Title: Patterns of space use in sympatric marine colonial predators reveals scales of spatial partitioning

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Abstract

Species distribution maps can provide important information to focus conservation efforts and enable spatial management of human activities. Two sympatric marine predators, grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* have overlapping ranges on land and at sea but contrasting population dynamics around Britain: whilst grey seals have generally increased, harbour seals have shown significant regional declines. We analysed two decades of at-sea movement data and terrestrial count data from these species to produce high resolution, broad-scale maps of distribution and associated uncertainty to inform conservation and management. Our results showed that grey seals use offshore areas connected to their haul-out sites by prominent corridors and harbour seals primarily stay within 50km of the coastline. Both species show fine-scale offshore spatial segregation off the east coast of Britain and broad-scale partitioning off western Scotland. These results illustrate that for broad-scale marine spatial planning, the conservation needs of harbour seals (primarily inshore, the exception being selected offshore usage areas) are different from those of grey seals (up to 100km offshore and corridors connecting these areas to haul-out sites). More generally, our results illustrate the importance of detailed knowledge of marine predator distributions to inform marine spatial planning; for instance, spatial prioritisation is not necessarily the most effective spatial planning strategy even when conserving species with similar taxonomy.

Keywords: Halichoerus grypus, Phoca vitulina, density estimation, propagating uncertainty, species distribution, telemetry, area-based conservation.

Introduction

The marine environment is affected to an increasing spatial extent and intensity through direct impacts of anthropogenic activities including fisheries, energy extraction and shipping traffic (Merchant et al. 2014) and through indirect impacts such as prey depletion due to fisheries or the effects of climate change (Guénette et al. 2006). Apex predators are particularly vulnerable to such impacts because their K-selected life histories limit the speed at which they can respond to reductions in population size. Anthropogenic activities at sea can affect marine predator distributions, particularly in the context of area-based conservation of species, and in relation to the management of these activities, such as the rapid development of renewable energy extraction. One focus of area-based conservation in the marine environment involves identifying areas with a high abundance of apex predators (Hooker et al. 2011). However, areas shared by multiple predator species may not include optimal habitat for any of those species (Williams et al. 2014). Williams et al. (2014) found that, at a regional scale, areas of greatest overlap in marine mammal distributions excluded areas of highest density for all species. Marine mammals are commonly used as indicators of ecosystem health (Boyd et al. 2006, Piatt & Sydeman 2007) and a good understanding of how their abundances are distributed is essential if marine protected areas for them are to be effective.

There are a number of habitat-based methods for mapping species distributions (Matthiopoulos & Aarts 2010). However, these methods require covariate data, which may limit the geographical area over which predictions can be made. When the focus is purely on spatial patterns, density estimation methodology offers a flexible alternative in which the spatial extent is not restricted by external covariates (Silverman 1986). Combining density-estimation methods with simple habitat models using only (distance-based) covariates that are universally available to predict to areas where movement data are absent, we develop a generalised framework to produce species distribution maps for terrestrial and marine animals integrating animal movement and population data. Obtaining robust population-level insights from individual animal data is challenging because such data can be difficult and expensive to collect and because the sample must be proportional to the animals' prevalence in the population. Many factors affect the precision of inference from limited sampling such as the underlying population structure and consistency in spatio-temporal behaviour. We propagate uncertainty through the entire analysis from movement and population data to estimated space use distributions.

Our study focusses on grey and harbour seals, two sympatric species that inhabit much of the coasts and continental shelf waters of northwest Europe. They are listed under Annex II of the European Habitats Directive, which requires designation of marine protected areas (MPAs); these exist for terrestrial sites but marine sites have not yet been proposed (JNCC 2010). As central place foragers, grey and harbour seal access to the marine environment is restricted by the need to return to shore periodically between foraging trips (Matthiopoulos et al. 2004). The two species have overlapping ranges on land and at sea, similar but variable diets, and comparable but asynchronous life-cycles (McConnell et al. 1999, Sharples et al. 2009, Brown et al. 2012). They may therefore be expected to display spatial niche partitioning to some extent. If the spatial component of niche partitioning at sea is strong, with little overlap in areas of highest density, this would have implications for designation of marine MPAs based on relative abundance. Designating MPAs for multiple species, sometimes known as "double badging", is one way for management authorities to strengthen conservation measures within limited resources. However, this would not be effective if there were strong evidence of spatial partitioning.

An issue of particular interest in our study area is that although grey and harbour seals are sympatric species and are therefore likely to be facing the same environmental stressors, they show opposing population trends in some areas around Britain. Grey seal numbers have generally increased since at least 1984 and, although stable in the Western and Northern Isles, are still increasing in the North Sea (Thomas 2013). Harbour seals have declined in Orkney, Shetland and the east coast of Scotland since around 2000 but are stable in the Western Isles (Lonergan et al. 2007, Duck et al. 2013). Possible causes of declines in harbour seal numbers include direct mortality from vessel interactions (Bexton et al. 2012), the effects of infectious diseases (Hall et al. 2006, Harris et al. 2008), biotoxin exposure (Hall & Frame 2010) or interspecific competition with grey seals (Bowen et al. 2003, Svensson 2012). Knowledge of regional variation in the extent of overlap in the at-sea distributions of grey and harbour seal populations could help to inform whether the two species compete for food.

Here, we synthesise more than two decades of population and movement data around the continental shelf of Britain, Ireland and France for two sympatric seal species. We describe species distributions for grey and harbour seals, defined as 'usage', with robust estimates of uncertainty and investigate patterns of spatial partitioning between the species. Our results are thus important to inform the placement of areas for conservation, including in the context of concern about harbour seal population declines. They are also important to inform other aspects of marine spatial planning, including local developments such as wind farms and tidal turbines. The methods developed here can readily be used in other situations where the ranges of central-place foragers (e.g. other pinnipeds, breeding seabirds, and terrestrial predators) overlap, and may be useful for informing marine spatial planning issues in these cases.

Methods

Figure 1 shows a schematic flowchart of the analytical process, which synthesises movement and population data to produce usage maps with accompanying uncertainty. Analyses were conducted using R 3.0.2 (R Core Team 2014) and maps were produced using Manifold 8.0.28.0 (Manifold Software Limited 2013).

(1) **Population data**: Grey and harbour seals are surveyed during August when harbour seals are moulting and haul-out on land for an extended period. During standard aerial surveys all seals along a specified coastline are counted and coordinates are recorded to an accuracy of up to 50m. Surveys take place within two hours of low tide when low tide is between 12:00 and 18:00 hours (Thompson et al. 2005, Lonergan et al. 2011).

Ground and boat-based count data collected by other organisations were also used in the analysis, and all sources of data collection are summarised in Table 1. Figure 2 shows the locations of terrestrial counts.

(2) **Movement data:** Telemetry data from grey and harbour seals were obtained from two types of logging device: Satellite Relay Data Logger (SRDL) tags that use the Argos satellite system for data transmission and GPS phone tags that use the GSM mobile phone network with a hybrid Fastloc protocol (McConnell et al. 2004, Argos 2011). Telemetry data were processed through a set of data-cleansing protocols to remove null and missing values, and duplicated records from the analysis. Details of telemetry data are available in Supplementary material, Appendix 1.

(3a) **Positional corrections:** Positional error, varying from 50m to over 2.5km affects SRDL telemetry points. Errors were assigned by the Argos system to six location quality classes. We developed a Kalman filter to obtain position estimates accounting for observation error (Royer & Lutcavage 2008). SRDL data were first speed-filtered at $2ms^{-1}$ to eliminate outlying locations that would require an unrealistic travel speed (McConnell et al. 1992). Observation model parameters were provided by the location quality class errors from Vincent et al. (2002), and process model parameters were derived by species from the average speeds of all GPS tags. GPS tags are generally more accurate than SRDL tags, and 75% of these data have an expected error of less or equal to 55m (Dujon et al. 2014). However, occasional outliers were excluded using thresholds of residual error and number of satellites.

(3b) **Interpolation**: Movement SRDL data were interpolated to 2-hour intervals using output from the Kalman filter and merged with linearly interpolated GPS data that had been regularised to 2-hour intervals. A regular grid of 5km resolution was created to encompass all telemetry data. 5km was selected based on the computational trade-off between the resolution and spatial extent of the final maps. Data from 259 grey seal tags (Supplementary material, Appendix 1 Table A1; Figure 3) and 277 harbour seal tags were used (Supplementary material, Appendix 1 Table A2; Figure 3). The patterns of movement of the tagged animals were assumed to be representative of the whole population (Lonergan et al. 2011). Tag deployment occurs outside each species breeding and moulting seasons, and tags usually fall off when animals moult. Therefore, telemetry data were primarily collected between June and December for grey seals, and between January and June for harbour seals.

(3c) **Haul-out detection:** Haul-out events for both SRDL and GPS tags were defined as starting when the tag sensor had been continuously dry for 10 minutes and ending when the tag had been continuously wet for

40 seconds. Haul-out event data were combined with positional data using date/time matching by individual animal. Each event was then assigned to a particular geographical location. In the intervening periods between successive haul-out events, a tagged animal was assumed to be at sea (if the tag provided such information) or in an unknown state (if the tag did not).

(3d) **Haul-out aggregation:** Haul-out sites (defined by the telemetry data as any coastal location where at least one haul-out event had occurred) were aggregated into $5x5km^2$ grids (defined above). Haul-out events occur on land or intertidal sandbanks. Haul-out sites were associated with a terrestrial count in order to scale the analysis to population level. Firstly, telemetry haul-outs were linked to terrestrial counts based on matching their grid cells. Secondly, if no match could be found, the nearest valid haul-out site visited by the animal either directly before or after the unmatched haul-out site event was chosen. Thirdly, if an animal had never been to a haul-out with associated terrestrial data during the time it was tagged, count information was assigned from the nearest haul-out based on Euclidean distance.

(3e) **Trip detection:** Seals move between different haul-out sites. Individual's movements at-sea were divided into trips, defined as the sequence of locations between defined haul-out events. Each location in a trip was assigned to a haul-out site. After spending time at sea an animal could either return to its original haul-out (classifying this part of the data as a return trip), or move to a new haul-out (giving rise to a transition trip). Journeys between haul-out sites were divided temporally into two equal parts and the corresponding telemetry data were attributed to the departure and termination haul-outs.

(3f) **Kernel smoothing**: Telemetry data are locations recorded at discrete time intervals. To transform these into spatially continuous data representing the proportion of time animals spend at different locations we kernel smoothed the data. The KS library in R (Chacón & Duong 2010) was used to estimate spatial bandwidth of the 2D kernel applied to each animal/haul-out map using the unconstrained plug-in selector ('Hpi') and kernel density estimator ('kde') to fit a usage surface. Kernel smoothing can be sensitive to the choice of smoothing parameter and serial correlation in the observations. However, thinning the data to eliminate autocorrelation would have meant a significant loss of information. Instead, the average tag duration (grey seals=124 days, harbour seals=99 days) was determined to be long enough to counteract bandwidth sensitivity (Blundell et al. 2001, Fieberg 2007). Only at-sea locations were smoothed because haul-outs were fixed locations and known without uncertainty at the scale of the analysis. Therefore, haul-out locations were incorporated back into the maps as discrete grid square usages.

(3g) **Information content weighting**: To account for differences in tag operation duration, an Index of Information Content (Supplementary material, Appendix 2) was derived. This ensured the importance of animals with short tag-lifespans was reduced and animals with heavily auto-correlated location data were not overrepresented. A 'discovery' rate was determined for each species, defined as the total number of new grid cells visited as a function of tag lifespan, and modelled using Generalised Additive Models (GAMs) (Wood 2006, 2011). Explanatory covariates were tag lifespan, type of tag (SRDL or GPS), and (for grey seals) age of each animal (1+ or pup). Each animal/haul-out map was multiplied by a normalised discovery rate (termed as an *Information Content Weighting*) and all maps connected to each haul-out were aggregated and normalised to 1.

4. **Population scaling**: The population at each haul-out was estimated from terrestrial count data, which was rescaled to allow for the proportion of animals that were at sea when surveys were carried out. Using the mean species haul-out probabilities over all available months and their variances, we derived a distribution (Supplementary material, Appendix 3) of population estimates ranging from the value of each terrestrial count (minimum population size) to 100 times the count (maximum population size). The distribution was sampled using parametric bootstrapping 500 times per count to produce a distribution of estimates. These data were then processed through a decision tree to produce current population estimates and variances, given the limitations in fine-scale data. From herein, population numbers are given based on these estimates.

5. **Population uncertainty**: Population-level uncertainty incorporated observational, sampling, and scaling errors (Supplementary material, Appendix 3). 'Population scaling' (explained above) produced estimates of population variance for each haul-out.

6. **Individual-level uncertainty**: Within haul-out uncertainty accounted for the differences in the magnitude of data collected by an animal over its tag lifespan, and for variation in the parameters of the tag itself. Variance was modelled using data-rich sites (determined experimentally to be those sites which had 7 or more animals associated with them) (Supplementary material, Appendix 3). Variance was estimated using linear models with explanatory covariates of sample size (number of animals at the haul-out), and mean usage of seals. The models predicted variance for data-poor and null usage sites (where population data existed but movement data did not, see 'Accessibility modelling' below). Within-haul-out variance was estimated for null usage sites by setting the sample size of the uncertainty model to 0. Individual and population-level variances were combined to form uncertainty estimates for the usage maps

(Supplementary material, Appendix 3). Usage and variance by haul-out were aggregated to a total usage and variance map for each species. Estimates of haul-out usage were then added to at-sea usage to generate maps of total usage.

7. **Accessibility modelling:** For haul-outs that had terrestrial counts but did not have associated telemetry data, we estimated usage in the form of accessibility maps (Supplementary material, Appendix 4). We modelled the expected decay of usage with increasing distance from the haul-out in the absence of between haul-out spatial heterogeneity. To ensure the spatial extent of the analysis was not restricted by availability of environmental data, simple habitat models were built using covariates of geodesic and shore distance from haul-out in a Generalised Linear Model (GLM) for each species (McCullagh & Nelder 1989). Previous studies have shown that UK grey and harbour seal habitat preference is primarily driven by distance to haul-out site (geodesic distance) (Aarts et al. 2008, Bailey et al. 2014). The model predicted usage for each haul-out that was normalised and weighted by the mean proportion of time animals spent not hauled out. Mean and variance were scaled to population size by combining each one with the population mean and variance estimates of each haul-out and these were aggregated to the total usage map for each species.

The methodology described above is based on (Matthiopoulos et al. 2004). However, the methodology was changed significantly and extended to ensure the analysis could be resolved to a fine-scale, that all available telemetry data could be included (see ‘Trip detection’), and that more sources of variability were incorporated and propagated through the analysis to produce continuous uncertainty estimates.

Spatial comparisons between species

To compare spatial use between species, an index ($s_i = M_{i(Hg)} - M_{i(Pv)}$) was calculated to show the global difference in the two species’ at-sea distributions, where estimated usage *(M_i)* was the number of animals expected to use grid cell *i*. (*Hg*) refers to grey seals, (*Pv*) to harbour seals.

Results

Movement data were analysed from 259 grey seal and 277 harbour seal telemetry tags deployed between 1991 and 2013. These were combined with terrestrial counts collected between 1996 and 2013. Combined hauled-out and at-sea usage of grey and harbour seals around Britain, Ireland, and France are shown in Figure 4, with uncertainty. Both species’ usage is concentrated around Scotland, reflecting the terrestrial distribution of seals around Britain, Ireland and France (Duck & Morris 2013). Grey seal distribution is widespread with high usage areas close to the coast linked with high usage offshore (Figure 4a). In some areas these offshore areas coincide with rocky ridges such as Stanton Banks south of Barra, west Scotland; and sandbanks such as West Bank in the Moray Firth, and Dogger Bank in the southern North Sea (see Figure 7 for named locations). The linking corridors of usage provide insight into how grey seals move between regions. Grey seal usage extends over the continental shelf off the west coast of Scotland and Ireland. The largest aggregation of high usage was around the Orkney Islands. Grey seal usage around Ireland was primarily coastal, with limited movement between Ireland and other areas of high usage around Britain.

By contrast, Figure 4b shows that harbour seals remain close to the coast in a number of apparently discrete local populations around Britain and Ireland, with little movement among them. However, in the Moray Firth and Firth of Tay, eastern Scotland, they spent time offshore at Smith Bank and Marr Bank, and from The Wash, England, they travelled to sandbanks up to 150km offshore (see Figure 7 for named locations). Offshore usage from The Wash in particular can be seen in fine-scale detail due to the large sample size (59 tagged animals) in this region. At-sea usage of each species calculated within buffers of increasing distance from the coast shows that harbour seals were more likely to stay close to the coast, spending only 3% of their time at distances greater than 50km from the coast (Figure 5). By contrast, grey seals spent 12% of their time at distances greater than 50km from the coast. Movements of harbour seals shown by the data underpinning the usage maps, confirm that although they do not usually travel as far offshore as grey seals, they show considerable movement parallel to the coast, resulting in concentrated patches of high coastal usage.

Figure 6 shows the difference, by grid cell, between the predicted abundance of grey and harbour seals as a measure of the distribution of each species relative to the other. Grey seal prevalence is expected because the population is much larger than that of harbour seals. From the usage maps, estimated total abundance of grey seals is 109,500 (95% CI=75,900-185,400), and the estimate of harbour seals is 44,000 (95% CI=20,800-68,000), which are similar to the published UK population estimates for 2012 for grey (O Cadhla et al. 2013, Thomas 2013) and harbour seals (Duck et al. 2013). Harbour seals were dominant in the southernmost part of the North Sea, around specific haul-out sites in northern France, west Scotland, parts of Ireland, and in localised offshore patches in the Moray Firth, off the west coast Orkney, and around Shetland.

Discussion

We describe for the first time the species distributions of two sympatric marine predators in fine resolution and at a broad-scale with estimates of uncertainty. Our analysis allows us to compare patterns of marine space use between the two species to provide insight into the extent to which they divide or share the common space available to them. In the context of variation in regional population trajectories, we can explore how patterns of spatial overlap between the species at sea relate to recent declines in some harbour seal populations. An application of our results is that they enable us to provide scientific advice on the areas of most importance to each species to inform conservation and management. Our results show that at-sea usage of harbour seals is heterogeneous with small patches of highly concentrated numbers of animals, indicative of the discrete regional populations found around Britain, Ireland, and France (Vincent et al. 2010, Cronin 2011, Sharples et al. 2012). On the east coast, harbour seals spend a high proportion of time at offshore sandbanks, indicative of foraging areas (Thompson et al. 1996). In contrast, grey seal usage is characterised by a series of interconnected highly utilised offshore areas that include known foraging sites (Matthiopoulos et al. 2004, McClintock et al. 2012). These differences in the way the two species use the marine environment may have consequences for their population dynamics in relation to changes in local prey availability (Sharples et al. 2009), disease transmission (Herreman et al. 2011), and their vulnerability to metapopulation collapses (Coltman et al. 1998, Matthiopoulos et al. 2005). In the south-eastern North Sea, where there is a separation of usage between grey and harbour seals, harbour seal numbers are increasing. This pattern is repeated at a finer-scale in the Moray Firth, an area where the harbour seal population has historically fluctuated but has appeared to stabilise in recent years (Duck et al. 2013). In both these areas, harbour seals utilise different offshore sandbanks, which are likely foraging areas (Tollit et al. 1998, McClintock et al. 2012). However, in the Firth of Tay (see Figure 7), where the population of harbour seals has declined to fewer than 200 animals (Duck et al. 2013), both species utilise the same offshore patch. West of Scotland and around Ireland, harbour seal populations are stable and use coastal areas (such as sea lochs and harbours) that grey seals do not, suggesting an inshore foraging distribution. These patterns give an indication that offshore spatial overlap may be detrimental to harbour seals but further studies incorporating information on seal diet and body condition, and prey distribution and abundance are required before conclusions can be reached. However, there is corroborating evidence from other populations where the species co-exist to demonstrate that interspecific competition between grey and harbour seals is prevalent. Within their range, grey and harbour seals co-exist in the northeast Atlantic and along the east coasts of North America and Canada. A decline in harbour seals throughout the 1990s at Sable Island, Canada has been partly attributed to inter-specific competition for shared food resources with grey seals (Bowen et al. 2003). On the east coast of the

US, in New England, seal haul-out sites that were once dominated by harbour seals are now designated as shared sites, or dominated by grey seals (Gilbert et al. 2005, Waring et al. 2010). Recent abundance estimates indicate the harbour seal population may be declining and therefore the increasing and spatially expanding grey seal population needs to be evaluated (Gordon Waring, pers. comm.).

Assumptions and limitations

We assumed that the spatial distributions of each species were in equilibrium to allow 22 years of movement data to be integrated. Inter-annual variability in the movement data was captured in the maps so that they show the largest extent to distributions possible. However, population dynamics of both species have changed considerably in recent history, and therefore pressures of density dependence at some haul-outs may have altered, speculatively leading to changes in the metapopulation dynamics of each species. Therefore, we recommend that future telemetry deployments should carry out repeat tagging for each species in similar areas to enable estimates of temporal heterogeneity in spatial distribution that could be integrated into haul-out uncertainty estimates. Parameters differed between telemetry tags depending on the purpose for which they were built. Two processes enabled the tags to be directly compared: Regularising the tracks accounted for differences in call attempts, call abortions, haul-out sampling rates, and the minimum number of satellites needed; weighting individual animals by their ‘Information Content Weighting’ (Supplementary material, Appendix 2) accounted for the cut-off date for call attempts and the wet/dry sensor failure criteria.

The at-sea and on-land distributions of grey and harbour seals vary seasonally (Thompson et al. 1996) and annually (Duck & Morris 2013, Duck et al. 2013). Therefore, to directly compare distributions at a population-level we used terrestrial count data from August. There were seasonal gaps in the telemetry data for each species at different times of the year. However, our examination of spatial partitioning between the two species is based on the assumption that patterns of usage remain constant. Grey seals show high pupping site fidelity to aggregated colonies during the breeding season (Pomeroy et al. 2005). However, some animals travel to a site to pup but return after only a few weeks to non-breeding haul-out regions (Russell et al. 2013). This suggests that animals providing telemetry data during the breeding season may deviate from their non-breeding behaviour for only a short time, having little impact on grey seal usage distribution. Male and female harbour seals have been shown to restrict their foraging range during the breeding season (Thompson et al. 1994, Van Parijs et al. 1997). However, lactation lasts around 24 days (Bowen et al. 1992), so this temporary behaviour is also unlikely to impact harbour seal usage distribution. To explore changes in the way that distributions of both species may vary annually and seasonally, more data collection is required. In future, this may be possible through telemetry devices encompassing new technology such as extended tag lifetimes (years rather than months) and with the advent of more affordable devices so that tags could be deployed to many more animals.

Informing conservation and management

Quantifying species distributions and understanding the differences in the way apex predators utilise the marine environment has important implications for the impacts of anthropogenic activities and management action to mitigate them. Grey and harbour seals are both listed in Annex II of the Habitats Directive, which has led to the designation by the governments of the UK and the Republic of Ireland of a number of terrestrial marine protected areas (MPAs), where grey or harbour seals are a qualifying feature (JNCC 2012), NPWS, unpublished data). No offshore MPAs have been proposed yet for these species, primarily because of the lack of robust science to inform this process. Here, we provide valuable new information, which together with other recent work (e.g. Russell et al. 2013), will allow governments to move towards selecting suitable sites to propose as marine MPAs for grey and harbour seals. We have shown that both species of seal spend the majority of their time at sea up to 50km from the coast but these areas are more important to harbour seals because they rarely move further from the coast; conservation and management action for harbour seals should therefore be focused in this zone. The exceptions are off The Wash and in the Moray Firth, where harbour seals spend more time further offshore. Grey seal distribution is more extensive and our results show that both offshore (presumed) foraging habitat and the transition corridors that link these foraging areas to haul-out sites are important to consider in the process of selecting marine MPAs. An important practical point arising from our results is that the uncertainty estimate for each grid square provides information about how representative the mean is of the underlying population. This provides information on the need for further data collection in areas of interest to conservation and management. Additionally, they can be used directly in conservation planning tools such as Zonation software (http://cbig.it.helsinki.fi/software/zonation/) that identifies areas important for habitat quality retention.

One issue of increasing conservation concern is the continuing rapid increase in marine renewable energy extraction in European waters (Edrén et al. 2010, Skeate et al. 2012, Thompson et al. 2013). Our results show that the impact of these developments on grey and harbour seals may vary because of differences in their spatial distributions. The effects of near-shore devices will potentially have a greater impact on harbour seals because a relatively greater proportion of the population will be exposed to the development. Conversely, a larger proportion of the grey seal population will be exposed to developments far offshore where corridors of usage form networks among offshore areas of high usage and haul-out sites. Through comparing grey and harbour seal distributions, we found spatial partitioning over varying spatial scales showing that sympatric apex predators have dissimilarities in their spatial patterns in this case. Therefore, it should not be assumed that spatial prioritisation can be used effectively to conserve species at similar trophic levels or taxonomic groups, and there is a requirement for careful analysis of their distributions, as presented here, to properly inform spatial planning mechanisms.

Broader applications

Animal-borne sensors have developed and advanced over the past 25 years, allowing many species to be tagged and producing large amounts of movement data (e.g. movebank.org). The species density estimation combined with simple habitat model framework presented here is applicable to a range of applications and datasets. This methodology will be pertinent to species where movement patterns of the whole population cannot be observed but population count data can be linked explicitly. In studies of marine central-place foragers, both sexes of seals and some seabirds can be counted reliably on land, tagged, and then tracked at sea, allowing insight into their spatial distribution. In the terrestrial environment, the methodology can be applied more widely as many terrestrial predators tend to be central-place foragers (e.g. wolves (*Canis lupus*) Sand et al. 2005) and so relevant movement and population data are more readily available. Additionally, for environments where covariate data are spatially extensive and continuous, the accessibility modelling framework presented here could be extended to include readily available environmental covariates.

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Figures & tables

Table 1. Summary of grey and harbour seal terrestrial surveys. Unless specified otherwise in the description, all surveys took place during August.

Area surveyed	**Method**	**Description**	**Data used**
Scotland	Aerial survey (helicopter)	Both species surveyed every 1-5 years using SMRU protocol	1996-2013
Moray Firth, Firth of Tay, Donna Nook, The Wash in East Anglia, and Thames estuary	Aerial survey (fixed-wing)	Both species surveyed annually using SMRU protocol	1996-2013
Chichester and Langstone harbour	Ground counts through Chichester Harbour Authority	Harbour seals surveyed annually	1999-2012
Cornwall and Isles of Scilly, south-west England	Boat survey (Leeney et al. 2010)	Grey seals surveyed in April	2007
Isles of Scilly	Ground counts (Sayer et al. 2012)	Grey seals	2010
North Wales	Ground counts (Westcott & Stringell 2004)	Grey seals counts extended over 12 months	2002, 2003
Skomer Island, West Wales	Ground counts	Adult grey seals	2013
Ramsey Island, West Wales	Ground counts	Grey seals	2007-2011
Northern Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol	2002
Strangford Lough, Northern Ireland	Aerial survey (helicopter)	Both species surveyed using SMRU protocol	2006, 2007, 2008 and 2010
Republic of Ireland	Aerial survey (helicopter)	Both species surveyed	2003

		using SMRU protocol	
Northern France	Ground counts with extrapolation (Hassani et al. 2010)	Harbour seals surveyed annually	1996-2008

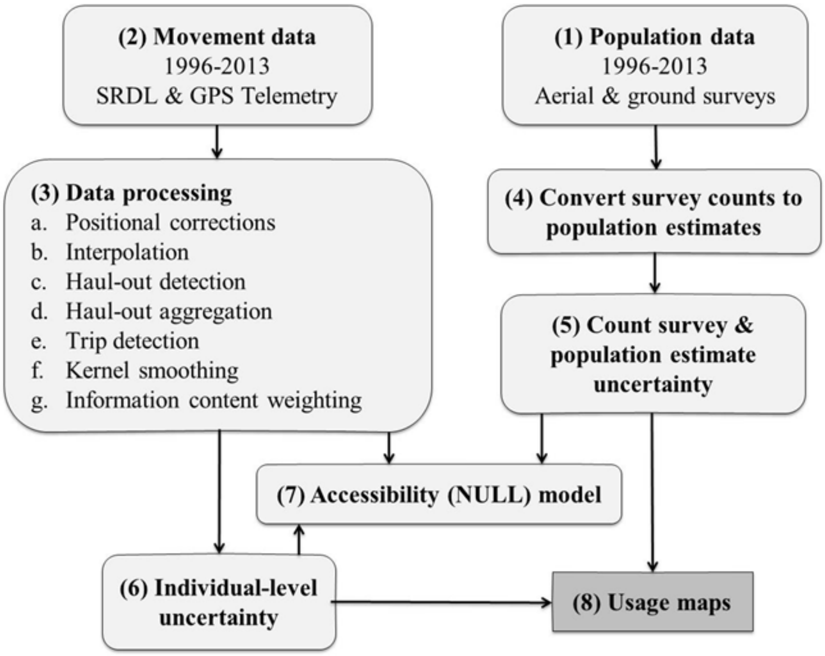


Figure 1. Flowchart representing high-level analytical methodology.

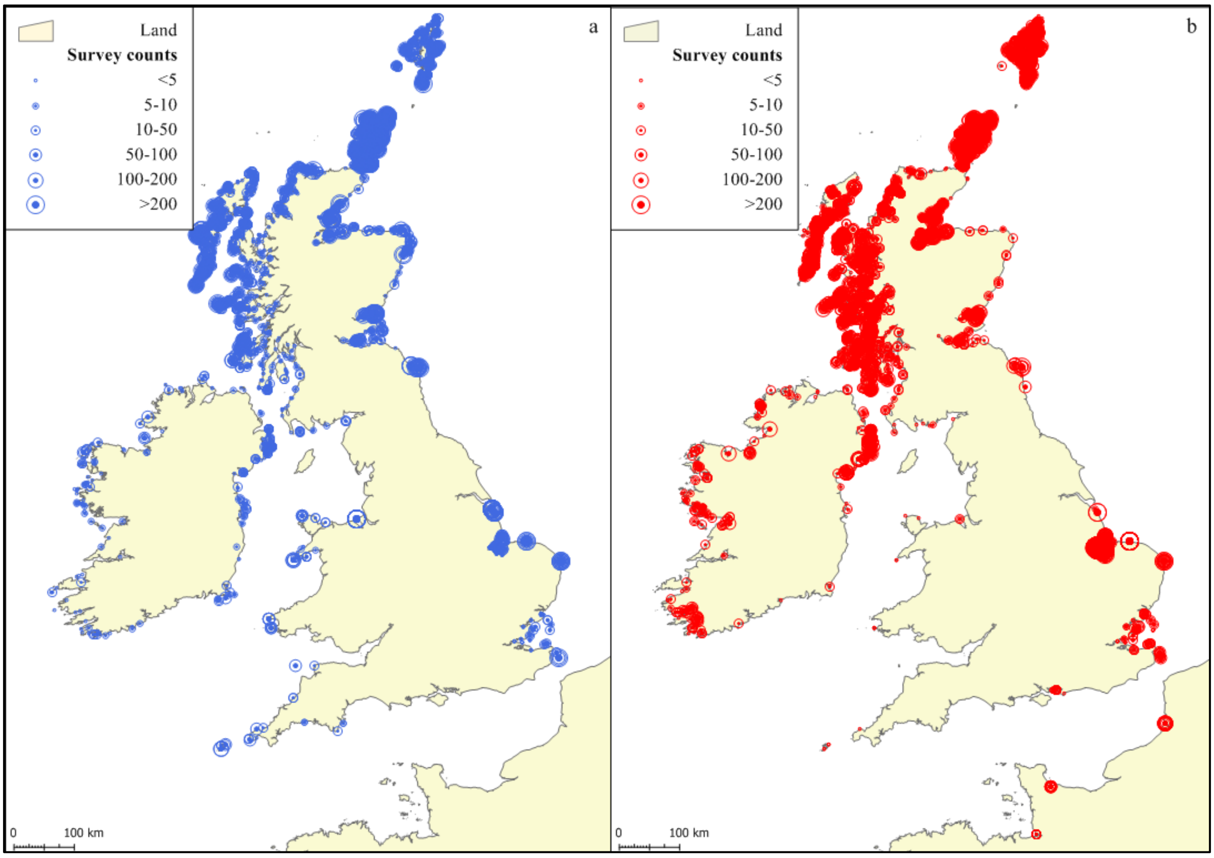


Figure 2. (a) Grey and (b) harbour seal terrestrial counts between 1996 and 2013. GSHHG shoreline data from NOAA were used in figures 2, 3, 4, 6 and 7, available from to download from http://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html.

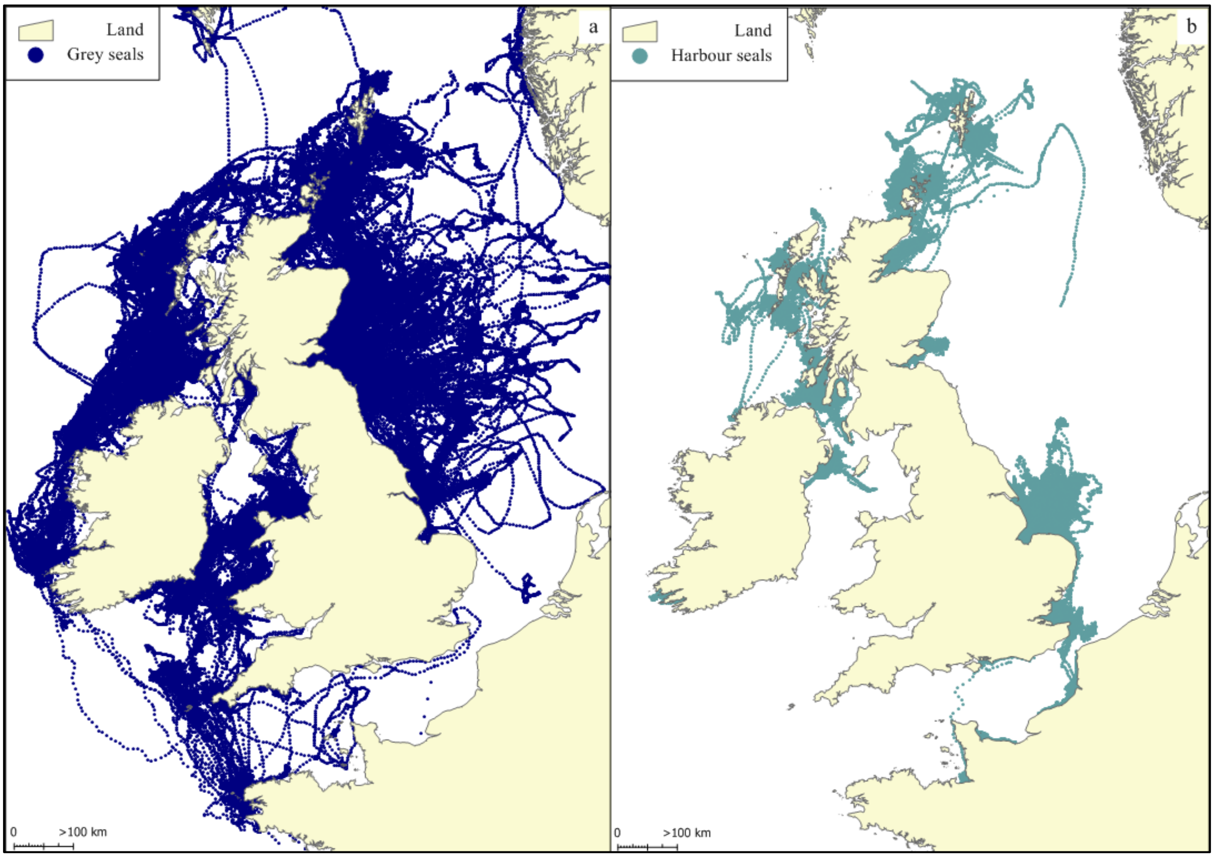
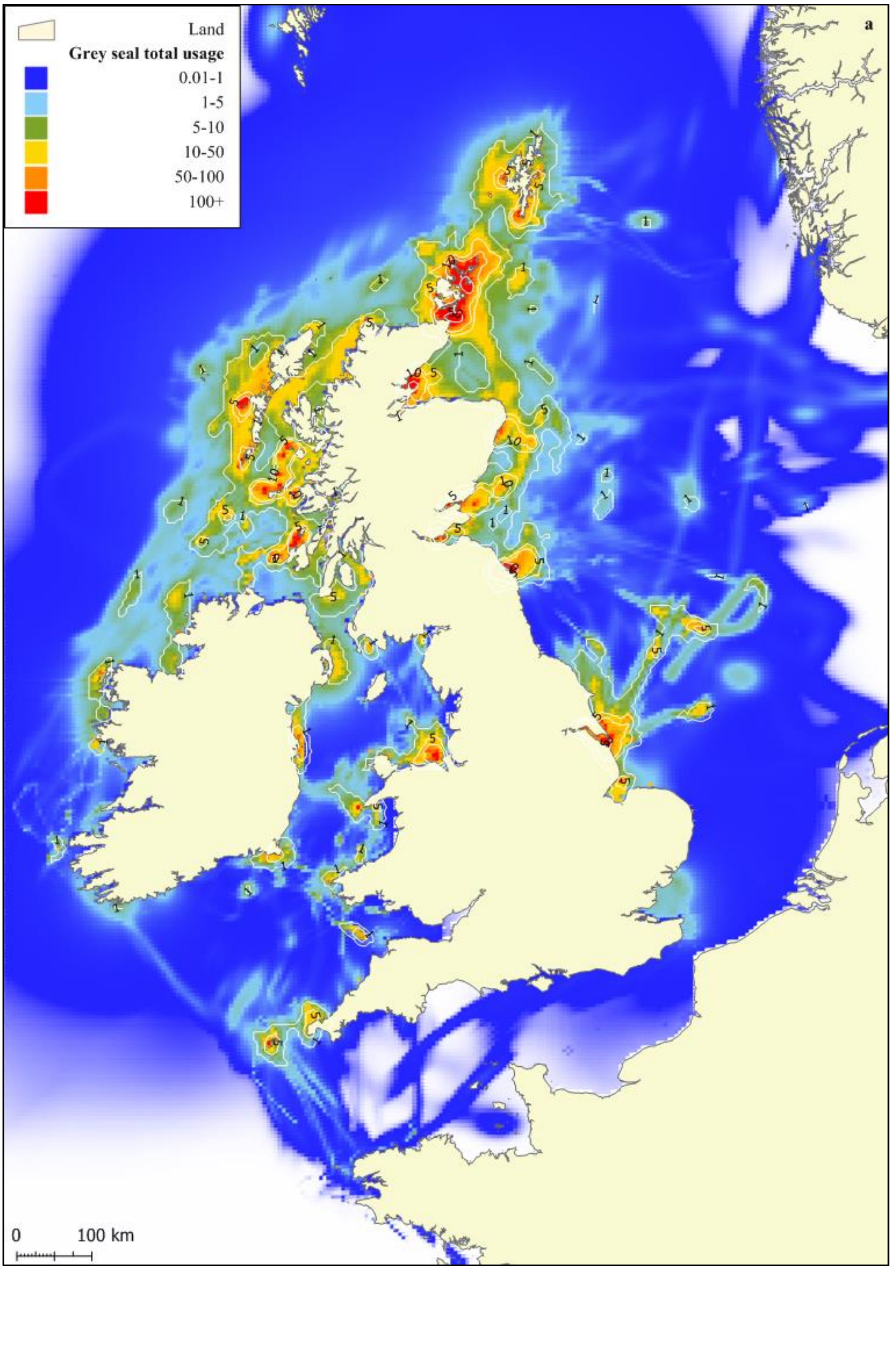


Figure 3. (a) Grey seal telemetry tracks between 1991 and 2013 showing 259 animals; and (b) harbour seal telemetry tracks between 2003 and 2013 showing 277 animals.


Land
Grey seal total usage
0.01-1
1-5
5-10
10-50
50-100
100+
a
0 100 km

538

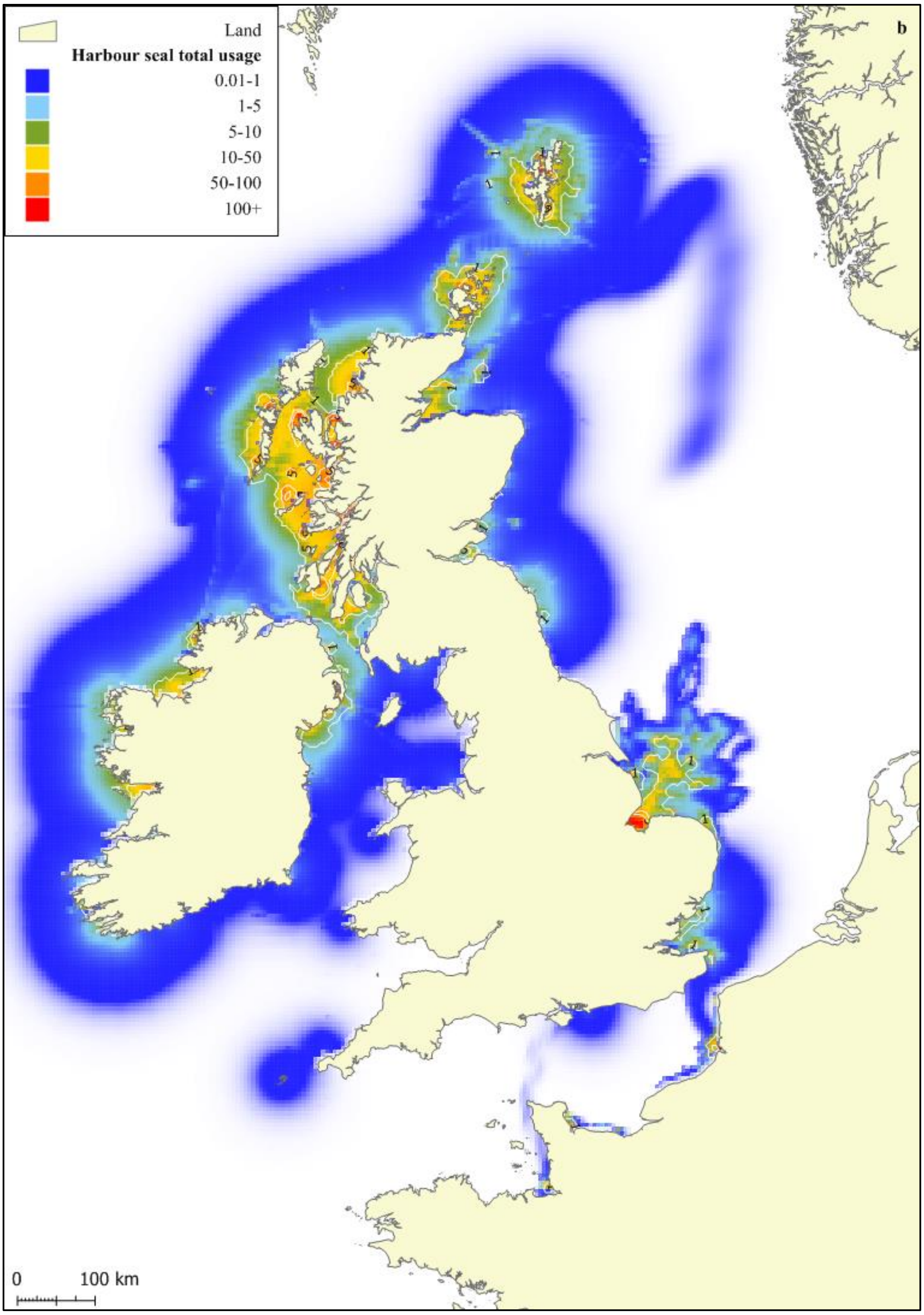


Figure 4. (a) Grey seals; (b) harbour seals; showing the predicted number of seals in each 5x5km^2 grid square. E.g. A yellow square denotes between 10 and 50 seals are within that grid square. White contour lines denote standard deviation from the mean as a measure of uncertainty around the estimated usage. Labels show the standard deviation value at each contour.

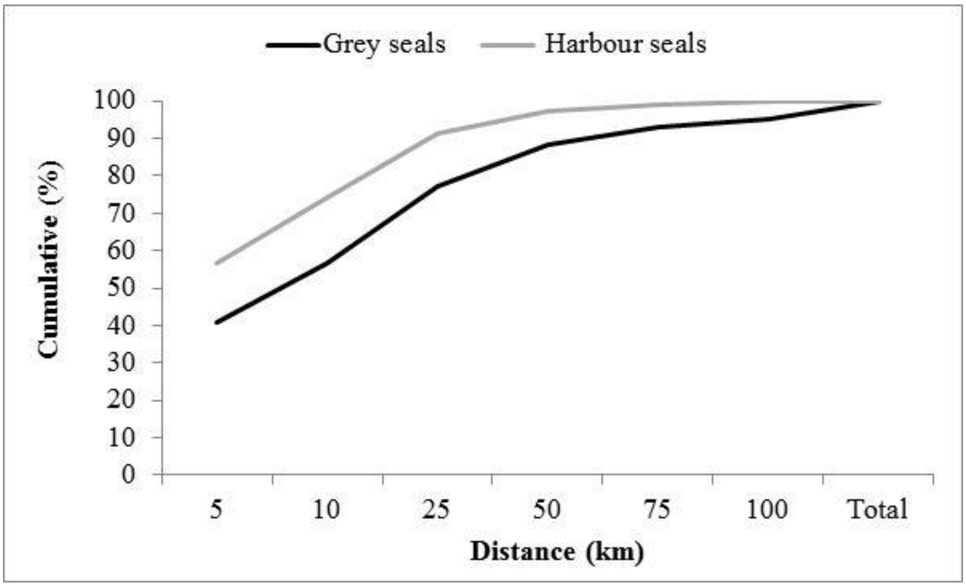


Figure 5. Cumulative spatial usage of grey and harbour seals as a function of distance from the coast.

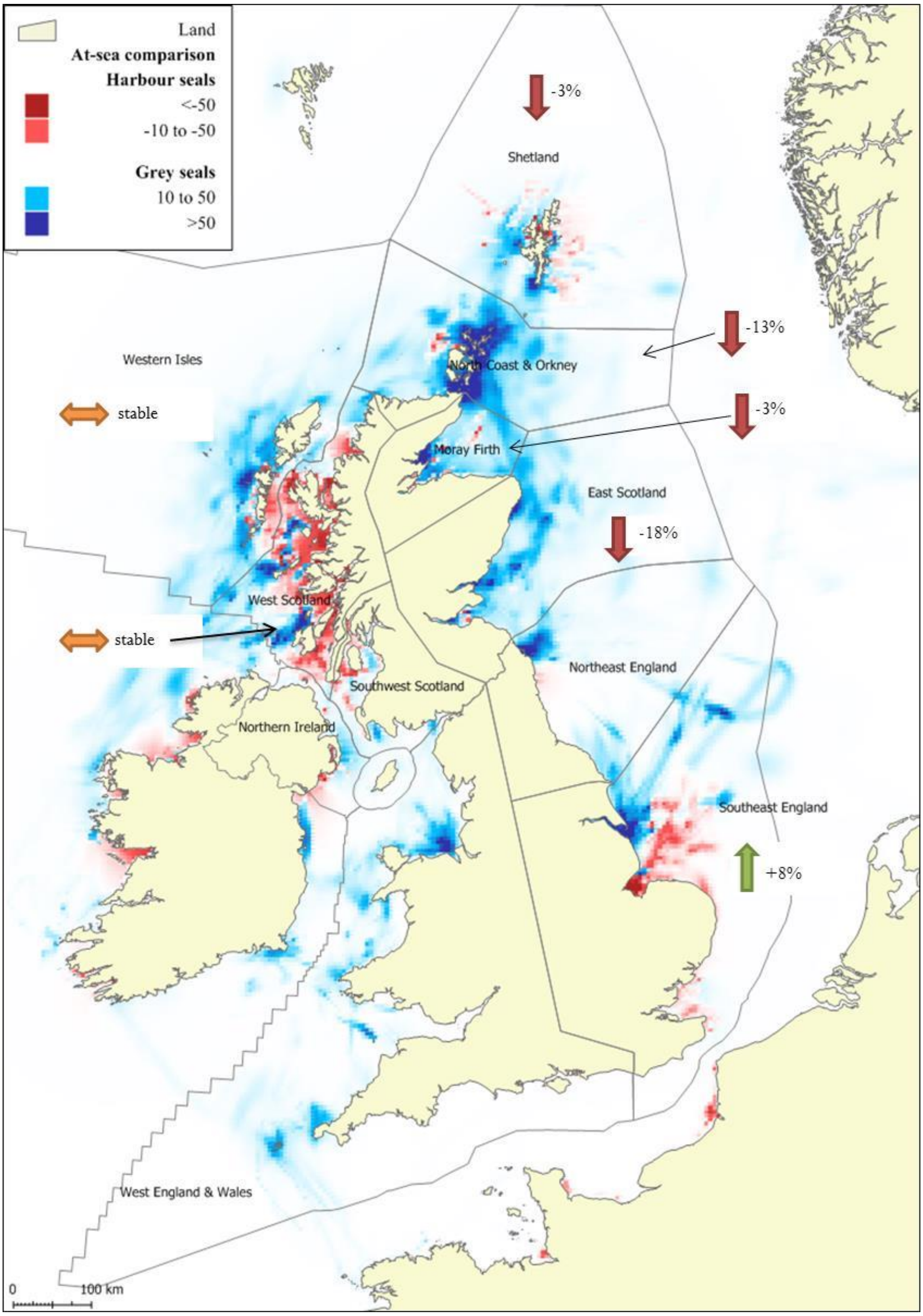


Figure 6. Spatial at-sea comparisons between grey and harbour seals at $5x5km^2$ resolution showing absolute difference in population numbers. Red denotes greater harbour seal usage, blue denotes greater grey seal usage. Traffic light indicator arrows show the population trajectories (2000-2010) of harbour seals in relation to each Seal Management Unit (SMU), and the accompanying text shows the per annum change in moult counts for harbour seals (Duck et al. 2013).

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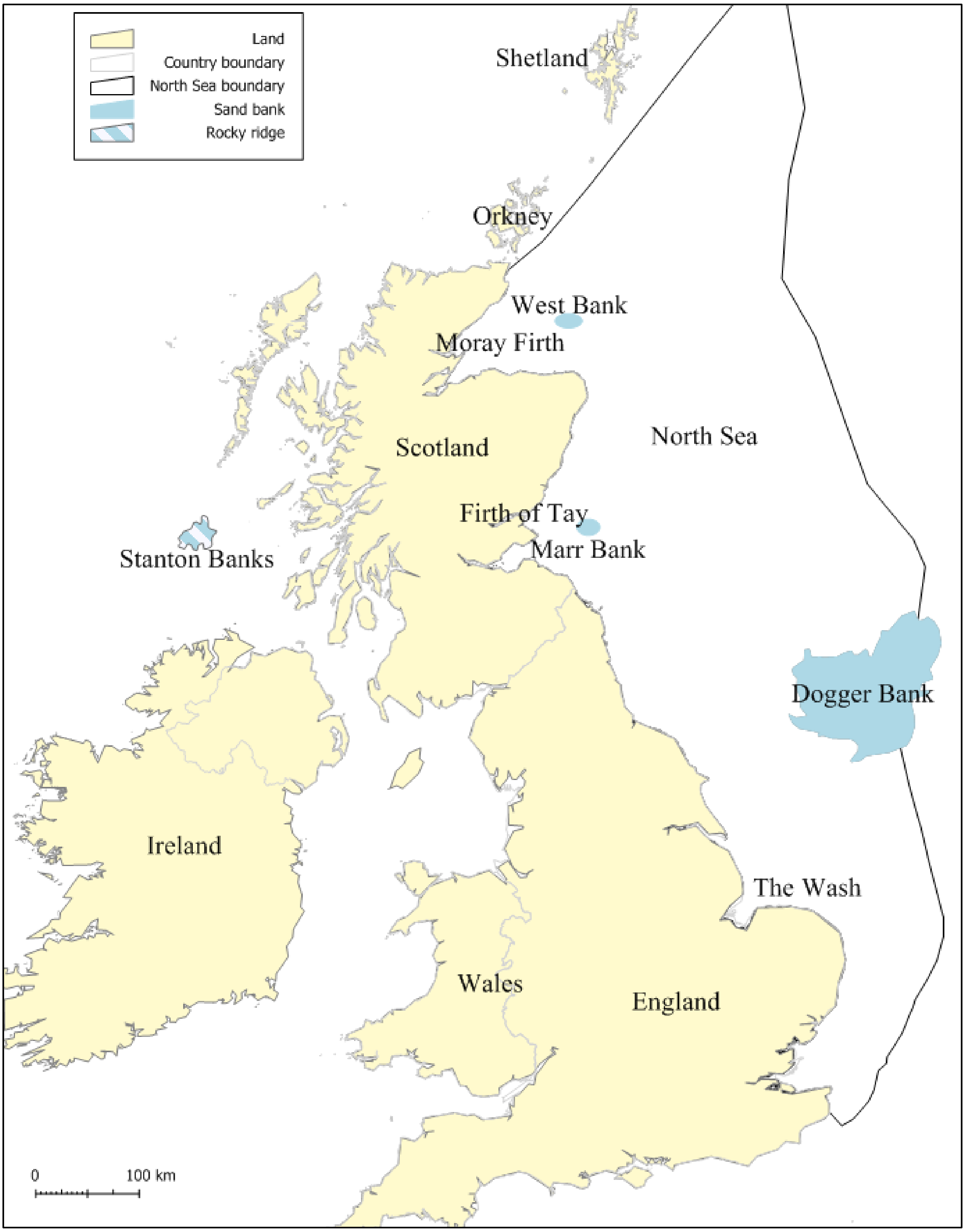

556 Figure 7. Map of the British Isles showing key areas and locations referred to in the text.

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