Moray Firth); East Coast (including East Scotland and Northeast England); and Southeast England. Wales was included as a further region to include tags deployed there during this project.

A4.2 Results

Of all tagged grey seal females in SMRU's dataset, 34 showed behaviour that met the criteria for breeding, and five (~15%) of those transitioned between distinct foraging and breeding regions. This is not indicative of the proportion that actually bred, as many tags failed before the breeding season, or the data were not adequate to assess breeding using the conservative criteria outlined above. Summaries of foraging and breeding regions are shown in Table A4.1 below. Pre- and post-breeding movements of grey seal females tagged during this study are shown in Fig. A4.1.

Table A4.1: Breeding and foraging regions of adult female grey seals. *Bold values indicate deployments not considered in Russell et al. (2013). *Asterisks indicate the number of females that were confirmed to have bred by ground sightings.*

Breeding Region	**Foraging Region**				
	Hebrides	**N. Scotland**	**E. Coast**	**S.E. Coast**	**Wales**
Hebrides	2003 (*n* = 2) 2004 (*n* = 2) **2017 (*n* = 3)** **2019 (*n* = 2)**				
N. Scotland	**2019 (*n* = 1)**	1992 (*n* = 1) 1998 (*n* = 2) **2017 (*n* = 3)** **2018 (*n* = 1)**	1998 (*n* = 1) 2004 (*n* = 1) 2008 (*n* = 1)		
E. Coast			2008 (*n* = 2)	**2015 (*n* = 1)**	
S.E. Coast				2005 (*n* = 3) **2015 (*n* = 4)*****	
Wales					**2017 (*n* = 1)*** **2018 (*n* = 3)*****

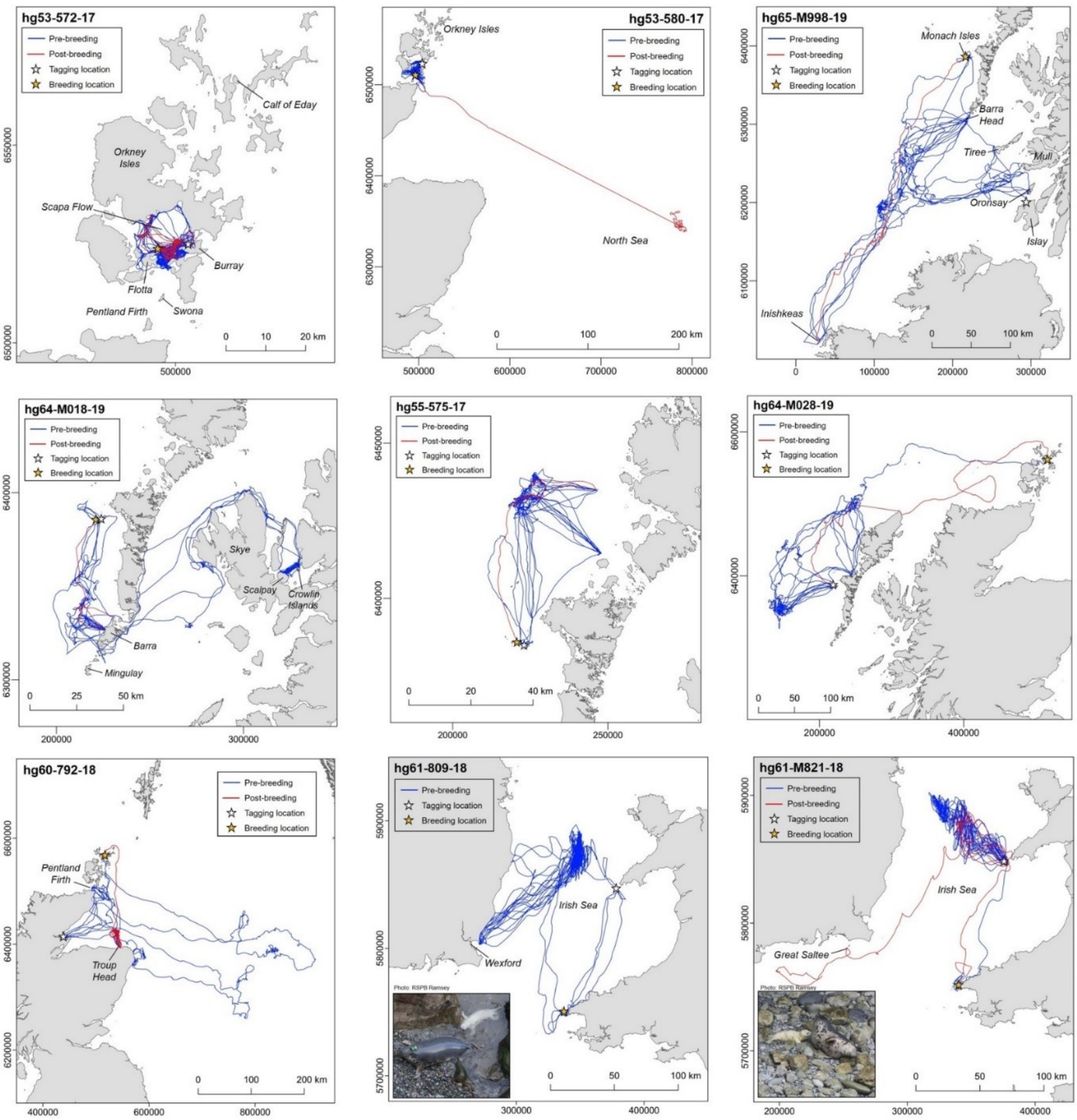

***Figure A4.1: Example tracks of breeding adult females tagged during this project**. Maps show tagging site (white stars), breeding site (gold stars), pre-breeding movements (blue lines) and post-breeding movements (red lines).*

A4.3 Discussion

Building on the results of Russell et al. (2013), seals generally appeared to forage and breed in the same region. However, the results presented here provide further evidence of seasonal movements between regions, including movements between the Hebrides (foraging) and North Scotland (breeding). Such inter-regional movements are likely to be related to variability in foraging conditions; for example, if foraging conditions in North

Scotland become unfavourable, females born in that region may choose to forage elsewhere, but return to breed, since grey seals display a degree of philopatry to where they were born, but also to where they first pupped (Pomeroy et al. 2000). Pup production in both the Hebrides and Orkney has plateaued in the last 20-25 years (Russell et al. 2019), suggesting that populations are at, or nearing carrying capacity (Thomas et al. 2019). Concurrently, pup production in the North Sea has been exponentially increasing (Russell et al. 2019). This was likely driven by relatively favourable foraging conditions in the southern North Sea, which initially resulted in disproportionately high summer (compared to breeding) numbers, composed in part of seals breeding further north (Russell et al. 2013). However, the rapid increase in pup production (Russell et al. 2019) means that there is now little mismatch between the foraging and breeding numbers, and thus less requirement for such seasonal movement. However, there is still evidence of some large-scale seasonal movements both within the British Isles (Table A4.1), and between the British Isles and the continent (Brasseur et al. 2015).

Seasonal movements were also detected on a finer spatial scale. For example, there was evidence of females tagged in the Moray Firth, breeding in Orkney (Fig. A4.1). In Wales, all three of the females that are known to have bred were tagged on Bardsey, and spent the summer foraging in the Irish Sea to the west of the island, hauling-out at Bardsey. For the two that transmitted data through to breeding, they made a sudden movement south to Ramsey to breed (Fig. A4.1), despite Bardsey being an established colony. A third seal was also observed with a pup on Ramsey, although the telemetry data did not cover her pre-breeding movements. This demonstrates that the scale of transitional movements between foraging and breeding grounds may vary among regions. In this case, for example, the seals did not leave Wales, but transitioned between sites within the Irish Sea. This highlights that seals hauling-out at one SAC (e.g. Lleyn Peninsula and Sarnau SAC) during the foraging season may comprise breeding stock from another SAC (e.g. Pembrokeshire Marine SAC). Inter-annual breeding site fidelity in this region is high (Langley et al. 2020), thus it is possible that natal philopatry could be driving this behaviour. Understanding the relationship between where seals breed, which is where trends are usually assessed against conservation objectives, and where they accumulate resources is essential to effective conservation management.