SPATIAL ECOLOGY OF MARINE TOP PREDATORS

Esther L. Jones

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Spatial ecology of marine top predators
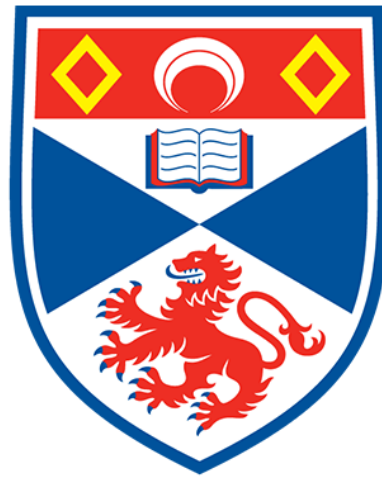
Esther L. Jones

This portfolio is submitted in partial fulfilment

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at the

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School of Mathematics & Statistics

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Declaration

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I, Esther L. Jones, hereby certify that this portfolio, which is approximately 50,000 words in length, is a record of work carried out by myself and co-authors as specified, and that it has not been submitted in any previous application for a higher degree. I carried out all work whilst I was a research student and/or employed by the University of St Andrews between 2014 and 2017. As the major author of the portfolio, I led the conception, execution, and writing of each of the four papers that comprise this submission.

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Acknowledgements

For you both, of course.

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 but contrasting population dynamics around the UK; whilst grey seals have generally increased, harbour seals have shown significant regional declines. A robust analytical methodology was developed to produce maps of grey and harbour seal usage estimates with corresponding uncertainty, and scales of spatial partitioning between the species were found. Throughout their range, both grey and harbour seals spend the majority of their time within 50 km of the coast.

The scalability of the analytical approach was enhanced and environmental information to enable spatial predictions were included. The resultant maps have been applied to inform consent and licensing of marine renewable developments of wind farms and tidal turbines. For harbour seals around Orkney, northern Scotland, distance from haul out, proportion of sand in seabed sediment, and annual mean power were important predictors of space-use.

Utilising seal usage maps, a framework was produced to allow shipping noise, an important marine anthropogenic stressor, to be explicitly incorporated into spatial planning. Potentially sensitive areas were identified through quantifying risk of exposure of shipping traffic to marine species. Individual noise exposure was predicted with associated uncertainty in an area with varying rates of co-occurrence. Across the UK, spatial overlap was highest within 50 km of the coast, close to seal haul outs. Areas identified with high risk of exposure included 11 Special Areas of Conservation (from a possible 25). Risk to harbour seal

populations was highest, affecting half of all SACs associated with the species. For 20 of 28 animals in the acoustic exposure study, 95% CI for M-weighted cumulative Sound Exposure Levels had upper bounds above levels known to induce Temporary Threshold Shift. Predictions of broadband received sound pressure levels were underestimated on average by 0.7 dB re 1μPa ($\pm$ 3.3).

An analytical methodology was derived to allow ecological maps to be quantitatively compared. The Structural Similarity (SSIM) index was enhanced to incorporate uncertainty from underlying spatial models, and a software algorithm was developed to correct for internal edge effects so that loss of spatial information from the map comparison was limited. The application of the approach was demonstrated using a case study of sperm whales (*Physeter macrocephalus*, Linneaus 1758) in the Mediterranean Sea to identify areas where local-scale differences in space-use between groups and singleton whales occurred. SSIM is applicable to a broad range of spatial ecological data, providing a novel tool for map comparison.

Contents

Chapter 1

Introduction

Objectives

This research is motivated by the spatial ecology of marine top predators. Methodologies were linked to provide solutions for some of the quantitative challenges that arise when analysing spatial data. The work primarily focuses on grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals, which are two sympatric species resident around the UK. In addition, existing methodology is enhanced to quantitatively compare maps, which has more general ecological applications. The key ecological objectives for the portfolio are to:

- Characterise grey and harbour seal distributions around the UK.

- Investigate whether grey and harbour seal distributions display spatial partitioning, and at which spatial scales.

- Determine which environmental drivers are important to harbour seal space-use.

- Quantify risk of exposure to shipping noise on seal populations and individuals.

This research fills important gaps in our knowledge around how seals use their marine environment, which has historically been examined in local areas around the UK (Thompson *et al.*, 1996; Aarts *et al.*, 2008). By expanding the study area, and with enhanced methodologies, we gain more general biological insights that are robust to spatial, temporal, and individual variability. Additionally, the portfolio addresses methodological problems by developing analyses to characterise species distributions using an approach coupling density estimation with regression modelling; and quantitatively compare geographically referenced maps, propagating uncertainty and correcting for edge effects. The research presented here is motivated by ecological questions of animal movement and offers bidirectional knowledge transfer between ecology, statistics and geographic information science, enabling ecological questions to be addressed from a novel perspective.

Conservation through spatial planning

There is an increasing drive towards the use of spatial planning as a tool for conservation in the marine environment (Gormley *et al.*, 2012). Marine top predators are often studied as due to various life history characteristics, populations are slow to recover from negative impacts such as overfishing, their loss can dramatically affect ecosystem functioning (Hooker *et al.*, 2011), and the conservation status of many marine mammals is directly protected by legislation. The designation of Marine Protected Areas (MPAs) is used to identify and protect areas that are important to focal species. However, a consequence of the high mobility of marine mammals is that MPAs may only afford partial protection because animals spend only a proportion of their time within them. Therefore, it is crucial to identify how and why these animals use habitats available to them (Wakefield *et al.*, 2014), and the impacts of natural and anthropogenic pressures that may act cause them to change their use of space over time so that appropriate areas can be protected (Thaxter *et al.*, 2012; Gormley *et al.*, 2012). Animal movement is driven by fundamental biological requirements to survive, mature, and reproduce by exploiting the available environment given their physiological constraints. Complex emergent behaviours can evolve from social interactions, avoiding predators and competitors, or responding dynamically to changing prey patches. These complexities are generally summarised into a chosen metric characterising spatial distribution to fulfil spatial planning requirements.

Data integration

Many marine mammals such as cetaceans and sirenians spend their entire lives at sea, surfacing only briefly to breathe. Estimating their abundance and distribution is challenging and methods such as distance sampling (Thomas *et al.*, 2002) and mark-recapture analyses (White, 1982) are often used. Other marine carnivores such as otters, polar bears, pinnipeds, some seabirds, and turtles spend some of their time on land, and through land-based surveys their population size can be estimated (Matthiopoulos & Aarts, 2010). Fitting animals with tracking devices

whilst on land provides a spatially explicit link between local population estimates and at-sea movement of telemetered animals, enabling species distributions to be characterised. Habitat selection models offer a modelling framework for areas where movement data are limited, and for predicting changes to species distribution time and space (Aarts *et al.*, 2012; Johnson *et al.*, 2013; Beyer *et al.*, 2010). Habitat selection models often use pertinent covariates to describe environmental and geographic space available to the focal species such as oceanographic variables (e.g. `http://marine.copernicus.eu/`).

Engineering technology of animal-borne sensors have developed and advanced over the past 25 years, evolving from simple locator devices to animals becoming oceanographic sensors themselves (e.g. SEaOS - `biology.st-andrews.ac.uk/seaos`). However, collecting these data is still a costly and time-consuming process, as large amounts of data are produced and robust analyses are required to integrate multiple data sources. An implicit issue with telemetry data is that an animal observed at a specific location and time is based partly on where the animal chooses to be and partly due to where it had been a short-time previously (spatial and temporal dependencies, termed as autocorrelation; Fieberg *et al.* (2010)). These underlying dependencies can vary due to animal behaviour, so that they may increase when an animal is foraging (e.g. making repeated movements in a small area), and decrease when an animal is travelling (e.g. moving directionally). Ignoring these dependencies can have serious consequences essentially resulting in misidentification of preference when predicting habitat selection, unless dependence is accounted for in space and time in appropriate, realistically complex statistical models. Both onshore and at-sea data are usually incomplete through time and space due to factors such as survey design constraints or technological issues (e.g. satellite uplink failure), and so modelling methodologies must be developed to handle partial data. Therefore, modelling frameworks need to account for regions in space and time where there were no data (unobserved regions). Uncertainty should be propagated through models so that mean estimates can be produced with an accompanying measure of uncertainty. However, this can be challenging when integrating many different sources of data, or where variance cannot be observed.

Analytical frameworks

Synthesising large, complex data of animal movement and population abundance requires a robust analytical framework. The first paper in the portfolio characterises grey and harbour seals around the UK. A requirement for the analysis was to incorporate a broad spatial extent around the UK so that the resultant usage maps could be used for both coastal and offshore spatial planning. Continuous coverage over the spatial extent was required, which included spatial predictions in areas where no animal movement data were collected but where animals were known (from terrestrial counts) to exist. To achieve these goals, density estimation and regression modelling were integrated into an analytical framework. There are a number of habitat-based established methods for mapping species distributions. In recent years, regression modelling (Aarts *et al.*, 2008; Wakefield *et al.*, 2011), and climate envelope modelling (Berry *et al.*, 2002; Cheung *et al.*, 2008) have become popular. However, these methods require covariate data that often limit the geographical extent of the analysis. When the focus is purely on spatial patterns, the batch of methods belonging to the area of density estimation (Silverman, 1986) offer a flexible alternative.

As central-placed foragers, UK seals spend much of their time on land or near the coast, but can also travel several hundred kilometres away from their haul outs. Environmental data such as prey fields and their potential physical proxies, which are often used for regression and climate envelope modelling can have limited geographical extent and variable resolution, limiting the spatial extent of predictions. Telemetry tags track individual seal locations, producing spatial non-uniformity. Therefore, imbalanced sampling effort needed to be accounted for, which is relatively easy to do using density estimation but not with the other proposed methodologies. Finally, fine-scale resolution over a broad-scale spatial extent was required. Climate envelope modelling uses coarse-scale data so fine-scale features may not be revealed. Density estimation was the only way to model fine-scale, broad-scale distributions and uncertainties given computational constraints. However, one limitation of density estimation is that it cannot be used for predictions. Therefore, to address spatial usage for unobserved regions,

regression models were implemented using the covariate shortest at-sea distance from haul out, which was available over the study area and was generated at the spatial resolution of the analysis. Predictions from these models provided general characterisations of animal distributions but cannot reveal fine-scale structure in usage.

Comparison between distributions

The fourth paper in the portfolio presents methodology to quantitatively compare geographically referenced maps, demonstrated using a case study of sperm whales (*Physeter macrocephalus*, Linneaus 1758) in the Mediterranean Sea. Map comparison techniques are useful to quantify similarity between two (or more) maps. In ecology, this problem has been explored in the context of comparisons of land-use where the underlying data is categorical (Hagen-Zanker & Lajoie, 2008). For many ecological data, such as species distributions, these methods are not appropriate because the underlying maps being compared are continuous density surfaces. There are currently several methods for comparing ecological data: (1) cell-by-cell comparisons between maps, which do not account for any spatial dependencies between cells within each underlying map being compared (Leitão *et al.*, 2011), and (2) overlap indices to assess spatial autocorrelation (e.g. Moran's I or Geary's C tests Cliff & Ord (1970)). Locational information is lost and only one form of spatial structure within the data is measured (Reid *et al.*, 2004; Manne *et al.*, 2007). These inadequacies were addressed by implementing a map comparison methodology originally developed in computer science (Wang *et al.*, 2004). Enhancements useful for ecology were developed by incorporating uncertainty of the underlying maps being compared into the map comparison calculation, and correcting for edge effects. By taking account of edge effects, the resultant maps produced from the comparison analysis had the same spatial extent as the underlying maps (i.e. the study area remained the same). This ensured that any important ecological processes taking place close to geographical borders at the edge of the study area were captured by the map comparison.

Portfolio summary

The portfolio is presented in a series of interlinked papers, which have been peer-reviewed to (1) characterise spatial distributions of grey and harbour seals and investigate scales of spatial partitioning between the species; (2) characterise space-use of harbour seals at a fine spatial scale; (3) quantify population risk and individual exposure of seals to ship noise; and (4) present novel methodology to compare maps in an ecological context.

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

Esther L. Jones, Bernie J. McConnell, Sophie Smout, Philip S. Hammond, Callan D. Duck, Christopher D. Morris, David Thompson, Deborah J.F. Russell, Cecile Vincent, Michelle Cronin, Ruth J. Sharples, Jason Matthiopoulos

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 50 km 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

100 km 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.

Fine-scale harbour seal usage for informed marine spatial planning

Esther L. Jones, Carol E. Sparling, Bernie J. McConnell, Christopher D. Morris, Sophie Smout

Abstract: High-resolution distribution maps can help inform conservation measures for protected species; including where any impacts of proposed commercial developments overlap the range of focal species. Around Orkney, northern Scotland, UK, the harbour seal population has decreased by 78% over 20 years. Concern for the declining harbour seal population has led to constraints being placed on tidal energy generation developments. For this study area, telemetry data from 54 animals tagged between 2003 and 2015 were used to produce density estimation maps. Predictive habitat models using GAM-GEEs provided robust predictions in areas where telemetry data were absent, and were combined with density estimation maps, and then scaled to population levels using August terrestrial counts from 2008 to 2015, to produce harbour seal usage maps with confidence intervals around Orkney and the North coast of Scotland. The selected habitat model showed that distance from haul out, proportion of sand in seabed sediment, and annual mean power were important predictors of space-use. Fine-scale usage maps can be used in consenting and licensing of anthropogenic developments to determine local abundance. When quantifying commercial impacts through changes to species distributions, usage maps can be spatially explicitly linked to individual-based models to inform predicted movement and behaviour.

Seals and shipping: quantifying population risk and individual exposure to vessel noise

Esther L. Jones, Gordon D. Hastie, Sophie Smout, Joseph Onoufriou, Nathan D. Merchant, Kate L. Brookes, David Thompson

Abstract: Vessels can have acute and chronic impacts on marine species. As the rate of increase in commercial shipping accelerates, there is a need to quantify and potentially manage the risk of these impacts. Usage maps characterising densities of grey and harbour seals and ships around the UK were used to produce risk maps of seal co-occurrence with shipping traffic. Acoustic exposure to individual harbour seals was modelled in a study area using contemporaneous movement data from 28 animals fitted with UHF GPS telemetry tags and AIS data from all ships during 2014 and 2015. Data from four acoustic recorders were used to validate sound exposure predictions. Across the UK, rates of co-occurrence were highest within 50 km of the coast, close to seal haul outs. Areas identified with high risk of exposure included 11 Special Areas of Conservation (from a possible 25). Risk to harbour seal populations was highest, affecting half of all SACs associated with the species. Predicted cumulative sound exposure level, $\text{cSELs}(M_{\text{pw}})$, over all seals was 176.8 dB re $1\mu\text{Pa}^2$ s (CI 95% 163.3, 190.4), ranging from 170.2 dB re $1\mu\text{Pa}^2$ s (CI 95% 168.4, 171.9) to 189.3 dB re $1\mu\text{Pa}^2$ s (CI 95% 172.6, 206.0) for individuals. This represented an increase of 28.3 dB re $1\mu\text{Pa}^2$ s over measured ambient noise. For 20 of 28 animals in the study, 95% CI for $\text{cSELs}(M_{\text{pw}})$ had upper bounds above levels known to induce Temporary Threshold Shift (TTS). Predictions of broadband received sound pressure levels were underestimated on average by 0.7 dB re $1\mu\text{Pa}$ ($\pm$ 3.3). We present a framework to allow shipping noise, an important marine anthropogenic stressor, to be explicitly incorporated into spatial planning. Potentially sensitive areas are identified through quantifying risk of exposure of shipping interactions to marine species, and individual noise exposure is predicted with associated uncertainty in an area with varying rates of co-occurrence. The detailed approach taken here facilitates spatial planning with regards to underwater noise within areas protected through the Habitats

Directive, and could be used to provide evidence for further designations. This framework may have utility in assessing whether underwater noise levels are at Good Environmental Status under the Marine Strategy Framework Directive.

Novel application of a quantitative spatial comparison tool to species distribution data

Esther L. Jones, Luke Rendell, Enrico Pirotta, Jed A. Long

Abstract: Comparing geographically referenced maps has become an important aspect of spatial ecology (e.g. assessing change in distribution over time). Whilst humans are adept at recognising and extracting structure from maps (i.e. identifying spatial patterns), quantifying these structures can be difficult. Here, we show how the Structural Similarity (SSIM) index, a spatial comparison method adapted from techniques developed in computer science to determine the quality of image compression, can be used to extract additional information from spatial ecological data. We enhance the SSIM index to incorporate uncertainty from the underlying spatial models, and provide a software algorithm to correct for internal edge effects so that loss of spatial information from the map comparison is limited. The SSIM index uses a spatially-local window to calculate statistics based on local mean, variance, and covariance between the maps being compared. A number of statistics can be calculated using the SSIM index, ranging from a single summary statistic to quantify similarities between two maps, to maps of similarities in mean, variance, and covariance that can provide additional insight into underlying biological processes. We demonstrate the applicability of the SSIM approach using a case study of sperm whales in the Mediterranean Sea and identify areas where local-scale differences in space-use between groups and singleton whales occur. We show how novel insights into spatial structure can be extracted, which could not be obtained by visual inspection or cell-by-cell subtraction. As an approach, SSIM is applicable to a broad range of spatial ecological data, providing a novel, implementable tool for map comparison.

Chapter 2

Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning

Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning

Esther L. Jones[1,2,*], Bernie J. McConnell[1], Sophie Smout[1,2], Philip S. Hammond[1,2], Callan D. Duck[1], Christopher D. Morris[1], David Thompson[1], Deborah J. F. Russell[1,2], Cecile Vincent[3], Michelle Cronin[4], Ruth J. Sharples[5], Jason Matthiopoulos[6]

[1]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, UK

[2]Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews KY16 9LZ, UK

[3]CEBC, UMR 7372 CNRS/University of La Rochelle, Institut du Littoral et de l'Environnement (ILE), 2 rue Olympe de Gouges, 17 000 La Rochelle, France

[4]Coastal & Marine Research Centre, University College Cork, Naval Base, Haulbowline, Co. Cork, UK

[5]Institute of Marine and Antarctic Studies, University of Tasmania, IMAS Sandy Bay, Private Bag 129, Hobart, TAS 7001, Australia

[6]University of Glasgow, Institute of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, Glasgow G12 8QQ, UK

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 2 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 50 km 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 100 km 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.

KEY WORDS: *Halichoerus grypus* · *Phoca vitulina* · Density estimation · Propagating uncertainty · Species distribution · Telemetry · Area-based conservation

INTRODUCTION

Anthropogenic activities directly (e.g. fisheries, energy extraction, shipping traffic; Merchant et al. 2014) and indirectly (e.g. prey depletion due to fisheries, climate change; Guénette et al. 2006) impact on the marine environment to an increasing spatial extent and intensity. 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 dis-

tributions, 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 is the identification of 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 (MPAs) for them are to be effective.

There are a number of habitat-based methods for mapping species distributions (Matthiopoulos & Aarts 2010). However, these methods are based on model predictions and 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). Density estimation is data-driven and does not rely on model predictions, making it particularly suitable for estimating species distributions where movement and population data are available and can be linked explicitly. Combining density-estimation methods with simple habitat models using (distance-based) covariates that are universally available to predict in 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, 2 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 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 2 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 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, which comprises the majority of our study area. 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) and 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 2 species compete for food.

Here, we synthesise >2 decades of population and movement data around the continental shelf of Britain, Ireland and France for 2 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
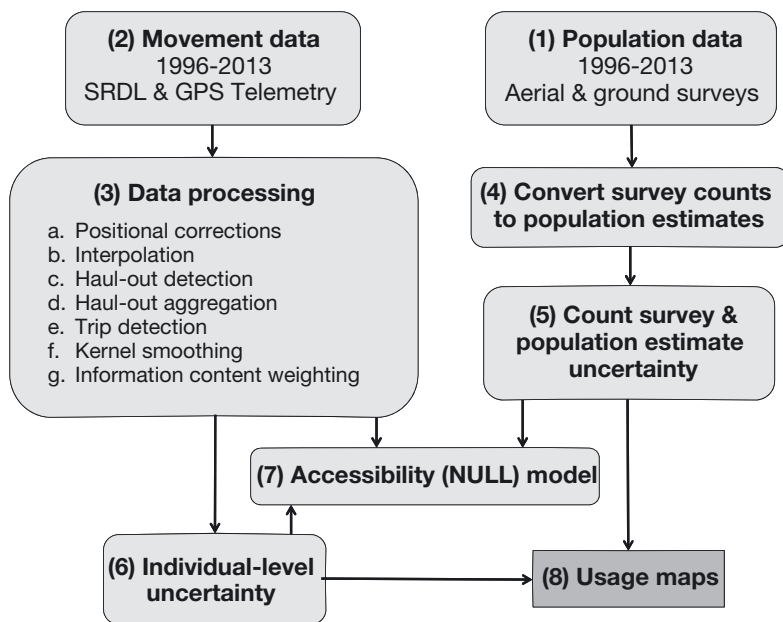
Fig. 1. Flowchart representing high-level analytical methodology

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

Fig. 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 2013).
(1) Population data. Grey and harbour seals are surveyed by the Sea Mammal Research Unit (SMRU) 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 50 m. Surveys take place within 2 h of low tide when low tide is between 12:00 and 18:00 h (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. Fig. 2 shows the locations of terrestrial counts.
(2) Movement data. Telemetry data from grey and harbour seals were obtained from 2 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 Supplement 1 at www.int-res.com/articles/suppl/m534p235_supp.pdf.
(3a) Positional corrections. Positional error, varying from 50 m to >2.5 km, affects SRDL telemetry points. Errors were assigned by the Argos system to 6 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 2 m s^{-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 ≤55 m (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 h intervals using output from the Kalman filter and merged with linearly interpolated GPS data that had been regularised to 2 h intervals. A regular grid of 5 km resolution was created to encompass all telemetry data; 5 km was selected based on the computational trade-off between the resolution and spatial extent of the final maps. Data from 259 grey seal tags (Fig. 3a; see Table S1 in Supplement 1) and 277 harbour seal tags were used (Fig. 3b; see Table S2 in Supplement 1). 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, although telemetry data

Table 1. Summary of grey and harbour seal terrestrial surveys. Unless specified otherwise in the description, all surveys took place during August. SMRU: Sea Mammal Research Unit

Area surveyed	Method	Description	Data used
Scotland	Aerial survey (helicopter)	Both species surveyed every 1 to 5 yr 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 seal counts extended over 12 mo	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 using SMRU protocol	2003
Northern France	Ground counts with extrapolation (Hassani et al. 2010)	Harbour seals surveyed annually	1996–2008

were collected year-round, data collection occurred primarily 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 min and ending when the tag had been continuously wet for 40 s. 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 1 haul-out event had occurred) were aggregated into 5×5 km^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. First, telemetry haul-outs were linked to terrestrial counts based on matching their grid cells. Second, 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. Third, 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. The movements of individuals 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 2 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 spent at different locations, we kernel smoothed the data. The KS library in R (Chacón & Duong 2010) was used to estimate spa-
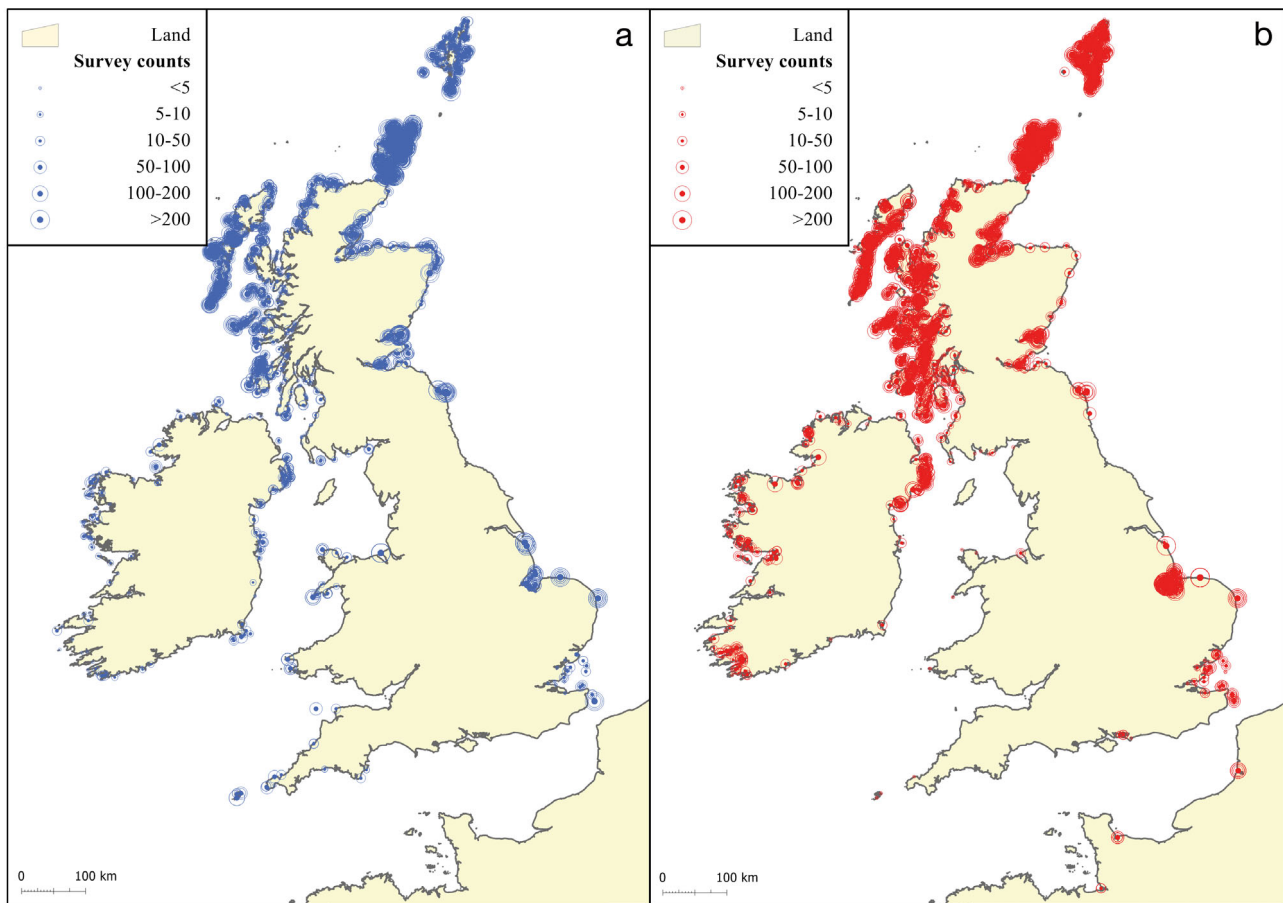
Fig. 2. (a) Grey and (b) harbour seal terrestrial counts between 1996 and 2013 for the British Isles and the European coasts of the English Channel. Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data from NOAA were used in Figs. 2, 3, 4, 6 & 7, available from www.ngdc.noaa.gov/mgg/shorelines/gshhs.html

tial 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 d, harbour seals = 99 d) 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 (Supplement 2 at www.int-res. com/articles/suppl/m534p235_supp.pdf) was derived. This process ensured the importance of animals with short tag-lifespans was reduced and animals with heavily auto-correlated location data were not over-represented. 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 (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 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 were rescaled to allow for the proportion of animals
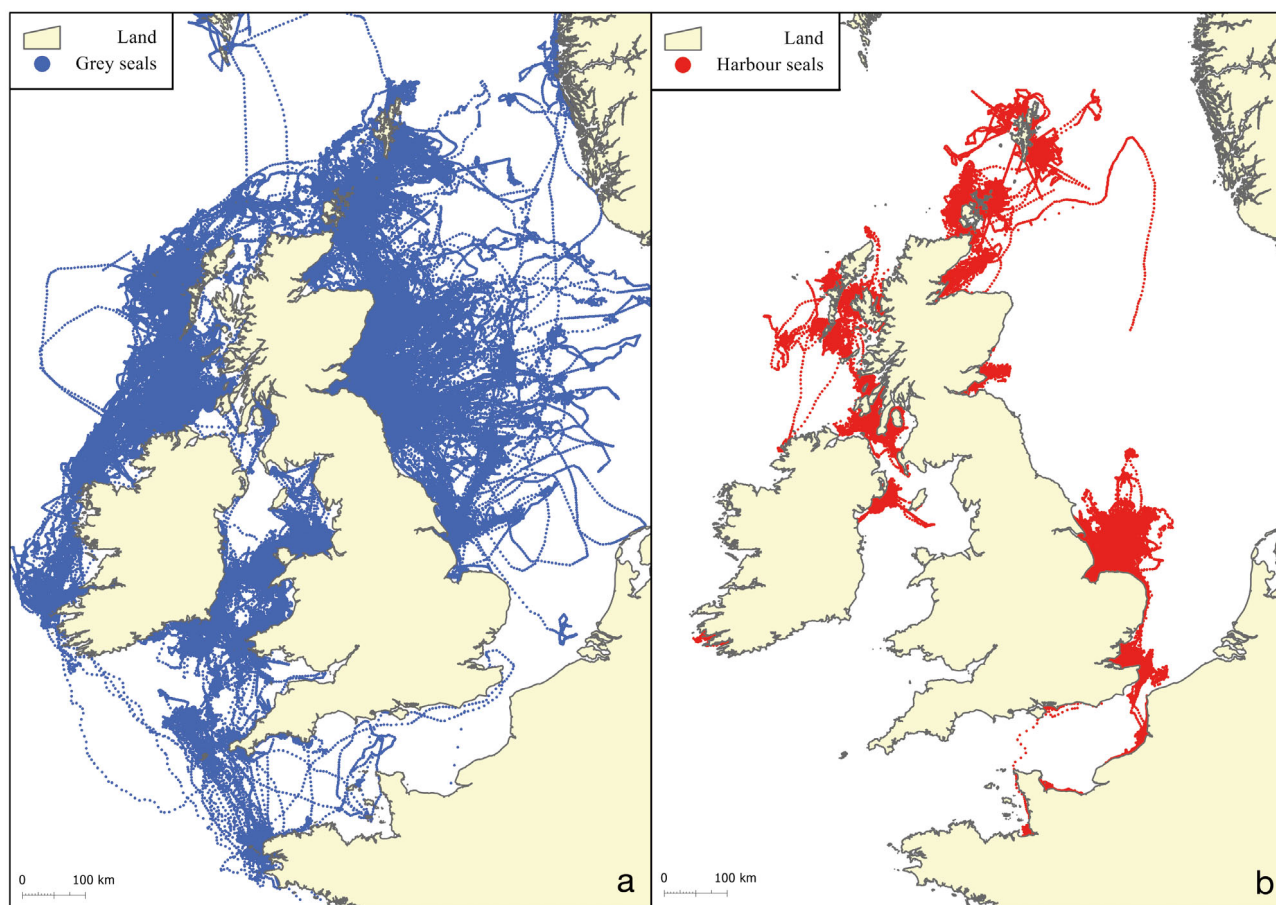
Fig. 3. (a) Grey seal telemetry tracks between 1991 and 2013 showing 259 animals; (b) harbour seal telemetry tracks between 2003 and 2013 showing 277 animals

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 (Supplement 3 at www.int-res.com/articles/suppl/m534p235_supp.pdf) 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. Hereon, population numbers are given based on these estimates.

(5) Population uncertainty. Population-level uncertainty incorporated observational, sampling and scaling errors (Supplement 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 animals associated with them) (Supplement 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 (Supplement 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 (see Supplement 4 at www.int-res.com/articles/suppl/m534p235_supp.pdf). 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 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.

(8) 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 2 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) refers to harbour seals.

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.

RESULTS

Using data from 259 grey seal and 277 harbour seal telemetry tags deployed between 1991 and 2013, we combined terrestrial counts collected between 1996 and 2013. Combined hauled-out and at-sea usage data of grey and harbour seals around Britain, Ireland and France are scaled to contemporary population levels (2013) and are shown in Fig. 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 (Fig. 4a). In some areas, these offshore areas coincide with rocky ridges, such as Stanton Banks south of Barra, west Scotland, and with sandbanks, such as West Bank in the Moray Firth and Dogger Bank in the southern North Sea (see Fig. 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.

In contrast, Fig. 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 150 km offshore (see Fig. 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 >50 km from the coast (Fig. 5). In contrast, grey seals spent 12% of their time at distances >50 km 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 do exhibit considerable movement parallel to the coast, resulting in concentrated patches of high coastal usage.

Fig. 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 to 185 400), and the estimate of harbour seals is 44 000 (95% CI = 20 800 to 68 000), which are similar
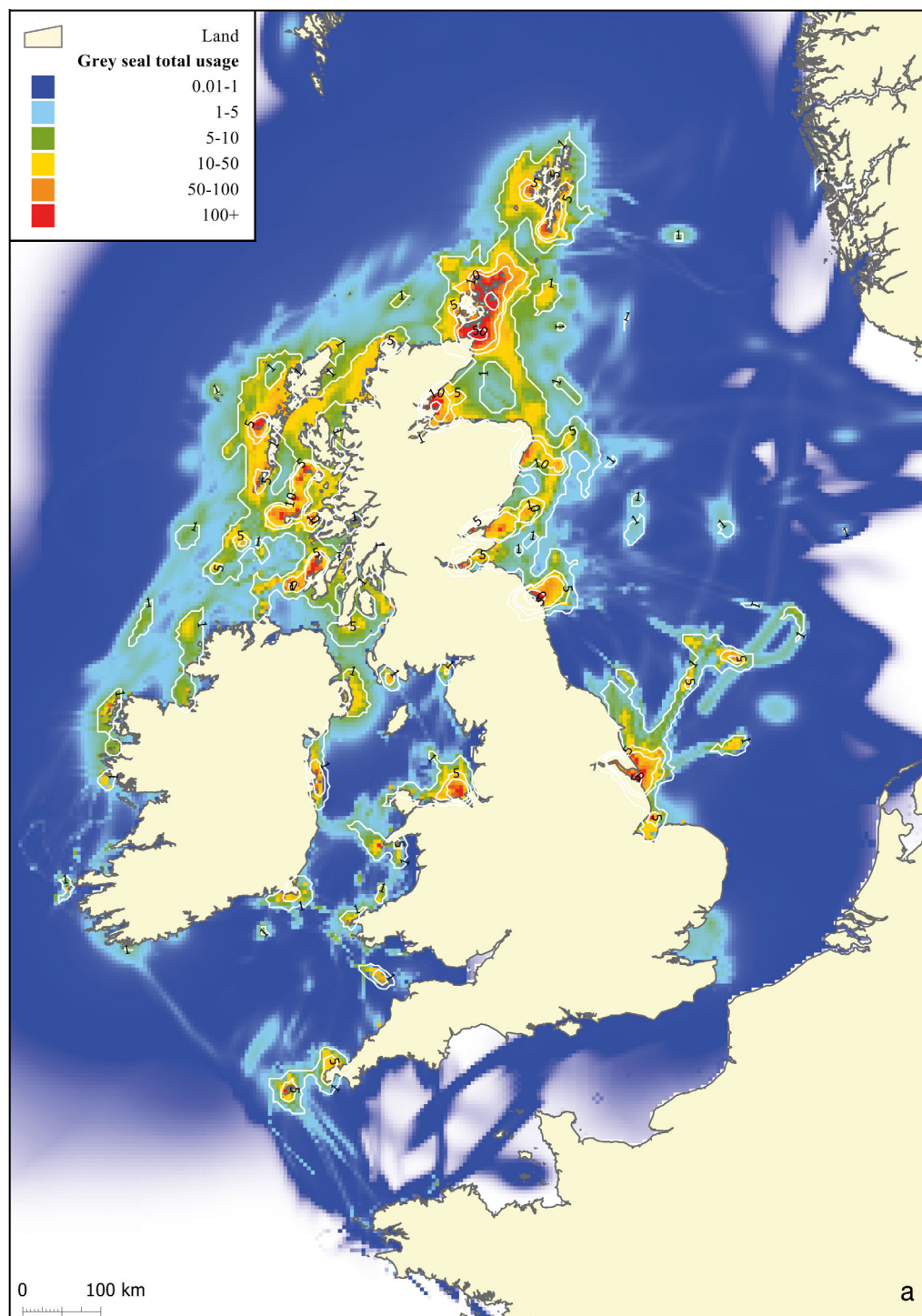
Fig. 4. The predicted number of (a) grey seals and (b) harbour seals in each 5 × 5 km² grid square, e.g. a yellow square denotes between 10 and 50 seals are within that grid square. White contour lines denote standard deviation from the mean as a measure of uncertainty around the estimated usage. Labels show the standard deviation value at each contour

to the published UK population estimates for 2012 for grey (Ó 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.
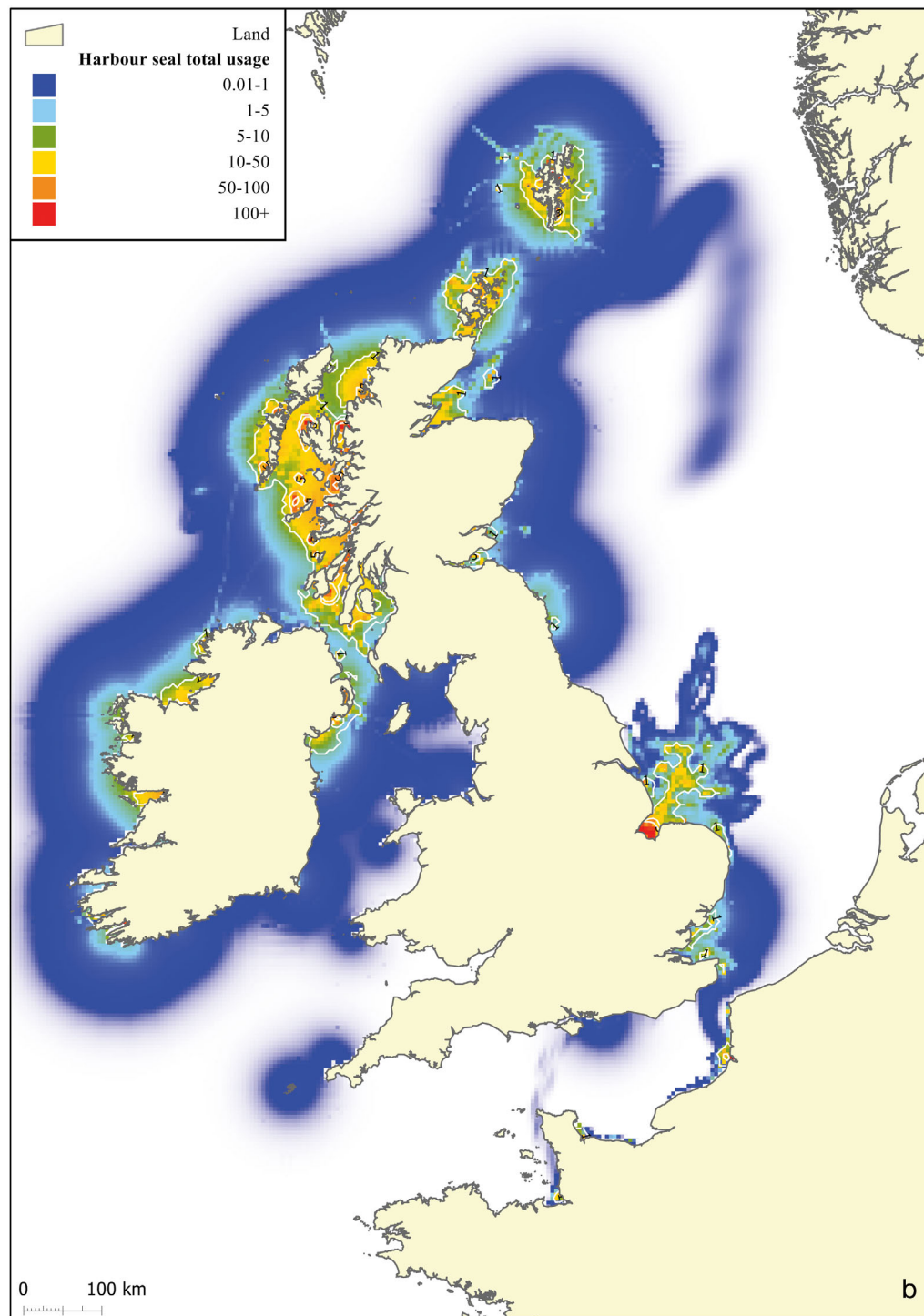
Fig. 4. Continued

DISCUSSION

We describe for the first time the species distributions of 2 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 2 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
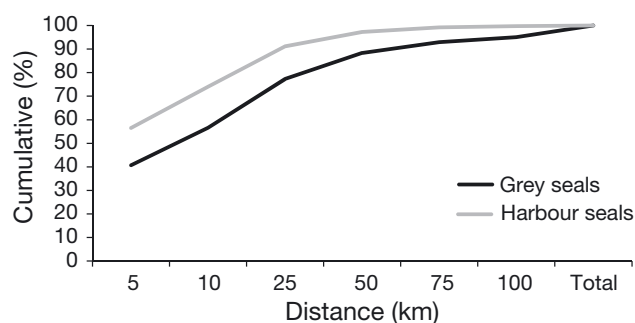
Fig. 5. Cumulative spatial usage of grey and harbour seals as a function of distance from the coast

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 2 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 southeastern 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 Fig. 7), where the population of harbour seals has declined to <200 animals (Duck et al. 2013), both species utilise the same offshore areas. West of Scotland and around Ireland, harbour seal populations are stable, and the seals use coastal areas (such as sea lochs and harbours) that grey seals do not, suggest-

ing 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, 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 USA, 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 yr 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 areas of recent population change, 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' (Supplement 2) accounted for
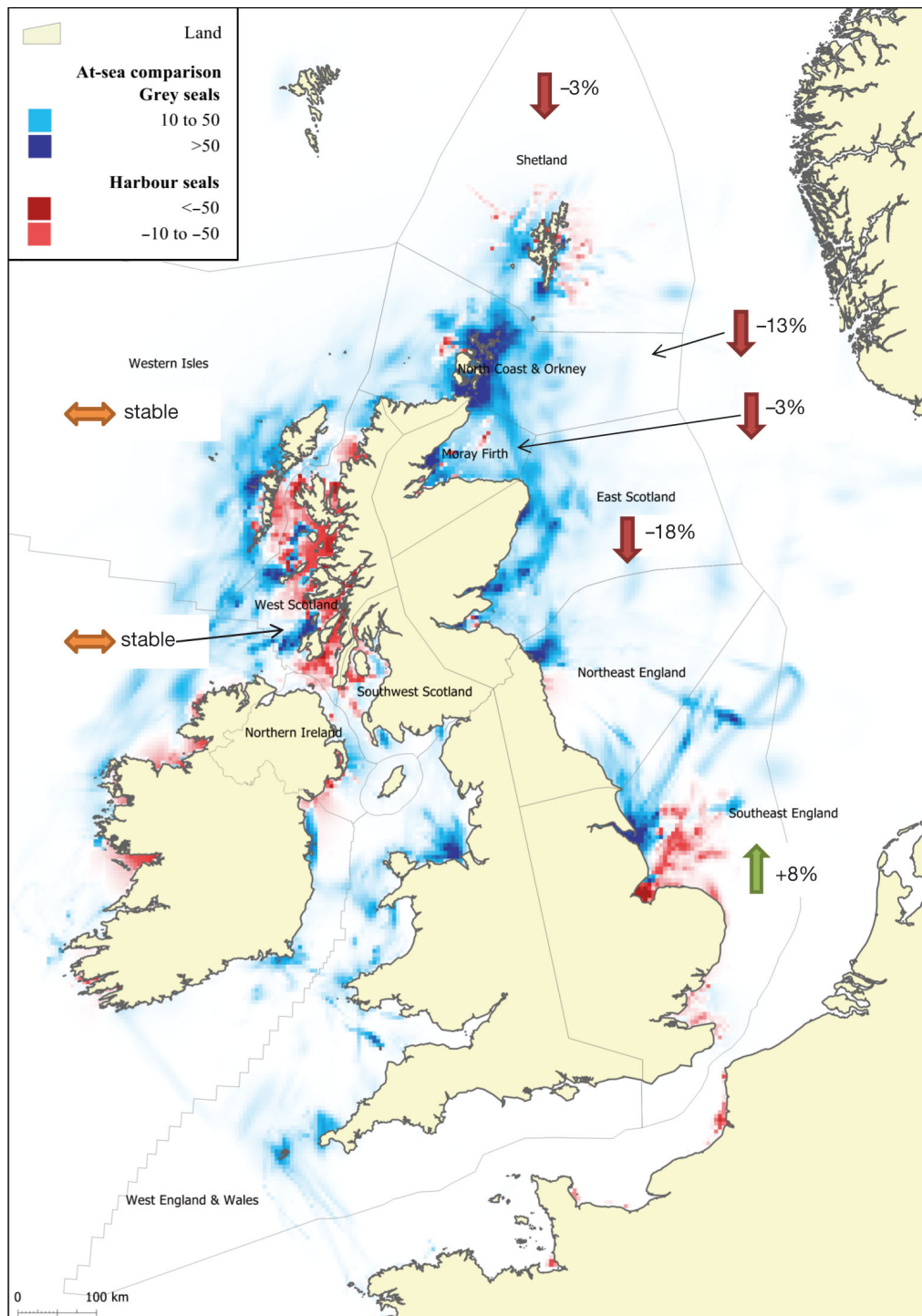
Fig. 6. Spatial at-sea comparisons between grey and harbour seals at 5 × 5 km² resolution showing absolute difference in population numbers. Red denotes greater harbour seal usage; blue denotes greater grey seal usage. Traffic light indicator arrows show the population trajectories (2000–2010) of harbour 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)

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 of both species from August. There were seasonal gaps in

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

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 the 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 on 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 such impacts. Grey and harbour seals are both listed in Annex II of the European Habitats Directive, which has led to the designation by the gove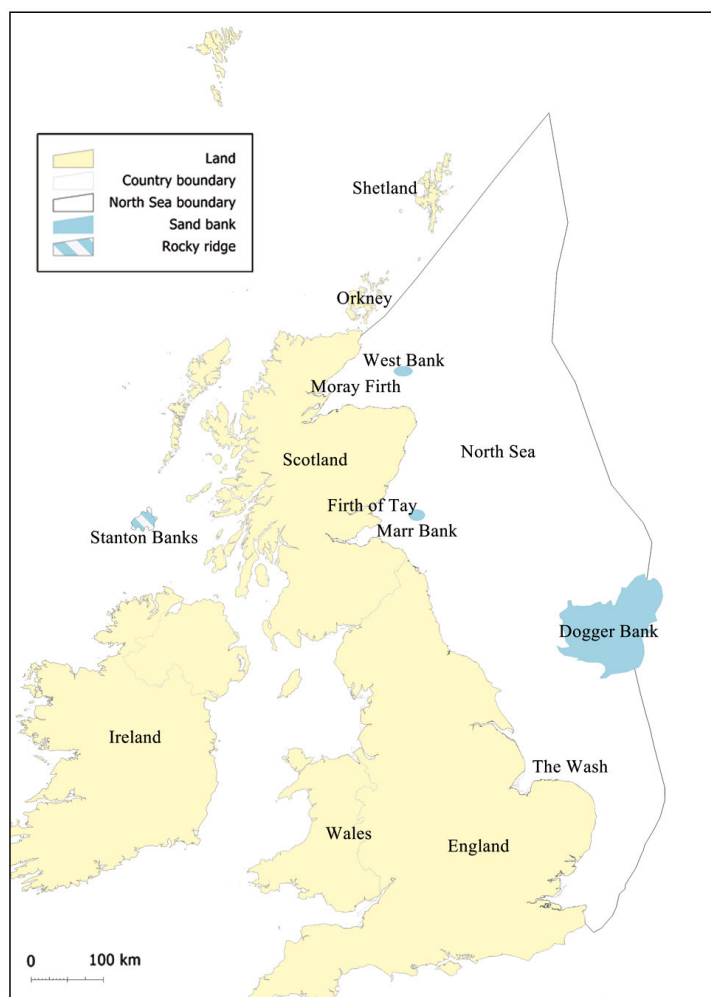rnments of the UK and the Republic of Ireland of a number of terrestrial MPAs, where grey or harbour seals are a qualifying feature (JNCC 2012, NPWS unpubl. data). No offshore MPAs have been proposed yet for these species, primarily because of the lack of robust science to inform this process. Here, 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 50 km 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 farther 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

the telemetry data for each species at different times of the year. However, our examination of spatial partitioning between the 2 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 d (Bowen et al. 1992), so this temporary behaviour is also unlikely to impact

data collection in areas of interest to conservation and management. Additionally, the results 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 yr, allowing many species to be tagged and producing large amounts of movement data (e.g. movebank.org). Density estimation is driven by movement data and does not rely on predictions of spatial usage, making it an ideal method where appropriate data are available. However, predictive modelling using underlying covariate data is suitable for areas where movement data are not available. The species density estimation combined with a simple habitat model framework presented here is applicable to a range of applications and datasets. The combined methodology presented here will be pertinent to species for which 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 therefore 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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The following supplements accompany the article

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

Esther L. Jones*, Bernie J. McConnell, Sophie Smout, Philip S. Hammond, Callan D. Duck, Christopher D. Morris, David Thompson, Deborah J.F. Russell, Cecile Vincent, Michelle Cronin, Ruth J. Sharples, Jason Matthiopoulos

*Corresponding author: el298@st-andrews.ac.uk

Supplement 1 - Seal deployments by year

Table S1. Summary of grey seal telemetry deployments by year. Tag type denotes satellite relay data logger (SRDL) or global postitioning satellite (GPS).

Year	Tag type	No. tags	Sex ratio (M:F)	Age (adult: pup)	Mean tag lifespan (days)	Tagging location
1991	SRDL	5	4:1	5:0	106	NE England
1992	SRDL	12	8:4	12:0	107	Moray Firth, NE England
1993	SRDL	3	1:2	0:3	59	NE England
1994	SRDL	4	2:2	0:4	59	NE England
1995	SRDL	21	15:6	15:6	92	Western Isles
1996	SRDL	20	8:12	20:0	59	Western Isles, Orkney & N coast, E Scotland
1998	SRDL	14	10:4	14:0	119	Orkney & N coast, Shetland
1999	SRDL	6	4:2	0:11	75	France
2001	SRDL	11	7:4	10:10	140	E Scotland
2002	SRDL	20	11:9	24:0	110	E Scotland, France
2003	SRDL	24	14:10	31:0	120	W Scotland, France
2004	SRDL	31	14:17	11:0	146	W Scotland, E Scotland, W England & Wales
2005	SRDL	11	5:6	2:0	155	E Scotland, SE England
2006	SRDL	2	1:1	19:0	66	E Scotland
2008	SRDL/GPS	10/9	9:10	7:5	186	E Scotland, NE England
2009	GPS	12	2:10	4:26	180	W England & Wales, Republic of Ireland
2010	GPS	30	13:17	3:0	128	Orkney & N coast, W England & Wales, France
2011	GPS	3	3:0	3:1	109	Republic of Ireland, France
2013	GPS	11	10:1	3:3	164	E Scotland, Republic of Ireland, France
TOTAL		**Mean=259**	**141:118**	**183:69**	**Mean=124**	

Table S2. Summary of harbour seal telemetry deployments by year.

Year	Tag type	No. tags	Sex ratio (M:F)	Age (adult: pup)	Mean tag lifespan (days)	Tagging location
2003	SRDL	26	11:15	26:0	161	W Scotland, Orkney & N coast, Shetland, SE England
2004	SRDL	29	15:14	29:0	116	W Scotland, Orkney & N coast, Shetland, SE England
2005	SRDL	21	12:9	21:0	94	W Scotland, Moray Firth, SE England
2006	SRDL/GPS	25/30	36:19	51:0	90	Western Isles, Moray Firth, SE England, Ireland, France, N Ireland
2007	SRDL/GPS	1/8	5:4	6:0	108	Moray Firth, N Ireland, France
2008	GPS	15	14:1	0	129	France
2009	GPS	10	3:7	10 : 0	84	W Scotland, Moray Firth, W England & Wales
2010	GPS	10	8:2	10:0	92	N Ireland
2011	GPS	31	22:9	31:0	96	W Scotland, Orkney & N coast, E Scotland
2012	GPS	68	40:28	68:0	77	W Scotland, Orkney & N coast, E Scotland, SE England
2013	GPS	3	2:1	3:0	56	E Scotland
TOTAL	**Mean=277**	**101:81**	**255:0**	**Mean=99**		

Supplement 2 - Information content weighting

The amount of data collected for each animal varies through differences in both individual behaviour and the functioning of the telemetry tag. Tag lifespan is a primary factor of the data richness an individual contributes. The rate of telemetry fixes is variable as it is dependent on how often the transmitter and receivers

communicate, which in turn depends on the location of an animal. Parameter settings on each batch of tags can be different; for example they can be adjusted to vary the number of attempted transmissions when an animal is hauled-out. To account for individual variation in the observation effort (telemetry points collected from each animal), information content weightings were devised using data from the entire study area. This approach reduced the importance of data-poor animals, whilst simultaneously not overstating the contribution of animals with heavily auto-correlated observations. For each species, models were built using a response variable of 'discovery rate', defined by the number of new 5 x 5 km^2 grid cells an animal visits during the lifespan of the telemetry tag. This rate was modelled as a function of the tag lifespan, tag type (SRDL or GPS), and (for grey seals) the age of the animal (1+ or pup). The intercept was set to zero and a quasi-poisson distribution with a log-link function was used within a Generalised Additive Model (GAM) framework utilising the R library *mgcv* (Wood 2006, 2011).

Results

Figure S1a shows a boxplot of grey and harbour seals tag type vs. discovery rate for total usage. The mean number of grid cells discovered throughout a tag's lifespan are shown by red triangles (grey: GPS = 312, SRDL = 213; harbour: GPS = 19, SRDL = 72). A Welch two-sided t-test demonstrated a statistical difference between species/tag type means at 80% confidence level. This was driven by a significantly higher tag lifespan, shown by green triangles in Figure S1b (grey: GPS = 3862 hours, SRDL = 2850 hours; harbour: GPS = 2175 hours, SRDL = 2929 hours). Model selection was based on Generalised (Approximate) Cross Validation (GCV; Craven & Wahba 1979). Similar models were selected for both grey and harbour seals, and tag lifespan was smoothed. Tag lifespan, tag type (SRDL or GPS), and age of animal (1+ or pup) were significant (p-value < 0.001) and explained 31.7% and 16.1% of variation in the data for grey and harbour seals respectively. Fitted values were normalised and used to weight the contribution of different animals to estimate usage associated with each haul-out location. Figure

S2 shows observed (points) and predicted (lines) values for the four subsets of animals (SRDL adults, SRDL pups, GPS adults, GPS pups) for (a) grey and (b) harbour seals.

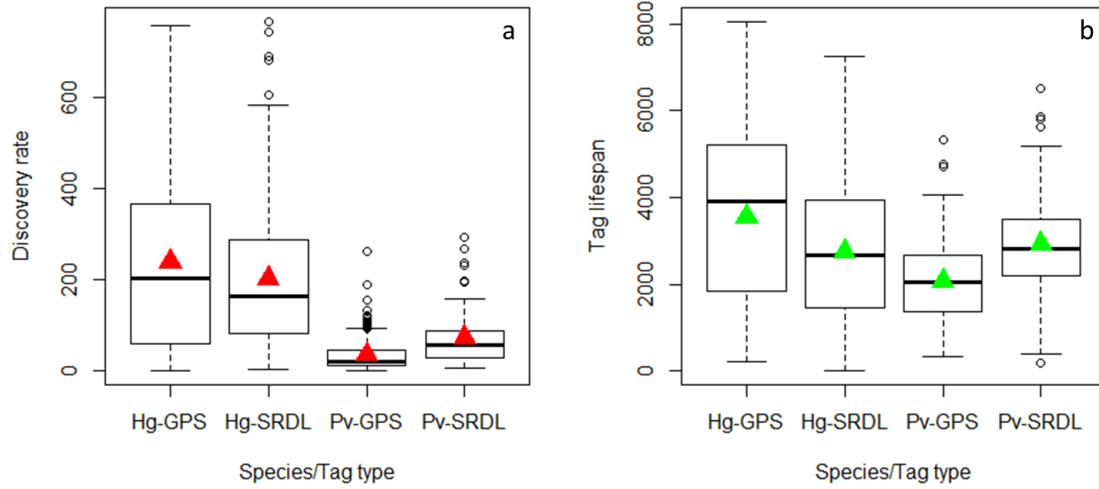Figure S1. (a) Discovery rate (number of new grid cells 'discovered' by each animal during the tag lifetime by species (Hg=*Halichoerus grypus*, Pv=*Phoca vitulina*) and tag type; (b) Total number of tag hours of by species and tag type.
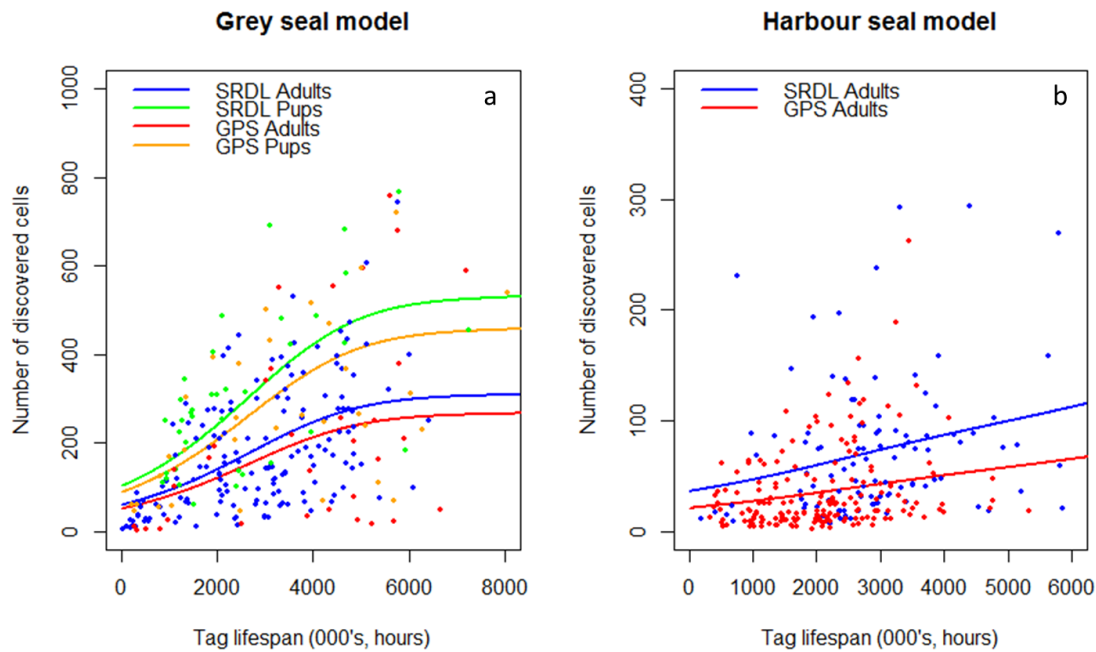
Figure S2. Plots showing tag lifespan vs. the number of discovered cells. Lines represent model predictions and points show observed data for (a) grey seals and (b) harbour seals.

Supplement 3 - Quantifying uncertainty and scaling terrestrial counts to estimate population

Uncertainty was accounted for at individual animal and population level.

Within haul-out (individual) uncertainty

From the movement data, some haul-outs (89) had many animals associated with them, termed as data-rich sites, but the majority (430 out of 536) of haul-out sites were data-poor and half of these had only one animal associated with them. We needed a way to estimate variance at haul-outs where there were small numbers of animals that could not be bootstrapped, and also at haul-outs where terrestrial count data existed but movement data did not (null sites; Supplement 4). To do this, we estimated individual variance in two stages. Firstly, assuming constant variance and coefficient of variation across space we used the data-rich haul-outs to fit models of variance. These were defined as all haul-outs with more than 7 animals associated with them, which were determined experimentally to be the minimum number of animals needed to robustly bootstrap each haul-out. At-sea kernel smoothed densities were bootstrapped 500 times for each data-rich haul-out, resampling with decreasing sample size to produce estimated logged variance and logged mean densities. Secondly, linear models (LMs) were fitted to these data by species with a response variable of logged variance and covariates of sample size (number of animals associated with a haul-out) and logged estimated mean density of seals weighted by information content. As expected, number of animals at a haul-out and logged mean densities explained 99.9% of the variation in the data. The variance increased asymptotically as the mean density increased, and simultaneously decreased as the number of animals at a haul-out increased (Figure S3). This allowed us to predict variance for any number of animals at a haul-out site. To predict uncertainty for the null sites, sample size was set to zero.

Scaling terrestrial counts to estimate population

Scaling terrestrial counts to estimate population size by haul-out with accompanying uncertainty was carried out through a two-stage process: A range of population estimates and associated uncertainty were generated, and were then processed through a decision tree to obtain a contemporary population estimate.

Several types of uncertainty are associated with terrestrial surveys and scaling to population level. Observational errors occur in surveys due varying to weather conditions, aircraft altitude (in aerial surveys), accuracy in recording animal locations, and possible disturbance to animals during surveying. Sampling errors occur because surveys by their nature are instantaneous counts in time. These errors are mitigated as much as possible through survey design and repeat surveying. Errors also occur when scaling to population estimates. We modelled these errors as follows: Parameters for the beta function in the likelihood function were calculated using the mean proportion of time each seal species spent hauled-out along with their corresponding confidence intervals (Matthiopoulos 2011, Lonergan et al. 2011, 2013).

$$\alpha = \frac{\mu}{\sigma^2}(\mu - \mu^2 - \sigma^2)$$
$$\beta = \frac{1 - \mu}{\sigma^2}(\mu - \mu^2 - \sigma^2)$$

Where:

μ = mean seal population hauled-out at any point in time.

σ^2 = variance in seal population hauled-out at any point in time.

A likelihood distribution was then derived as:

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

Where:

N_i = Seal population of ith haul-out.

m_{ij} = Number observed on i[th] haul-out on j[th] survey.

For each haul-out the estimated population size was allowed to vary from the value of each terrestrial count (minimum population size) to 100 times the count (maximum population size). Parametric bootstrapping using the derived likelihood distribution was repeated 500 times per count to produce a range of population estimates.

Surveying the entire coastline of the UK each year is infeasible, and therefore estimating the current populations of both species was challenging; many haul-out sites had limited count data and/or the data was not contemporary. Both species' populations have varied over the temporal scale of the analysis and there are also local fluctuations in population levels. To obtain a single population estimate for each haul-out from the bootstrapped estimates, a decision tree approach was taken to provide robust population estimates with uncertainty that reflected contemporary population dynamics as much as possible (Figure S4).

Population means and variances, and means and variances for each haul-out were combined using formulas for the product of independent variables, where X represents population estimates and Y represents individual estimates.

$$mean = E\left(X\right)E\left(Y\right)$$

$$variance = E\left(Y\right)E\left(Y\right)\mathrm{Var}\left(X\right) + E\left(X\right)E\left(X\right)\mathrm{Var}\left(Y\right) + Var\left(X\right)\mathrm{Var}\left(Y\right)$$

Visualising spatial sampling effort

To quantify spatial sampling effort the coefficient of variation was calculated by grid cell (x) as the ratio of uncertainty (expressed by the standard deviation (σ)) to the estimated proportional usage (μ). The coefficient of variation was higher in areas of the usage maps where telemetry tagging effort was low relative to the local population size or where null maps contributed to the majority of the estimated usage. This provides information on telemetry data gaps and where future tagging effort can be concentrated (Figure S5).
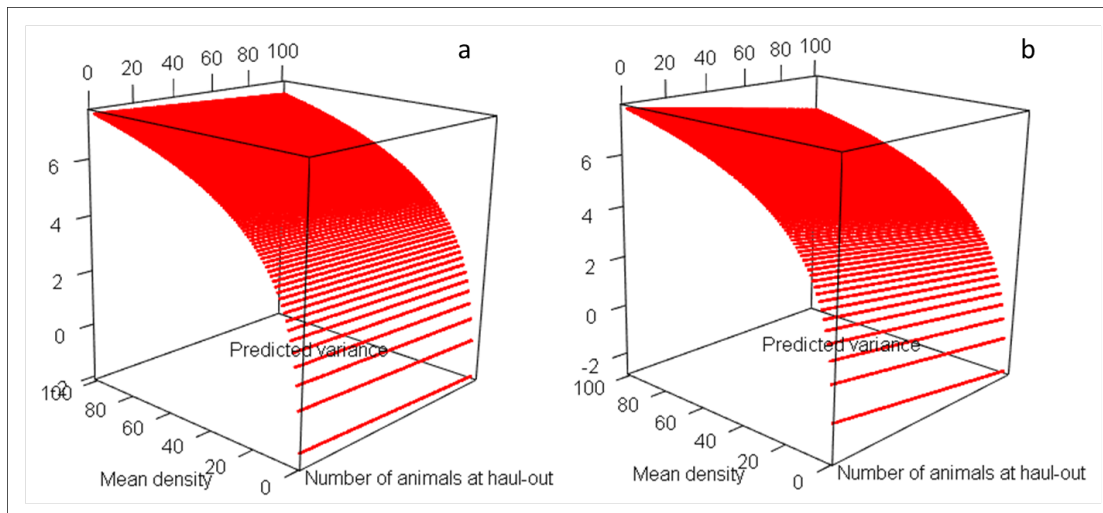
Figure S3. Grey (left) and harbour (right) plots to show the predicted variance of the chosen models when mean density and the number of animals at a haul-out are varied from 1 to 100 respectively.
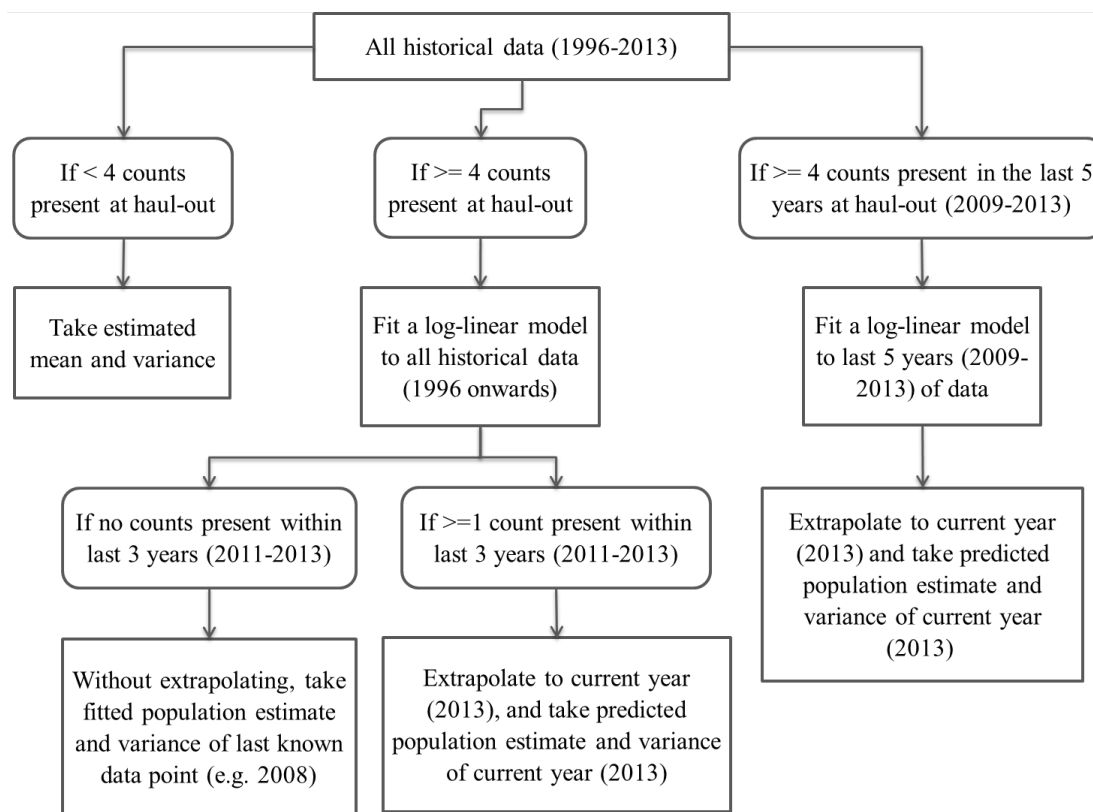
Figure S4. Flow chart showing population estimates by haul-out depending on the terrestrial count data available.
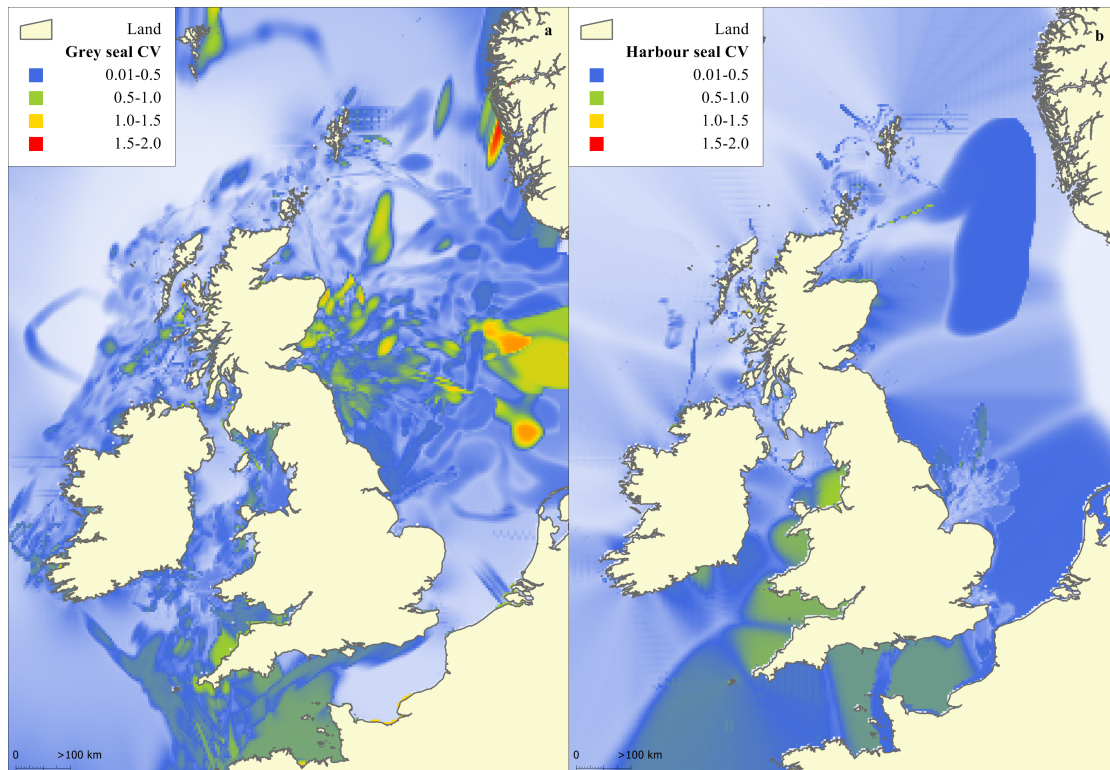
Figure S5. (a) Grey and (b) harbour seal coefficients of variation, showing areas where uncertainty deviates from the expected uncertainty.

Supplement 4 - Accessibility modelling

Sampling effort in the telemetry data was unbalanced because tag deployments tend to focus on larger seal colonies or specific study areas. Therefore, to account for areas in the maps where survey count data were present but telemetry data were not, models were derived to estimate likely usage in those areas using a sub-sample of telemetry data. The number of telemetry locations in each 5 x 5 km^2 grid were modelled using Generalised Linear Models (GLM; McCullagh & Nelder 1989) as a function of distance to the shore to represent accessibility to the coast (in 5 km bins) and accessibility to a given haul-out, termed as geodesic distance, which is the distance to any given grid square from a haul-out taking land into account. Previous studies of UK grey and harbour seals have shown that habitat preference is primarily driven by geodesic distance (Aarts et al. 2008, Bailey et al.

2014). Geodesic distance and distance-to-shore were continuous, but additional environmental covariates could not be considered because they would reduce the spatial extent of the analysis. A sub-sample of 50 adult tracks from each species were selected without replacement and the number of available grid squares at each combination of distance to shore and geodesic distance was used as an offset in the log link quasi-Poisson distribution models.

Telemetry and accessibility maps

Continuous coverage of usage around the UK was achieved by combining telemetry and accessibility maps. 927 and 1018 haul-outs were used for grey and harbour seals respectively: 466 (50%) and 398 (39%) haul-outs had telemetry data associated with them. Figure S6 and Figure S7 show (a) telemetry, (b) accessibility, and (c) combined usage maps. Population scaling and uncertainty were estimated for telemetry and accessibility usage separately and so the total usage maps were a result of directly combining the telemetry and accessibility maps. Grey and harbour seal accessibility usage maps (Figure S6b and Figure S7b) contribute to the aggregate maps in similar areas. Harbour seals have more disaggregated haul-outs than grey seals, and distribute themselves diffusely along the coast. Therefore, tagging effort was concentrated over a relatively small area, when compared to the species distribution on land. This, combined with harbour seals prevalence in west Scotland and Ireland, which have long complex coastlines meant the accessibility map contributed 48% of the total usage for harbour seals, compared to 16% for grey seals.
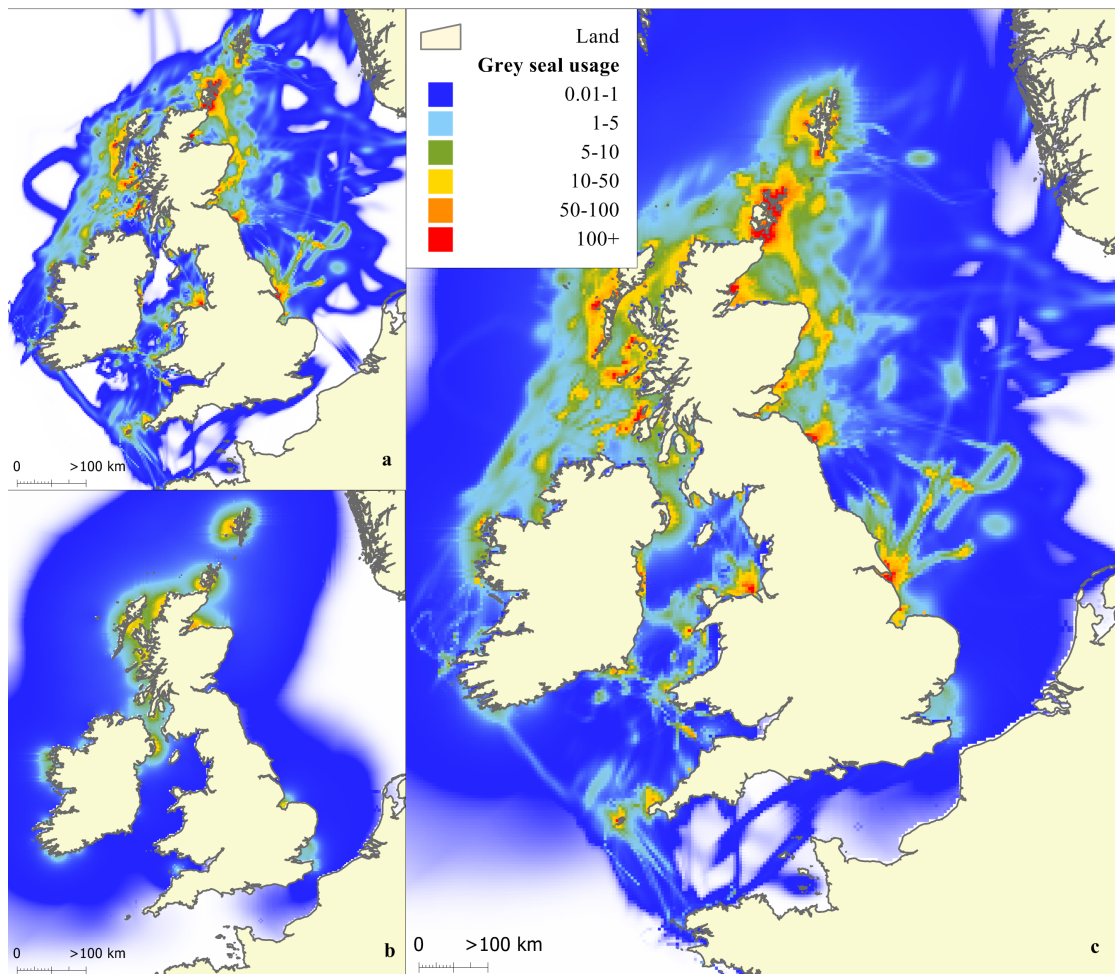
Figure S6. Grey seal (a) telemetry map; (b) accessibility map; (c) telemetry and accessibility maps combined to produce final usage map.
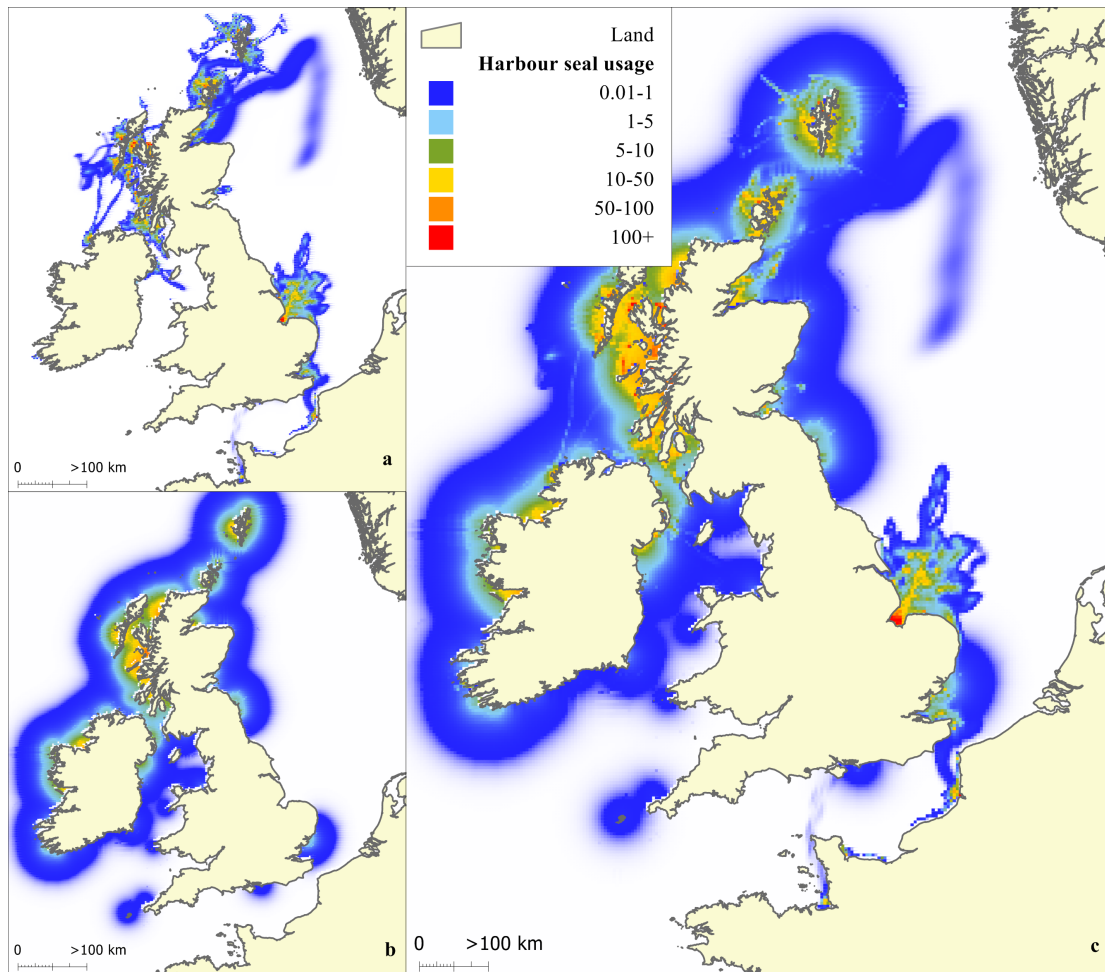
Figure S7. Harbour seal (a) telemetry map; (b) accessibility map; (c) telemetry and accessibility maps combined to produce final usage map.

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Chapter 3

Fine-scale harbour seal usage for informed marine spatial planning

Fine-scale harbour seal usage for informed marine spatial planning

Esther L. Jones*[1,2], Carol E. Sparling[3], Bernie J. McConnell[2], Christopher D. Morris[2], Sophie Smout[2,1]

1. *Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews, KY16 9LZ, UK*

2. *Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, KY16 8LB, UK*

3. *Sea Mammal Research Unit Consulting, New Technology Centre, North Haugh, St Andrews, Fife, KY16 9SR, UK*

Corresponding author: Esther Jones, Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews, KY16 9LZ, `el298@st-andrews.ac.uk`, 01334 461829

Abstract

High-resolution distribution maps can help inform conservation measures for protected species; including where any impacts of proposed commercial developments overlap the range of focal species. Around Orkney, northern Scotland, UK, the harbour seal population has decreased by 78% over 20 years. Concern for the declining harbour seal population has led to constraints being placed on tidal energy generation developments. For this study area, telemetry data from 54 animals tagged between 2003 and 2015 were used to produce density estimation maps. Predictive habitat models using GAM-GEEs provided robust predictions in areas where telemetry data were absent, and were combined with density estimation maps, and then scaled to population levels using August terrestrial counts from 2008 to 2015, to produce harbour seal usage maps with

confidence intervals around Orkney and the North coast of Scotland. The selected habitat model showed that distance from haul out, proportion of sand in seabed sediment, and annual mean power were important predictors of space-use. Fine-scale usage maps can be used in consenting and licensing of anthropogenic developments to determine local abundance. When quantifying commercial impacts through changes to species distributions, usage maps can be spatially explicitly linked to individual-based models to inform predicted movement and behaviour.

Introduction

Within the context of increasing anthropogenic activities in coastal environments, understanding movement and distributions of top predators is critical to deliver effective marine spatial planning and ensure adequate management and protection[1-4]. However, marine animals are challenging to study as they spend all or most of their lives at sea, and much of this time underwater. Robust estimates of space use at appropriate spatial and temporal scales are required and should include estimates of uncertainty to ensure that risks to the population can be identified and managed objectively.

In early-stage marine spatial planning, constraint mapping is carried out to reduce conflicts and ensure sustainable use of marine resources. For example, areas are identified for potential commercial development, such as defining lease areas for proposed offshore marine renewable projects, whilst ensuring the conservation of protected species and habitats (e.g. marine protected areas; `www.gov.uk/government/publications/east-inshore-and-east-offshore-marine-plans`). During consenting and licensing stages, a common approach is to overlay spatial layers within a Geographical Information System (GIS) framework, such as anthropogenic activities and species distributions, so that areas of interest and associated risks can be identified[5]. Anthropogenic activities in the marine environment are often resolved to a fine spatio-temporal scale (e.g. locations of marine energy leasing areas or oil and gas

pipelines), and to improve efficacy in marine spatial planning it is important to also use high resolution and robust maps of species distributions and habitats prioritised for conservation. Estimates of uncertainty in species distributions should be generated to inform decision-making regarding the level of identified risks.

Harbour seals (*Phoca vitulina*) are one of two resident seal species around the UK, spending the majority of their time within 50 km of the coast[6]. Around Orkney, their diet (in 2010/11) was dominated by sandeel (*Ammodytes spp*), cod (*Gadus morhua*), and saithe (*Pollachius virens*) in spring and summer, and pelagic and gadid fish (mainly herring (*Clupea harengus*) and cod) in autumn[7]. They haul out for extended periods to breed in June and July, and moult in August[8]. The Habitats Directive (1992 Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC)), is one of the main policy drivers for nature conservation in European waters including the UK. The Habitats Directive is transposed into Scottish law by the Conservation (Natural Habitats) Regulations 1994 (as amended in Scotland), and under these Regulations Special Areas of Conservation (SACs) have been established for harbour seals. The harbour seal population has been in decline in some areas around the UK since at least 2000. Animals within the Orkney and the North Coast management region have been particularly affected with numbers decreasing by 78% between 1997 and 2013[9]. Concern around the status of the population, coupled with uncertainty surrounding the risk of collisions between tidal turbines and seals, has led to constraints being placed on tidal energy generation developments in this area until more information is available on the potential risks presented to this species by tidal turbines. A key element of models for assessing collision risk is determining the abundance of animals that may use the area close to the turbines.

Orkney and the North coast of Scotland is an interesting study area: it has a convoluted coastline with diverse physical environment and sediment dynamics, including the Pentland Firth, an area with strong tidal currents[10]. The declining local harbour seal population, coupled with the worlds first commercial tidal stream array (www.meygen.com) now in place, makes characterisation of seal usage

at a more appropriate scale for assessing individual project development essential for effective spatial management.

Maps of at-sea usage of harbour seals around Orkney and the North coast of Scotland were produced with associated 95% confidence intervals. Based on established methodology[6], analytical capabilities were enhanced to address scalability, uncertainty, and predictive power. We implemented an analytical solution with high spatial resolution to more appropriately reflect underlying heterogeneity in seal movement, reduced uncertainty by clustering similar haul outs to ensure underlying telemetry data were retained in the analysis, and incorporated environmental covariates pertinent to the species in a more sophisticated modelling framework to predict space use in regions where telemetry data were unavailable.

Results

Year and shortest at-sea distance from haul out were included in the selected habitat model. Shortest at-sea distance was required so that predicted usage for each null cluster was limited according to the distance that an animal could realistically travel from the cluster. Fig. 1 shows the occurrence rate for each covariate (response variable on the scale of the exponential of the linear predictor; y-axes) with accompanying 95% confidence intervals calculated through parametric bootstrapping. As expected, shortest at-sea distance had a strongly negative coefficient, indicating that usage decreased with increasing distance from haul out. Proportion of sand in sediment and annual mean tidal power were retained in the selected model as polynomial terms. High usage of low proportions of sand was associated with wide confidence intervals, as data were limited. Space use then increased with increasing proportion of sand, peaking when sediment was 54% sand. The relationship between usage and annual mean tidal power shows that usage generally decreases with increasing tidal power, although confidence intervals are wide. The relative contribution of each covariate to model selection is shown in Fig. 2. The model with only year and at-sea distance covariates produced

a fold pass score (FPS = 0.84), above threshold (0.80) using 40 equal-size bins. Including sand increased the cross-validation score (FPS = 0.86) and including tidal power raised the score (FPS = 0.89). This FPS could not be improved upon with additional covariates. We speculate that the decrease in score when tidal power was added to the baseline model was due to an unquantified interaction between tidal power and at-sea distance. Interactions could not be included in model selection due to non-convergence of the GAM-GEEs.

Usage based on telemetry observations comprised 82% and the habitat modelling contributed 18% to the at-sea map. Fig. 3a shows at-sea distributions of harbour seals around Orkney and the North coast of Scotland, and can be interpreted as the estimated mean number of seals present in each 0.6 km x 0.6 km cell. The map shows that harbour seals spend the majority of their time within 30 km of the coast around Orkney and the North coast of Scotland, and that much of the centre of the channel of the Pentland Firth (Fig. 4) is not well utilised. Figs. 3b and 3c show lower and upper 95% confidence intervals and can be interpreted as the bounds on the estimated number of seals in each cell. Harbour seal at-sea usage across the whole map is estimated as 2444 (95% CI 946, 4006). Aggregating haul outs at 3.6 km gave rise to 246 telemetry clusters (haul out clusters that had telemetry data associated with them). Seven of these clusters had only one tagged animal and a terrestrial count greater than one, which contributed to approximately to 7% of the total at-sea mean usage calculated from the maps. 45% of total at-sea usage (over half of the telemetry usage contribution to the maps) arose from data-rich clusters with geq 7 tagged animals associated with them (Fig. S3 in Supplementary information). It is important to note that at-sea usage in any given cell is influenced by density estimation from multiple telemetry clusters, and predicted usage from null clusters. Therefore, in cases where few tagged animals were explicitly associated with a haul out cluster did not necessarily mean that only usage from these individuals influenced the total usage of that cluster.
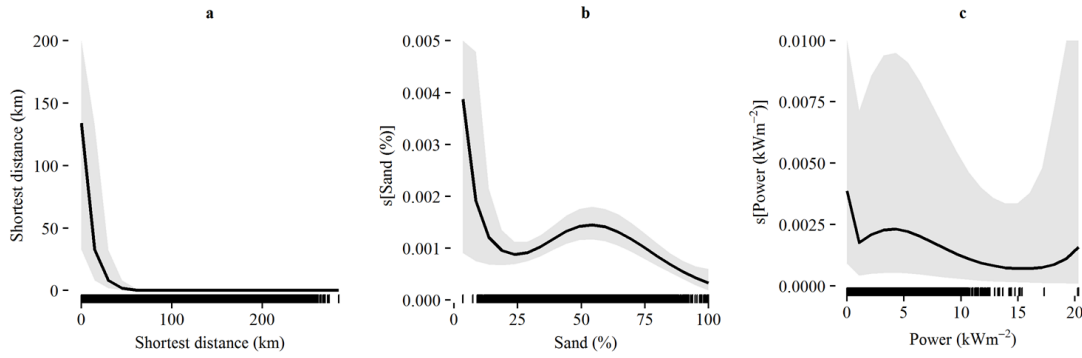
Figure 1. Occurrence rate of animals, predicted by the selected model (i.e. mean population responses) for each covariate (a) Shortest at-sea distance to haul out, (b) Proportion of sand in sediment, (c) Annual mean tidal power. Occurrence rate is calculated on the scale of the exponential of the linear predictor (proportional to usage; y-axes) with shaded areas representing 95% confidence intervals (using parametric bootstrapping). Rug plots showing data values are displayed on the x-axis of each plot.
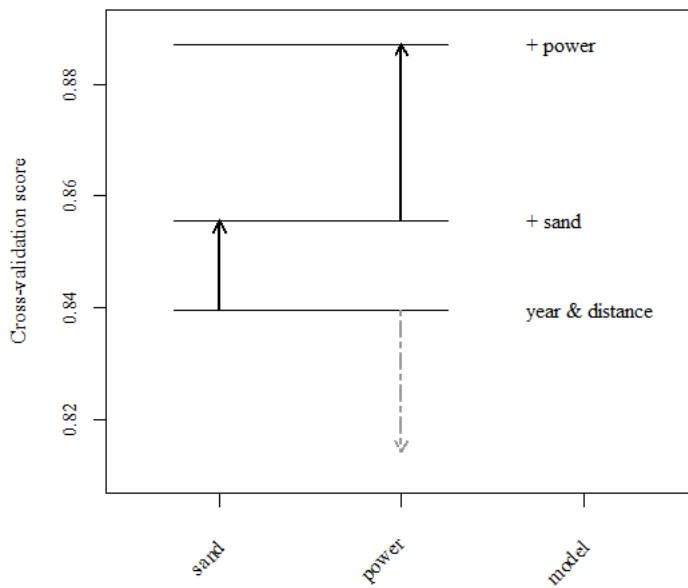
Figure 2. Forwards model selection resulted in increasingly complex models until five-fold cross-validation scores (using 40 equal bins areas) did not improve. The length and direction of the arrows indicate change in cross-validation following the addition of each covariate. Solid arrows indicate the variables that led to the largest improvement in score.
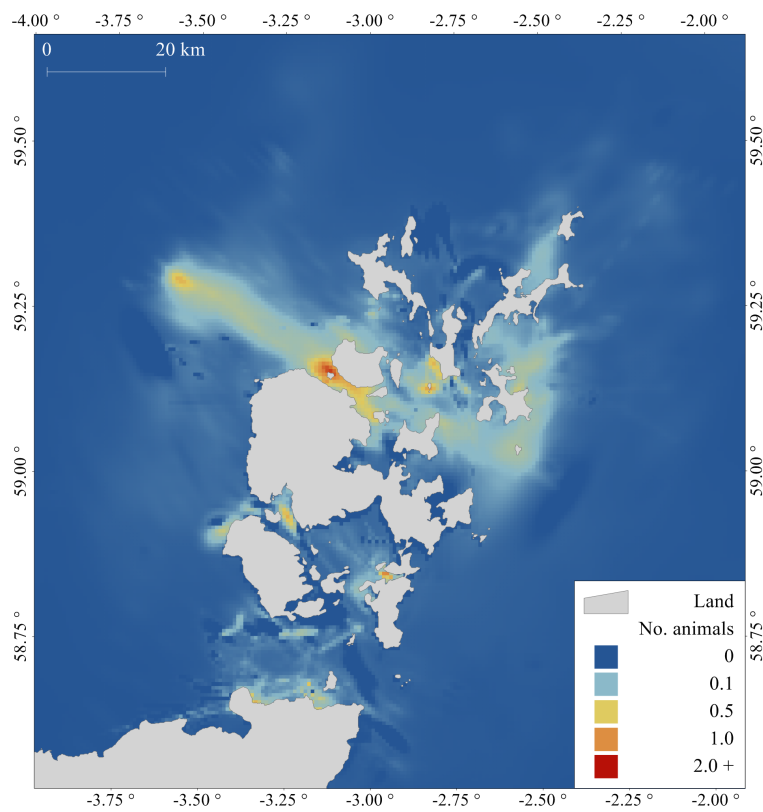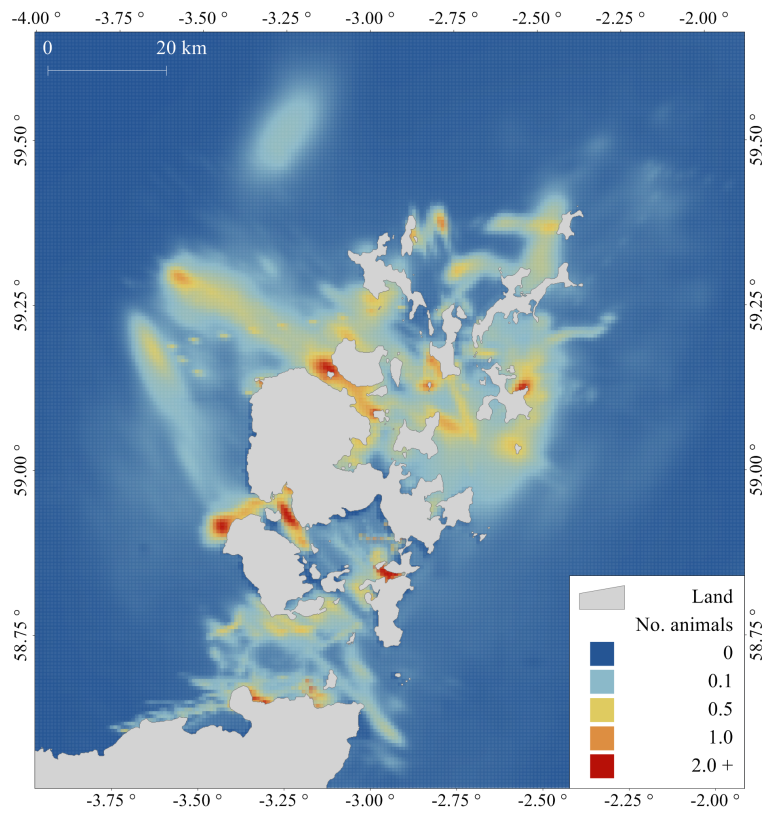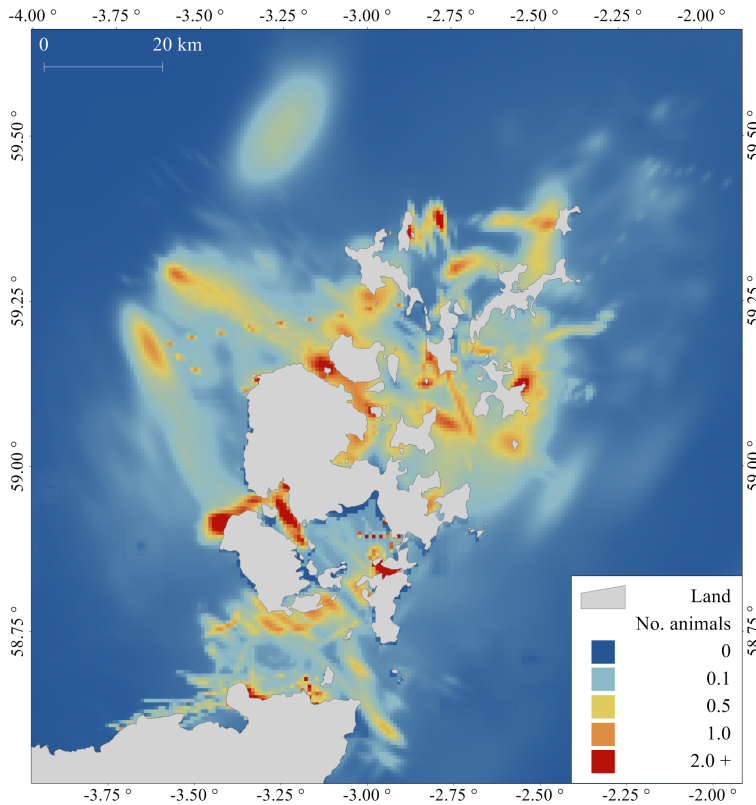
Figure 3. At-sea harbour seal usage (a) mean, (b) lower 95% confidence interval, (c) upper 95% confidence interval. The figure was produced using R 3.3.23[4] and GIS software Manifold 8.0.29.03[5].

Discussion

Maps of harbour seal at-sea usage were produced for the area around Orkney and the North coast of Scotland, with associated 95% confidence intervals. These high spatial resolution maps with levels of uncertainty around the mean distribution of animals can be used to inform spatial management of the marine environment.

Harbour seals are central-place foragers, regularly hauling out on land in between spending time at sea travelling and foraging. Therefore, their at-sea distribution is likely to be strongly linked to their haul out locations. At-sea usage maps show that harbour seals around Orkney concentrated space-use within 30 km of their haul outs, a behaviour consistent with other areas around the UK[6,11-13]. The primary driver of space-use was distance from haul out in the predictive habitat

model; usage declined with increasing distance from haul out. More specifically, animals spent the majority of time within a few kilometres of the coast in shallow water (less than 50 m); an exception was to the north-west of the Orkney mainland where animals spent time further offshore presumably foraging at sand banks[14].

From the habitat model, the second driver of seal usage was the proportion of sand in sediment. Excluding the lower range where data were limited, harbour seal usage increased until 54% sand, whereby usage then declined. Sandeels are non-migratory resident species that live in sand/gravel mix sediment[15,16]. They are a primary component in the diet of harbour seals around Orkney[7], and the relationship found between seal space-use and sand could be driven by this predator-prey interaction.

The Pentland Firth, an area with strong tidal currents, is of commercial interest as a number of leased tidal developments are situated within it. Usage within the Pentland Firth itself was limited although haul outs were situated to the north and south of the channel. The relationship between seal usage and annual mean tidal power showed that harbour seal space use generally declined with increasing power. Relationships found between shortest at-sea distance from haul out and seabed sediment corroborate with other literature that have found these relationships in grey seal habitat preference in the North Sea[17]. Like any predator, seals most likely respond dynamically to their environment with regards to the location of their prey species, and sand in sediment and annual mean tidal power are likely to act as proxies for prey distribution[18,19]. Free-ranging marine animals such as seals must be influenced by currents, either positively by using currents to travel more efficiently and utilise concentrated prey patches, or negatively by swimming against currents when travelling to a haul out, which may vary regionally[19-22]. Relevant environmental covariates were used for habitat modelling but other covariates likely to be good predictors of space use could be included. The composition of harbour seal diet is known to change over time and region[7]. Where available, temporally and spatially aligned prey data may be likely candidates to increase predictive ability[23] (although see [24]).

It is important to understand how species distributions change over time. However,

animal location data are usually not complete across time and space as a result of patchy data collection. The modelling framework was developed to handle partial data, accounting for areas where no data were available (unobserved regions), as well as quantifying the accompanying uncertainty. This methodology could be extended using historical data sets to investigate temporal changes in distribution such as seasonal changes and inter-annual fluctuations, so that long-term changes in abundance and distribution can be captured to inform conservation of the species. Usage maps were scaled to population estimates using terrestrial counts collected during August. During this time, harbour seals moult, spending much of their time hauled out, and the terrestrial counts provide information about the abundance and distribution of seals at this stage in their lifecycle. Intra-annual movement of individuals outside of the study area, or the distribution of animals between haul out sites within the study area were not accounted for. To identify these, and seasonal changes in distribution, additional terrestrial counts outside of moult season would be required, as well as an estimate of proportion of animals hauling out when these additional surveys were carried out[25].

Usage in a given at-sea grid cell was a complex summation (including weightings) of maps from different haul out clusters. For any given grid cell, there are likely to be substantial contributions from several clusters, and those with few seals associated with them are likely to have low weights. A grid cell will be influenced by null maps from clusters where there are no telemetry data. To account for any extreme seal behaviour from one animal at one haul out cluster, each kernel smooth was reweighted by the index of information content (by individual) based on the relative amount of information that animal contributed (hours tagged per animal and tag type). This method ensured that fine-scale features in space use were retained, whilst not emphasizing abnormal behaviour of individuals. Uncertainty in the usage where results from some haul out clusters having few seal trips are influential is represented in the confidence interval maps (i.e. wider confidence intervals in those areas). Usage was displayed over all types of seal activity without distinguishing between habitat that may be important for specific events, such as foraging or breeding, from areas that might be used as commuting corridors between such sites. Anthropogenic activities can have chronic impacts on marine

species such as avoidance of important habitats, or changes to behaviour[26]. One way to assess these impacts is to quantify the population effects on the species; energetic costs to animals vary by activity[27] and therefore explicitly accounting for activity budgets would be required. When marine spatial planning objectives are to identify risks to animals given their space use, then usage including all activity types is required. However, specific events such as foraging can be prioritised for some applications (e.g. population consequences of disturbance; PCOD[28]), and under these circumstances, information in addition to usage maps would be required to fulfil conservation objectives.

Species distribution analyses often require underlying data to be aggregated into a static map[29]. The analysis presented here does not take patterns of residency and site turnover of animals into account. For example, mean usage does not differentiate between occasional use of an area by many individuals, or a small number of individuals utilising an area intensively. The number of individuals exposed to collision risk from marine renewable developments (e.g. tidal turbines) is likely to be different between these two situations. This is true of any static density inputs into collision risk models, and implications of not accounting for individual turnover in an area include predictions of collision risk that can exceed the total local population of animals, affecting the efficacy of the spatial management process[30].

Spatial management can be informed through predicting movement of animals under given conditions, termed individual-based models (IBM)[31]. These models can be used to assess changes in species distributions over time and space, and as predictive tools to assess the impact of anthropogenic activities[32]. For central-place foragers in particular, predicting changes in distribution can be challenging. Central places can transition over time (e.g. seals can move to different haul outs; bats change roosting sites seasonally[33]), but the locations and time of switching to new central places can be difficult to predict. To provide more accurate analyses of changes in species distributions, environmental space can be parameterised within IBMs using underlying maps of habitat preference or space-use[31]. These can provide information about the range of the species, areas of important habitat (e.g.

optimal, sub-optimal, and infeasible) to better inform movement and behaviour. For example, energetic costs of displacement when animals move from optimal to sub-optimal habitat due to anthropogenic activities can be quantified. High-resolution usage maps such as the ones presented here can be integrated within IBMs to produce a powerful analytical framework to predict change in species distributions and assessment the impact of direct and indirect anthropogenic activities on protected species.

Methods

Study area

A study area centred on Orkney was delineated from 58.52°N to 59.66°N and 3.98°W to 1.88°W, to include the majority of telemetry data from the surrounding area (Fig. 4). To ensure that usage in the outer regions of the study area was not underestimated, a larger analytical area was delineated to capture telemetry data from animals that spent time at-sea within the study area. Emphasis was placed on determining a high grid resolution so that detailed space-use could be represented. The underlying telemetry data were regularised to two-hourly intervals and the degree of kernel smoothing (see Movement data) to produce density surfaces was dependent on this regularisation. An appropriate spatial resolution of 0.6 km x 0.6 km was determined through estimation of median distance (median = 0.64 km; variance = 2.7 km) between each location of an individual. Analyses were conducted using R 3.3.2[34] and GIS software Manifold 8.0.29.0[35] and all maps were projected using Universal Transverse Mercator 30° North, World Geodetic System 1984 datum (UTM30N WGS84). Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data version 2.2.2 from NOAA were used to represent land, available from `http://www.soest.hawaii.edu/pwessel/gshhg/`.
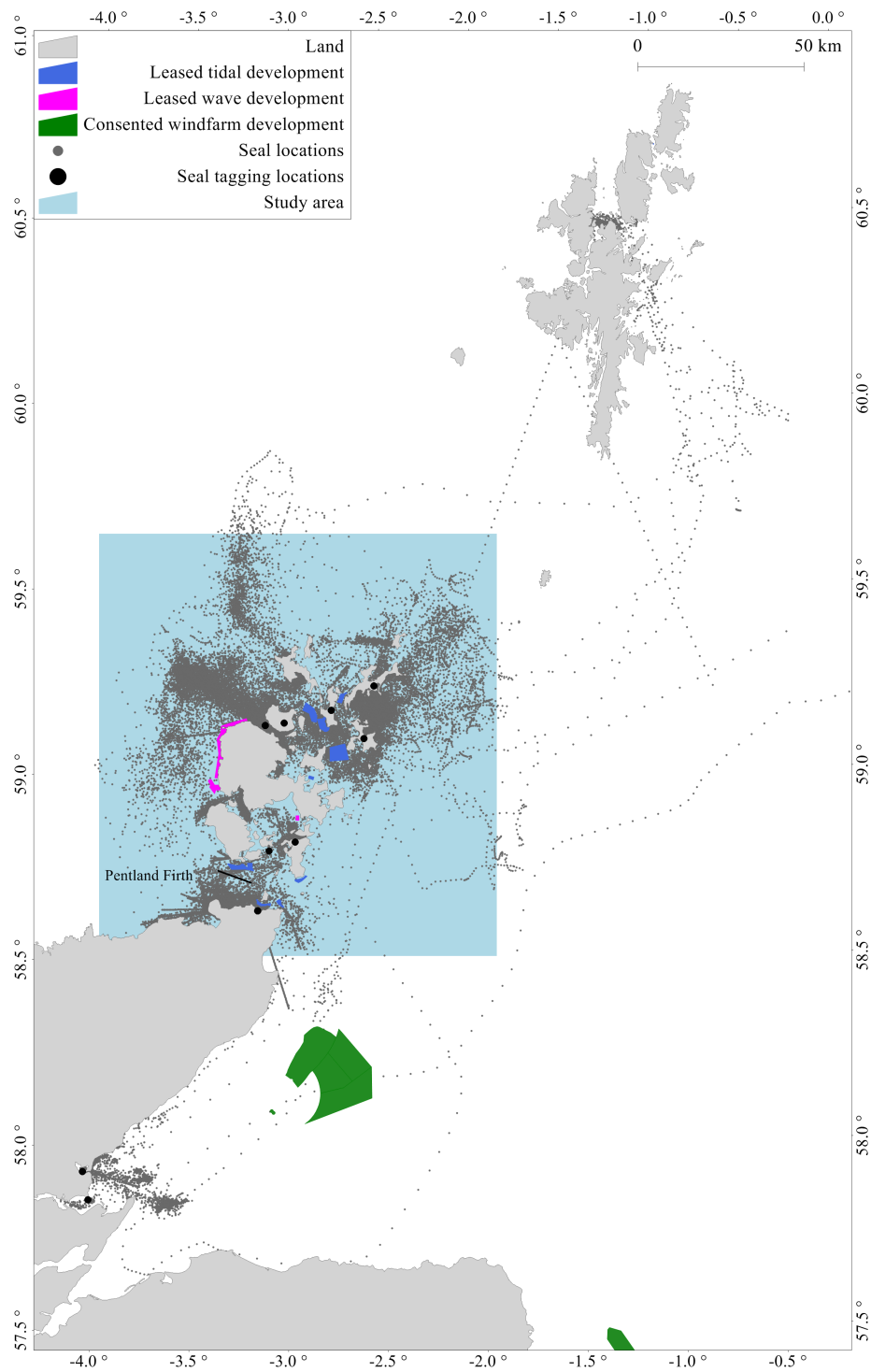
Figure 4. Map showing the spatial extent of the analysis, tracks of 54 animals (dark grey points), their tagging locations (black circles), proposed offshore marine renewable developments [tidal stream (blue), wave (pink), wind (green) areas], and study area centred on Orkney (blue background). The figure was produced using R 3.3.23[34] and GIS software Manifold 8.0.29.03[35].

Movement data

60 adult animals (defined as older than one year old), tagged between 2003 and 2015, spent time within the study area. Between 2003 and 2005, Satellite Relay Data Loggers (SRDL) were deployed that use the Argos satellite system for data transmission[36]. Between 2011 and 2015, GPS phone tags that use the GSM mobile network with a Fastloc©hybrid protocol were deployed[37]. All animal handling procedures were carried out under Home Office Animals (Scientific Procedures) Act licence numbers 60/2589, 60/3303, 60/4009, and 60/7806. Telemetry data were processed through a set of data-cleansing protocols to remove observations with null and missing values, and duplicated records from the analysis.

SRDL positional error was corrected using a Kalman filter and data were used to estimate positions at two-hourly intervals[6,38]. The majority of GPS locations have an expected error of ≤ 55 m[39], although occasional outliers were excluded using thresholds of residual error and number of satellites, and then straight-line interpolated to regularise to the same two-hourly intervals as the SRDL data[6]. Three animals had few locations within the study area, and three animals did not have any haul out records, so these six animals were excluded, bringing the total number of animals used in the analysis to 54 (Table S1 and Fig. S1; Supplementary information).

Continuous spatial surfaces to represent the proportion of time animals spent in different areas were derived by kernel-smoothing the telemetry data. The *ks* R library[40] was used to estimate spatial bandwidth of the 2D kernel applied to each animal/haul out site map. A multivariate plug-in bandwidth selector was determined for each individual by combining all locations associated with that individual. Individual-level weightings were applied to account for differences in the magnitude of data collected by an animal over its tag lifespan and for variation in the operational settings of the tag itself[6]. This ensured that individuals with long tag lifespans, which could be highly auto-correlated, were not overrepresented, whilst also ensuring the individual with short tag lifespans were not under-represented in the analysis. A discovery rate (termed index of information content[6]) was determined as the total number of new grid cell that

an individual visited during the tag lifespan. The *mgcv* library in R[41] was used to fit a Generalised Additive Model (GAM) with a quasi-poisson distribution with a log-link function. The response variable was discovery rate and explanatory variables were the smooth of tag lifespan (hours) and tag type (SRDL or GPS) as a factor. Each animal/haul out map was multiplied by a normalised discovery rate and all density maps connected to each haul out cluster were aggregated and normalised to one.

Terrestrial counts

Harbour seals are surveyed during their moult in August when the greatest number of animals haul out on land for an extended period. Different sections of coastline are surveyed each year. During aerial surveys all seals along a specified section of coastline are counted and coordinates are recorded to an accuracy of approximately 50 m. Surveys take place within two hours of low tide, when low tide is between 12:00 and 18:00 hours[42]. Surveyed coastline was gridded to 0.6 km x 0.6 km and the most recent available count (ranging from 2008 to 2015) was recorded in each onshore grid cell (Fig. 5 & S2 in Supplementary information). Grid cells that were surveyed but in which no animals were located were given a value of zero. For each grid cell, the local population was estimated with associated uncertainty. Full details of this method are available from (Supplementary information `www.int-res.com/articles/suppl/m534p235_supp.pdf`[6]).
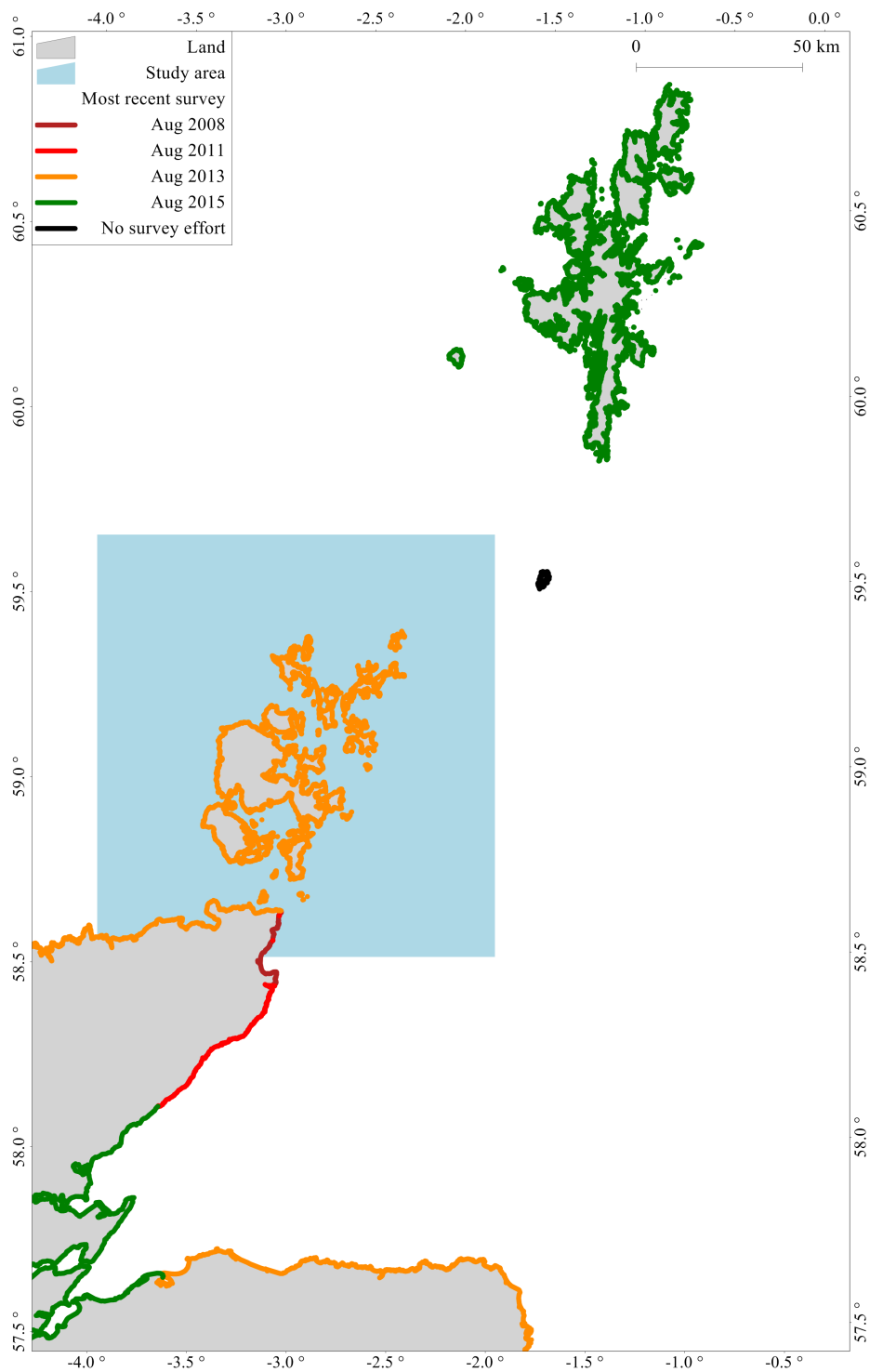
Figure 5. Map showing the most recent terrestrial surveys within the spatial extent of the analysis. Black lines represent no survey effort. The figure was produced using R 3.3.23[34] and GIS software Manifold 8.0.29.03[35].

Environmental data

1. **Shortest at-sea distance from haul out location** By definition, central-
   place foragers have a home-range. For seals, this was represented by the
   shortest distance between a haul out site and an at-sea location taking into
   account land barriers (such as islands) that animals must swim around.
   Shortest at-sea distance was calculated using the *gdistance* R library[43] at
   a resolution of 0.6 km x 0.6 km to determine distance between each seal
   location and the associated haul out (either departure or destination).

2. **Bathymetry** The bathymetric metadata and Digital Terrain Model
   data products were derived from the European Marine Observation and
   Data Network (EMODNet) Bathymetry portal (`http://www.emodnet-
   bathymetry.eu`) released August/September 2015. Seabed depth data had a
   resolution of 1/8 minutes (about 230 m) and are based on the seabed depth
   at the Lowest Astronomical Tide (Fig. 6a).

3. **Tidal power and peak flow** Seals haul out on exposed areas of rock and
   sandbanks at low tide, and tidal information is likely to play an important
   role in their distribution[12]. Tidal energy resources were characterised by
   annual mean tidal power (kWm^{-2}; Fig. 6b), peak flow for mean spring
   tide (ms^{-1}; Fig. 6c), and peak flow for mean neap tide (ms^{-1}; Fig. 6d),
   calculated using the Pentland Firth and Orkney Waters Hydrodynamic
   Model (PFOW)[10]. Mean peak current speeds were calculated using two
   tidal harmonics (M2; lunar and S2; solar) from 60 days of mid-depth velocity
   from the PFOW climatology run. The east and west components of current
   velocity were used to produce M2 and S2 amplitudes and phases. The semi-
   major axis amplitudes for each ellipse (M2 and S2) were then summed to
   produce peak flow for mean spring/neap tide[44]. To represent the kinetic
   energy available throughout the tidal cycle, annual mean tidal power ($\overline{P_T}$)
   was calculated. Average power available over 365 days from the PFOW
   climatology run was calculated taking a complete tidal cycle into account
   (rather than only peak values): $\overline{P_T} = 1/2\rho\overline{U^3}$, where ρ is density of water,
   taken as 1027 kg m^{-3}, and U is the mid-depth current speed[10,44]. Model

predictions were available in an unstructured grid ranging from a resolution of 150 - 250 m at the coast to 3 km at the outer edges of the study region.

4. **Sediment type** was derived from the British Geological Survey (available to download `http://www.bgs.ac.uk`), obtained from core samples spaced 5 km apart on average (Figs. 6e-g). A simplified Folk classification system[45] was applied to derive variables containing proportions of sand, gravel, and mud. Data were given as a percentage-by-weight of gravel (particles > 2.0 mm in diameter), sand (0.0625 – 2.0 mm in diameter), and mud (particles < 0.0625 mm in diameter). Spatial autocorrelation between the three covariates was calculated by randomly sub-sampling the cores to calculate semi-variograms[46]. Each sediment covariate was kriged at a 1 km resolution using the semi-variograms and the resultant local estimates were normalised[17]. These covariates did not account for other substrate (such as underlying rock or biotope information) that may have been present on the seabed.
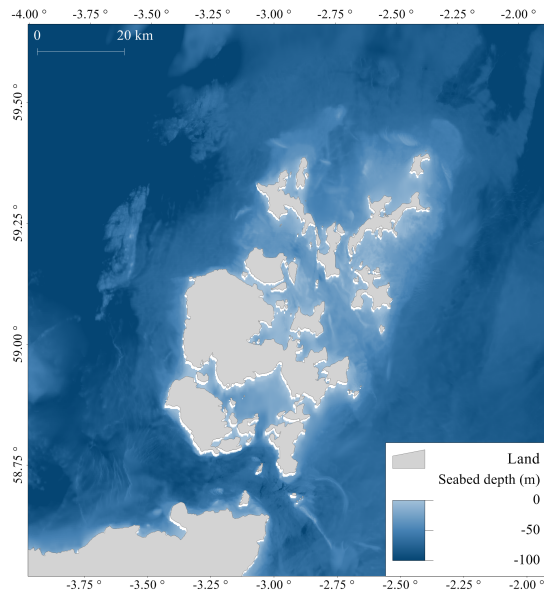
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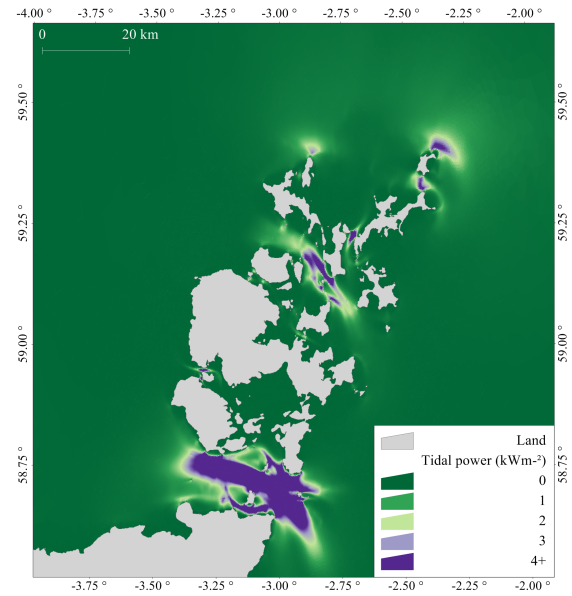
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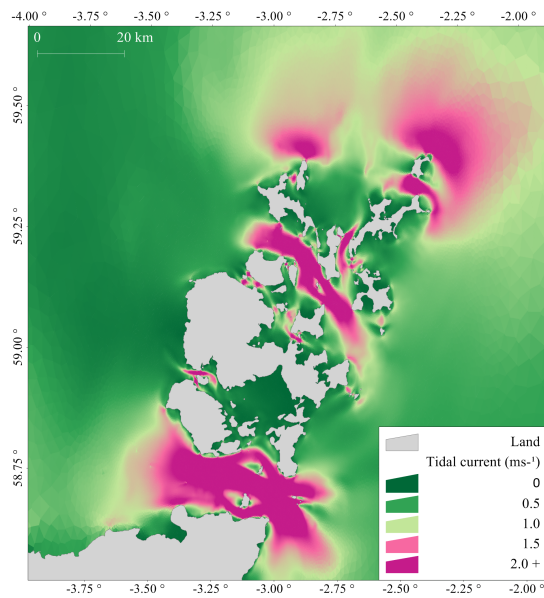
(c)
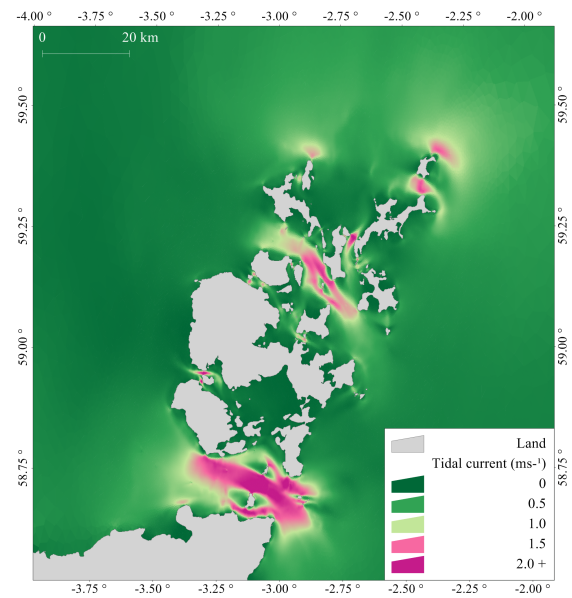
(d)
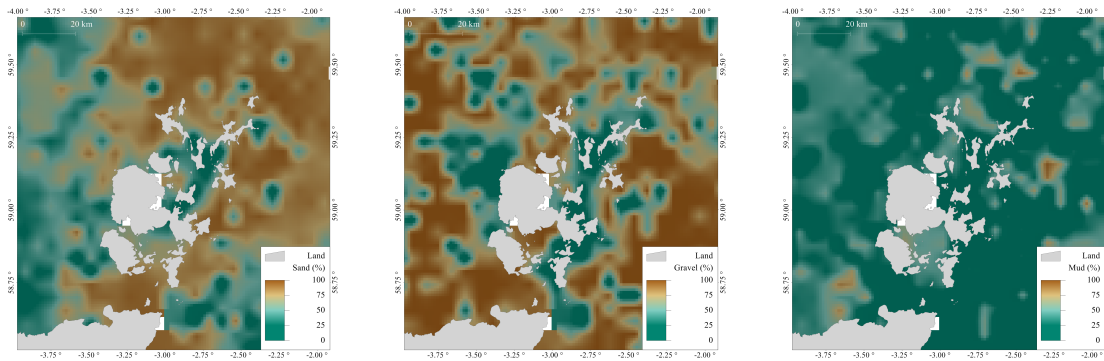
(e)   (f)   (g)

Environmental covariates (except shortest at-sea distance) used for habitat
modelling: (a) Seabed depth, (b) Annual mean tidal power, (c) Peak flow for
mean spring tide, (d) Peak flow for mean neap tide, (e) Proportion of sand in
seabed sediment, (f) Proportion of gravel in seabed sediment, (g) Proportion of
mud in seabed sediment. The figure was produced using R 3.3.23[34] and GIS
software Manifold 8.0.29.03[35].

Haul out clustering

A 0.6 km x 0.6 km grid cell was identified as an onshore haul out either from
the telemetry data where animals moved onto land, or from the terrestrial count
data where animals were counted within that cell. Haul out cells were aggregated
for the purpose of scaling to a local population level because: (a) The resolution
of a 0.6 km x 0.6 km cell may not have been consistent with the scale of animal
behaviour and space use if more than one haul out formed part of a connected
aggregation (e.g. seals may return to an onshore location close to departure haul
out); (b) using non-aggregated haul outs maximised the number of haul out cells
defined by the terrestrial count data which did not have telemetry data directly
associated with them. This would have resulted in inflated uncertainty as the
habitat model would contribute more usage to the analysis than necessary; and
(c) using non-aggregated haul out cells associated with telemetry data but where
the terrestrial count was zero reduced the importance of telemetry data (effectively
removing telemetry data from the usage surface). Haul out cells were aggregated

using a clustering algorithm based on shortest at-sea distance between them. To define an appropriate spatial scale, hierarchal cluster analysis with a centroid agglomeration method was used to generate clustering ranges from a minimum separation of 0.6 km (no clustering) to 15 km (maximum clustering) in increments of 0.6 km[47]. A change point analysis was performed based on the number of clusters using the *changepoint* R library[48]. A single change point occurred at 3.6 km and haul outs were aggregated to this scale for the remainder of the analysis. Telemetry clusters were defined as having telemetry data from at least one tagged animal associated with any haul out cell in the cluster. Null clusters were those where terrestrial count data showed seals were present, but no tagged animals visited any haul out cells within the cluster. To retain telemetry clusters with zero terrestrial counts in the analysis, their counts were changed to one, and the total was rescaled to the original count.

Habitat modelling

Predictions of at-sea usage were required for null clusters (where seals were known to haul out from the terrestrial count data but for which no telemetry data were available). Augmenting the approach taken in Jones *et al.* (2015), a Generalised Additive Modelling - Generalised Estimating Equation (GAM–GEE) modelling framework was used to predict at-sea seal usage. Models were fitted using all telemetry locations with five pseudo-absences associated with each presence point by repeatedly selecting at-sea locations within the study area to associate a representative range of underlying environmental covariates with the pseudo-absence points[49]. Multicollinearity between the covariates was tested using Variation Inflation Factor (VIF) analysis from the *car* R library[50]. Peak flows for mean spring and neap tides were highly correlated (based on a threshold for high collinearity > 5) so these covariates were not included in the same model during model selection. All other covariates had a VIF score between 1.5 and 3.7. The *geepack* R library[51] was used to fit binomial GAM–GEEs with a logit link function and an independent working correlation structure to account for any residual autocorrelation within defined panels of data[52]. Panels were defined for

individual animal and for pseudo-absences separately to avoid underestimating autocorrelation within presences of an individual, and each pseudo-absence was assumed to be independent[26]. Covariates were standardised (mean = 0, sd = 1) to aid model fitting[53]. Year of tag deployment was included as a factor and shortest at-sea distance was included as a linear covariate within the linear predictor. The *splines* R library was used to implement cubic β-splines to allow all other covariates to vary as a function of one-dimensional smooth terms within the linear predictor (4 degrees of freedom) with one internally positioned knot at the mean of each covariate[52]. Linear and spline terms were offered in model selection for all covariates. Allowing interactions between covariates was not possible due to non-convergence in the models. Models were assessed on their ability to predict spatially, and similar-sized spatial blocks were delineated based on haul out cluster using the sample function in R. Forwards model selection was carried out using k-fold cross-validation, using four blocks to fit a model and predicting from the fifth block. This was repeated five times until all blocks had been used in prediction. For each fold, equal-areas with 40 bins with a moving window were used and Spearman rank correlations were calculated based on n = 40 and $\alpha = 0.05$. Folds passing this test were summed and the count divided by five. The threshold for fold pass score (FPS) for five-folds was FPS > 0.8[54].

The selected model was used to estimate usage for the study area for each null cluster. The median value for tag deployment year (2011) was used for all predictions and shortest at-sea path from haul out cluster was calculated. Predicted (mean population) space-use was calculated from the exponential of the linear predictor[17]. For each null cluster, space-use was normalised to one, so that it could be scaled to the local population estimate.

Propagating uncertainty and population-scaling

Uncertainty within each grid cell of the usage maps was calculated. Within-cluster variance was modelled using data-rich telemetry clusters (determined experimentally to be those sites which had ≥ 7 tagged animals associated with them). Variance was estimated from linear models with explanatory covariates

of sample size (number of tagged animals in the telemetry cluster) and mean usage by seals. The models predicted variance for data-poor telemetry and null clusters (by setting the sample size of the uncertainty model to zero). Predicted within-cluster variance increased as the mean usage and number of tagged animals decreased (Supplementary information, Fig. S4). The harbour seal population in each cluster was estimated from terrestrial count data, which were rescaled to allow for the proportion of animals at sea when surveys were carried out[55]. Population-level variance for each cluster was calculated from bootstrapping, based on the uncertainty in estimates of haul-out probability[6]. Within-cluster and population-level variances were combined to give uncertainty estimates for each grid cell in the usage maps. Maps for all clusters were then scaled according to the local harbour seal population, also accounting for the mean proportion of time animals spent at sea (calculated from the telemetry data). Density estimation maps (using telemetry data) were combined with habitat model predictions of usage for null clusters to create total usage maps, showing mean usage with associated 95% confidence intervals.

Data availability

The datasets analysed during the current study are available in the Pure repository, `http://dx.doi.org/10.17630/4f86d1c0-f999-4ca2-b6a8-6ea63a83400b`.

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Author Contributions Statement

ELJ analysed the data and drafted the manuscript, CDM provided data, and ELJ, SS, CES, BJM, and CDM provided intellectual input and editorial content to the manuscript.

Additional Information

The authors declare no competing financial interests.

The following supplements accompany the article

Fine-scale harbour seal usage for informed marine spatial planning

Esther L. Jones*, Carol E. Sparling, Bernie J. McConnell, Christopher D. Morris, Sophie Smout

*Corresponding author: el298@st-andrews.ac.uk

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Supplementary information

Table S1. Animals included in the analysis showing animal reference number, tag type, age-class, region, location of tagging, sex, year tagged, and number of days of movement data collected.

#	Animal reference	Tag type	Age	Management region	Tagging location	Sex	Year	Tagged days
1	pv1-ali-03	SRDL	1+	Orkney & N coast	Sanday	F	2003	187
2	pv1-Arnie-03	SRDL	1+	Orkney & N coast	Eynhallow	M	2003	179
3	pv1-bo-03	SRDL	1+	Orkney & N coast	Sanday	F	2003	184
4	pv1-Bob-03	SRDL	1+	Orkney & N coast	Eynhallow	M	2003	131
5	pv1-cat-03	SRDL	1+	Orkney & N coast	Sanday	F	2003	217
6	pv1-dot-03	SRDL	1+	Orkney & N coast	Sanday	F	2003	273
7	pv1-erin-03	SRDL	1+	Orkney & N coast	Rousay	F	2003	165
8	pv6-Ken-04	SRDL	1+	Orkney & N coast	Stronsay	M	2004	143
9	pv6-Len-04	SRDL	1+	Orkney & N coast	Stronsay	M	2004	112
10	pv6-Max-04	SRDL	1+	Orkney & N coast	Rousay	M	2004	78
11	pv6-Oli-04	SRDL	1+	Orkney & N coast	Eynhallow	M	2004	92
12	pv6-pat-04	SRDL	1+	Orkney & N coast	Stronsay	F	2004	115
13	pv6-Pete-04	SRDL	1+	Orkney & N coast	Eynhallow	M	2004	26
14	pv6-queenie-04	SRDL	1+	Orkney & N coast	Rousay	F	2004	99
15	pv6-sally-04	SRDL	1+	Orkney & N coast	Eynhallow	F	2004	74
16	pv11-James-05	SRDL	1+	Moray Firth	Dornoch	M	2005	32
17	pv11-Kath-05	SRDL	1+	Moray Firth	Dornoch	F	2005	108
18	pv24-112-11	GPS	1+	Orkney & N coast	Pentland	M	2011	167
19	pv24-148-11	GPS	1+	Orkney & N coast	Pentland	M	2011	143
20	pv24-150-11	GPS	1+	Orkney & N coast	Pentland	F	2011	113
21	pv24-151-11	GPS	1+	Orkney & N coast	Pentland	M	2011	72
22	pv24-153-11	GPS	1+	Orkney & N coast	Pentland	F	2011	121
23	pv24-155-11	GPS	1+	Orkney & N coast	Pentland	M	2011	36
24	pv24-165-11	GPS	1+	Orkney & N coast	Pentland	M	2011	48
25	pv24-394-11	GPS	1+	Orkney & N coast	Pentland	M	2011	88
26	pv24-541-11	GPS	1+	Orkney & N coast	Pentland	M	2011	133
27	pv24-580-11	GPS	1+	Orkney & N coast	Pentland	F	2011	94
28	pv24-590-11	GPS	1+	Orkney & N coast	Pentland	M	2011	71
29	pv24-598-11	GPS	1+	Orkney & N coast	Pentland	F	2011	110
30	pv24-622-11	GPS	1+	Orkney & N coast	Pentland	M	2011	76
31	pv24-x625-11	GPS	1+	Orkney & N coast	Pentland	M	2011	84

#	Animal reference	Tag type	Age	Management region	Tagging location	Sex	Year	Tagged days
32	pv44-003-12	GPS	1+	Orkney & N coast	Eday	F	2012	41
33	pv44-004-12	GPS	1+	Orkney & N coast	Eday	F	2012	41
34	pv44-005-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	51
35	pv44-007-12	GPS	1+	Orkney & N coast	Eday	F	2012	40
36	pv44-011-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	51
37	pv44-014-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	44
38	pv44-017-12	GPS	1+	Orkney & N coast	Eday	M	2012	41
39	pv44-018-12	GPS	1+	Orkney & N coast	Eday	M	2012	26
40	pv44-020-12	GPS	1+	Orkney & N coast	Eday	F	2012	32
41	pv44-021-12	GPS	1+	Orkney & N coast	Eday	F	2012	25
42	pv47-392-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	110
43	pv47-427-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	17
44	pv47-539-12	GPS	1+	Orkney & N coast	Eday	M	2012	143
45	pv47-583-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	99
46	pv47-585-12	GPS	1+	Orkney & N coast	Eday	M	2012	151
47	pv47-588-12	GPS	1+	Orkney & N coast	Eynhallow	M	2012	93
48	pv57-197-14	GPS	1+	Orkney & N Coast	St Margarets	F	2014	88
49	pv57-199-14	GPS	1+	Orkney & N Coast	Switha	M	2014	5
50	pv57-200-14	GPS	1+	Orkney & N Coast	St Margarets	F	2014	151
51	pv57-913-14	GPS	1+	Orkney & N Coast	St Margarets	F	2014	176
52	pv59-05-15	GPS	1+	Moray Firth	Loch Fleet	F	2015	121
53	pv59-07-15	GPS	1+	Moray Firth	Loch Fleet	F	2015	141
54	pv59-12-15	GPS	1+	Moray Firth	Loch Fleet	F	2015	128
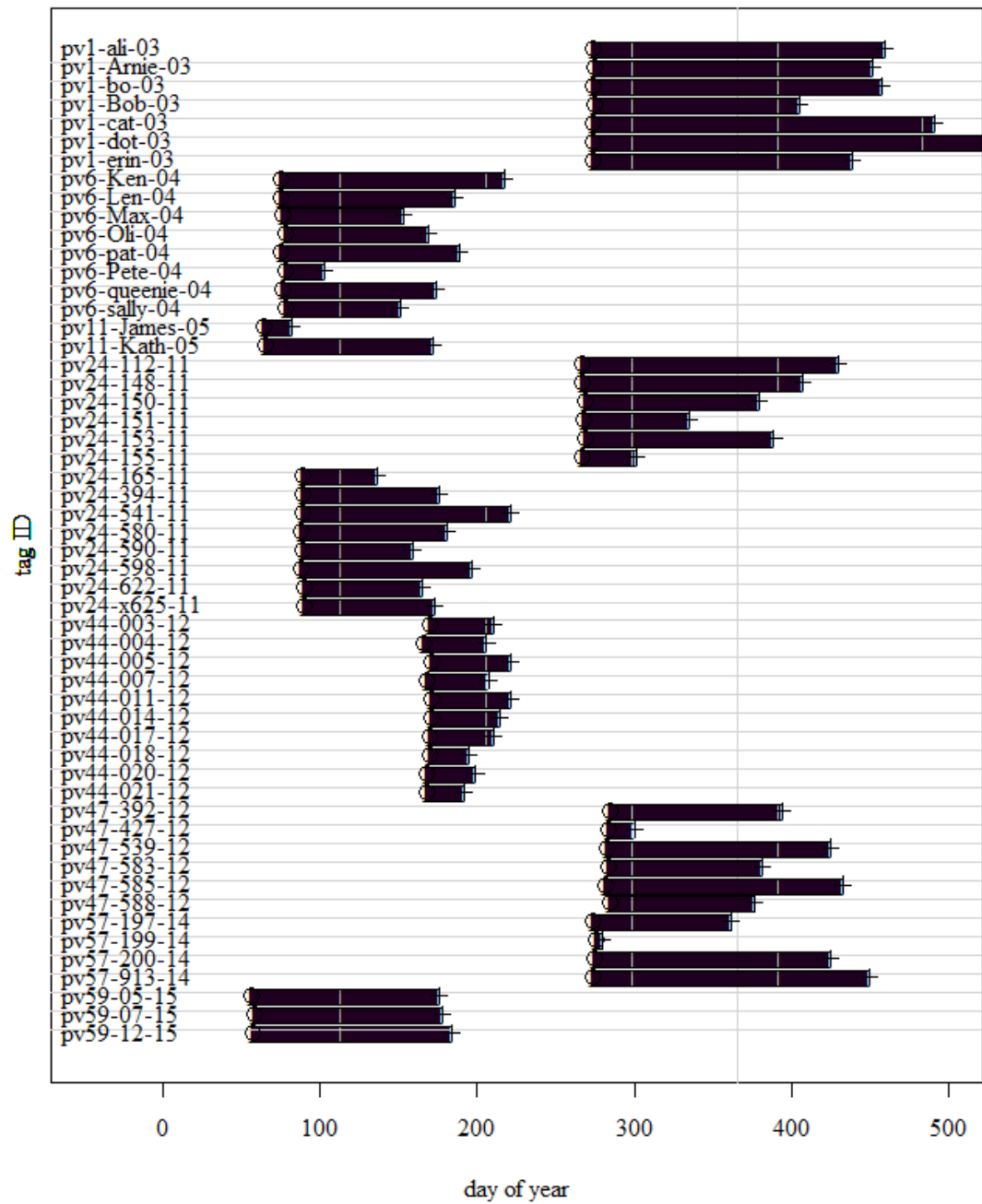
Figure S1. Temporal extent (day of year) of movement data by animal.
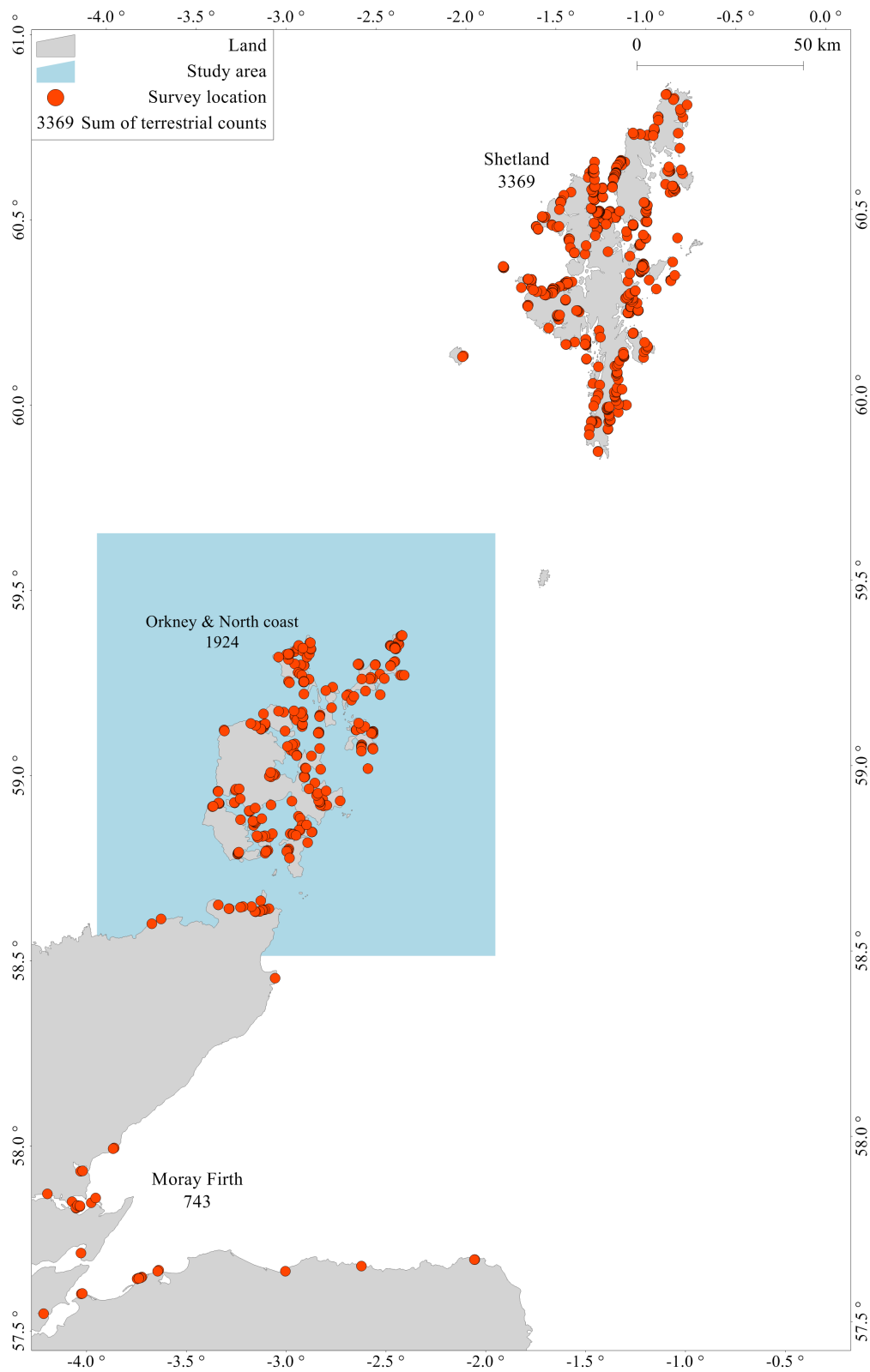
Figure S2. Locations of most recent terrestrial survey counts (ranging from 2008 to 2015 for individual locations) within the study area. The figure was produced using R 3.3.2[34] and GIS software Manifold 8.0.29.0[35].
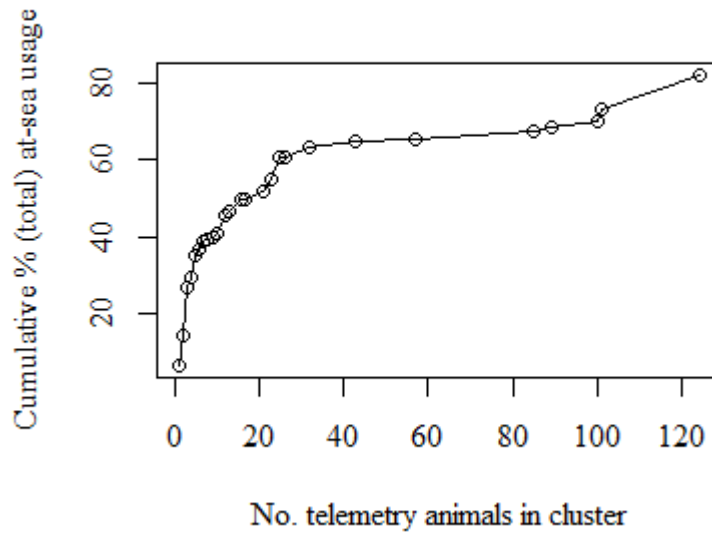
Figure S3. Cumulative usage contribution that haul out clusters with increasing numbers of tagged animals make to the total mean at-sea usage.
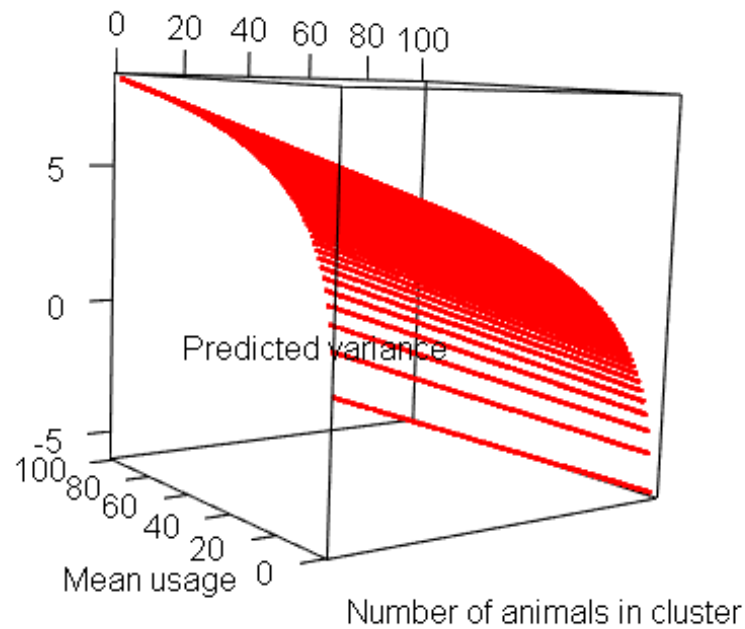
Figure S4. Predicted within-cluster variance when mean density and number of animals in a haul out cluster are varied from 1 to 100 respectively.

Chapter 4

Seals and shipping: quantifying population risk and individual exposure to vessel noise

Seals and shipping: quantifying population risk and individual exposure to vessel noise

Esther L. Jones*[1,2] (iD), Gordon D. Hastie[2] (iD), Sophie Smout[1,2], Joseph Onoufriou[2], Nathan D. Merchant[3], Kate L. Brookes[4] and David Thompson[2]

[1]*Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews KY16 9LZ, UK;* [2]*Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, UK;* [3]*Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, Suffolk NR33 0HT, UK; and* [4]*Marine Scotland Science, 375 Victoria Road, Aberdeen AB11 9DB, UK*

Summary

1. Vessels can have acute and chronic impacts on marine species. The rate of increase in commercial shipping is accelerating, and there is a need to quantify and potentially manage the risk of these impacts.

2. Usage maps characterising densities of grey and harbour seals and ships around the British Isles were used to produce risk maps of seal co-occurrence with shipping traffic. Acoustic exposure to individual harbour seals was modelled in a study area using contemporaneous movement data from 28 animals fitted with UHF global positioning satellite telemetry tags and automatic identification system data from all ships during 2014 and 2015. Data from four acoustic recorders were used to validate sound exposure predictions.

3. Across the British Isles, rates of co-occurrence were highest within 50 km of the coast, close to seal haul-outs. Areas identified with high risk of exposure included 11 Special Areas of Conservation (SAC; from a possible 25). Risk to harbour seal populations was highest, affecting half of all SACs associated with the species.

4. Predicted cumulative sound exposure level, $cSELs(M_{pw})$, over all seals was 176·8 dB re 1 μPa^2 s (95% CI 163·3–190·4), ranging from 170·2 dB re $1\mu Pa^2$ s (95% CI 168·4–171·9) to 189·3 dB re 1 μPa^2 s (95% CI 172·6–206·0) for individuals. This represented an increase in 28·3 dB re 1 μPa^2 s over measured ambient noise. For 20 of 28 animals in the study, 95% CI for $cSELs(M_{pw})$ had upper bounds above levels known to induce temporary threshold shift. Predictions of broadband received sound pressure levels were underestimated on average by 0·7 dB re 1 μPa ($\pm 3\cdot3$).

5. *Synthesis and applications.* We present a framework to allow shipping noise, an important marine anthropogenic stressor, to be explicitly incorporated into spatial planning. Potentially sensitive areas are identified through quantifying risk to marine species of exposure to shipping traffic, and individual noise exposure is predicted with associated uncertainty in an area with varying rates of co-occurrence. The detailed approach taken here facilitates spatial planning with regard to underwater noise within areas protected through the Habitats Directive, and could be used to provide evidence for further designations. This framework may have utility in assessing whether underwater noise levels are at Good Environmental Status under the Marine Strategy Framework Directive.

Key-words: acoustic propagation, AIS, *Halichoerus grypus*, marine stressor, MSFD, noise pollution, *Phoca vitulina*, spatial overlap, telemetry, uncertainty

Introduction

Major shipping routes converge around populated coastlines with relatively high densities of ships accessing ports.

Coastal regions serve as important habitats (e.g. for breeding, foraging) for many species of marine mammals leading to the potential for interactions with ships in these areas. Marine mammal habitats are often conserved through protected areas or other spatial planning measures. There is a perceived requirement for effective

spatial planning where shipping traffic and marine mammals share the same environment (Erbe *et al.* 2014; Williams *et al.* 2015), but the level of management required will depend to a large extent on the scale and intensity of interactions and the effects these have on the behaviour and welfare of the species of interest. Injury due to collisions with vessels is widely recognised as a serious risk for large cetaceans and sirenians (Beck, Bonde & Rathbun 1982; Panigada *et al.* 2006). Trauma ascribed to ship strikes has also been identified in a proportion of both live stranded (Goldstein *et al.* 1999) and dead stranded seals in the United States (Swails 2005), suggesting that mortality resulting from these collisions may pose a risk, albeit lower, for pinnipeds. However, difficulties in observing these unpredictable events mean that mortality rates are still poorly understood.

Shipping traffic is a major component of underwater low-frequency ambient noise in the oceans, and has increased by 10 dB since the mid-1960s in monitored areas of the Pacific (Andrew *et al.* 2002). A focus of the Marine Strategy Framework Directive (MSFD, 2008/56/EC; European Commission 2008) requires EU member states to ensure that noise levels do not adversely affect the marine environment. Phocid seals rely on sound for communication (van Parijs *et al.* 1997), and potentially navigation and predator–prey detection, and have good low-frequency hearing from a few hundred Hz to 70–80 kHz (Cunningham & Reichmuth 2016). Vessel noise is likely to be audible to seals at relatively long ranges and has the potential to lead to a range of chronic effects. For marine mammals, these include avoidance of important habitats (Morton & Symonds 2002), changes in behaviour such as interference with vocalisations (Payne & Webb 1971) and auditory damage (Southall *et al.* 2007), which may pose a significant risk of detrimental long-term population consequences (Tyack 2008). Reviewing previous studies of auditory damage in marine mammals, Southall *et al.* (2007) proposed sound pressure level [SPL; dB re: 1 µPa (peak) (flat)] and sound exposure level (cSEL; dB re 1 μPa^2 s), a measurement of cumulative acoustic energy over time, as noise assessment metrics for auditory damage in marine mammals. Hearing loss can be characterised as permanent threshold shift (PTS) in hearing sensitivity that is unrecoverable over time, or a temporary threshold shift (TTS) where hearing recovers completely over a specified time. For pinnipeds exposed to non-pulse underwater sounds, cSEL was predicted as 203 dB re 1 μPa^2 s and 183 dB re 1 μPa^2 s for the onset of PTS and TTS, respectively.

Potential impacts of exposure to shipping noise are likely to increase concomitantly with growth in the commercial shipping industry (Hatch *et al.* 2008). Despite this, little is known about the levels of noise exposure from shipping in relation to the distribution, movements or behaviour of pinnipeds. Shipping traffic is known to disturb seals from haul out sites (Jansen *et al.* 2015), but there is little published information using at-sea movements of seals in relation to vessel activity (Chen *et al.*

2016). Several studies have called for monitoring of areas where there is high incidence of shipping traffic (Merchant *et al.* 2012; Williams *et al.* 2015) so that acute and chronic impacts on marine species can be addressed. It is important to identify areas of greatest risk within the marine environment (Erbe, MacGillivray & Williams 2012; Erbe *et al.* 2014), and to develop techniques to assess long-term sound exposure (Merchant *et al.* 2012).

Grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals are abundant around much of the UK coastline; they are central-place foragers spending the majority of their time within 50 km of the coast (Jones *et al.* 2015). With similar but asynchronous lifecycles, they haul out on land (to rest, breed and moult) and spend time at-sea travelling to their foraging grounds and moving between haul out sites. Important areas for both species are protected under Annex II of the Habitats Directive (JNCC 2010) and Special Areas of Conservation (SAC) have been designated around the British Isles to protect their terrestrial breeding habitats.

We propose a generalisable framework to characterise co-occurrence between seals and shipping on a broad spatial scale (i.e. nationally). Predicted exposure to shipping noise on individual seals is then investigated in an area where an SAC is designated and where varying spatial overlap occurred.

Materials and methods

SPATIAL CO-OCCURRENCE

To characterise spatial overlap between seals and shipping traffic, two modelled data sources were used: seal at-sea usage maps (Jones *et al.* 2015) and ship usage maps (MMO 2014). Rate of co-occurrence was calculated to quantify spatial overlap between seals and ships in each grid cell. This was defined as the daily number of co-occurrences between seals and ships in each 5 km × 5 km grid cell, i, described as $S_i B_i$, where S_i = mean number of seals in i; B_i = mean daily number of vessel transits in i. The resolution of the co-occurrence maps was not explicitly linked to the spatial scale of potential auditory damage. Rather, the scale was chosen so that broad-scale analysis could be produced to identify potentially acoustically sensitive areas around the British Isles.

Seal at-sea usage maps for grey and harbour seals around the British Isles were produced at a 5 km × 5 km resolution (Appendix S1: Fig. S1, Supporting Information). Methodology to generate usage maps from Jones *et al.* (2015) is summarised: Usage was estimated using a combination of terrestrial counts of seals at haul out sites and animal-borne telemetry data from 259 grey seals and 277 harbour seals. Animals were tagged with satellite relay data loggers (SRDL) or global positioning satellites (GPS) phone tags between 1991 and 2013. A series of data processing protocols removed observations with null, missing or duplicated data. SRDL data were speed filtered at a maximum of 2 ms^{-1} and Kalman filtered to correct for positional errors. Occasional outliers in the GPS data were excluded using thresholds of residual error and number of satellites (Russell *et al.* 2015). To account for sampling bias, telemetry locations were

regularised to 2-hourly intervals. Locations were kernel-smoothed into continuous spatial surfaces to represent the proportion of time animals spent in different areas. Tagged seals did not haul out in some areas, but terrestrial surveys showed that animals were present. To complete the usage maps in these areas, a null model was fitted using all telemetry data to model usage as a function of distance from haul out site. Local usage maps were scaled to local population estimates for 2013. Telemetry-based maps were aggregated with predictions from the null model to create a usage map for the area of the study. Uncertainty was propagated by combining variance in onshore counts with variation between spatial usage of haul outs to produce confidence intervals of usage estimates.

Ship usage maps showing the distribution of vessels around the British Isles in 2012 were developed using automatic identification system (AIS) ship tracking data, available to download from the Marine Management Organisation (https://data.gov.uk/dataset/ mmo1066-vessel-density-grid-2012). Due to international maritime legislation on the requirement for use of AIS (IMO 1974), vessels greater than 299 gross tonnes and all passenger vessels in British Isles waters over the study period were represented in the data. Where available, smaller vessels that carried AIS (but were not required to) were also included in the data. Positional data were supplied by the Maritime and Coastguard Agency, collected by their network of ground-based receiving stations around the British Isles. Methodology to generate ship usage at a resolution of 2 km × 2 km from MMO (2014) is summarised: Due to computational constraints, AIS data were sampled over 42 days throughout 2012 (3–9 January, 1–7 March, 1–7 May, 1–7 July, 1–7 September and 1–7 November) to remove seasonality. Positional data were translated into vessel transits to produce a continuous track. A transit began when speed over ground (SOG) exceeded 0·5 knots and normally ended when SOG stayed below 0·2 knots for more than 5 min (or other specified threshold; Appendix S1: Table S1). Density was defined as the number of vessel transits in a grid cell rather than the number of times a vessel transited across a grid cell. Data processing to translate raw AIS locations into a usage surface is summarised in Appendix S1: Table S2. AIS data had maximum locational error of 50 m (Russell *et al.* 2015), so uncertainty in locations around mean usage was not considered. Vessels were categorised into 11 groups: cargo vessels (48%), tankers (18%), passenger (9%), fishing (8%) and the other groups (unknown, non-port and port service, dredging, high-speed craft, military and sailing craft) comprised the remaining usage (Appendix S1: Table S3). To calculate rates of co-occurrence, all vessel types were used to create ship usage, defined as the mean daily number of vessel transits in each grid cell at the same 5 km × 5 km resolution as the seal usage maps (Appendix S1: Fig. S2).

ACOUSTIC EXPOSURE

A study area including high rates of co-occurrence (≥100 per day) was identified. Located 57.5°N to 58.6°N and 2.2°W to 4.4°W, the area was centred on the Moray Firth, north-east Scotland (Fig. 1a), and encompassed the Dornoch Firth and Morrich More SAC where harbour seals were a primary reason for site selection. Harbour seals spend time around haul out sites and foraging in offshore areas in the Moray Firth (Thompson *et al.* 2013). The study area has a mean depth of 54 m (max = 202 m) and sediment in the area is primarily sand, with a mixture of gravel and mud. A series of acoustic propagation approaches were used to predict exposure to shipping noise for individual harbour seals.

Seal telemetry data were collected using Fastloc© GPS Ultra High Frequency tags (Pathtrack Ltd, Leeds, UK). Over 2 years, 35 tags were deployed on harbour seals. Of these, 28 tags transmitted sufficient information to be analysed, between 19 May–17 August 2014 and 6 January–2 August 2015 (Table 1). Seals were captured whilst hauled out and anesthetised with intravenous Zoletil100® (Virbac, Bury St Edmunds, UK) at a dose rate of 0·5 mg kg^{-1}. Tags were attached to fur on the back of the neck using Loctite® 422 (Henkel, Hemel Hempstead, UK) Instant Adhesive. All procedures were carried out under Home Office Animals (Scientific Procedures) Act licence number 70/7806. Data from each tag were uploaded to one of five archiving UHF receiver base stations positioned at locations around the Moray Firth (Fig. 1a). Data transfers were made when animals surfaced or hauled out within range (line-of-sight) of a receiver station. High-resolution movement data were generated by sampling animal locations every 3 min. Erroneous locations were removed using thresholds of residual error and number of satellites (Russell *et al.* 2015). Locations were interpolated and sub-sampled to estimate noise exposure every 15 min and at-sea locations were retained.

Ship tracking data were provided by MarineTraffic (www.ma rinetraffic.com) for all vessels with operational AIS transmitters in the Moray Firth. AIS data mostly extended over the same spatio-temporal range as the seal telemetry data to enable acoustic exposure of seals to be modelled in the context of surrounding ship traffic (19 May–17 August 2014 and 11 March–2 August 2015). Information was provided on individual vessel name, type, length and width. The sampling rate was set to 2-min intervals and true speed at each vessel location was derived from the on-board vessel log system. Course, heading, date and time were also recorded. Data were cleaned and locations with missing attributes or stationary vessels (speed = 0 knots) were removed. Vessel data were grouped to the same 15-min intervals as the seal data, and one location for each vessel present by interval was selected randomly. Data from 1689 vessels were retained (Table 2).

Predictions of acoustic exposure were made. Source levels (SPLs referenced to 1 m; dB re 1 µPa at 1 m) were estimated for each ship by date and time within one-third octave bands (centre frequencies: 12·5 Hz to 20 kHz) based on ship length and speed, using the 'Research Ambient Noise Directionality' model (Breeding *et al.* 1996; Table 2; Appendix S2). Transmission losses (dB) and associated uncertainty were estimated using spherical and cylindrical spreading models (Marsh & Schulkin 1962; Urick 1983), based on empirical measurements in shallow water in the frequency range 0·1–10 kHz. In coastal waters, estimations of ship noise need to account for the dependence of sound wave attenuation on highly variable local environmental factors (Jensen *et al.* 2011), and so seabed depth and sediment type were incorporated into acoustic modelling. Bathymetric metadata and Digital Terrain Model data products were derived from the European Marine Observation and Data Network (EMODNet) Bathymetry portal (http://www.emodnet-bathymetry.eu) released August/ September 2015, and were based on the seabed depth at the Lowest Astronomical Tide (LAT).

Skip distance (H; km) represents the distance at which sound waves make first contact with either the sea floor or surface, where (D; m) is the water depth (Schulkin & Mercer 1985).

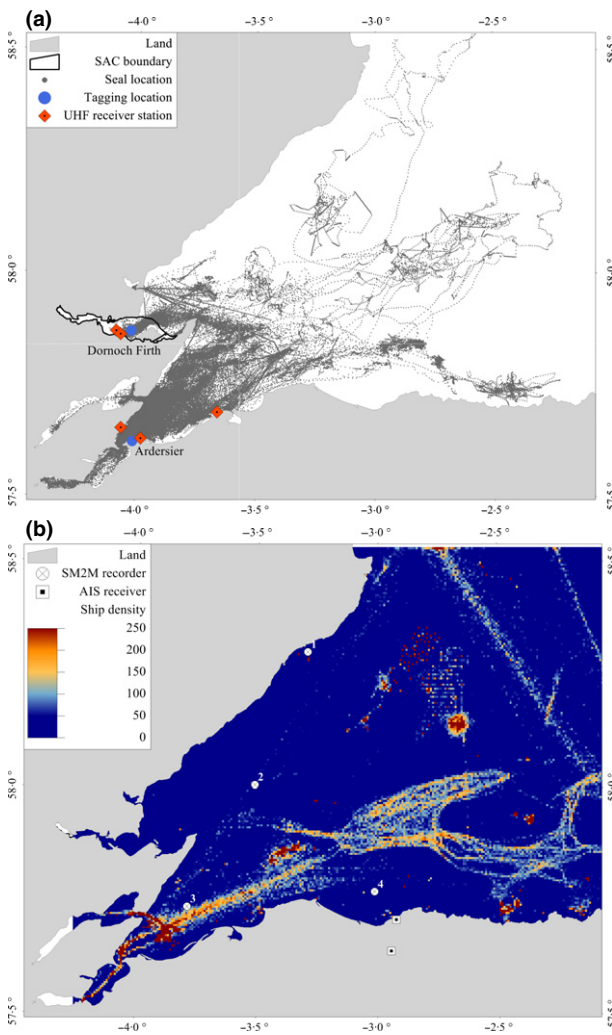$$H = [2D/3]^{1/2} \qquad \text{eqn 1}$$

Fig. 1. (a) At-sea telemetry locations from 28 tagged seals, regularised to 15-min intervals (grey points), tagging locations (blue points), UHF GPS receiver stations (orange diamonds), and boundary of Dornoch Firth and Morrich More SAC (black outline); (b) AIS shipping density over the study period at 0.5×0.5 km resolution, AIS receiver stations (squares), and labelled SM2M recorders (circles with cross). Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data version 2.2.2 from NOAA were used to represent land, available from http://www.soest.hawaii.edu/pwessel/gshhg/.

Transmission loss (TL; dB) was calculated using the distance between source (ship location) and receiver (seal location), range (R; km), absorption coefficient in seawater (α; dB km^{-1}) where $\alpha = 0.036f^{1.5}$ with each one-third octave band centre frequency (f; kHz; Richardson *et al.* 1995), near-field anomaly (k_L; dB) and shallow water attenuation coefficient (a_T; dB).

$$\text{Short-range } R \leq H \qquad \text{TL} = 20 \log_{10} R + \alpha R + 60 - k_L \qquad \text{eqn 2}$$

$$\text{Mid-range } H \leq R \leq 8H \qquad \text{TL} = 15 \log_{10} R + \alpha R + a_T\left(\frac{R}{H} - 1\right) + 5 \log_{10} H + 60 - k_L \qquad \text{eqn 3}$$

$$\text{Long-range } R \geq 8H \qquad \text{TL} = 10 \log_{10} R + \alpha R + \alpha T\left(\frac{R}{H} - 1\right) + 10 \log_{10} H + 64.5 - k_L \qquad \text{eqn 4}$$

Sand was the predominant sediment in the study area [seabed sediment data (BGS Geology: marine sediments 250k) used with permission of the British Geological Survey, http://www.bgs.ac.uk, and available to view on Maremap, http://www.maremap.ac.uk/index.html], and estimates of k_L and a_T in shallow water with sand sediment were used in eqns (2)–(4), where sea state was assumed to be 2 on the Beaufort scale (Appendix S2: Table S4).

Uncertainty in transmission loss was modelled using data of error estimates at selected frequencies and ranges (Appendix S2: Table S5). A linear model was produced with a response variable of standard deviation and explanatory covariates of range and frequency (up to 2.85 kHz). The maximum standard deviation predicted from the model was used for higher frequencies (up to 20 kHz). Received SPLs (dB re 1 µPa$_{(RMS)}$) were calculated by subtracting transmission loss from source levels and integrating over frequency to produce broadband received SPL at each seal location. For analytical purposes, sound sources (vessels) and receivers (seals) were assumed to be located at the mid-point of the water column. Uncertainty in transmission loss was propagated through the acoustic models: Parametric bootstrapping was used to create a set of realisations, sampling from transmission loss mean and standard deviation. Estimated mean ambient noise in the study area (see Acoustic validations below) was used as a minimum threshold for predictions of SPL. Mean SPL was calculated by seal for each 15-min interval. Based on the tracks of seals through predicted sound fields, and using the M-weighting function for pinnipeds in water (Southall *et al.* 2007), cSEL (M$_{pw}$) was calculated every 15-min for each individual over each 24 h period. Mean cSEL(M$_{pw}$) for ambient noise (see Acoustic validations below) was used as a minimum threshold for the predictions. Using bootstrapped data, estimates of mean cSEL(M$_{pw}$) and 95% CI were produced for each 15-min interval over 24 h for individual animals and as an aggregation over all individuals.

ACOUSTIC VALIDATIONS

Predictions from the acoustic models were compared to field measurements of underwater sound made using remote acoustic recorders deployed on the seabed. Four recorders (Wildlife Acoustics SM2M recorders; Maynard, MA, USA) with a sample rate of 96 kHz and gain of 12 dB were deployed within the study area and were set to record on a 33% duty cycle (10 min on, 20 min off) (Fig. 1b). Recordings were available from 27 June to 17 August 2014, overlapping the study period by 53 days. Details of the data analysis procedure are given in Merchant *et al.* (2016); the monitoring data selected for comparison were resolved to one-second resolution in one-third octave bands between 25 Hz and 1 kHz. Broadband received SPL over this frequency range were calculated at the same 15-min intervals used in the predictive model. SPL mean and variance were calculated if there was more than one observation within an interval. Daily ambient noise at each receiver location was calculated as a median SPL (Merchant *et al.* 2016).

Table 1. Animals used to predict acoustic exposure

Animal ID	Year	Tagging site	Sex	Mass at capture (kg)	Tag duration (days)	Number of days used in analysis
65170	2014	Ardersier	M	74·8	57·9	56
65180	2014	Ardersier	M	77·8	92·3	86
65181	2014	Ardersier	M	83·6	59·9	53
65184	2014	Ardersier	M	81·8	39·4	36
65185	2014	Ardersier	M	88·8	73·2	70
65186	2014	Ardersier	F	90·2	35·9	35
65187	2014	Ardersier	M	60·6	39·1	38
65190	2014	Ardersier	M	51·8	50·4	36
65194	2014	Ardersier	M	90·6	67·8	52
65196	2014	Ardersier	F	74·2	66·0	59
65198	2014	Ardersier	F	82·0	45·5	40
65145	2015	Ardersier	M	77·3	61·5	60
65202	2015	Ardersier	M	57·2	156·7	154
65204	2015	Ardersier	M	87·2	97·5	79
65206	2015	Ardersier	F	82·7	96·6	96
65207	2015	Ardersier	M	89·7	131·8	107
65209	2015	Ardersier	M	79·1	145·8	120
65212	2015	Ardersier	M	87·1	98·3	92
65213	2015	Ardersier	F	94·3	91·0	89
65214	2015	Ardersier	F	79·7	89·7	82
65217	2015	Ardersier	M	85·1	111·0	106
65219	2015	Ardersier	F	80·3	98·2	95
65220	2015	Ardersier	M	87·7	114·2	109
65226	2015	Dornoch Firth	M	90·3	37·9	37
65233	2015	Dornoch Firth	M	65·5	131·9	126
65234	2015	Dornoch Firth	M	88·5	38·6	33
65255	2015	Dornoch Firth	M	62·7	84·1	79
65258	2015	Dornoch Firth	F	72·7	20·9	15

Table 2. Moray Firth AIS data summarised by vessel group (italicised sub-totals)

Group	Vessel type	Number of vessels	Mean vessel length (min, max; m)	Mean vessel speed (min, max; kts)	Mean source level (min, max; dB re 1 μPa at 1 m)	Number of locations (15-min intervals)	Proportion of locations (%)
1	Tug	*82*	*53 (13, 95)*	*6 (0·1, 14)*	*148 (113, 196)*	*22 217*	*8·9*
2	Cargo	526	126 (15, 335)	11 (0·1, 23)	160 (112, 187)	33 409	13·4
	Tanker	110	159 (40, 333)	10 (0·1, 16)	160 (137, 178)	24 979	10·0
		636	*132 (15, 335)*	*11 (0·1, 23)*	*160 (112, 187)*	*58 388*	*23·4*
3	Dredger	13	83 (15, 207)	6 (0·1, 13)	150 (123, 191)	1648	0·7
	Fishing	192	32 (9, 143)	7 (0·1, 65)	144 (113, 202)	73 982	29·7
		205	*35 (9, 207)*	*7 (0·1, 65)*	*144 (113, 202)*	*75 630*	*30·3*
4	Local Vessel	5	24 (15, 28)	6 (0·1, 18)	173 (154, 194)	784	0·3
	Pilot Vessel	1	5	16	144	970	0·4
	Pleasure Craft	126	13 (7, 60)	6 (0·1, 23)	134 (113, 205)	5461	2·2
	Port Tender	1	19	8	137	122	0·0
	Sailing Vessel	323	14 (6, 59)	5 (0·1, 33)	133 (113, 203)	15 018	6·0
		456	*14 (5, 60)*	*5 (0·1, 33)*	*134 (113, 205)*	*22 355*	*9·0*
5	Dive Vessel	*15*	*75 (17, 157)*	*9 (0·1, 21)*	*149 (129, 170)*	*1370*	*0·5*
6	High Speed Craft	8	20 (17, 26)	13 (0·1, 24)	156 (127, 198)	3180	1·3
	Law Enforcement	4	66 (24, 84)	7 (2, 11)	140 (118, 156)	828	0·3
	Reserved	9	41 (11, 92)	7 (0·1, 20)	145 (116, 201)	2168	0·9
	Search and Rescue	32	35 (12, 105)	7 (0·1, 26)	151 (113, 198)	8773	3·5
		53	*36 (11, 105)*	*8 (0·1, 26)*	*150 (113, 201)*	*14 949*	*6·0*
7	Military Operations	*9*	*69 (6, 176)*	*18 (0·1, 102)*	*157 (118, 219)*	*552*	*0·2*
8	Passenger	*75*	*155 (11, 333)*	*12 (2, 24)*	*160 (115, 181)*	*5513*	*2·2*
9	Unclassified	*158*	*69 (2, 208)*	*8 (0·1, 22)*	*151 (113, 204)*	*48 379*	*19·4*
Total		1689	76 (2, 335)	8 (0·1, 102)	149 (112, 219)	249 353	100·0

The acoustic exposure model was run contemporaneously for these four locations at the same temporal resolution. Uncertainty in transmission loss was propagated and mean and variance of SPL were estimated. The minimum predicted SPL in the four locations was used as a threshold of daily ambient noise. Estimates of SPL from the acoustic exposure model were then compared with measurements from the acoustic monitoring data at each of the four locations to validate the noise estimations. Mean ambient noise over all four locations was also calculated by taking an average over median daily values of SPL. To represent ambient noise over a 24-h period, cSEL (M_{pw}) was calculated. These data represented a spatial, temporal and frequency sample, which was assumed to be representative of daily ambient noise over the study area.

Results

SPATIAL CO-OCCURRENCE

Estimated number of daily co-occurrences per grid cell between grey and harbour seals and vessels around the British Isles are shown in Fig. 2. For both species, high spatial overlap (≥100 per day) occured within 50 km of the coast close to seal haul outs. Due to low densities of shipping in the west coast of Scotland, there were relatively low rates of co-occurrence than would be expected given the high usage by both species of seals.
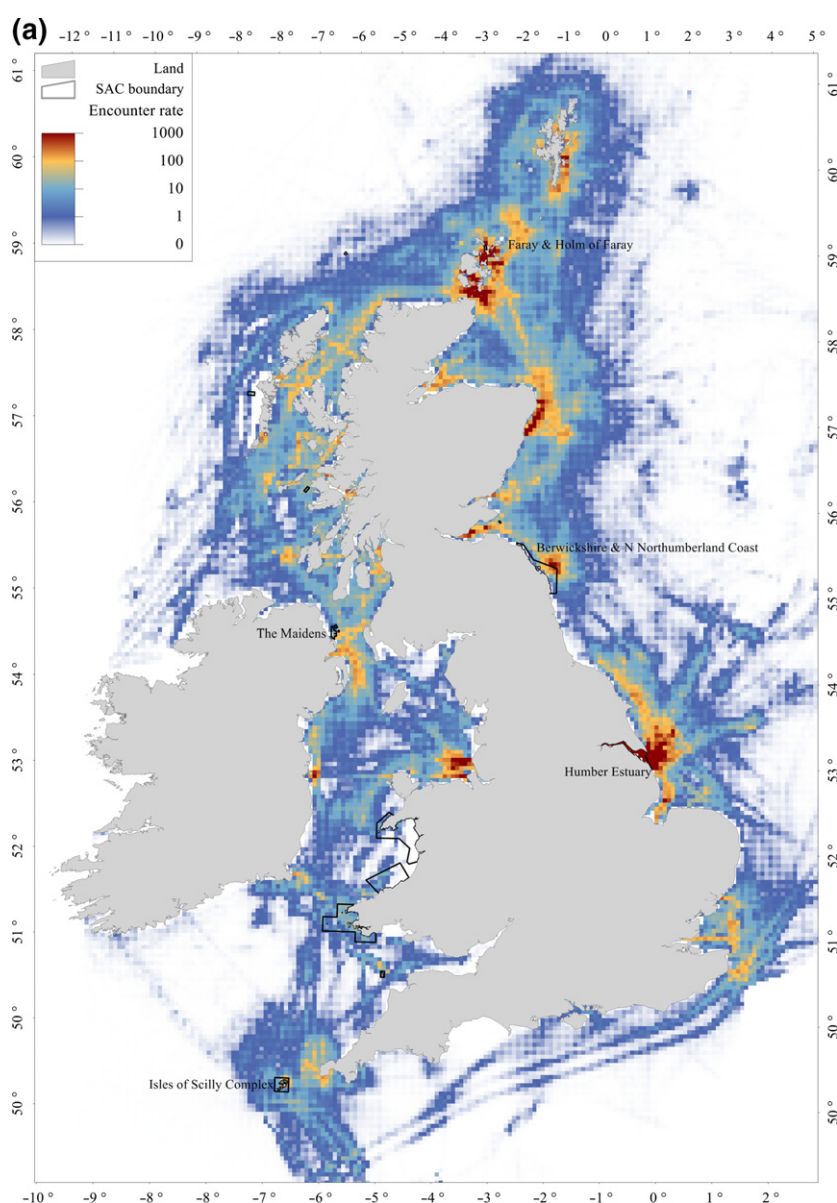
Fig. 2. Estimated number of daily co-occurrences around the British Isles between vessels and (a) grey seals; (b) harbour seals. Boundaries of SACs are shown (black outlines), available to download from http://jncc.defra.gov.uk/protectedsites/SACselection/gis_data/te rms_conditions.asp, and are labelled to show where the daily rate of co-occurrence ≥100 (yellow cells) within an SAC.
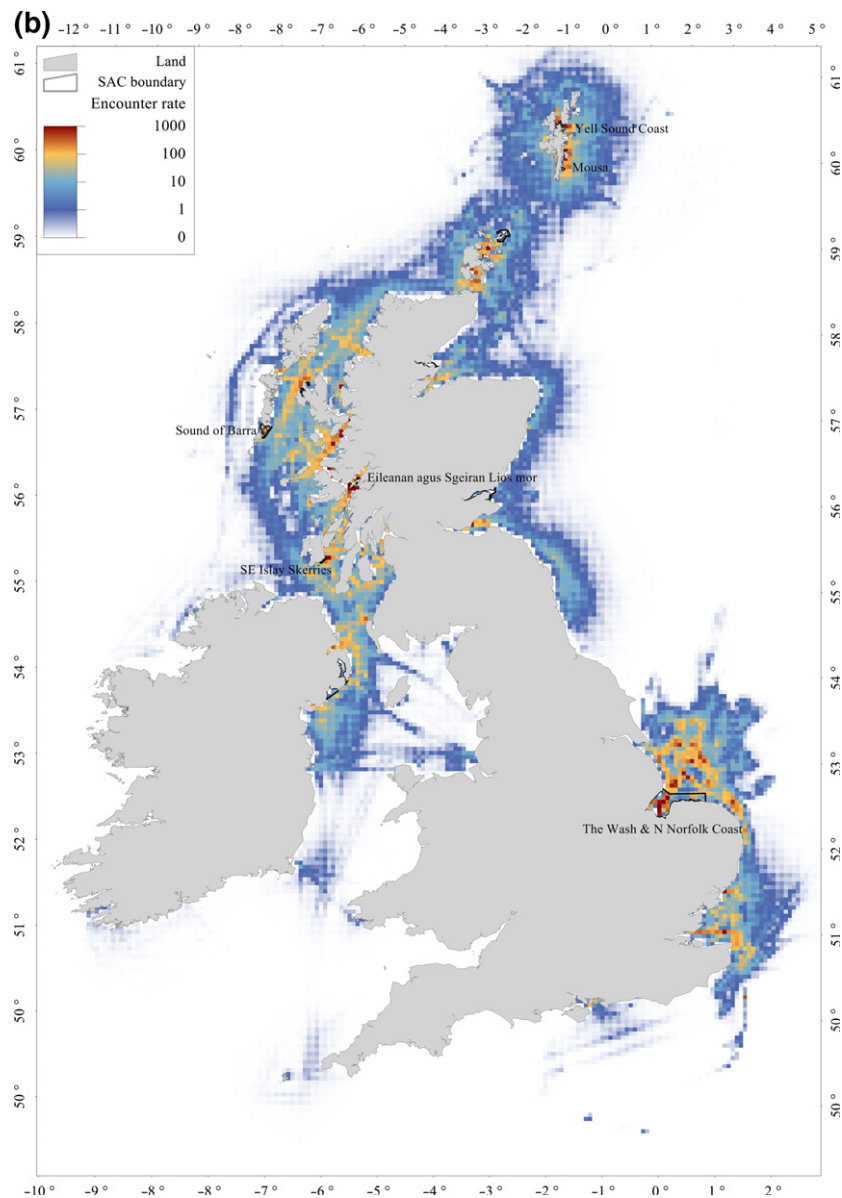
Fig. 2. Continued.

Of the 13 SACs designated for grey seals, five were associated with high co-occurrence, in Orkney (Faray and Holm of Faray), north-east England (Berwickshire and North Northumberland Coast), east England (Humber Estuary), Isles of Scilly off the west coast of England and Northern Ireland (The Maidens) (Fig. 2a). Six of the 12 SACs designated for harbour seals were in areas of high overlap, in west Scotland (South-East Islay Skerries; Eileanan agus Sgeiran Lios mor), Outer Hebrides (Sound of Barra), Shetland (Mousa; Yell Sound Coast) and east England (The Wash and North Norfolk Coast) (Fig. 2b). Fig. 3 shows that variable spatial overlap occurs within the Moray Firth, the detailed study area where acoustic exposure was estimated.

ACOUSTIC EXPOSURE

Locations (corresponding to 2040 seal days) from 28 animals (M = 20; F = 8; Table 1) were combined with locations from 1689 vessels to estimate mean SPL at each seal location and mean $cSEL(M_{pw})$ for seals over each 24-h period. The majority of location data came from three groups of vessels: fishing and dredging (30·3%), cargo and tankers (23·4%), and unclassified (19·4%) (Table 2).

Mean SPL was estimated for each seal location (Fig. 4). Higher mean SPLs (≥140 dB re 1 μPa) were predicted close to the ports of Nigg in the Cromarty Firth, Inverness in the inner Moray Firth, and Banff. The spatial pattern in mean SPL corresponds well with areas of
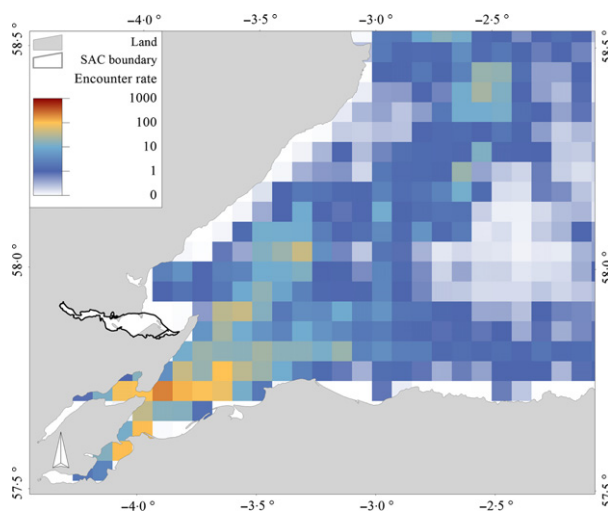
Fig. 3. Estimated number of daily co-occurrences between harbour seals and vessels within the Moray Firth study area. The boundary of Dornoch Firth and Morrich More SAC is shown (black outline).

Fig. 4. Predicted mean SPL (higher than ambient levels) for seal locations within the study area, with ascending order of plotting to show locations where highest values occurred.

high co-occurrence previously identified (Fig. 3), with the exception of Banff, which did not feature as an area of high spatial overlap because a single animal spent time there, and therefore it was not representative of seal movement at the population level.

Maximum daily cSEL(M_{pw}) for each individual ranged from 170·2 dB re 1 μPa^2 s (95% CI 168·4–171·9) to 189·3 dB re 1 μPa^2 s (95% CI 172·6–206·0) (Appendix S3: Fig. S3). Figure 5 shows the cSEL($M_{pw}$) over all individuals with a maximum of 176·8 dB re 1 μPa^2 s (95% CI 163·3–190·4). Mean cSEL(M_{pw}) based on ambient noise levels was calculated as 150·0 dB re 1 μPa^2 s, suggesting that 26·8 dB re 1 μPa^2 s of sound exposure above this level could be attributed to shipping traffic.

ACOUSTIC VALIDATIONS

Predictions from the acoustic exposure model underestimated SPL on average by 0·7 dB re 1 μPa (±3·3) when compared with measurements of underwater sound (Appendix S4: Fig. S4). The four locations (Fig. 1b) varied in prediction accuracy: location 1 (0·9 dB re 1 μPa; ±2·3), location 2 (1·1 dB re 1 μPa; ±2·6) and location 4 (0·6 dB re 1 μPa; ±6·3). Location 3, which had the highest volume of ship traffic in close proximity corroborated to within 0·1 dB re 1 μPa (±2·0) of field measurements.

Discussion

We describe a framework to identify exposure risk to marine species from vessel traffic, and predict acoustic exposure to shipping noise for individuals, validated using measurements of underwater sound. Distributions of seals and shipping traffic around the British Isles were analysed to identify persistent spatial patterns of co-

Fig. 5. Predicted mean cSEL (M_{pw}) over all individuals by hour of day (orange line) with 95% CI (dotted orange lines). The maximum elevation above mean ambient noise (grey line) with 95% confidence intervals (dotted grey lines) is 26·8 dB re 1 μPa^2s.

occurrence. Caveats and limitations associated with the analysis of spatial overlap of seals and vessels, and the acoustic exposure approach taken here are discussed in Appendix S5. Both seal and vessel distributions have low stochasticity at a broad spatial scale; seals are central-place foragers, and ships travel on defined shipping routes. Co-occurrence was most intense within 50 km of the coast close to seal haul outs, and given their relatively coastal range (Jones *et al.* 2015), any impacts may affect more of the harbour seal population compared with grey seals. Some offshore areas greater than 50 km from the coast also exhibited high spatial overlap; this was generally limited to areas where seal usage was coincident with offshore shipping lanes. When considering exposure to shipping

traffic in isolation, we found no evidence relating declining seal population trajectories with high levels of co-occurrence between animals and vessels. Particularly, counts of harbour seals in east Scotland have decreased (by over 90% between early 2000s and 2015), where there are relatively lower levels of shipping, compared with east England where the harbour seal population is increasing and there are high intensities of vessels (Duck & Morris 2016). Our results show that 11 SACs around the British Isles have high risk of exposure within their boundaries.

Predicted exposure levels in the Moray Firth were below those previously estimated to cause PTS (203 dB re 1 μPa^2 s) for pinnipeds in water (Southall *et al.* 2007). However, upper confidence interval bounds of 20 from 28 animals did exceed levels previously shown to cause TTS as a result of 25 min exposure to 2·5 kHz Octave Band Noise with a source level of 152 dB re 1 μPa (183 dB re 1 μPa^2 s) (Kastak *et al.* 2005). When making this comparison, it is important to highlight that shipping noise in the current study was generally below this frequency, but studies investigating TTS have not included lower frequencies. Nevertheless, this demonstrates the importance of propagating uncertainty in predictive modelling of vessel noise, particularly close to the coast where sound propagation can be highly variable. There is a degree of uncertainty in the TTS estimates as published TTS values (Kastak *et al.* 2005) were based on unweighted cSELs, whereas our predicted cSELs were M-weighted; for a discussion of the implications of applying different weighting systems during the data collection and subsequent prediction stages, see Tougaard, Wright & Madsen (2015). However, as the signals used to derive TTS estimates (2·50 and 3·53 kHz) in Kastak *et al.* (2005) were within the functional hearing range of seals as defined by Southall *et al.* (2007), they effectively had an M-weighting of 0 dB, making our comparisons valid. While the definition of injury from exposure to noise is not written into law, guidance regarding European Protected Species (EPS) only refers to permanent shifts in hearing thresholds of cetaceans. TTS would not be considered to be an injury under EPS, and in this context, the definition is transferable to seals. However, where high levels of noise have been identified, the acoustic modelling approach presented here could be used further to test the potential effectiveness of pragmatic mitigation measures. For example, the impact of rerouting shipping lanes or speed restrictions at different levels (Bagočius 2014; Merchant *et al.* 2014) in these areas could be modelled so that predicted sound levels received by individuals (assuming consistent behaviour) are reduced to acceptable limits. Although high spatial co-occurrence was present in the Moray Firth, by comparison with other areas around the British Isles, it has relatively less intense shipping traffic. Predictions of exposure to ship noise are likely to be considerably higher in other areas where very high intensities of spatial overlap occur for one or both species of seals (e.g. daily rate ≥1000) such as Orkney, Shetland, north-east Scotland,

east and south-east England, west Scotland and north Wales. The framework could also be used to identify the potential consequences of changes in shipping traffic. This is particularly relevant to areas that currently experience lower levels of anthropogenic noise where ecosystems may undergo relatively large changes if shipping traffic increases.

Auditory masking of biologically significant sounds for seals is a potential risk, defined as the amount by which the audibility threshold for one sound is raised by the presence of another (Moore 1982). This may be particularly important where higher levels of sound above ambient noise are estimated in and around SACs, designated due to their importance for breeding. Vocalisations, which overlap in frequency with shipping noise appear to play a role in harbour seal reproduction, through male–male competition or advertisement to females (Hanggi & Schusterman 1994; van Parijs, Hastie & Thompson 2000). A reduction in the ability of seals to detect these calls has the potential to lead to biologically significant effects. Furthermore, behavioural responses by seals to anthropogenic sound (e.g. Russell *et al.* 2016) have the potential to lead to avoidance of important foraging habitats with possible impacts on energy acquisition by individuals. However, paucity of empirical studies on behavioural responses by seals to shipping noise means that impacts associated with avoidance have not been quantified in the current study. This remains a clear data gap when considering the potential risks posed by shipping to seal populations. Although our results do not suggest an acute effect on individuals, where populations are affected (90% decline in harbour seals in some regions over the last 15 years; Duck & Morris 2016) by other stressors, cumulative impacts may have a significant effect.

Identifying levels of risk of marine stressors for spatial planning is a focus of legislation in the EU (European Commission 2008). EU member states are required to manage the marine environment to ensure 'Good Environmental Status' (GES), but given the paucity of information on population or ecosystem level effects of underwater noise (descriptor 11 of MSFD), measuring whether GES is being achieved remains challenging. The framework presented here offers a basis to begin assessing GES by identifying areas where high levels of noise coincide with areas of greatest usage by sensitive species. This provides evidence for further investigation and the application of mitigation measures (Bagočius 2014; Merchant *et al.* 2014). Here, we demonstrate areas where high rates of co-occurrence between seals at-sea and shipping coincide with SACs; designated to protect these species at a population level during important periods of their life history through the Habitats Directive. To manage this risk and develop properly targeted mitigation solutions, there remains a need to improve understanding of the implications of cumulative exposure to elevated ambient noise levels for both individual- and population-level effects.

FUTURE RECOMMENDATIONS

We describe a framework to identify risk of exposure to marine species populations from shipping traffic, through spatially explicitly calculating rates of co-occurrence between animals and vessels. We then predict exposure to individuals using acoustic models to estimate mean SPL and cSEL(M_{pw}) with associated uncertainty. Where there are increasing populations of animals combined with a growing volume of ship traffic, spatial co-occurrence can be used to identify new regions of overlap. In areas where levels of noise exposure to individuals are above acceptable thresholds, the framework could inform mitigation measures to reduce noise to tolerable levels. However, there remains a need to investigate the impact of elevated noise exposure on avoidance behaviour of individuals. To understand the long-term implications of exposure to noise from shipping, targeted studies to assess the effects on individual survival and reproductive parameters in areas with quantified but differing levels of shipping would be useful.

Authors' contributions

E.L.J., S.S., G.D.H., J.O., D.T. conceived the manuscript; E.L.J. drafted the manuscript; J.O. and K.L.B. provided data; E.L.J., G.D.H. and N.D.M. analysed the data. All authors provided intellectual input and editorial content to the manuscript.

Acknowledgements

Data accessibility

Ship usage maps are available to download from the Marine Management Organisation, https://data.gov.uk/dataset/mmo1066-vessel-density-grid-2012. Bathymetric metadata and Digital Terrain Model data products were derived from the European Marine Observation and Data Network (EMODNet) Bathymetry portal, available to download http://www.emodnet-bathymetry.eu. Sediment data are available from the British Geological Survey, http://www.bgs.ac.uk and available to view on Maremap, http://www.maremap.ac.uk/index.html. Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data version 2.2.2 from NOAA were used to represent land, available from http://www.soest.hawaii.edu/pwessel/gshhg/.

Seal at-sea usage maps, location data for individual seals, locations and source levels for vessels, and SPLs from monitoring data used for acoustic validations are available from the Pure repository, https://doi.org/10.17630/89ac9345-240a-41bb-8f53-b3f14bb114c0. Data files SealAtSeaUsage-Maps, SealTelemetryData, SourceLevelData, SoundMonitoringData (Jones *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Usage maps.

Appendix S2. Modelling acoustic exposure.

Appendix S3. Sound exposure levels for individuals.

Appendix S4. Validating acoustic predictions with underwater sound measurements.

Appendix S5. Caveats and limitations.

Appendix S6. Spatial co-occurrence using 2011 ship usage maps.

Seals and shipping: quantifying population risk and individual exposure to vessel noise

Esther L. Jones*, Gordon D. Hastie, Sophie Smout,

Joseph Onoufriou, Nathan D. Merchant, Kate L. Brookes

& David Thompson

*Corresponding author: `el298@st-andrews.ac.uk`

Appendix S1 - Usage maps

Seal at-sea usage maps
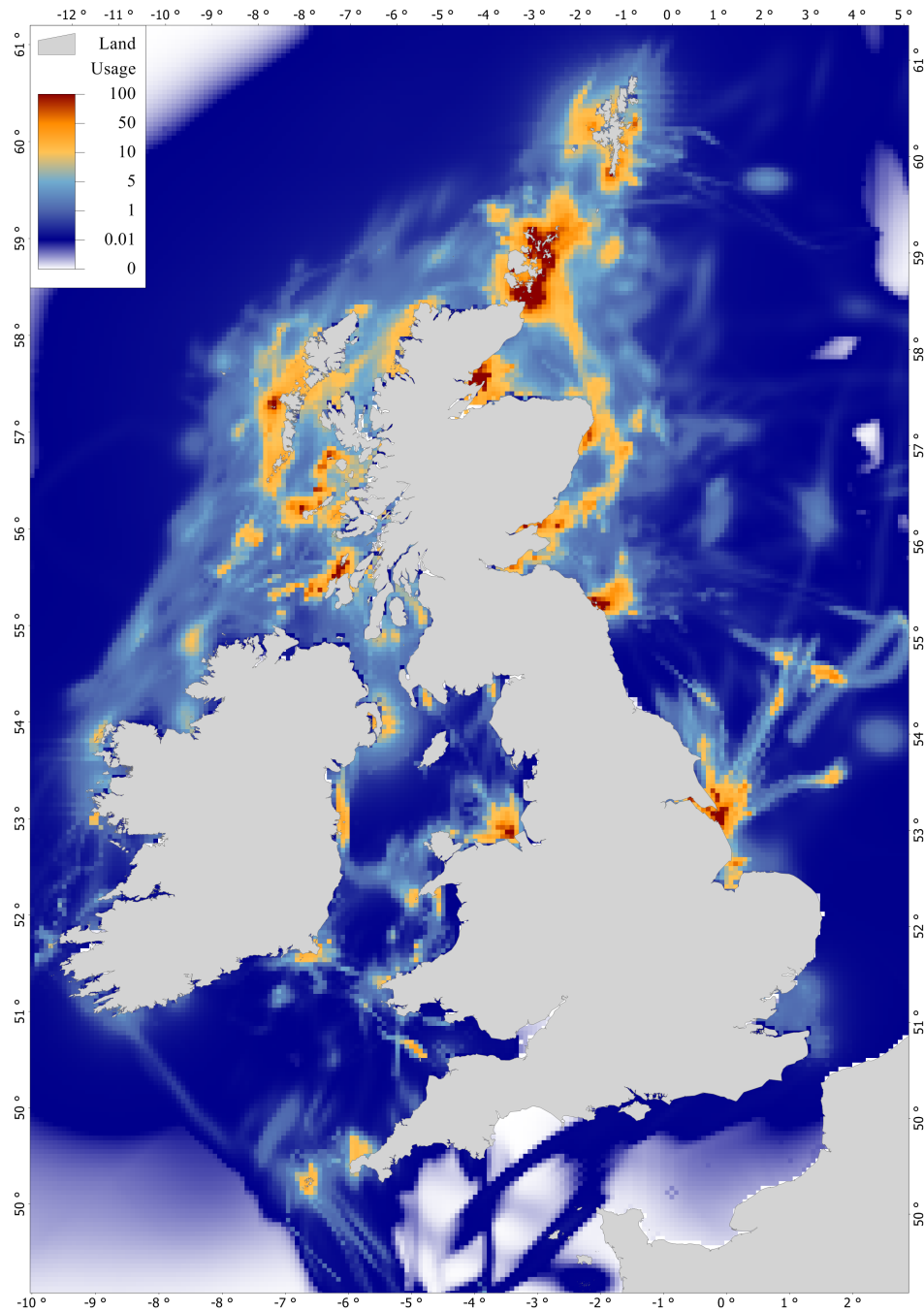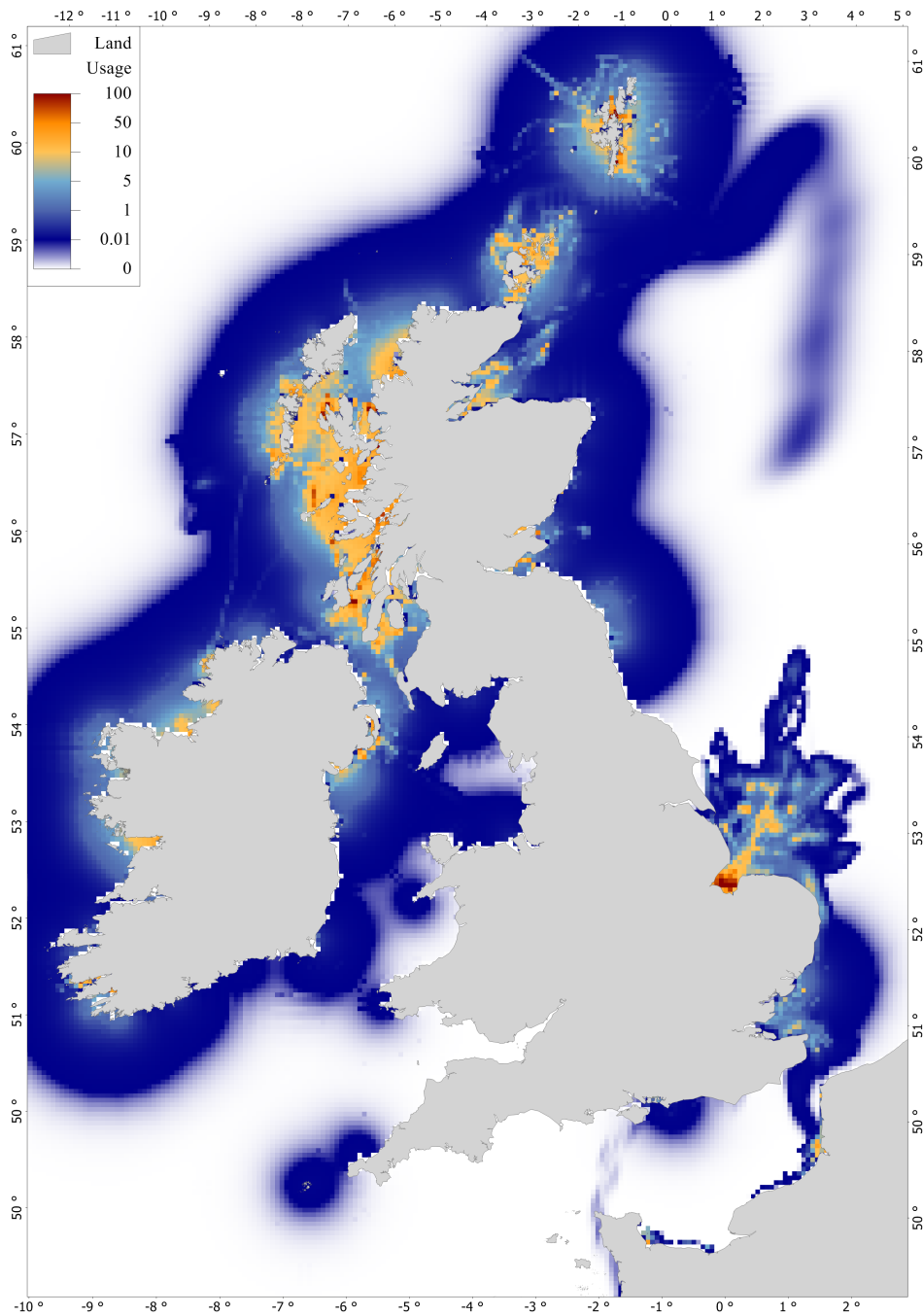
Fig. S1. (a) Grey and (b) harbour seal at-sea usage maps showing number of seals in each 5 km x 5 km grid cell, scaled to 2013 population levels, adapted from Fig. 4; Jones *et al.* (2015). Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data from NOAA were used to represent land, available from `http://www.soest.hawaii.edu/pwessel/gshhg/`.

Ship usage maps

AIS shipping data were processed to produce daily ship usage by vessel type.

Table S1. Vessel transit termination codes, extracted from Table 3; MMO (2014).

Code	Transit termination reason
0	End of the period of the input dataset.
1	Position outside the national area of interest.
2	Contact lost.
3	Intermittent contact (position reports greater than 10 minutes apart, start of an inferred transit).
4	Intermittent contact finished, normal contact restored (end of an inferred transit).
5	Normal transit termination, which includes speed over ground falls below 0.2 knots for more than 5 minutes.
6	Quality Assurance (QA) checks on consecutive positions result in repeated invalid points and therefore a termination of the transit line.

Table S2. Summary of AIS shipping data processing, adapted from MMO (2014).

Stage 1	• Decoding and sorting of AIS signal (positional reports and voyage information). • Associating ship static and voyage information with positional reports for each vessel.
Stage 2	• Identification of vessel transits. • Quality assurance of vessel transit lines. • Transit simplification. • Identification and reporting of vessel AIS processing statistics.

Stage 3	- Plotting of vessel transits in GIS. - Spatial QA of transit lines to remove overland transit segments. - Identification of vessel transit start/finish points within regional zones. - Validation and correction of vessel information against a third party vessel statistics database.
Stage 4	- Calculation of Vessel Transit Classification (VTC). - Creating density grids. - Calculating temporal differences. - Calculation of regional shipping statistics.

Table S3. AIS data vessel groupings, adapted from MMO (2014).

Group	Type	Description	Usage
0	Unknown		6%
1	Non-Port service craft	Search and rescue vessels, towing, medical transports, ships according to resolution no. 18, other special craft.	1%
2	Port service craft	Pilot vessels, tugs, port tender and vessels with anti-pollution facilities or equipment.	3%
3	Vessels engaged in dredging or underwater operations	Vessels engaged in dredging or underwater operations, vessels engaged in diving operations.	2%
4	High Speed Craft		2%
5	Military or law enforcement vessels		1%
6	Passenger vessels		9%
7	Cargo vessels		48%

8	Tankers		18%
9	Fishing*	Fishing vessels.	8%
10	Sailing and Pleasure craft	Pleasure craft, sailing vessels.	2%

*Fishing vessels are not required to carry AIS beacons. As a result AIS data may not be a fully accurate representation of fishing activity. All fishing vessels > 15 m are required to carry Vessel Monitoring System (VMS) beacons.
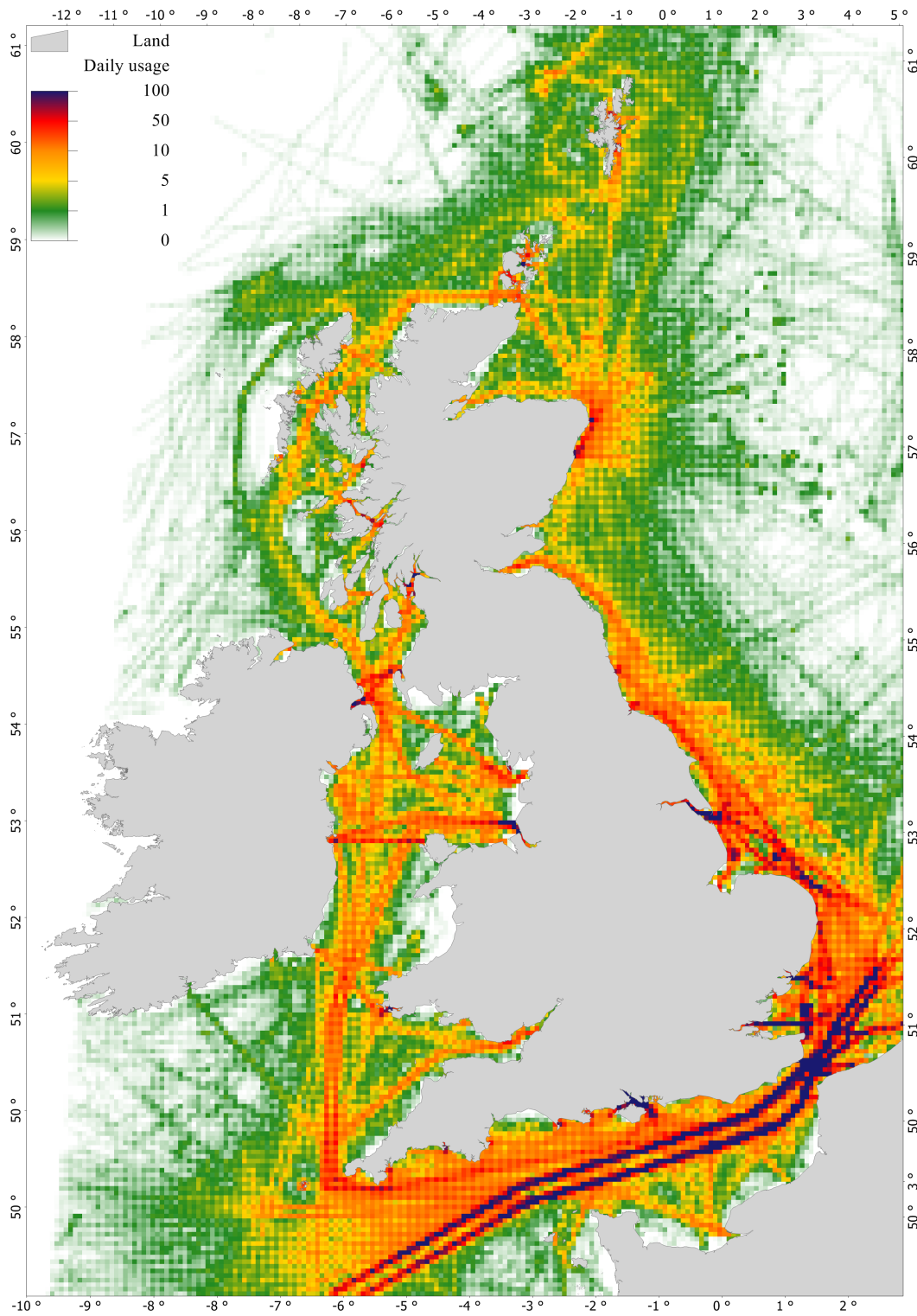
Fig. S2. Mean daily ship usage in 2012 showing the mean number of vessel transits in each 5 km x 5 km grid cell (e.g. red denotes between 50 and 100 vessel transits within a grid cell in one day).

Processing ship and seal usage maps to calculate spatial co-occurrence

Ship and seal usage maps were assessed to ensure they could be compared. Ship usage maps were scaled from 2 km x 2 km resolution to the same 5 km x 5 km resolution as the seal at-sea usage maps implementing 'Spatial Overlay' with averaged proportionality using Manifold v8.0.29.0 (Manifold Software Limited 2015). Both data layers were originally projected in Universal Transverse Mercator 30° North, datum World Geodetic System 1984 (UTM30N WGS84) and this projection was used for subsequent analysis. The spatial extent for the comparison was defined by the ship usage maps. Density surfaces by vessel type were aggregated and the resulting weekly density was divided by 7 to give daily ship usage (Fig. S2). Usage maps were produced for shipping traffic throughout 2012. Population data for seals were collected in August each year. Therefore, seal usage maps were scaled to the most contemporary seal population estimate in 2013. Here, we estimate overlap based on the mean temporal distribution of seals and ships (i.e. mean over the year). Seal at-sea usage maps used movement data available over many months and years, analogous to their long-term marine distribution, but not accounting for significant lifecycle events such as breeding and moulting that occur primarily on land. Likewise, ship usage maps were produced as a mean daily distribution, and seasonality was accounted for by sampling AIS data throughout the year.

Appendix S2 – Modelling acoustic exposure

Ship source levels

Source levels (SL) of noise from ships were estimated by third-octave frequency band (f; Hz) from ship length (l; ft) and speed (v; kt) using the Research Ambient Noise Directionality 3.1 model (Breeding *et al.* 1996). Mean ship speed ($\bar{v} = 4.26$ kt) and length ($\bar{l} = 185.24$ ft) were calculated over all available ship data.

$$\text{SL}\left(f, v, l\right) = L\left(f\right) + 60\ \log_{10}\left(v/\bar{v}\right) + 20\ \log_{10}\left(l/\bar{l}\right) + df.dl + 3 \qquad \text{(S1)}$$

$$df = \begin{cases} 0 \ \le f \ \le 28.4 & df = 8.1 \\ f > 28.4 & df = 22.3 - 9.77 \ \log_{10}(f) \end{cases} \tag{S2}$$

$$dl = l^{1.15}/3643 \tag{S3}$$

$$L(f) = \begin{cases} f \le 500 & L(f) = -10 \ \log_{10}(10^{-1.06 \ \log_{10} f - 14.34} + 10^{3.32 \ \log_{10} f - 21.425}) \\ f > 500 & L(f) = 173.2 - 18 \ \log_{10}(f) \end{cases} \tag{S4}$$

Transmission loss

Transmission loss in shallow water and associated uncertainty were calculated using spherical and cylindrical spreading models (Marsh & Schulkin 1962), based on empirical measurements in shallow water in the frequency range 0.1 – 10 kHz. The equations use spherical spreading for short ranges and cylindrical spreading at long ranges. Estimates of k_L and a_T in shallow water from Marsh & Schulkin (1962), reproduced in Urick (1983) were used where sea state was assumed to be 2 on the Beaufort scale, and primary sediment was sand (Table S4). Uncertainty in transmission loss was modelled using data from the semi-interquartile error estimates (Table S5), also from Marsh & Schulkin (1962), reproduced in Urick (1983).

Table S4. Estimates for near-field anomaly and attenuation coefficient in shallow water by frequency assuming Beaufort sea state 2 and sand sediment (Marsh & Schulkin (1962), reproduced in Urick 1983).

Frequency (f; kHz)	k_L; dB	a_T; dB
0.1	7.0	1.0
0.2	6.2	1.3
0.4	6.1	1.6
0.8	5.9	1.9
1.0	5.7	2.1
2.0	4.2	3.1

Frequency (f; kHz)	k_L; dB	a_T; dB
4.0	3.6	3.7
8.0	2.9	4.5
10.0	2.7	4.8

Table S5. Error estimate in transmission loss by range and frequency, assuming Beaufort sea state 2 and sand sediment (Marsh & Schulkin (1962), reproduced in Urick 1983).

Range (R; km)	Frequency (f; kHz)			
	0.112	0.446	1.12	2.82
2.7432	2	4	4	4
8.2296	2	4	5	6
27.432	4	9	11	11
54.864	5	9	11	12
82.296	6	9	11	12

Appendix S3 – Sound exposure levels for individuals

Predicted mean cumulative sound exposure levels, cSEL(M_{pw}), and associated 95% confidence intervals were calculated for each individual over a typical 24-hour period (Fig. S3). Mean maximum cSELs(M_{pw}) for each individual ranged from 170.2 dB re $1\mu Pa^2$ s (CI 95% 168.4, 171.9) to 189.3 dB re $1\mu Pa^2$ s (CI 95% 172.6, 206.0).
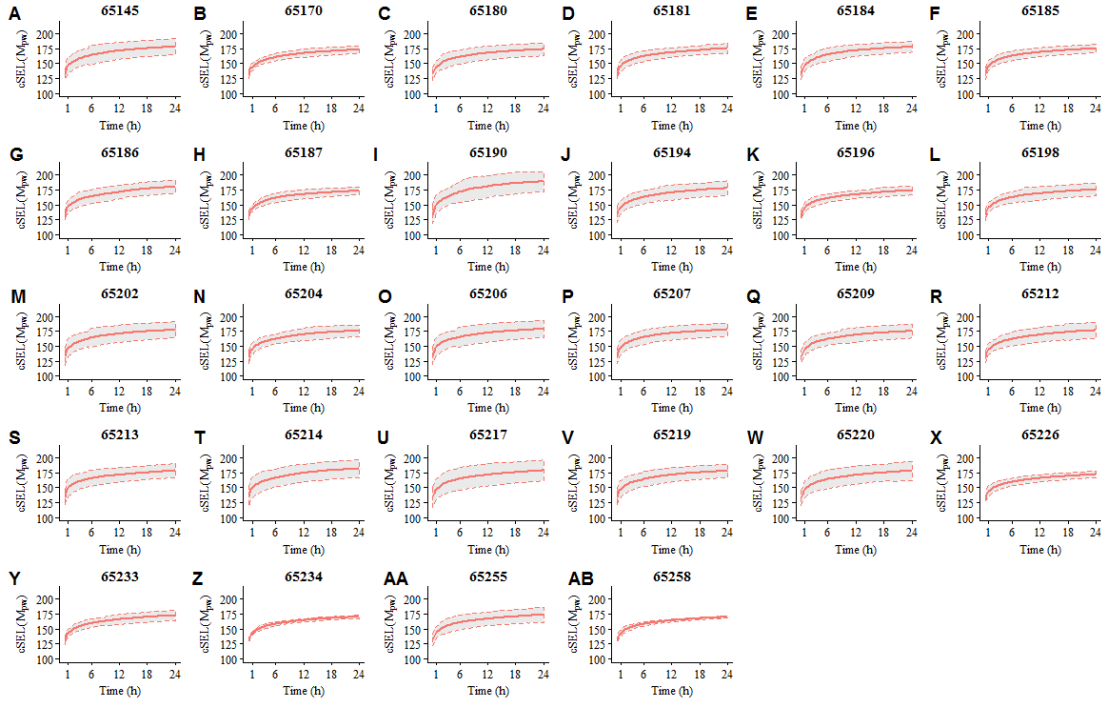
Fig. S3. Mean cumulative Sound Exposure Level (cSEL(M_{pw}); dB re $1\mu Pa^2$s) by hour of day for each seal (solid line) with 95% confidence intervals (dotted lines).

Appendix S4 – Validating acoustic predictions with underwater sound measurements
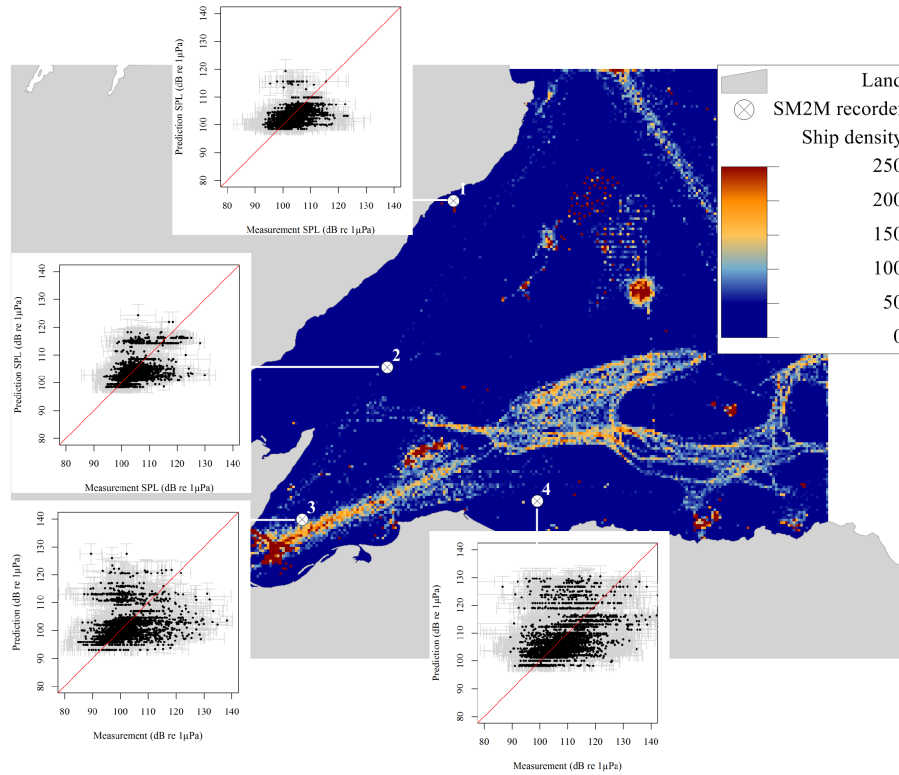
Fig. S4. AIS shipping density in the Moray Firth study area, labelled (1,2,3,4) SM2M sound recorders (white circles), and plots of SPL for measurements vs. predictions (black points) with 95% CI (pale grey lines). The red lines delineate accordance.

Appendix S5 – Caveats and limitations

AIS data have been shown to effectively characterise shipping noise (McKenna, Wiggins & Hildebrand 2013; Merchant *et al.* 2014, 2016; Farcas, Thompson & Merchant 2016). These data represent vessels > 299 gross tonnes and all passenger vessels, and smaller vessels such as fishing fleets that are arguably likely to contribute to close-to-coast underwater noise are under-represented. Spatial overlap and noise level predictions presented here may be underestimated in coastal waters, quantified by the disparity between acoustic predictions and

measurements (Appendix S4). Although the assumed relationship between ship speed and broadband source level (Breeding *et al.* 1996) breaks down for bulk carriers and container ships (McKenna *et al.* 2012), McKenna, Wiggins & Hildebrand (2013) showed that speed and length covariates remain significant when modelling ship noise production levels. Information about vessel loads, propeller type, or year of build, which can all potentially affect ship noise production levels should be included in future modelling. Source characteristics may also have been underestimated given that directivity of sound emissions from ships can be highly variable; for example, the level of stern aspect noise from vessels can be 8 – 12 dB higher than bow aspect noise (over frequency range 160 Hz to 4 kHz; Trevorrow, Vasiliev & Vagle 2008). Noise levels were propagated from the middle of the water column so the diving depth of seals or change in propeller depth (unloaded ships have a shallower depth of propeller, radiating less noise) could not be accounted for explicitly. Vessels with speeds of 0 knots were excluded but we could not distinguish vessels that were moving at low speeds under way from those that were at anchor but moving with the tide because AIS data did not provide this information reliably. Sound propagation in shallow water environments can be highly variable due to complexity in hydrography and bathymetry, and the effects of weather and tidal currents. Model validation has shown that spreading law models such as those used here can underestimate sound levels close to the source and overestimate sound levels further from the source (Farcas, Thompson & Merchant 2016). However, balancing computational constraints with model complexity prohibited the use of more sophisticated acoustic models.

Ship usage was derived from 42 days of tracking data throughout 2012, and seal at-sea usage was scaled to a population estimate in August 2013, providing the most contemporaneous temporal alignment between the two datasets. Shipping lanes are well-defined and although the volume of ship traffic can vary year-by-year, the routes of these vessels generally do not. We conducted the spatial overlap analysis using vessel densities in 2011, which produced similar results (Appendix S6, Fig. S5).

Appendix S6 – Spatial co-occurrence using 2011 ship usage maps

Spatial co-occurrence was calculated between seal at-sea usage maps (Jones *et al.* 2015) and ship usage maps generated from AIS data in 2011 (MMO 2014), available to download from `https://data.gov.uk/dataset/mmo1066-vessel-density-grid-2011`. AIS data were sampled at two-month intervals throughout 2011, from the first 7 days of per month commencing with January. Results showed that similar spatial patterns arise when ship usage in 2011 and 2012 were used (Fig. S4). This demonstrates that between these years, inter-annual fluctuation in vessel density is minimal on the broad-spatial scale considered in these analyses.
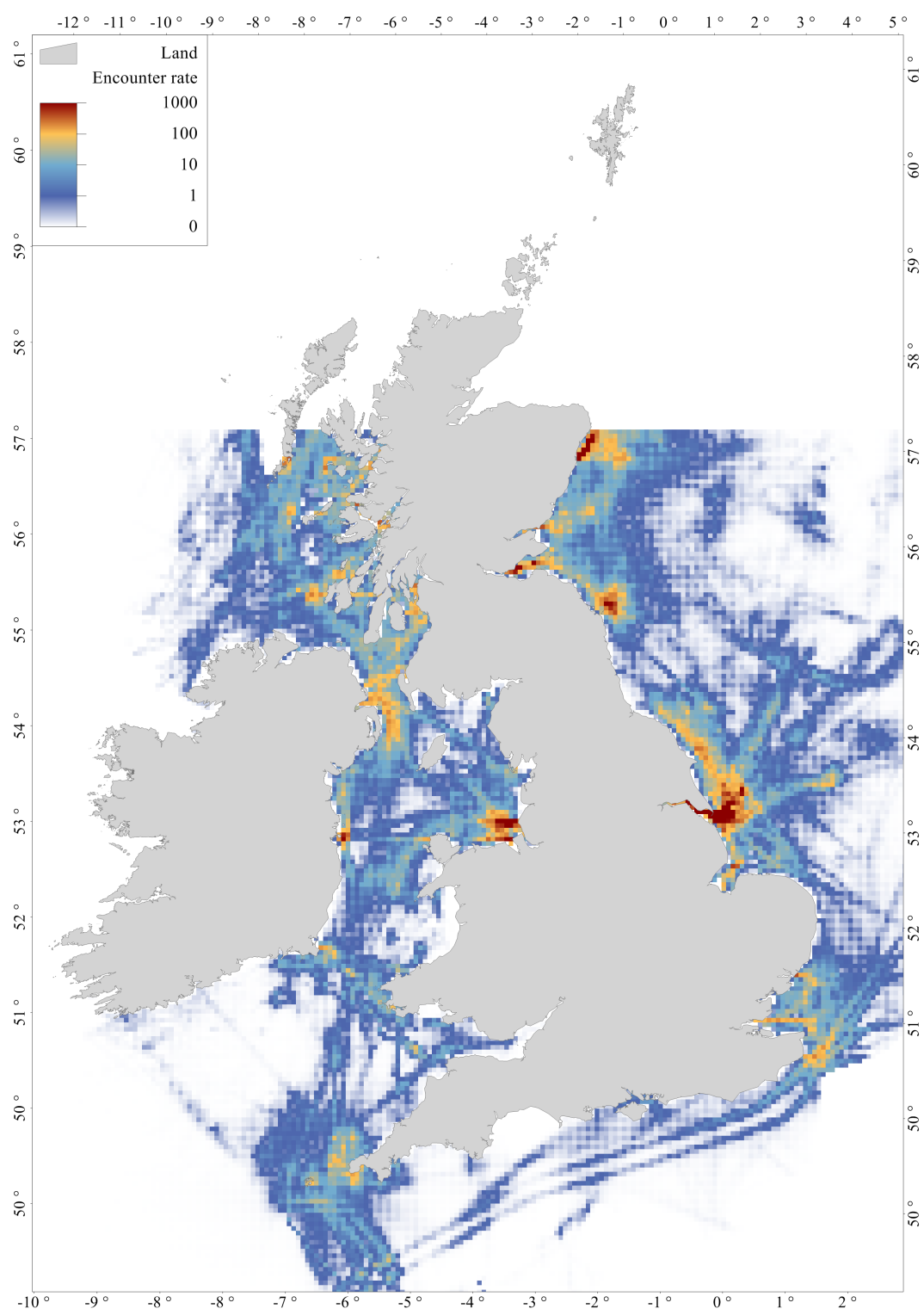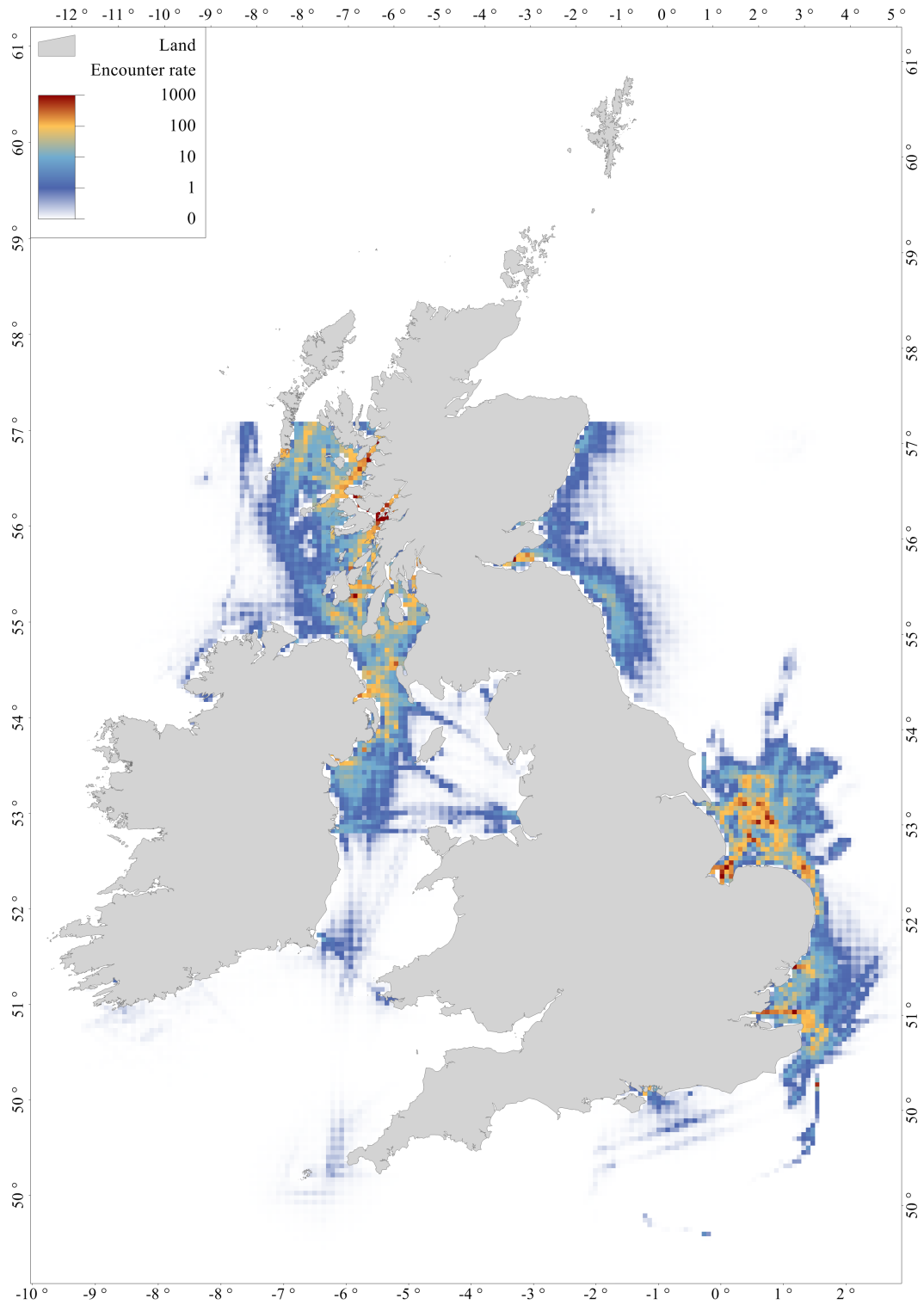
Fig. S5. Estimated number of daily co-occurrences around the UK in 2011 between vessels and (a) grey seals; (b) harbour seals. Ship usage maps were available in a reduced study area for 2011, which did not extend to northern Scotland.

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Chapter 5

Novel application of a quantitative spatial comparison tool to species distribution data
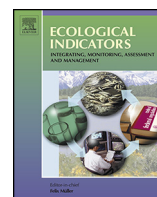
Novel application of a quantitative spatial comparison tool to species distribution data

Esther L. Jones [a,b,*], Luke Rendell [a], Enrico Pirotta [c], Jed A. Long [d]

[a] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, United Kingdom
[b] Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews KY16 9LZ, United Kingdom
[c] School of Mathematics, Washington State University, Vancouver 98686, WA, USA
[d] Department of Geography and Sustainable Development, School of Geography and Geosciences, Irvine Building, University of St Andrews, St Andrews, Fife, Scotland KY16 9AL, United Kingdom

ARTICLE INFO

ABSTRACT

Comparing geographically referenced maps has become an important aspect of spatial ecology (e.g. assessing change in distribution over time). Whilst humans are adept at recognising and extracting structure from maps (i.e. identifying spatial patterns), quantifying these structures can be difficult. Here, we show how the Structural Similarity (SSIM) index, a spatial comparison method adapted from techniques developed in computer science to determine the quality of image compression, can be used to extract additional information from spatial ecological data. We enhance the SSIM index to incorporate uncertainty from the underlying spatial models, and provide a software algorithm to correct for internal edge effects so that loss of spatial information from the map comparison is limited. The SSIM index uses a spatially-local window to calculate statistics based on local mean, variance, and covariance between the maps being compared. A number of statistics can be calculated using the SSIM index, ranging from a single summary statistic to quantify similarities between two maps, to maps of similarities in mean, variance, and covariance that can provide additional insight into underlying biological processes. We demonstrate the applicability of the SSIM approach using a case study of sperm whales in the Mediterranean Sea and identify areas where local-scale differences in space-use between groups and singleton whales occur. We show how novel insights into spatial structure can be extracted, which could not be obtained by visual inspection or cell-by-cell subtraction. As an approach, SSIM is applicable to a broad range of spatial ecological data, providing a novel, implementable tool for map comparison.

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1. Introduction

Ecological systems typically exhibit spatial heterogeneity arising from underlying processes that influence species occurrence, abundance, and diversity. Characterising spatial heterogeneity, and changes to it, are essential to understanding the structure of ecological systems (Fortin and Dale, 2005). Spatial ecological data range from spatially discrete events or individuals, represented as basic plots of locations in space referenced by a point (e.g. vegetation assemblages in geographical space, Penttinen et al., 1992), to distributions of species across habitats, characterised by continuous density maps (McKinney et al., 2012). Geographically referenced maps are an effective way to convey complex spatial information

because the human visual system excels at recognising structure in these familiar and intuitively read images. However, visual interpretation of spatial patterns in such maps is subjective (Da Silva-Buttkus et al., 2009), which can be further complicated by the characteristics of the mapped data, such as scale (e.g. grain and extent) and the particular cartographic representation used (e.g. projection, colour, symbology) (MacEachren, 1995). Therefore, methods have moved towards objectively quantifying the patterns observed in mapped data to produce consistent and repeatable analyses (Fortin and Dale, 2005).

The comparison of two (or more) geographically referenced maps aims to characterise differences in spatial heterogeneity and structure, and calculate defined spatial metrics between them. The problem of map comparison (Jacquez, 1995) has been studied for decades by geographers (Tobler, 1965), as well as ecologists (Levine et al., 2009). There are many ecological applications where map comparison can lead to new insights. Ecological data often have intrinsic properties that make them challenging to compare spa-

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tially: data tend to be continuous-valued (e.g. spatially explicit model predictions) and have underlying spatial dependencies (e.g. neighbouring cells are not independent). However, there are few established spatial comparison techniques documented in the ecological literature directly relating to the type of problems outlined above, as available methods generally only address one or other of these properties.

In recent years, emphasis has been placed on comparisons of mapped categorical data (Hagen-Zanker and Lajoie, 2008) and methods for assessing spatial structure in maps of continuous valued data or spatially explicit model predictions on a regular spatial lattice remain limited in both scope and sophistication (Hagen-Zanker, 2006a). Cell-by-cell comparisons and non-spatially explicit indexes weighted by grid cell are widely used in remote sensing, but do not account for spatial dependencies between cells (Horn, 1966; Leitão et al., 2011). Likewise, Moran's I or Geary's C tests (Cliff and Ord, 1970) assess spatial autocorrelation but provide single indices across space, which do not retain locational information. Metrics used to investigate niche similarity between species distributions predicted with Environmental Niche Models also lose spatial information to give a single measure of overlap or equivalency (Warren et al., 2008). Overlap indices and tests for spatial autocorrelation measure only one form of spatial structure in the data, and this may not be sufficient for the ecological question being posed.

A Structural Similarity Index (SSIM index) was proposed originally by Wang et al. (2004) for comparing compression techniques used in digital imaging (e.g. JPEG compression). The index uses a spatially-local moving window to generate independent components relating to local similarities in the mean, variance, and spatial correlation between the two maps being compared. SSIM can assess continuous data and simultaneously considers local magnitude and spatial structure, making it suitable to be adapted for the application of comparing spatial ecological data. Map comparison methods to ecological problems should allow uncertainty associated with the data or model predictions to be included in the map comparison to aid interpretation. Ecological maps often have uncertainty estimates associated with each grid cell when values are obtained using spatially explicit predictive models (Rocchini et al., 2011), and these should be incorporated in a map comparison approach. Additionally, local statistics such as the SSIM index are susceptible to edge effects arising from the use of a spatially local neighbourhood (Boots, 2002). Edge effects (i.e. the inclusion of null areas outside the study) are exacerbated by irregularly shaped boundaries caused by arbitrarily shaped administrative units or geographical features (e.g. islands). These may or may not influence the spatial process under study. Ecological processes often change on or near boundaries (Wiens et al., 1985), for example, the boundary of the Antarctic Circumpolar Current affects the surrounding marine ecosystem (Tynan, 1998), and so these areas can be of specific interest. Therefore, we propose two enhancements to the SSIM index to address common issues faced in spatial ecological analysis by incorporating uncertainty associated with the underlying data into the map comparison, and correcting for edge effects. We demonstrate use of the SSIM methodology and our enhancements by applying them to a case study to compare habitat preference by groups and singletons of sperm whales (*Physeter macrocephalus,* Linneaus 1758) in the Mediterranean Sea (Pirotta et al., 2011).

2. Methods

2.1. Map comparison

Consider two continuous valued maps (A and B) each represented as regular grids. For each cell, a local neighbourhood is defined by (n) neighbouring spatial units given a weighting (w).

The size of the neighbourhood is user-defined, has a lower limit of 3×3 cells and can take any non-even value. Wang et al. (2004) proposed the use of a (circular) Gaussian weighting function of $w = \{w_i | i = 1, 2 \ldots, n\}$ where w_i is obtained from a Gaussian kernel centred on the focal cell. The standard deviation, $\sigma = n/3$, is normalised so that $\sum_{i=1}^{n} w_i = 1$.

The index i iterates through all n cells within each local region to produce means and variances for each map as well as covariance between the two gridded maps.

$$\mu_a = \sum_{i=1}^{n} w_i a_i \tag{1}$$

$$\sigma_a^2 = \sum_{i=1}^{n} w_i (a_i - \mu_a)^2 \tag{2}$$

$$\sigma_{ab} = \sum_{i=1}^{n} w_i (a_i - \mu_a)(b_i - \mu_b) \tag{3}$$

μ_a, σ_b^2, and σ_{ab} represent spatially local measures of mean, variance and covariance, computed for each cell, where a_i and b_i represent the values in cell i for maps A and B respectively. The three components of the SSIM method are then calculated from these statistics, giving spatially local measures of similarity in the mean, variance, and covariance of the two maps.

$$SIM(A, B) = \frac{2\mu_a\mu_b + c_1}{\mu_a^2 + \mu_b^2 + c_1} \tag{4}$$

$$SIV(A, B) = \frac{2\sigma_a\sigma_b + c_2}{\sigma_a^2 + \sigma_b^2 + c_2} \tag{5}$$

$$SIP(A, B) = \frac{\sigma_{ab} + c_3}{\sigma_a\sigma_b + c_3} \tag{6}$$

The statistics are named Similarity in Mean (SIM), Similarity in Variance (SIV), and Similarity in Pattern (SIP) of spatial covariance, so that they can be interpreted intuitively in ecological terms (Table 1). Constants (c_1–c_3) are used in equations (4)–(6) to aid stability when the denominators of the equations, sum of the squared means $\left(\mu_a^2 + \mu_b^2\right)$, sum of the squared variances $\left(\sigma_a^2 + \sigma_b^2\right)$, and product of the standard deviations ($\sigma_a\sigma_b$) are close to 0. Following guidelines proposed by Wang et al. (2004), the constants can be estimated heuristically from the range of values of the underlying maps being compared (R) together with k_1=0.01 and k_2=0.03. Therefore, $c_1 = (k_1R)^2$, $c_2 = (k_2R)^2$, and $c_3 = c_2/2$.

An overall measure for comparison can be computed as the product of all three components.

$$SSIM(A, B) = [SIM(A, B)]^{\alpha} \cdot [SIV(A, B)]^{\beta} \cdot [SIP(A, B)^{\gamma}] \tag{7}$$

Constants α, β, γ can be used to weight individual components in SSIM and can take any value where ($\alpha > 0$, $\beta > 0$, $\gamma > 0$). Default values of $\alpha = \beta = \gamma = 1$ are used for the case study below. The overall comparison measure meets the following criteria: (1) symmetry: $SSIM(A, B) = SSIM(B, A)$; (2) boundedness: $-1 \leq SSIM(A, B) \leq 1$; and (3) unique maximum: $SSIM(A, B) = 1$ if $A = B$. SSIM is bounded by $(-1,1)$ where -1 indicates complete dissimilarity between the spatial structure of the underlying maps, and 1 shows the maps are identical (Table 1). Similarity in pattern (SIP) of spatial covariance is of interest to ecologists because it reveals differences in spatial structure that are difficult to capture visually or through simple comparison methods such as direct map subtraction. In the context of species distribution models, low values ($SIP \to -1$) will show local-scale differences in space use that may indicate underlying mechanisms such as competitive exclusion, niche partitioning, or habitat segregation, whereas high values ($SIP \to 1$) could indicate areas where direct competition or some

Table 1
Description of local statistics calculated in SSIM index, using pairs of images (maps A and B) to demonstrate high and low similarity. The interpretation column provides a general ecological interpretation of each metric using the case example of one species in Map A and a different species in Map B.

Index	Description	Bounds	Interpretation	Map A	Map B
Similarity in means (SIM)	Ratio of twice the product of the local means to their summed squares.	(0, 1)	0 = Map A has high values; map B low values. The means are dissimilar (e.g. species have different local abundances).		
			1 = Both maps A and B have similarly high (or low) values (e.g. species have similar local abundances).		
Similarity in variance (SIV)	Ratio of twice the product of the local standard deviations to their summed variances.	(0, 1)	0 = Map A has high variance; map B low variance. The variances are dissimilar (e.g. one species is spatially clustered, the other has a homogeneous distribution).		
			1 = Both maps A and B have similarly high (or low) variance (e.g. both species have similar degrees of spatial clustering, or both have homogeneous local distributions).		
Similarity in pattern (SIP) of spatial covariance	Ratio of the local covariance to the product of the local standard deviations.	(−1, 1)	−1 = Map A has high values in some cells; Map B has high values in alternate cells. Spatial correlation is negative (e.g. species exhibit spatial partitioning).		
			0 = Map A and B exhibit no spatial correlation (e.g. species distributions are independent).		
			1 = Map A and B have high and low values in the same cells. Spatial correlation is positive (e.g. species are using the same resources, or have predator–prey interactions).		

form of ecological interaction, such as predation, are occurring. The means of each metric can be calculated to produce summary statistics ($\overline{SIM}$, $\overline{SIV}$, $\overline{SIP}$) if required. The mean of SSIM ($\overline{SSIM}$) will provide an overall metric of map comparison, capturing the similarities between means, variances, and covariance in a single value.

The mean and variance of each grid cell in the underlying maps are resampled to generate a series of realisations (N). SSIM statistics are calculated for each set of realisations ($1 \cdots N$) of the two maps being compared. A variance-adjusted measure of SSIM is calculated by taking the mean of each statistic over the resulting comparisons. Upper and lower 95% confidence limits of the statistics can be calculated from the mean and variance of the sampled comparisons. To correct for edge effects, a reflection algorithm is implemented to generate synthetic buffers and ensure the spatial extent of the map comparison is preserved (Appendix A in Supplementary).

2.2. Case study: sperm whales in the Mediterranean

2.2.1. Introduction

In the Mediterranean, a small population of sperm whales persist. Sperm whales show sexually dimorphic behaviour as adults: males become increasingly solitary as they mature, and segregate from long-term social units of adult females and their offspring, excepting short term associations for mating purposes (Whitehead, 2003). It is unclear what drives this segregation and hypothe-

ses include: groups of females outcompeting solitary males when exploiting mid-water squid patches, males and females having different dietary and hence habitat preferences, or higher male growth rates that require wider search areas to locate high prey densities (Whitehead, 2003). Understanding habitat use in areas where both sexes co-occur is of obvious interest with respect to these hypotheses. Pirotta et al. (2011) predicted habitat preferences of sperm whales in the waters around the Balearic archipelago in the Mediterranean Sea. In this area both groups (assumed to be female social units) and singleton whales (assumed to be males) were regularly observed, suggesting a breeding ground. Measures of uncertainty around the estimated probability of occurrence were obtained from the modelling process to characterise variance around the mean estimate in each grid cell. Uncertainty arises in all ecological models and could result, for example, from sampling design and data collection, the resolution of environmental variables used in the model, modelling process, or the dynamic nature of species' distribution (Rocchini et al., 2011; Tessarolo et al., 2014). The SSIM index and our enhancements can be implemented accounting for any sources of uncertainty. Here, we use habitat preference maps and associated uncertainty to compare spatial patterns of use between assemblages. We demonstrate that the proposed map comparison methodology can quantify differences in the local spatial patterns observed between the maps and
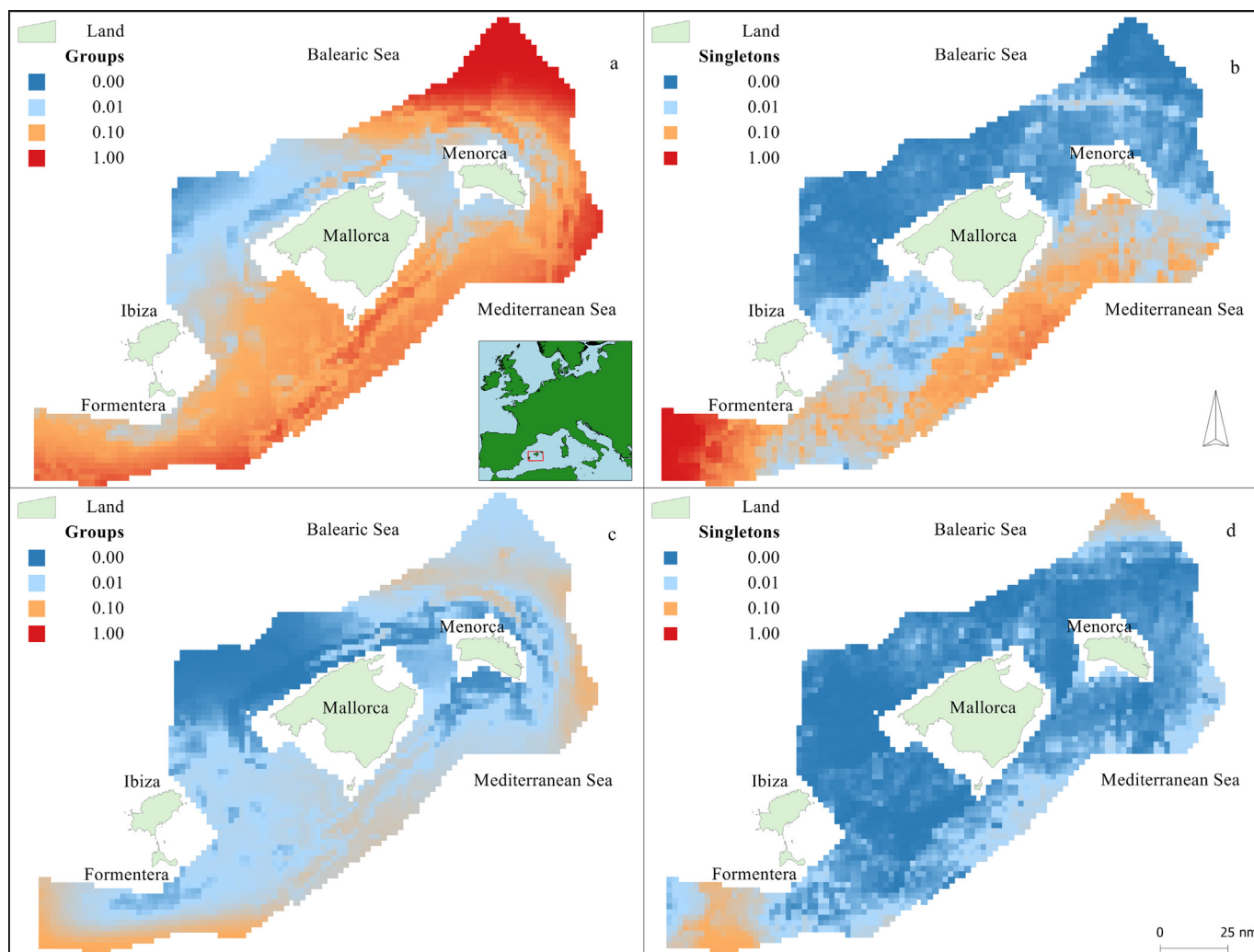
Fig. 1. Predicted probability of occurrence for both social assemblages: (a) groups; (b) singletons (c) variance in group presence; and (d) variance in singleton presence. (a) and (b) are modified from Pirotta et al. (2011). Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) shoreline data from NOAA were used, available to download from http://www.ngdc.noaa.gov/mgg/shorelines/gshhs.htmlhttp://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html.

provide novel biological insights not readily apparent from visual assessments alone.

2.2.2. Data

The study area was located from 38 to 41°N and 0.5–5°E, centred on the islands of Ibiza, Mallorca and Menorca (Fig. 1). Information on sperm whale occurrence was collected during dedicated summer research cruises covering the waters around the Balearic archipelago. Each cruise lasted for approximately a month and was repeated over 6 consecutive years (2003–2008). Whales were located and tracked acoustically from their echolocation clicks, and an encounter was defined as a period of continuous acoustic contact with one or more animals. Pirotta et al. (2011) used a Generalised Additive Modelling (GAM) approach to model sperm whale occurrence as a function of several environmental and temporal predictors, combined with Generalised Estimating Equations (GEEs) to account for autocorrelation in the residuals. Further details on the environmental datasets and analytical approach can be found in Pirotta et al. (2011) and are summarised here: Separate analyses were carried out for singletons and groups to determine whether habitat preference was characterised by different extrinsic drivers. The final model for sperm whale groups included latitude, longitude, weekly sea surface temperature (SST) and slope gradient. For singletons, latitude, longitude, year, monthly SST and slope aspect were retained by model selection. The authors noted

qualitatively different spatial patterns emerging for the two social assemblages in the final prediction maps, quantitatively supported by an inverse relationship with SST, and suggested that these might be the result of fine-scale habitat segregation.

2.2.3. Analysis

The predicted probability of presence of groups and singletons, and corresponding estimates of variance were mapped at a spatial resolution of 2 nautical miles (NM) on a regular grid. To calculate SSIM statistics, the size of the local neighbourhood for both maps should be defined by taking the nature of the underlying data and ecological process in question into account. Lewis et al. (2007) examined the nearest-neighbour distances between sperm whales in the Mediterranean Sea using a similar acoustic survey approach to data used in Pirotta et al. (2011) and found that animals defined as belonging to a 'cluster' mostly had an upper limit of 2.7 NM of perpendicular distance between them, whereas dispersed (singleton) animals were separated by distances beyond this threshold. The size of the local neighbourhood was defined in a 3×3 ($n = 9$) cell window (6 NM x 6 NM), such that the edge of the window was at least 2 NM (1 grid cell) from any animals encountered in the centre cell. A circular Gaussian weighting kernel ($w = \{w_i \mid i = 1,2\ldots,9\}$) with a standard deviation ($\sigma = n/3$) was set to 3 NM. Sensitivity tests were applied to verify that varying the size of local neighbourhood and using a Gaussian weighting kernel did not affect results
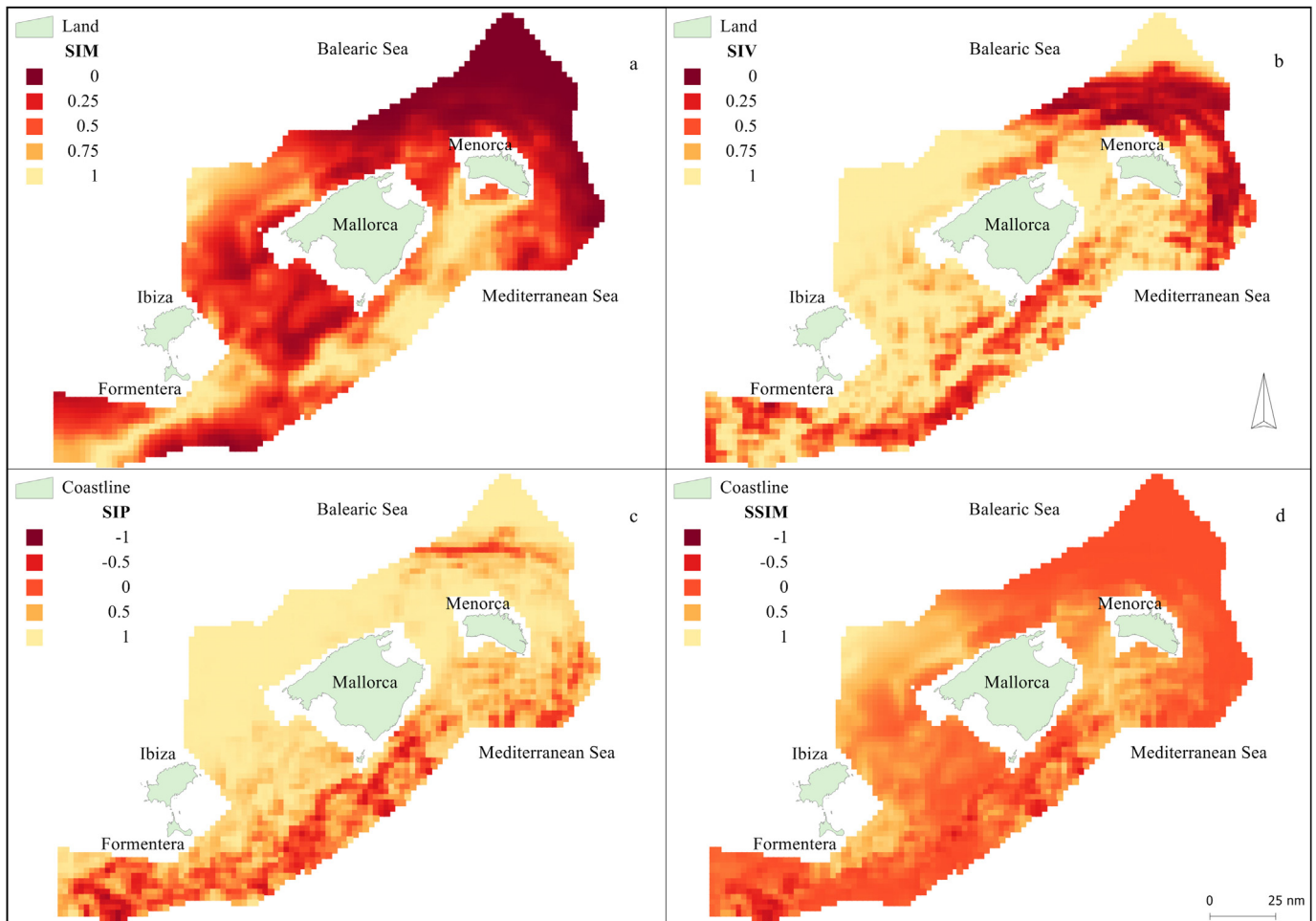
Fig. 2. Map comparison between the predicted probability of occurrences of group and singleton sperm whales. A reflection algorithm was used to counteract internal edge effects: (a) Similarity In Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (−1 to 1); and (d) Structural Similarity index (−1 to 1).

from the case study (Section 2.2.4 and Appendix B in Supplementary). Uncertainty from the underlying data was included in the map comparisons using parametric bootstrapping. Samples from a multivariate normal distribution were generated using model coefficients and each covariance matrix to produce 500 realisations of model coefficients for the group and singleton models. These were used to predict 500 sets of probabilities for the group and singleton models. SSIM statistics were calculated for each pair of maps generated from bootstrapped data. Mean and variance of predicted probabilities in each grid cell were taken for each statistic (SIM, SIV, SIP, and SSIM). All analysis was conducted using the statistical software package R (R Core Team, 2014), and code and data used for calculating the SSIM index can be obtained from Appendices C and D in Supplementary respectively.

2.2.4. Sensitivity testing

Sets of sensitivity tests were conducted to demonstrate how varying specific (user-defined) parameters could potentially affect results of the map comparison analysis for the sperm whale data: (1) A circular Gaussian weighting kernel was applied to the local neighbourhood window vs. no weighting; (2) the size of the local neighbourhood was varied, using 3×3, 5×5, and 7×7 grid cells; and (3) a reflection algorithm to correct for edge effects was applied vs. no edge correction. For Gaussian weighting tests, the size of the local neighbourhood (w) was set at 3×3 grid cells and the reflection algorithm was implemented. For local neighbourhood tests, Gaussian weighting and the reflection algorithm were applied. For edge

effects tests, the size of the local neighbourhood (w) was set at 3×3 grid cells and Gaussian weighting was applied. In all tests, $\sigma = n/3$ and only mean values from the underlying maps being compared were used. SSIM statistics were calculated for each set of tests and means and variances of each statistic (SIM, SIV, SIP, SSIM) were calculated to provide summary statistics. Welch two-sample t-tests were used to compare the SSIM statistic for each set of tests.

3. Results

SSIM was used to compare the predicted probability of occurrence between groups and singleton sperm whales (Fig. 2). Fig. 2a, showing similarity between the local means (SIM), aligns with visual differences seen between the underlying maps (Figs. 1a and b). Areas where SIM is close to 1 (yellow) are found in regions of the study area where habitat preference is high for both social assemblages (east and south of Mallorca, and east and south of Formentera), or low for both social assemblages (north-west of Mallorca). Values of SIM close to 0 (red) denote areas where one social assemblage has low habitat preference and the other has high habitat preference. An example is to the north of Menorca, where fewer data were collected: the sperm whale group model in particular was subject to sampling bias, resulting in a high estimate for habitat preference, whereas predicted probability of occurrence for singletons was low (Pirotta et al., 2011). Fig. 2b shows similarity in local variance (SIV) between the maps. Values close to 1 (yellow) show areas where assemblages have similar variance in the
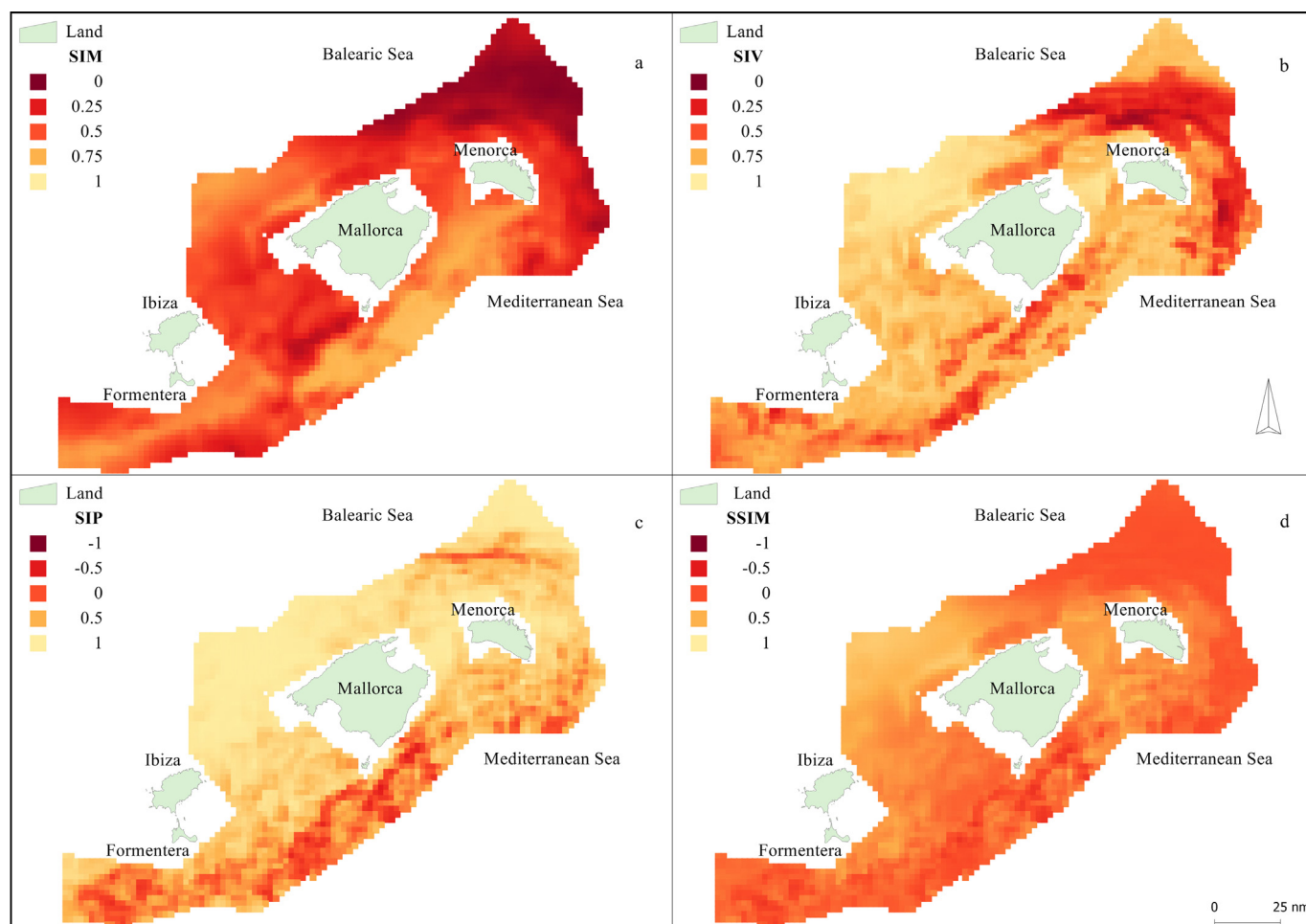
Fig. 3. Map comparison between the predicted probability of occurrence of group and singleton sperm whales using bootstrapped uncertainty from the habitat preference models of both social assemblages. A reflection algorithm was used to counteract internal edge effects: (a) Similarity In Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (−1 to 1); and (d) Structural Similarity index (−1 to 1).

probability of occurrence, and values close to 0 (red) show areas where the variance is different. For example, the area to the north of Menorca shows a transition zone where groups and singletons are using space differently—groups have heterogeneous, sporadic space use (i.e. high variance), singletons are utilising space in a consistent, homogeneous way (i.e. low variance). Fig. 2c shows the similarity in patterns (SIP) of spatial covariance between the maps. The SIP metric is the most difficult to capture through visual comparison of habitat use between groups and singletons (c.f. Figs. 1a and b). Values close to 1 (yellow) denote local regions where the spatial structure between predicted probability of occurrence of groups and singletons is similar, meaning grid cells with relative high and low variance are in the same locations in each underlying map. Underlying mechanisms of direct competition for resources could be occurring, for example to the north, east and west of Menorca, and north and west of Mallorca. Values close to −1 (red) indicate areas where local spatial structure is dissimilar, suggesting spatial partitioning may be occurring (north of Menorca in the transition zone discussed previously, and the southern edge of the study area). Fig. 2d shows SSIM, which is the product of the other three statistics. Differences in spatial structure detected in SIV (Fig. 2b) and SIP (Fig. 2c) at the southern edge of the study area remain apparent in the SSIM index. Some spatial structural similarities seen throughout Figs. 2a–c to the north-west and east of Mallorca, and south-east of Formentera are also retained in SSIM. The mean

value of SSIM was calculated ($\overline{SSIM} = 0.22$), showing positive spatial structure between the underlying maps.

Results incorporating uncertainty from the underlying maps into the comparison calculation are provided in Fig. 3, and show similar inferences to those in Fig. 2, although each of the four comparison metrics exhibit less extreme values. An area of particular interest is south of Mallorca (Fig. 3c), where SIP is close to −1 (red), characterising different spatial patterns in habitat use between groups and singletons. Fig. 4 focuses on this area, which is situated over the continental slope and has previously been identified as a feeding ground for sperm whales (Gannier and Praca, 2007; Gannier et al., 2002). Although Fig. 4a shows that both social assemblages have similar (high) habitat preference (SIM is close to 1), there is strong negative SIP in specific areas (Fig. 4c), indicating local-scale spatial partitioning between groups and singletons. These patterns occur mostly along bathymetric contours at depths ranging between 1000 to 2000 m. The spatial structure can be seen in SSIM (Fig. 4d).

The results of sensitivity tests are shown in Table 2 (visual results are available in Appendix B in Supplementary). When comparing Gaussian weighting vs. no weighting, there was no significant difference in $\overline{SSIM}$ (t = 0.06, p-value = 0.95). By varying the size of the local neighbourhood between 3 × 3 and 5 × 5 grid cells $\overline{SIV}$ and $\overline{SIP}$ show differences (calculated from the variance and covariance in the underlying maps being compared), leading to a significant t-test result when comparing $\overline{SSIM}$ (t = 4.14, p-value < 0.00005). Likewise,

Table 2

Results determining sensitivity of the SSIM index when user-defined parameters were varied: applying Gaussian weighting to the local neighbourhood vs. no weighting; varying the size of the local neighbourhood; and implementing the reflection algorithm vs. not countering for edge effects.

Sensitivity analysis	Parameters	SIM			SIV			SIP			SSIM			t-test on SSIM
		Mean	Low 95%CI	Upp 95%CI	Mean	Low 95%CI	Upp 95%CI	Mean	Low 95%CI	Upp 95%CI	Mean	Low 95%CI	Upp 95%CI	t; p-value
Weighting	Gaussian weighting	0.432	−0.183	1.048	0.741	0.169	1.313	0.654	−0.127	1.434	0.218	−0.293	0.729	0.06; 0.95
	No Gaussian weighting	0.432	−0.183	1.048	0.740	0.167	1.313	0.652	−0.130	1.435	0.218	−0.294	0.729	
Local neighbourhood	3 × 3 cells	0.432	−0.183	1.048	0.741	0.169	1.313	0.654	−0.127	1.434	0.218	−0.293	0.729	4.14; 0.00
	5 × 5 cells	0.433	−0.174	1.041	0.706	0.104	1.308	0.567	−0.229	1.362	0.191	−0.284	0.666	
	7 × 7 cells	0.435	−0.169	1.039	0.684	0.063	1.306	0.515	−0.284	1.314	0.177	−0.279	0.633	2.34; 0.02[a]
Edge effects	Reflection algorithm	0.432	−0.183	1.048	0.741	0.169	1.313	0.654	−0.127	1.434	0.218	−0.293	0.729	0.79; 0.43
	No reflection algorithm	0.435	−0.177	1.047	0.734	0.155	1.314	0.639	−0.150	1.427	0.212	−0.287	0.712	

[a] 5 × 5 Window vs. 7 × 7 were compared to give this t-test result.

when comparing 5×5 and 7×7 tests, there is a significant difference between $\overline{SSIM}$ (t = 2.34, p-value = 0.02). When the reflection algorithm was not applied, the value of $\overline{SSIM}$ was not affected significantly but there was a reduction in the spatial extent of the map comparison (as values for edge cells could not be calculated) (Appendix B in Supplementary).

4. Discussion

We have described an approach to objectively compare spatial patterns between two continuous valued maps. We enhanced the original SSIM index (Wang et al., 2004) by incorporating uncertainty from underlying maps into the comparison calculation and correcting for edge effects. Application of the SSIM approach, including our enhancements, was demonstrated with a case study using sperm whale distribution data in the Mediterranean Sea. Quantitative map comparison tools are currently limited in their extent and application in the ecological literature (Hagen-Zanker, 2006b; Robertson et al., 2014), possibly because ecological data have characteristic properties such as continuous values and inherent spatial dependencies that make quantifying the underlying spatial structure between geographically referenced maps challenging. As well as accounting for these characteristics, the SSIM index has several key advantages making it ideal for broader ecological applications. First, the methodology can be easily implemented regardless of the prediction or estimation method used to obtain the underlying maps. For instance, a useful application of the method would be to compare two maps where different statistical methods were used to address similar questions. Second, the SSIM index produces a number of underlying statistics, as well as an overall measure of similarity in spatial structure. By comparing local means, variances, and covariance between underlying maps, different aspects of spatial patterns are characterised, potentially providing insight into underlying processes that drive these patterns. Finally, the size of the local neighbourhood in the map comparison calculation is user-defined. Prior knowledge of spatial scale of the data can be used to inform the map comparison analysis, providing more meaningful results.

Dependent on the size of the local neighbourhood, edge effects occur when comparing maps because non-valued cells beyond the boundary of the study area are included. To ensure the map comparison produced the same spatial extent as the underlying maps, a reflection algorithm was chosen to correct for edge effects because of its ability to deal with complex edges and ease of implementation. The algorithm reflected known data along edges to extrapolate outside of the study area. A limitation of this method is that it can emphasise fine-scale or local patterns in areas where it is implemented, and so care should be taken when interpreting results close to edges in the study area.

The definition of spatially local neighbourhoods and the effects of their size have been well studied (Chefaoui, 2014; Long et al., 2010; Zurlini et al., 2007). In ecology, local neighbourhood size must be considered in the context of spatial resolution of the data and the underlying ecological processes being investigated (Wiens, 1989; Wu, 2004). Therefore, local neighbourhood sizes are often varied to examine their influence on results and inferences. However, there can still be subjectivity in selecting the appropriate local scale for spatial analysis (Nelson and Boots, 2008). In the case study, a local neighbourhood was selected based on the spatial scale present in the ecological process (i.e. the distance between the assemblages being compared). As the local neighbourhood size increases fine-scale differences in patterns identified through SSIM will disappear, resulting in a smoothing effect. Similarly, using the minimum local neighbourhood (3×3 grid squares) may produce results that show fine-scale differences in patterns which do not make sense ecolog-
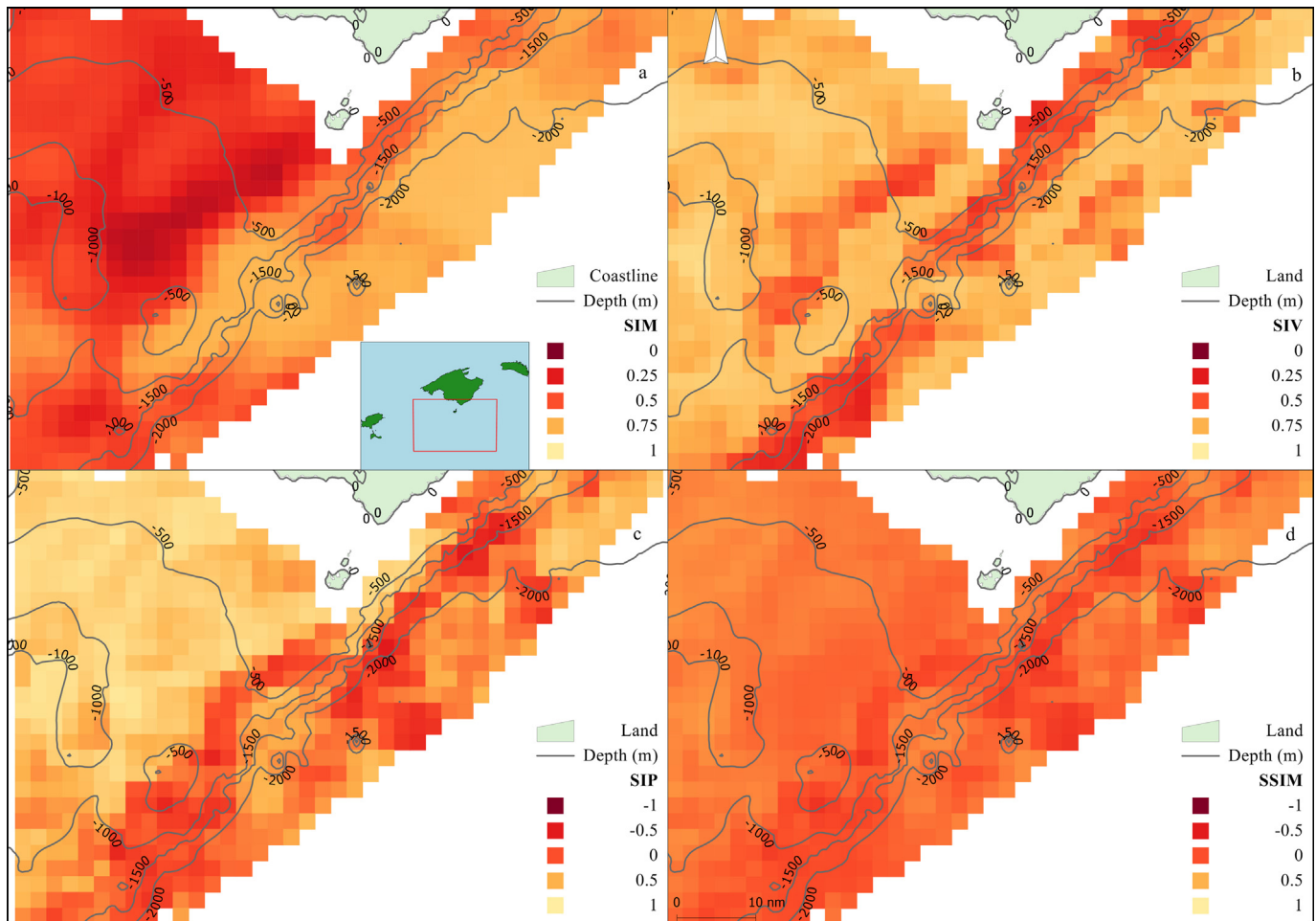
Fig. 4. Map comparison between the predicted probability of occurrence of group and singleton sperm whales using bootstrapped uncertainty from the habitat preference models of both social assemblages. A reflection algorithm was used to counteract internal edge effects. Focusing on the area of interest south of Mallorca: (a) Similarity In Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (−1 to 1); and (d) Structural Similarity index (−1 to 1).

ically. We recommend use of a local neighbourhood in the SSIM index that bears relation to: (1) the scale of underlying data (e.g. movement of animals) represented in the maps being compared, (2) ecological questions being investigated through map comparisons, and, (3) scale-dependent patterns of underlying ecological processes being investigated.

4.1. Case study

The map comparison showed differences in space use between groups and singleton sperm whales. The area south of Mallorca was also identified by Pirotta et al. (2011) as important to both social assemblages. Data sampling effort was greatest here and therefore groups and singleton models suffered less from sampling bias than in other areas. In this area, both social assemblages had high predicted probability of occurrence. Statistical differences in patterns of space-use were associated with fine-scale features at depths between 1000 and 2000 m, and the probability of occurrence for both social assemblages was previously found to be driven by bathymetric features (Pirotta et al., 2011). Although the sex of animals included in the study was not verified, singletons showed diving behaviour typical of solitary males, and groups of sperm whales are generally associated with adult females and their immature offspring (Drouot et al., 2004; Whitehead, 2003). Whitehead (2003) suggested that reduced foraging success for males in areas where both social assemblages exist may be a result of resource

competition. Our results reveal that groups and singletons do interact spatially in some mutually exclusive way. This has implications for both understanding local space use, and informing more general hypotheses about the evolution of extreme behavioural sexual dimorphism in sperm whales (Whitehead and Weilgart, 2000). The results provide a specific target area so that efficient resources can be put into studying sexual segregation of groups and singletons. Hypotheses could be investigated to determine whether patterns of mutually exclusive (presumed) foraging of groups and individuals show stable resource partitioning (in which case both social assemblages may be foraging optimally), or whether patterns are the result of one social assemblage being outcompeted and forced to utilise sub-optimal habitat. Sensitivity tests indicated that comparison results were affected by neighbourhood size, and any interpretation should take account of this.

4.2. Broader applications and further development

Comparisons of spatially referenced data provide a mechanism for linking observed spatial patterns with underlying ecological processes (Turner, 1989). Methodology presented here has wider applications for ecology, where quantitative comparisons of spatial patterns are often required to understand underlying processes and guide management decisions. Application of the SSIM index with our enhancements provides spatially explicit comparisons to identify areas where there are underlying differences in space-

use. There are many applications to spatial ecology problems such as identifying areas of conflict between anthropogenic activities and wildlife: depredation on domestic livestock and farmed species by apex predators (Berland et al., 2008; Ripple et al., 2014; Suryawanshi et al., 2013). An important application is the assessment of change in distribution between and within species, such as comparing density maps obtained using different methods (Bailey et al., 2014), assessing competition and spatial segregation between species (Suryawanshi et al., 2013; Wilson, 2010), and seasonal changes in distribution (Millspaugh et al., 2015).

The Marine Strategy Framework Directive uses an ecosystem-based approach to management of anthropogenic activities within the marine environment (Olenin et al., 2010). Under this framework, ecosystems are assessed through a set of environmental abundance and distribution indicators to determine conservation status. Spatially-explicit indicators such as biodiversity indices (species richness and diversity) present mean values over time (Piroddi et al., 2015). The SSIM index and enhancements presented here can be used to elevate these indicators to a spatio-temporal context and assess biodiversity over time. When used in conjunction with abundance estimates, these can further inform the spatial management process.

The methodology could be developed further. Currently, spatial resolution and extent of the maps being compared must be regularly spaced and identical, and the case study used to demonstrate the methodology benefitted from having these characteristics. However, comparing animal distributions (e.g. using line transect data from animal sightings surveys) may result in varying spatial resolution and extent because sampling effort and survey area can change over time. Adapting SSIM methodology to allow for maps with non-regular lattices and point-process patterns to be compared, would be beneficial for effective analyses. For longer time-series (Bailey et al., 2014) or multiple species comparisons (Wilson, 2010), map comparison functionality could be extended to compare more than two maps at once, either sequentially, or through pair-wise comparisons.

5. Conclusions

The SSIM index and enhancements presented here offer a comprehensive tool to objectively compare spatially explicit ecological data within an implementable framework. An advantage of the SSIM index is that different aspects of spatial comparison can be investigated: maps of SIM, SIV, and SIP (relating to similarities in local means, variances, and covariance, respectively) can be calculated to reveal spatial patterns that cannot be seen through visual inspection of the underlying maps. The SSIM metric summarises SIM, SIV, and SIP into one map because summary statistics are often required to condense information. This can be further summarised by calculating the mean over SSIM to give a single value representing similarity between the underlying maps.

We presented enhancements to the SSIM index by incorporating uncertainty from the underlying maps and correcting for edge effects so that the methodology can be broadly applied to many types of spatial ecological data. Using an ecological case study to compare groups and singletons sperm whale distribution in the Mediterranean Sea, we demonstrated the presence of local-scale spatial structure that could not be detected either visually or using map subtraction techniques. We found that in these areas where (presumed) foraging was taking place, singletons and groups of whales were spatially mutually exclusive. This enabled us to recommend that future behavioural studies focusing on interactions between singletons and groups of whales whilst foraging could most effectively be carried out in the areas of interest we have identified.

Appendices. Supplementary Material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.05.051.

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The following supplements accompany the article

Novel application of a quantitative spatial comparison tool to species distribution data

Esther L. Jones*, Luke Rendell, Enrico Pirotta & Jed A. Long

*Corresponding author: el298@st-andrews.ac.uk

Appendix A - Edge effects

Edge effects (i.e. the inclusion of null areas outside the study region) are encountered in a number of problems such as point pattern analysis (Gignoux et al., 1999; Haase, 1995), geostatistics (Xu and Dowd, 2012), and local regression models (Fotheringham et al., 2002). Edge effects are exacerbated by irregularly shaped boundaries caused by arbitrarily shaped administrative units or geographical features (e.g. islands) that may influence the spatial process under study. In order to account for edge effects one of three general methodologies are typically used: (1) exclude edge data (i.e. those locations where the spatially local neighbourhood extends beyond the study area) from final results (Ripley, 1991); (2) buffer the study area with empirical or synthetic data (Haase, 1995; Sterner et al., 1986); or (3) re-shape the local neighbourhood in the presence of an edge (Fotheringham et al., 2002; Getis and Franklin, 1987; Gignoux et al., 1999). Excluding edge locations has the undesirable effect of reducing the study area proportional to the local neighbourhood size. This is especially problematic for ecological studies where important spatial processes may occur near study site boundaries (Tynan, 1998). Increased sampling effort to collect additional empirical data is not always feasible, and is only realistic where the spatial process continues unabated outside of the study area edges. In many cases, such a sampling strategy cannot be employed due to the nature of the edge (e.g. a boundary such as a coastline). Any of the above strategies for mitigating edge effects can be readily implemented with the SSIM index.

Here we employ a reflection algorithm that is appropriate with regular lattice (gridded) data to generate a buffer of synthetic data around the study area (Figure A1). Let $Z(x,y)$ be the value of the known data at location (x, y) where x and y index columns and rows. Let the parameter n be the size of the spatial local neighbourhood to be used in analysis (e.g. 7 in a 7 x 7 kernel window), which controls how many iterations ($n/2$-1) are required. The reflection algorithm is a four-step process, and begins with the incrementing parameter $k = 1$.

Define all edge cells in the map as the set $E\left\{e\left(x,y\right)\right\}$

For each edge cell calculate values of the reflected synthetic data, $\hat{Z}_e$ using:

$$\hat{Z}_e\left(x, y\right) = \frac{Z(x,y-k)+Z(x,y+k)+Z(x-k,y)+Z(x+k,y)}{m} \quad (A1)$$

where m is the number of non-null Z values in the calculation.

For any edge cell, e^*, that is null after step 2 (i.e. outer corners) calculate $\hat{Z}_{e*}$ using:

$$\hat{Z}_{e*}\left(x, y\right) = \frac{Z(x-k,y-k)+Z(x-k,y+k)+Z(x+k,y+k)+Z(x+k,y-k)}{m} \quad (A2)$$

$Z = \{Z, \hat{Z}\}$. If $k < n$ increment k by 2 and return to step 1, otherwise the algorithm is complete.
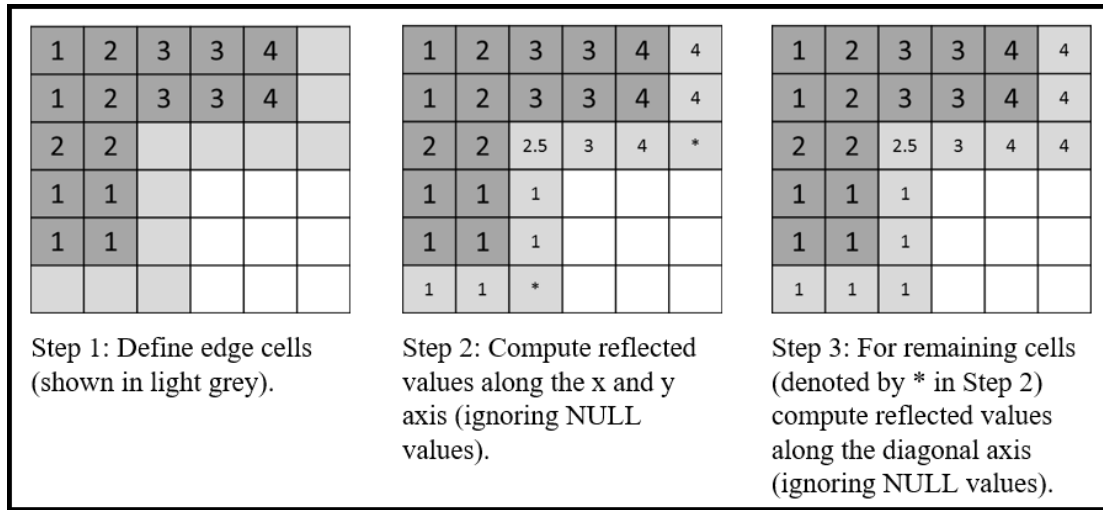
Figure A1. Description of steps 1–3 in the reflection algorithm. The example is shown for $k = 1$, but the algorithm is extensible to larger windows.

Appendix B - Sensitivity analysis

Sets of sensitivity tests were conducted to demonstrate how changing specific user-defined parameters could potentially affect results of the map comparison analysis: (1) A circular Gaussian weighting kernel was applied to the local neighbourhood window vs. no weighting; (2) the size of the local neighbourhood was varied, using 3x3, 5x5, and 7x7 grid cells; and (3) a reflection algorithm to correct for edge

effects was applied vs. no edge correction.

Method

For Gaussian weighting tests, the size of the local neighbourhood (w) was set at 3x3 grid cells and a reflection algorithm was implemented. For local neighbourhood tests, Gaussian weighting and reflection algorithm were applied. For edge effects tests, the size of the local neighbourhood (w) was set at 3x3 grid cells and the Gaussian weighting was applied. In all tests, $\sigma = n \mathbin{/} 3$ and only mean values from the underlying maps being compared were used. SSIM statistics were calculated for each set of tests and means and variances of each statistic (SIM, SIV, SIP, SSIM) were calculated to provide summary statistics. Welch two-sample t-tests were used to compare the SSIM statistic for each set of tests.

Results

Figures B1 and B2 show map comparisons when a Gaussian weighting was applied to the local neighbourhood and no weighting was applied, respectively. Figures B1, B3, and B4 show map comparisons where the local neighbourhood is 3x3, 5x5, and 7x7 grid cells, respectively. As the size of the local neighbourhood increases, local-scale features from the map comparison show less prevalence. However, even when a large (when compared to the scale of the local features) local neighbourhood (7x7) is used, spatial partitioning between groups and singletons identified in the main paper can be seen (Figure B4d). Figure B1 shows the results of applying a reflection algorithm to correct for edge effects. Figure B5 shows that when edge effects are not countered, the spatial extent of the map comparison is reduced due to missing values.
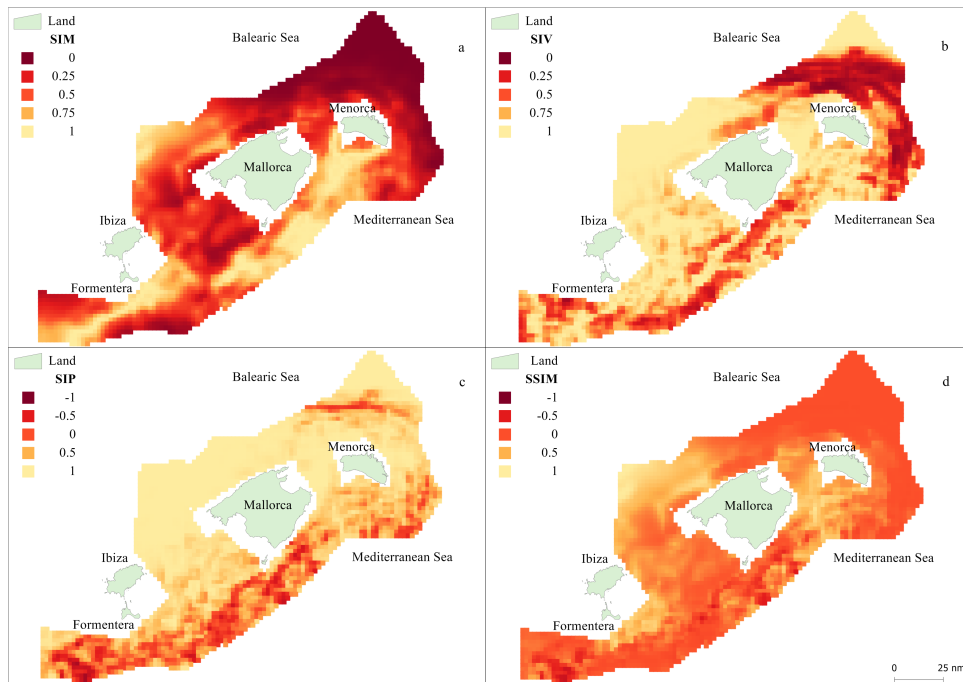
Figure B1. Map comparison between the predicted probability of occurrences of group and singleton sperm whales using a Gaussian weighting (w=3x3 and reflection algorithm implemented) (from top-left): (a) Similarity in Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (-1 to 1); and (d) Structural Similarity index (-1 to 1).
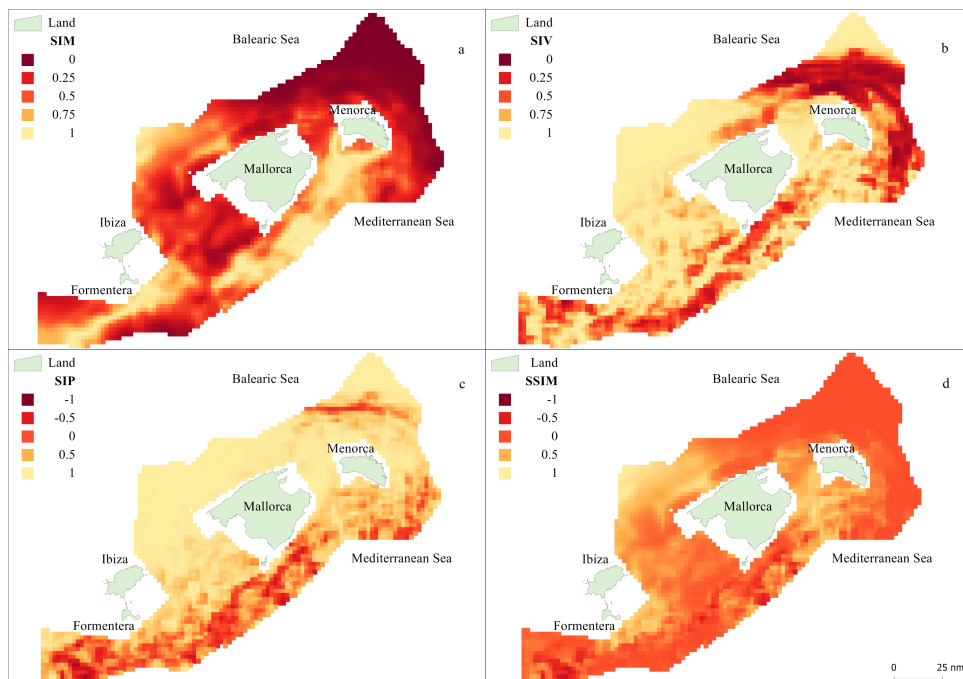
Figure B2. Map comparison between the predicted probability of occurrences of group and singleton sperm whales using **no weighting function** (w=3x3 and reflection algorithm implemented) (from top–left): (a) Similarity in Means (0–1);

(b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (-1 to 1); and (d) Structural Similarity index (-1 to 1).
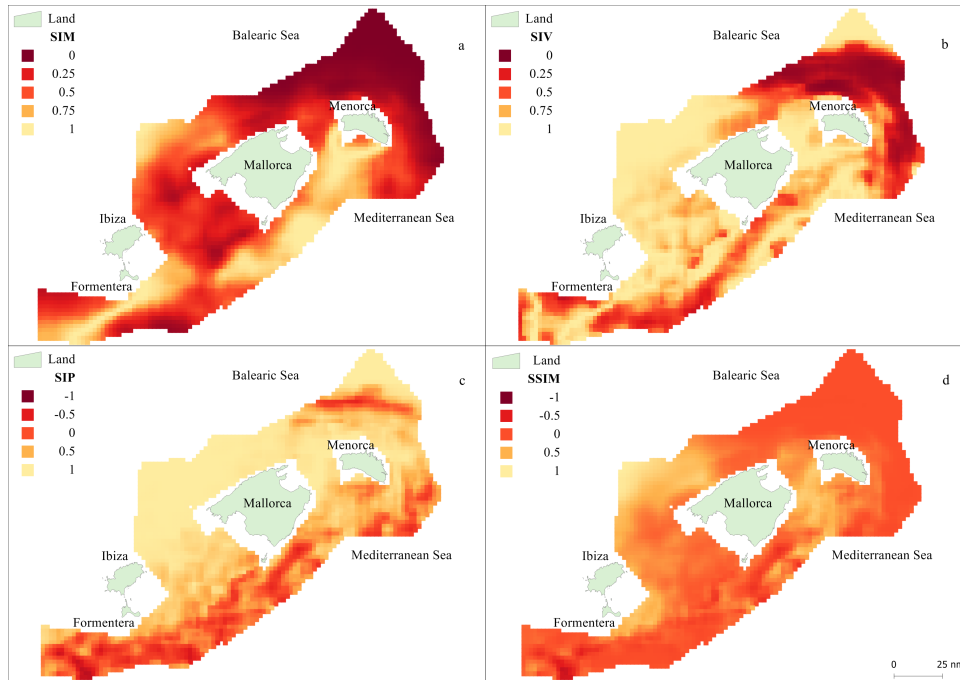
Figure B3. Map comparison between the predicted probability of occurrences of group and singleton sperm whales using a **local neighbourhood of 5x5 grid cells** (Gaussian weighting and reflection algorithm implemented) (from top-left): (a) Similarity in Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (-1 to 1); and (d) Structural Similarity index (-1 to 1).
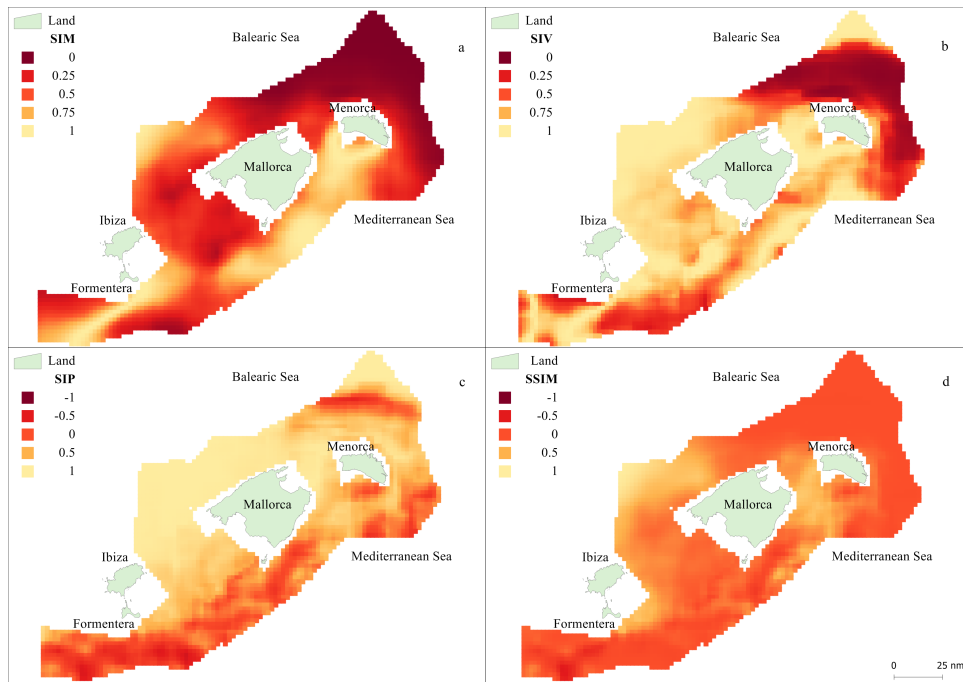
Figure B4. Map comparison between the predicted probability of occurrences of group and singleton sperm whales using a **local neighbourhood of 7x7 grid cells** (Gaussian weighting and reflection algorithm implemented) (from top-left): (a) Similarity in Means (0–1); (b) Similarity In Variance (0–1); (c) Similarity In Pattern of spatial covariance (-1 to 1); and (d) Structural Similarity index (-1 to 1).
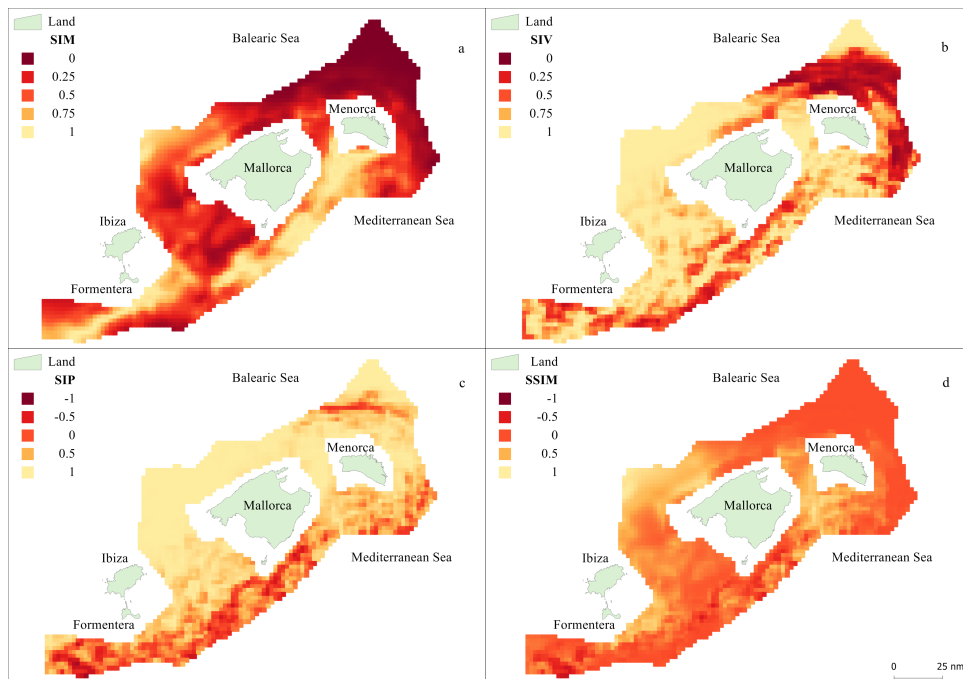
Figure B5. Map comparison between the predicted probability of occurrences of group and singleton sperm whales with no correction for edge effects (w=3x3 and

Gaussian weighting implemented) (from top-left): (a) Similarity in Means (0-1);
(b) Similarity In Variance (0-1); (c) Similarity In Pattern of spatial covariance (-1
to 1); and (d) Structural Similarity index (-1 to 1).

Appendix C - R code

```
library(maptools)
library(geepack)
library(splines)
library(SpatialTools)



#***********************************************************
#SSIM - R implementation of the Structural Similarity
#Index using raster package
#***********************************************************


library(raster)  ### Requires raster >= 2.3-12


#Function for iterative edge correction via map
#reflection (and averaging)
edge.cor.ref <- function(ras,w){
        iter.edge.cor.ref <- function(ind, ras, cel){
                #reflect along vertical/horizontal edges
                i <- cel*2-1
                col. <- colFromCell(ras,ind)
                row. <- rowFromCell(ras,ind)
                cols <- c(col.-i, col.,   col.+i, col.)
                rows <- c(row.,   row.-i, row.,
row.+i)
                celly <- cellFromRowCol(ras,rows,cols)
                subr <- ras[celly]
```

```
                    est <- mean(subr,na.rm=TRUE)
                    if (!is.nan(est)){
                            return(est)
                    } else {
                            #Reflect along diagonal if it is
                            #only corner connected.
                            cols <- c(col.-i, col.-i,
                                    col.+i, col.+i)
                            rows <- c(row.-i, row.+i,
                                    row.+i, row.-i)
                            celly <- cellFromRowCol(ras,
                                    rows,cols)
                            subr <- ras[celly]
                            est <- mean(subr,na.rm=TRUE)
                            if (!is.nan(est)){
                                    return(est)
                            } else {return(NA)}
                    }
            }
            #-------------
            #Assume NA values (edge padding or donut holes)
            #exist for edge correction.
            for (cel in 1:w){
                    temp <- boundaries(ras,type='outer')
                    loc <- Which(temp==1,cells=T)
                    for (ind in loc){
                            ras[ind] <- iter.edge.cor.ref(ind.
                                    ras,cel)
                    }
            }
    return(ras)
}
```

```r
#Gaussian filter weights matrix
filter.g <- function(w,sigma){
        f.g <- function(x,y,sigma){ (1/(2*pi*sigma^2))
                        *exp(-(x^2+y^2)/(2*sigma^2))}
        w.i <- seq(-w,w,1)
        xy <- expand.grid(x=w.i,y=w.i)
        xy$w <- f.g(xy$x,xy$y,sigma)
        w.m <- matrix(xy$w,nrow=length(w.i),byrow=T)
                /sum(xy$w)
        return(w.m)
}


#==========================================
ssimMap <- function(img1, img2, w=3, sigma=1.5,
        gFil=FALSE, outer.edge.pad=FALSE,
        edge.cor=FALSE) {

        #Check to see if extents are equal
        img1.extent <- extent(img1)
        img2.extent <- extent(img2)
        img1.na <- Which(is.na(img1),cells=TRUE)
        if (img1.extent != img2.extent){stop('Warning:
SSIM calculation aborted. The raster extents
do not match.')}

        #set constants
        l <- max(cellStats(img1, max),
                cellStats(img2, max))
        globalMin <- abs(min(cellStats(img1, min),
```

```
                        cellStats(img2, min)))
l <- l - globalMin
k <- c(0.01, 0.03)
C1 <-(k[1]*l)^2
C2 <-(k[2]*l)^2
C3 <-C2/2


#Create Null filter
filterx <- matrix(1,ncol=w*2+1,nrow=w*2+1)
            /(w*2+1)^2
if(gFil) {
        #create Gaussian filter
        filterx <- filter.g(w,sigma)
}


#Optionally pad edges with NA's for
#edge correction
if (outer.edge.pad){
        img1 <- extend(img1,2*w)
        img2 <- extend(img2,2*w)
}


#Compute iterative edge correction 'reflect'
if (edge.cor=='reflect'){
        img1 <- edge.cor.ref(img1,w)
        img2 <- edge.cor.ref(img2,w)
}


#get mu
mu1 <- focal(img1, filterx)
mu2 <- focal(img2, filterx)
```

```r
        sig1 <- abs(focal(img1*img1,filterx)
                - mu1*mu1)^0.5
        sig2 <- abs(focal(img2*img2,filterx)
                - mu2*mu2)^0.5
        #sig12 relates to correlation
        sig12 <- focal(img1*img2, filterx) - mu1*mu2


        #compute components
        L <- ((2*mu1*mu2)+C1) / (mu1^2 + mu2^2 + C1)
        C <- ((2*sig1*sig2)+C2) / (sig1^2 + sig2^2 + C2)
        S <- (sig12 + C3) / (sig1 * sig2 + C3)
        #compute SSIM
        SSIM2 <- L * C * S


        #Compute RasterBrick
        ssim.brick <- brick(SSIM2, L, C, S)
        ssim.brick <- crop(ssim.brick,img1.extent)
        ssim.brick[img1.na] <- NA


        ssim.brick@data@names <- c('SSIM', 'SIM',
                                        'SIV', 'SIP')
        return(ssim.brick)
}



###################################################
# SSIM comparisons using paramteric bootstrapping &
# reflection edge-correction algorithm
###################################################
dat<-read.csv("Balearics_dataset.csv",header=T)


n=500     # Define number of boostraps
```

```
w <- 1      # window size in pixels - window
            # size = (2w+1)^2 , w=2 is a 5x5 window
sigma <- ((2*w+1)^2)/3  # sigma of gaussian window


#**********************************************
# Singletons
#**********************************************


# To select only sightings with single males
dat1<-subset(dat,Group!=1)


# Fit single model
mod_single<-geeglm(Pres ~ bs(Lat,knots=mean(Lat))+
        bs(Long,knot=mean(Long))+as.factor(Year)
        +SST_monthly+bs(Aspect,knots=mean(Aspect)),
        family=binomial, corstr="independence",id=Line_Id,
        data=dat1)


# Bootstrap model coefficients
BootstrapParametersSingles<-rmvnorm(n, coef(mod_single),
             summary(mod_single)$cov.unscaled)


# Import the prediction dataset as a shapefile
sshape <- (readShapeSpatial("Prediction_final_
           single_2005.shp",
        proj4string=CRS("+proj=utm +ellps=WGS84
           +datum=WGS84 +zone=31 +north +units=m")
        , repair=T))
        # Read in *.shp file
# Define general raster
r <- raster(xmn=bbox(sshape)[1,1],
```

```
        xmx=bbox(sshape)[1,2],

        ymn=bbox(sshape)[2,1],

        ymx=bbox(sshape)[2,2],

        crs="+proj=utm +ellps=WGS84 +datum=WGS84
         +zone=31 +north +units=m",

        resolution=((3706*8)+3)/8, vals=NULL)
## Rasterize the shapefile
rs <-rasterize(sshape,r)


snewdata <- data.frame(Long=values(rs)[,3],

        Lat=values(rs)[,4],

        Aspect=values(rs)[,5], Year=values(rs)[,6],

        SST_monthly=values(rs)[,7])


# Set up a matrix for the predictions to go into
smatrix <- matrix(data = NA, nrow = nrow(snewdata),

        ncol = n, byrow = FALSE, dimnames = NULL)


for (i in 1:n) {
        # Substitute the model coefficients
        #for each of the bootstraps
        mod_single$coefficients <-
        BootstrapParametersSingles[i,]
        # predict
        smatrix[,i] <- predict(mod_single,
                        newdata=snewdata,
                        type="response")
}



#*******************************************
# Groups
```

```
#*********************************************


# To select only sightings with groups
dat2<-subset(dat,Group!=0)


# Fit group model
mod_group<-geeglm(Pres ~ bs(Lat,knots=mean(Lat))+
            bs(Long,knot=mean(Long))+
            bs(SST_weekly,knots=mean(SST_weekly))+
            bs(Slope1x,knots=mean(Slope1x)),
            family=binomial,
            corstr="independence",id=Line_Id,data=dat2)


# Bootstrap model coefficients
BootstrapParametersGroups<-rmvnorm(n, coef(mod_group),
        summary(mod_group)$cov.unscaled)


# Set up a matrix for the predictions to go into
gmatrix <- matrix(data = NA, nrow = nrow(values(rg)),
            ncol = n, byrow = FALSE, dimnames = NULL)


# Import the prediction dataset as a shapefile
gshape <- (readShapeSpatial("Prediction_final_group.shp",
            proj4string=CRS("+proj=utm +ellps=WGS84
            +datum=WGS84 +zone=31 +north +units=m"),
            repair=T)) # Read in *.shp file
## Rasterize the shapefile
rg <-rasterize(gshape,r)


gnewdata <- data.frame(Slope1x=values(rg)[,3],
            Long=values(rg)[,4],
            Lat=values(rg)[,5],
```

```
                SST_weekly=values(rg)[,6])


for (i in 1:n) {
        # Substitute the model coefficients for each
        # of the bootstraps
        mod_group$coefficients <-
        BootstrapParametersGroups[i,]
        # predict
        gmatrix[,i] <- predict(mod_group,
                        gnewdata, type="response")
}




#*******************************************************
# Comparisons
#*******************************************************
# Set up output matrices
rSSIM <- rSIM <- rSIV <- rSIP <-
matrix(data = NA, nrow = nrow(snewdata), ncol = n,
        byrow = FALSE, dimnames = NULL)



# Comparison loop
for (j in 1:n) {


        # Define each raster in the loop j
        s <- g <- r
        values(s) <- smatrix[,j]
        values(g) <- gmatrix[,j]


        reflectedge <- ssimMap(s, g, w=w, sigma=sigma,
        gFil=TRUE, outer.edge.pad=TRUE,
```

```
        edge.cor='reflect')


        rSSIM[,j] <- values(reflectedge$SSIM)

        rSIM[,j]   <- values(reflectedge$SIM)

        rSIV[,j]   <- values(reflectedge$SIV)

        rSIP[,j]   <- values(reflectedge$SIP)


        print(j)


}




#****************************************************
# Take mean & variance of sampled comparisons
#****************************************************
meanSSIM <- apply(rSSIM, 1, mean)

varSSIM <-  apply(rSSIM, 1, var)

meanSIM <- apply(rSIM, 1, mean)

varSIM <-  apply(rSIM, 1, var)

meanSIV <- apply(rSIV, 1, mean)

varSIV <-  apply(rSIV, 1, var)

meanSIP <- apply(rSIP, 1, mean)

varSIP <-  apply(rSIP, 1, var)
```

Appendix D - Data

Corresponding data for Appendix C - R Code is available to download from `https: //doi.org/10.1016/j.ecolind.2016.05.051`

References for Appendices

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Chapter 6

Discussion

An analytical framework to produce grey and harbour seal usage maps with accompanying uncertainty around the UK was developed in Jones *et al.* (2015). The framework was enhanced in Jones *et al.* (2017c) to produce fine-scale at-sea usage maps of harbour seals around Orkney and the north coast of Scotland. In Jones *et al.* (2017a), usage maps from Jones *et al.* (2015) and ship usage maps were used to quantify risk to seals of co-occurrence with vessels through identifying potentially acoustically sensitive areas. Sound exposure levels to vessel noise with associated uncertainty were predicted for individuals in an area with varying rates of co-occurrence, and validated using field sound measurements. A map comparison methodology was applied to an ecological case study in Jones *et al.* (2016), to compare groups and singleton assemblages of sperm whales in the Mediterranean Sea. Figure 1 shows a synthesis of the portfolio, ecological insights, and the outputs made available for practitioners.
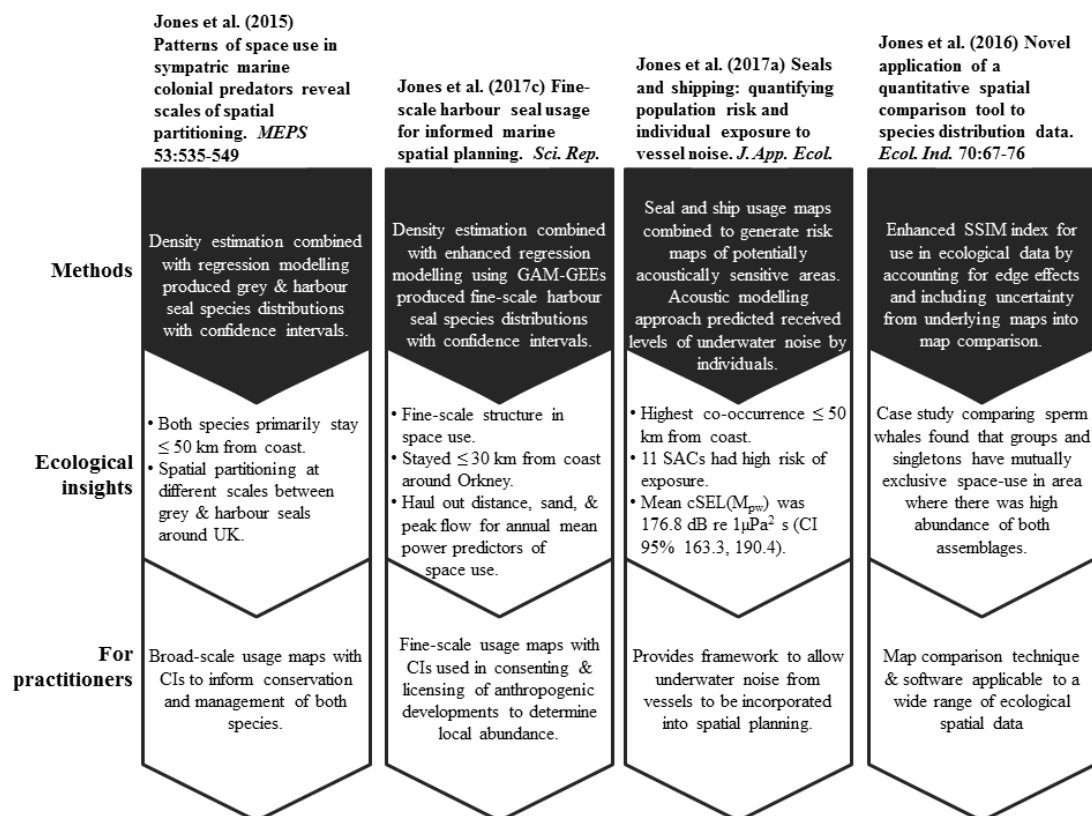

Fig. 1. Flowchart to highlight the contents of the portfolio, primary ecological insights, and the applied nature of each paper.

Patterns of space-use in sympatric marine colonial predators reveal scales of spatial partitioning

Grey and harbour seal usage maps with accompanying uncertainty were produced by developing an analytical framework to combine density estimation and regression modelling approaches. Fulfilling a conservation objective to identify seal space-use over a large spatial extent (i.e. nationally), the framework was developed so that space use could be characterised over the study area. A trade-off of the approach was that a coarse spatial resolution was used due to computational limitations. This was appropriate for understanding the broad-scale species distribution of grey and harbour seals, and has since been used by practitioners in many applied contexts: informing general conservation (Hayhow *et al.*, 2016), offshore energy strategic environmental assessment (Jones & Russell, 2016), licensing and consenting of offshore marine renewable developments (Jones & Matthiopoulos, 2011; Sparling *et al.*, 2012), and contributing to advice for the planning of Marine Protected Areas (Jones *et al.*, 2017b).

Grey and harbour seal usage maps showed how both species heavily utilised coastal areas close to their haul outs. Although both species are central-place foragers, individuals may transition between haul outs regularly; they are generalist predators, foraging on a wide range of benthic and demersal species in the neritic environment (Prime & Hammond, 1990), which vary spatially and temporally (Brown *et al.*, 2012; Wilson & Hammond, 2015; Hammond & Wilson, 2016). An advantage of characterising species distributions is that generalised movement patterns can be identified visually. In particular, contrasts between the two species showed that harbour seals exist in localised populations close to their haul outs, and stay within 50 km of the coast for over 95% of the time. An exception is the Wash, east England ($52.924°$ N, $0.249°$ E), a wide harbour with sand banks and mud flats (Hall *et al.*, 1998). The increasing harbour seal population consistently use haul outs within the Wash between travelling to offshore sandbanks (Duck *et al.*, 2015). Grey and harbour seals exhibit spatial partitioning in this region, with grey seals hauling out further north at Donna

Nook (53.476° N, 0.153° E), and utilising offshore sandbanks further north-east than harbour seals (McClintock *et al.*, 2012). Grey seal distribution was also concentrated close to their haul outs. However, by contrast with harbour seals, grey seal offshore distribution had spatial structure, and often connected haul outs between regions through corridors of offshore usage. Grey seals travel farther offshore than harbour seals, and are likely to be physiologically more capable of exploiting dynamic prey patches, which may drive differences in diet between the two species (Wilson & Hammond, 2016).

Seal Management Units (SMUs) inform the conservation management of the two species by dividing the UK into spatial regions (SCOS, 2015). Comparing predicted abundance of both species by grid cell as a measure of the distribution of each species relative to each other, it was shown that SMUs where grey and harbour seals overlapped heavily coincided with areas of harbour seal decline (3 – 18%) over the previous 10 years (2000 – 2010). By contrast, SMUs where grey and harbour seals exhibited spatial partitioning were in regions where harbour seal numbers remained stable or were increasing (SCOS, 2015). Although no causal link could be established in this analysis, the authors suggest that increasing grey seal numbers from lower historic levels to current population size may be adversely impacting harbour seal numbers in areas where there is strong spatial overlap between the species, either through direct competition for resources, or more indirect means. Since publication of this paper, evidence has arisen for interspecific (and possibly intraspecific) competition of grey seals with sympatric species through grey seal predation on harbour porpoise (Leopold *et al.*, 2015), juvenile grey seals (Bishop *et al.*, 2016; Brownlow *et al.*, 2016), and harbour seals (van Neer *et al.*, 2015). Examination of the carcasses showed that characteristic corkscrew lesions on dead stranded animals, that had previously been attributed to ship strikes (Bexton *et al.*, 2012), were in fact caused by grey seal predation. Matthiopoulos *et al.* (2014) showed that proximate causes for the Moray Firth harbour seal decline were juvenile mortality and decreased fecundity rate. It is likely that a combination of factors contribute to the harbour seal decline in regions of the UK; an increasing grey seal population creating interspecific competition directly through predation of harbour seals, and indirectly through competition for

shared resources. Additionally, pressure on the harbour seal population in some regions may cause outbreak of disease or reduced fitness of individuals through exposure to toxins (Hall & Frame, 2010; Jensen *et al.*, 2015).

Characterising species distributions is a central insight in ecology, and the grey and harbour seal usage maps have utility for informing conservation objectives and marine spatial planning. However, managing changes to populations facilitated by external pressures such as climate change and anthropogenic activities requires an understanding of ecosystem functioning to explicitly link source-based (e.g. foraging distributions) with process-based information (e.g. trophic linkages). Faecal analysis provides a comprehensive and quantitative estimate of prey composition. However, constraints in data collection and processing limit broad-scale analysis to decadal occurrences around the UK (in 1985, 2006, 2010; Wilson & Hammond (2015); Hammond & Wilson (2016)). Studies of faecal analysis have shown that diet composition of both grey and harbour seals, which vary regionally and seasonally, have changed over the past 20 years. For long-lived generalist predators like seals, changes in diet linked to shifts in foraging distribution and/or trophic level depredation are likely to manifest over long temporal scales, and other means of dietary analysis such as stable isotopes can provide a long-term view of trends in diet composition. Recent work has found that in the North Sea, the grey seal isotopic niche has contracted, signifying both a decline in trophic position and change in foraging habits over the 20th century (Hanson *et al.*, In review). Corroborating previous studies of an increased reliance on sandeels (*Ammodytes marinus*) by composition, long-term change in diet could be the response of grey seals adapting to larger prey items being removed from the ecosystem by overfishing (Speirs *et al.*, 2016). Additionally, a contributory factor could be intraspecific competition; where the grey seal population is increasing, individuals may be constrained to more reliable prey patches as resources become more valuable.

The usage maps assume that telemetry data are in equilibrium, e.g. an animal tagged 20 years ago used space in a similar way to the same animal tagged 10 years ago at the same location. This assumption was necessary to produce static usage

maps across time. However, given the weight of evidence showing shifts in grey seal diet (Hanson *et al.*, In review; Wilson & Hammond, 2015; Hammond & Wilson, 2016), spatio-temporal boundaries (Fietz *et al.*, 2016), and population dynamics (Thomas, 2015), it seems implausible that space use has not changed over the last 20 years (when the first telemetry tags used in the usage maps were deployed). Foraging is a primary at-sea behaviour of seals, and they must respond dynamically to their environment. Telemetry deployments used for the usage maps, whilst providing detailed locational information, were not part of an experimental design for this purpose, as individual deployments had differing objectives. Therefore, there have been few repeat tagging events (i.e. animals tagged in different years at the same place), and none that can be reliably compared (e.g. adults and juvenile deployments took place in the same location between years). A regime of repeat tagging over time at selected sites would give a baseline of inter-annual differences in space-use, and provide insight into how space use changes over time with respect to intrinsic and extrinsic factors. Additionally, Hanson *et al.* (In review) found that juveniles have foraging distributions relatively closer to the coast than adults. This has implications for conservation objectives in terms of protection of the species, as well as marine spatial planning objectives. Although the grey and harbour seal usage maps used telemetry data from juveniles, there were limited deployments, and so juvenile space use could not be characterised. Therefore, a gap in our understanding is the at-sea distribution of juvenile seals, how this differs from adults, and the potential implication for management of the species.

Fine-scale harbour seal usage to inform marine spatial planning

The second paper characterises fine-scale harbour seal at-sea usage around Orkney and the North coast of Scotland, and addresses limitations of scalability, uncertainty, and predictive power in Jones *et al.* (2015). In areas where proposed offshore marine renewable developments are at consenting or licensing

stages, estimates of abundance of protected species in the area around the proposed development are required (Marine Scotland, 2010). For offshore marine renewables, these can range in size from large windfarms to localised tidal power streams. Therefore, scalability of the analytical framework to produce species distribution maps at an appropriate spatial resolution was required. As part of the consenting process, regulations call for an assessment of the potential impact to the ecosystem of the proposed development. For developments with moving parts, such as underwater tidal turbines, an assessment of potential collision risk with animals in the area is required.

Collision risk models often use mean density estimates and uncertainty of animals as initial values for individual based models (IBMs), and therefore it is important to use accurate abundance estimates values where possible (Donovan *et al.*, 2017). Fine-scale maps were produced at the most highly resolved spatial resolution supported by the underlying telemetry data. To scale to local population levels, each at-sea telemetry location was explicitly linked with terrestrial count data from onshore counts. To avoid inflating estimates of uncertainty, haul outs within a specified distance from each other were aggregated. Harbour seal distribution on land is often disaggregated along the coastline and they may return from an at-sea trip to within several kilometres of their departure haul out. Aggregating haul outs for the purposes of scaling to population levels ensured that terrestrial counts were utilised more effectively, and maps of density estimation (which had lower uncertainty associated with them) were used more often than maps of predicted space use from the regression model (which had higher uncertainty associated with them), reducing the uncertainty around the mean population estimate for the study area.

When considering analytical methodology to characterise species distributions that will be used in evidence-based decisions such as in consenting and licensing, sources of uncertainty, and the method of propagating these through the analysis should be considered to ensure the methodology can be used appropriately by practitioners. Regression modelling was used to understand how animals interact with geographical and environmental space by predicting space use in areas where

telemetry data were not present. In Jones *et al.* (2015), additional environmental covariates could not be implemented because the spatial extent of the analysis extended around the UK, where many different habitats types exist, making it challenging to more generally characterise habitat use from environmental predictors. For example, seal diet changes by region (Wilson & Hammond, 2016), which may affect habitat preference and seal behaviour. However, the smaller study area centred on Orkney was occupied by a local harbour seal population, allowing the prediction of space-use from environmental covariates more plausible.

Enhancements in the analytical framework combined with additional movement data resulted in at-sea usage of harbour seals that showed fine-scale structure, which was not visible in Jones *et al.* (2015). They remained primarily within 30 km of the coastline, and their distribution was linked to seabed sediment of sand, and annual mean tidal power. Sandeels are a non-migratory species that live in a sand/gravel mix of sediment (McConnell *et al.*, 1999; Reay, 1970) and are an important aspects of harbour seal diet around Orkney (Wilson & Hammond, 2015). Harbour seal space use generally declined with increasing tidal power. The Pentland Firth is an area with strong tidal currents and is of commercial interest as a number of tidal turbine developments are situated within it. There were seal haul outs on the north and south coasts but harbour seal space use was limited within the channel.

There are two limitations of the analysis. First, for central placed foragers that have daily cycles of hauling out between making foraging trips at sea, the most important covariate will always be distance from haul out. Grey and harbour seals are strongly linked to the coast, and this covariate dominates their selection of space use. When predicting space use by aggregated haul out, as was the case in this analysis, it is essential that distance from haul out is included in a predictive model, otherwise predictions are simply not accurate. Second, analysing movement data as a static distribution and subsequently using dynamic hydrographic and environmental information as static covariates inevitably results in a loss of information. Therefore, it is difficult to accurately associate animal space use with the environment, making the interpretation of that association

challenging. Modelling space use or habitat preference in a more dynamic flexible analytical framework would go some way towards a more realistic scenario of modelling, and provide more useful interpretations of how and why seals use the environment available to them.

Seals and shipping: quantifying population risk and individual exposure to vessel noise

At-sea usage maps from Jones *et al.* (2015) were used to investigate the risk to seals of co-occurrence with vessel traffic. Overlaying grey and harbour seals with ship usage maps, potentially acoustically sensitive areas were identified. A key finding was that 11 from 25 Special Areas of Conservation (SACs) for seals, which protect habitat important for breeding, had high levels of co-occurrence within them. There are some important caveats when interpreting this finding; high co-occurrence was defined by the authors as over 100 co-occurrences per day. This was not related to sound levels received by animals but was derived according to the data from spatial overlap. SACs are primarily onshore delineations, with facility to extend up to 500 m from land. However, seal distributions showed that animals were at-sea within the boundaries of SACs, although it is unknown whether individuals were under the water or at the surface. The results highlight an important gap in regulation as anthropogenic noise is not currently considered in marine spatial planning.

In an area identified as potentially acoustically sensitive, acoustic exposure models predicted received levels of noise from 1,689 vessels to 28 individuals. To reduce processing times, a simple acoustic approach was used. Spatio-temporal movements of seals and vessels were modelled and received levels were calculated in 15-minute intervals. Variance in transmission loss was propagated through the analysis, so that received levels were produced with estimates of uncertainty associated with them. There were several sources of variance that could not be accounted for, particularly uncertainty arising from source levels. Source levels were estimated by vessel at each location based on ship length and speed

(Breeding *et al.*, 1996). This was a simplification as noise generated by vessels are dependent on many other characteristics such as load weight (which can affect draft), propeller type, and aspect of vessel in relation to receivers (Trevorrow *et al.*, 2008). Although adjustments in the acoustic exposure modelling were made for bathymetry and sediment, it was assumed that both source (vessels) and receivers (seals) were consistently in the middle of the water column. Seals forage on a wide range of benthic and demersal species in the neritic environment (Prime & Hammond, 1990; Hammond & Wilson, 2016) before surfacing between dives (Thompson & Fedak, 1993). Although on average they may be in the middle of the water column, when calculating received noise levels, their placement in the water column at each time interval is likely to be an important consideration. Despite these assumptions, predictions of acoustic exposure corroborated with contemporaneous sound field measurements.

The framework presented here can serve to understand the impact of changes over time. Localised changes in both marine species populations and vessel traffic could alter the acoustic sensitivity of areas. For example, changes to local seal populations; grey seal numbers increasing in the North Sea, or the harbour seal population decreasing in Orkney (Duck *et al.*, 2015; Thomas, 2015). Although shipping lanes are fairly static, vessel numbers are generally increasing (Tournadre, 2014). The framework can be used to identify new areas of potentially acoustic sensitivity for seals under changing conditions. Further studies are required to understand seal behavioural responses to shipping noise, and more broadly anthropogenic noise. Some understanding is known about their behavioural responses to acute noise (Hastie *et al.*, 2015; Russell *et al.*, 2016), but research has not been published on behavioural responses to chronic anthropogenic noise. There is a clear data gap when considering the impacts of shipping on seal populations and individuals. Although the study did not find an acute effect from the received levels to individuals of shipping noise, where populations of animals may be already under stress, chronic impacts that contribute to cumulative effects may have a significant effect, and these effects should be considered when assessing population vulnerability.

Novel application of a quantitative spatial comparison tool to species distribution data

Motivation for this paper came from the spatial comparison between grey and harbour seal at-sea usage in Jones *et al.* (2015). One aspect of the study was to identify areas where spatial partitioning between the species was relevant and investigate the spatial scales of the partitioning. However, techniques were limited because cell-by-cell comparisons do not take interdependencies between cells into account (Horn, 1966; Leitão *et al.*, 2011), and locational information is lost when indices across space are applied (Cliff & Ord, 1970). Additionally, spatial comparisons using within-model methods (Scott-Hayward *et al.*, 2013) were not appropriate for these data because the analytical framework (density estimation and regression modelling) meant that single predictive models for each species were not produced. Methods were investigated that could be adapted for spatial ecology, which often use continuous data with spatial autocorrelation and uncertainty around the mean estimate in each grid cell of the underlying maps being compared. In ecology, maps of predicted distribution are often the endpoint of an analysis (e.g. Embling *et al.* (2010); Hammond *et al.* (2013)), and changes in distribution over time are compared qualitatively or by using simple metrics such as utilisation distributions (Fieberg & Kochanny (2005) but see Demšar *et al.* (2015) for a sophisticated analysis). Map comparisons need to be objective so that the any additional ecological findings from the interpretation of the comparison are quantified and robust. The paper showed how a map comparison methodology can be enhanced for use in spatial ecology. Using the Structural Similarity index (SSIM; Wang *et al.* (2004)), different aspects of spatial comparison can be identified, and the similarities in spatial structure between the two images being compared can be examined in different ways. These metrics can also be collapsed into single metrics or even an overall metric. This could be particularly useful if many sets of maps were compared.

An appropriate ecological case study was used in the paper to demonstrate the map comparison index. A small population of sperm whales exist in the

Mediterranean Sea. As males mature sexually, they disaggregate from females and their offspring, becoming increasingly solitary (Whitehead, 2003). The mechanism for this behaviour is unknown, and theories include female social units outcompeting solitary males when exploiting mid-water squid patches, or male growth rates driving wider search areas for additional prey resources. Centred on Mallorca and including surrounding islands in the Mediterranean Sea, the habitat preference for singles and groups of cohorts of sperm whales were compared using the SSIM index. Identifying differences in spatial patterns showed that in an area of strong habitat preference for both social assemblages where presumed foraging was taking place, there was mutually exclusive spatial segregation. This provided a focused area for future data collection to investigate the mechanisms for this behaviour. Hypotheses include whether this pattern of behaviour shows stable resource partitioning (optimal foraging for both assemblages) or whether one assemblage is being outcompeted into sub-optimal habitat. The study showed that there wass spatial structure that cannot be detected either visually or by using simple map subtraction techniques.

Most data collection, particularly involving animals is expensive, time-consuming, and sometimes intrusive. Therefore, if additional ecological insights can be extracted using previously collected and analysed data, these insights will provide added value. There are advantages to using map comparison techniques that can be applied after analysis of data are complete. For the production of species distributions maps, data collection can occur across decades with results being produced years apart with different underlying data collection and analytical methods (Hammond *et al.*, 2002, 2013). The SSIM index does not require reanalysis of underlying data, which may be problematic to obtain, or even that data are analysed using similar methods. Uncertainty can also be used in the map comparison software, resulting in more robust spatial comparisons.

There are several limitations discussed in the paper regarding the implementation of the SSIM index software that would be useful to address for practitioners: the spatial resolution and extent of the maps being compared must be identical. Surveys carried out through time often use varying transects, meaning that

spatial extent and resolution are likely to be dissimilar between years. A fairly simple software change would allow non-identical spatial resolutions and extents to be incorporated into the map comparison index. A significant addition would be to allow more than two maps to be compared. Species distributions are often available over time, or multiple species analyses are produced. Pairwise comparisons or sequential analysis, and corresponding metrics could be incorporated into the software to allow this. The comparison algorithm could be improved for accessibility and usability by developing an R library to increase its appeal.

Synthesis and future research

The aim of the studies contained within this portfolio was to develop robust analytical tools and innovative analyses to gain meaningful ecological insights into the study species, interactions with their environment, and potential impacts of anthropogenic activities. These findings were then disseminated to inform the guidance given by regulators to practitioners in the commercial sector. A theme of this portfolio was to combine many different data sets to provide robust analysis and ecological findings. This has enhanced our knowledge of how seals use space, what is important to them in their environment, and how anthropogenic activities may impact them.

Ultimately, using movement data to produce static distributions results in a loss of information such as temporal and behavioural data. There remains a challenge to preserve and use as much information as possible whilst producing outputs from analysis that can used by practitioners in an applied context. Animals continuously interact with their environment, producing dynamic distributions through time, and predicting more realistic space use to include three dimensions would undoubtedly bring additional insights. There is a requirement for the development of innovative analytical tools, and the interpretation of cutting-edge techniques to integrate into working practice by end-users.

Modelling approaches using Integrated Nested Laplace Approximations (INLA;

Rue *et al.* (2009)), is a promising approach that may provide solutions to some of the analytical and software challenges for analysing complex telemetry data. Although the issue of scalability was addressed in Jones *et al.* (2017c), the resultant analysis mapped usage in regularly gridded cells. This was effective as the usage surfaces could be mapped easily using Geographic Information System (GIS) software, and interpretation was 'number of animals per km^2', for example. However, justification of spatial resolution was based on limitations of data collection (e.g. mean time between GPS locations), rather than the inherent behaviour of the species. Limitations in data collection are inevitable but one solution would be to implement a mesh, available using the Stochastic Partial Differential Equation approach (SPDE; Lindgren *et al.* (2011)). This approach can be combined with INLA to flexibly fit complex spatio-temporal models. In data-rich regions mesh would be finer, and in areas where there are less data the mesh would be coarser, representing the underlying data more appropriately and enabling the analysis to characterise fine-scale features (e.g. movements in a focal area).

Identifying spatial partitioning between species then raises the question of how to explicitly link causal mechanisms with mutually exclusive behaviour. Jones *et al.* (2015) compared grey and harbour seal usage maps using simple map subtraction to identify spatial partitioning. One approach to determine the nature of the relationship between sympatric species would be to model the presence of one species on the other using joint species distribution modelling, which the INLA framework allows. Extending this, different trophic levels could also be added to determine relationships within the ecosystem, giving additional insight into food web associations and ecosystem functioning. Changes in species distributions are ultimately important for the purposes of predicting future change to manage populations and marine spatial planning. Incorporating dynamic spatio-temporal environmental covariates as well as other information such as diet and potential prey fields into spatial models is vital. The INLA-SPDE approach offers a flexible analytical framework that produces interpretable results. Although habitat selection models can associate environmental information with animal locations, a challenge remains to include more dynamic covariates that

are likely to be pertinent to top marine predators. Marine predators such as seals are known to respond quickly to changes in their environment, and their movements are explicitly linked to shifts in prey availability as well as constraints of the environment available to them. Likewise, prey availability is explicitly linked to dynamic environmental covariates such as currents and thermal mixing, and spatial models need to incorporate these (Scott *et al.*, 2010). There has been progress in recent years associating predator movements and space-use with environmental features (Scales *et al.*, 2014). However, work needs to be done to build methodological bridges between spatial and movement ecology and close the gap between modelling populations and individuals.

A branch of spatial ecology has arisen to address space use of animals through bespoke analytical methods of their movements (Patterson *et al.*, 2008). State-space methods feature process and observation models that are explicitly linked to predict future states through a time series approach. Hidden Markov Models use a state-space approach with unobserved (hidden) states, and have become increasingly popular for ecological data; they are can be reasonably straightforward to fit and typically have rapid processing times (Zucchini *et al.*, 2016). Covariates can be included, and so they can describe space use of individuals within the context of geographic and environmental space. In this way, usage maps could be included as habitat covariates to inform HMMs. By contrast, individual based models (IBMs) use simulations of many individuals, whose movements are defined by a set of criteria to investigate space use. Incorporating usage maps into IBMs can aid model fitting, as estimated densities in each grid cell can inform the model about the local seal population abundance at the beginning of the simulation (Donovan *et al.*, 2017). The models can be validated using movement data but depending on complexity, this can be challenging (Nabe-Nielsen *et al.*, 2014).

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