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RESEARCH ARTICLE

At-sea distribution of seals on the Northwest European Shelf: Towards transboundary conservation and management

Matt I. D. Carter[1] | Geert Aarts[2,3] | Floris M. van Beest[4] | Matt Bivins[1] | Sophie M. J. M. Brasseur[2] | Rune Dietz[4] | Callan D. Duck[1] | Anders Galatius[4] | Anita Gilles[5] | Jan Haelters[6] | Gordon D. Hastie[1] | Mark Jessopp[7,8] | Chris D. Morris[1] | Simon E. W. Moss[1] | Jacob Nabe-Nielsen[4] | Dominik A. Nachtsheim[5] | Tobias Schaffeld[5] | Jessica Schop[2] | Ursula Siebert[5] | Jonas Teilmann[4] | Dave Thompson[1] | Paul M. Thompson[9] | Cécile Vincent[10] | Debbie J. F. Russell[1,11]

[1]Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, UK; [2]Wageningen Marine Research, Wageningen University & Research, Den Helder, The Netherlands; [3]Royal Netherlands Institute for Sea Research, Texel, The Netherlands; [4]Section for Marine Mammal Research, Department of Ecoscience, Aarhus University, Roskilde, Denmark; [5]Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Büsum, Germany; [6]Institute of Natural Sciences, Ostend, Belgium; [7]School of Biological, Earth and Environmental Science, University College Cork, Cork, Ireland; [8]MaREI Centre, Environmental Research Institute, University College Cork, Cork, Ireland; [9]Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, Cromarty, UK; [10]Pelagis, UAR 3462, University of La Rochelle/CNRS, La Rochelle, France and [11]Centre for Research into Ecological & Environmental Modelling, University of St Andrews, St Andrews, UK

Correspondence
Matt I. D. Carter
Email: midc@st-andrews.ac.uk

Debbie J. F. Russell
Email: dr60@st-andrews.ac.uk

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Abstract

1. Quantifying and mitigating transboundary effects of anthropogenic activity is a key challenge in environmental management, particularly for wide-ranging species such as large predators, fish and migratory birds, relying on habitats across multiple national jurisdictions. This challenge is especially complex in marine ecosystems, where the movement of species and impacts across borders is largely unobserved. Central-place foragers, such as pinnipeds and seabirds, exemplify this complexity: abundance is typically assessed on local (regional or national) scales on land, yet at-sea movements and drivers of abundance occur on broader transboundary scales. Resolving this mismatch is critical to effective conservation, especially in areas such as the Northwest European Shelf (NWES), which features globally important predator populations (including two pinniped species) alongside growing anthropogenic pressures and a mosaic of national maritime borders.
2. We model an unprecedented GPS dataset from 236 grey (*Halichoerus grypus*) and 606 harbour seals (*Phoca vitulina*) tracked in waters of seven countries across the NWES (United Kingdom, Ireland, France, Belgium, Netherlands, Germany and Denmark). Using regional habitat association models, we generate at-sea

distribution estimates for both species at 5 km resolution, scaled to haulout counts, producing country-specific and NWES-wide density maps.
3. Analysis of the extent to which seals making foraging trips from one country occupy the Exclusive Economic Zones (EEZs) of other countries revealed substantial transboundary overlap, particularly for grey seals, and harbour seals in the southern North Sea.
4. A case study apportioning grey seal density within three adjacent offshore marine protected areas in different EEZs revealed that, where total density in a given area is required, overlooking transboundary distribution can underrepresent numbers by an order of magnitude.
5. *Synthesis and applications*. This study provides the first comprehensive, regionally scalable distribution estimates for pinnipeds across the NWES and its constituent countries. The modelling framework is adaptable to other central-place and migratory species, supporting transboundary biodiversity assessments and international conservation policy. We discuss common limitations and misconceptions of species distribution estimates, highlight priorities for future work and underscore the need for transboundary efforts to manage wide-ranging species, providing a foundation for future ecological modelling and decision-making across shared ecosystems.

KEYWORDS
central-place forager, density map, environmental impact assessment (EIA), marine protected areas (MPAs), marine spatial planning (MSP), marine vertebrate predators, pinnipeds, species distribution model (SDM)

1 | INTRODUCTION

Throughout the past century, the footprint of human activity has extended into over 80% of Earth's terrestrial (Sanderson et al., 2002) and marine ecosystems (Halpern et al., 2008), driving unprecedented biodiversity loss and ecosystem change. As species ranges and ecological processes frequently cross political boundaries, effective conservation management requires strategic international cooperation (Kark et al., 2015). However, the ability to quantify and mitigate transboundary effects of anthropogenic activity remains a significant challenge (Mason et al., 2020), particularly in the marine environment where impacts are diffuse, cumulative and expanding rapidly (Halpern et al., 2008, 2015). Marine ecosystems are highly connected, and the movement of species and impacts across borders is largely unconstrained and unobserved. Indeed, over 90% of marine species are estimated to require multinational governance, with 58% covering more than 10 national jurisdictions (Roberson et al., 2021). Addressing the mismatch between the scale of ecological connectivity and the scale at which populations are managed is critical for achieving global biodiversity targets and the sustainable use of shared ecosystems.

Highly mobile marine vertebrate predators readily cross national borders and are particularly vulnerable to anthropogenic threats (Maxwell et al., 2013; Nelms et al., 2021). Given their top-down influence on food webs, predators have a disproportionate effect on ecosystem structure and function (Heithaus et al., 2008). They also assimilate bottom-up effects, making them sentinels of ecosystem health (Hazen et al., 2019). Indeed, these taxa are often used as indicators of biodiversity status in Regional Seas Convention (RSC) assessments. Pinnipeds and breeding seabirds are particularly useful indicators as they frequently return to land between foraging trips, allowing populations to be monitored at breeding colonies and haulouts with relatively high accuracy (Banga et al., 2022; Frederiksen et al., 2022). Their central-place foraging strategy and dependence on terrestrial habitat mean that individual countries have jurisdiction over the component of a wider population that breeds or hauls out within national borders. However, there is a mismatch between the local (regional or national) scale at which abundance is assessed, and the broader transboundary scale of at-sea distribution where potential impacts are most likely to occur (Carter et al., 2022).

The Northwest European Shelf (NWES) hosts globally important marine predator populations, including ~36% of the world's grey seals (*Halichoerus grypus*) (>200,000 individuals, >95% of the Northeast Atlantic metapopulation; SCOS, 2024) and ~60% of Eastern Atlantic harbour seals (*Phoca vitulina*; >75,000 individuals—SCOS, 2024, comprising two metapopulations—Carroll et al., 2020). The NWES is also an area of particularly high cumulative anthropogenic impacts, with stressors such as fisheries, marine traffic, habitat modification (including a fast-growing marine renewable energy sector) and climate change (Halpern et al., 2008). Transboundary management is especially important in this region, where eight countries (the United Kingdom [UK], Ireland, France, Belgium, the Netherlands, Germany, Denmark and Norway) share complex maritime borders (Figure 1). As signatories to the Oslo-Paris (OSPAR) RSC (OSPAR Commission, 1992), these countries have a shared responsibility to assess and conserve marine ecosystems, as set out in OSPAR's North-East Atlantic Environment Strategy (OSPAR Commission, 2021). Effective marine spatial planning and the implementation of a marine strategy (such as the European Union [EU] Marine Strategy Framework Directive (Directive 2008/56/EC) or national equivalents), in co-operation with other Contracting Parties, are therefore legally binding. Moreover, NWES countries have ratified the United Nations Economic Commission for Europe (UNECE) Convention on Environmental Impact Assessment in a Transboundary Context (Espoo Convention), which provides a legal framework for assessing and managing environmental impacts of planned activities across national borders (UNECE, 1991). These regional commitments align with broader international goals, including the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022) and the UN Sustainable Development Goals (United Nations General Assembly, 2015), which emphasise the need for a cross-border approach to ecosystem management.

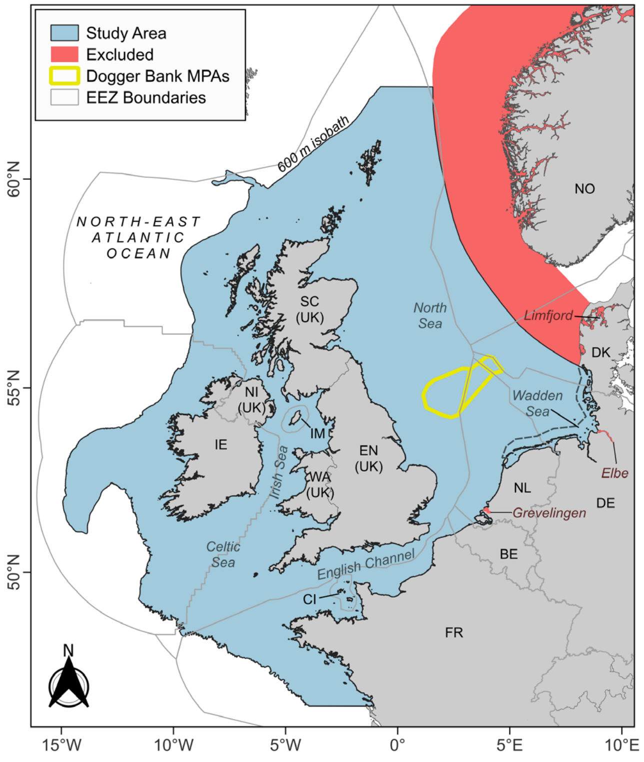

FIGURE 1 Study area comprising the Northwest European Shelf. Red areas were excluded (see Section 2.1). Yellow polygons denote the marine protected areas (MPAs) used in the Dogger Bank case study. Grey lines denote Exclusive Economic Zone (EEZ) boundaries. Dashed line delimits the Wadden Sea. SC, EN, WA, NI (UK): Scotland, England, Wales, Northern Ireland (United Kingdom); IM, CI: Isle of Man, Channel Islands (UK dependencies); BE, Belgium; DE, Germany; DK, Denmark; FR, France; IE, Ireland; NL, Netherlands; NO, Norway.

Mapping the broadscale distribution of species at sea is key to facilitating transboundary conservation and management (Roberson et al., 2021). For cetaceans in the Northeast Atlantic, this has been achieved through at-sea surveys (Gilles et al., 2016; Hammond et al., 2013); this Eulerian approach naturally lends itself to population-level estimates (Aarts et al., 2008). For seals and seabirds, the data used are usually from animal-borne tags; generating at-sea density estimates from such Lagrangian data requires ancillary information on total abundance at the central place (Aarts et al., 2008). Through international collaboration, progress has been made in recent years for seabirds; colony-level abundance data were combined with geolocator data to generate coarse-scale distribution estimates for six species across the Northeast Atlantic (Fauchald et al., 2021). For grey and harbour seals, studies have provided high-resolution at-sea distribution estimates, but these are restricted to representing density from particular haulouts in particular countries (Aarts et al., 2016; Carter et al., 2022; Vincent et al., 2017) or discrete non-contiguous regions (Huon et al., 2021). These estimates are frequently used in ecological research (e.g. ecosystem models) and applied contexts (e.g. environmental impact assessments [EIAs]), yet their limitations are often overlooked. Indeed, such at-sea distribution estimates will not be representative of overall mean seal density in some areas since they do not account for seals making trips from haulouts outside of the study country or region. Without a single broadscale distribution map, users therefore risk distorting inference of top-down effects in ecosystem models and overlooking transboundary impacts, hindering effective conservation and management. Grey and harbour seals therefore represent a valuable model to understand and address the spatial mismatch between ecological processes and jurisdictional boundaries—a challenge that is increasingly relevant across both marine and terrestrial systems.

The aim of this study is to generate broadscale distribution maps for the NWES, alongside country-specific estimates, for both seal species using an extensive GPS satellite tracking dataset, unprecedented in size (236 grey and 606 harbour seals) and spatial extent (covering most major centres of abundance across Northwest Europe). First, we build regional habitat association models and predict at-sea distributions for seven NWES countries at a 5 km resolution, scaled using haulout count data. Combined, these predictions represent NWES-wide estimates of at-sea seal density. Second, we use the outputs to examine the extent to which seals hauling out in one country are present in the Exclusive Economic Zones (EEZs) of other countries during foraging trips. Third, we demonstrate an application of the distribution estimates in a case study, apportioning grey seal density within three adjacent offshore marine protected areas (MPAs) in different national jurisdictions to the source countries. By providing a scalable framework for estimating transboundary distributions of central-placed and migratory species, this study contributes to the growing toolkit for ecosystem-based management in shared seascapes.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area comprises the seas of the NWES, representing the available habitat for seals hauling out in seven European countries: the UK (and dependencies: the Isle of Man and the Channel Islands), Ireland, France, Belgium, the Netherlands and the Wadden Sea coast of Germany (including Helgoland) and Denmark (Figure 1). Here, the NWES is defined by the continental shelf edge in the west and the limits of the North Sea in the east. The 600 m isobath (EMODnet Bathymetry, 2022) was used to delimit the shelf edge since it represents the likely limit of viable foraging habitat for seals (Carter et al., 2022). The International Council for the Exploration of the Sea (ICES) Statistical Areas (ICES, 2016) were used to delimit the North Sea boundary at the mouth of the channel between Denmark and Norway. Some areas on the NWES were excluded due to a lack of comparable tracking and/or count data (Limfjord and Northwest Denmark and the coast of Norway) or because they host a relatively small number of seals with likely unique habitat associations (Elbe Estuary and Grevelingen Lake) (Figure 1). Together, these areas comprise ~1% of grey and ~11% of harbour seals on the NWES (ICES, 2024).

2.2 | Tracking data

Tracking data were from Fastloc® GPS-GSM satellite telemetry devices (SMRU Instrumentation, UK) deployed between 2005 and 2023 on grey and harbour seals at >50 capture locations in the UK, Ireland, France, the Netherlands and Germany (Figure 2a,b). Data were pooled across years to ensure maximum spatial coverage (see Appendix S1). Seals were captured on, or close to, haulouts. All seals were estimated to be at least 6 months old; pups were not included in the study because their distribution is likely to be unpredictable (Carter et al., 2017) and tracking data are lacking in many regions. Tags were glued to fur on the neck, falling off before or during the annual moult. Median transmission duration was 100 days (IQR: 66–138). The tags collected high-resolution positional, dive and haulout information and transmitted via Global System for Mobile Communications (GSM) mobile networks (McConnell et al., 2004). Data cleaning and preparation followed protocols described in Carter et al. (2022). Briefly, cleaned data were regularised to a constant 30 min time step, partitioned into trips at sea and assigned to discrete habitat association regions (see Appendix S1). Regularised location fixes were excluded from analysis if there was a gap >6 h between the surrounding observed locations. Data during the first week post capture were removed as they are potentially unrepresentative of normal foraging behaviour. As per Carter et al. (2022), data were restricted to discrete "study seasons" (grey seals: summer [May–August], harbour seals: autumn-winter-spring [September–May]) since behaviour during these periods is unlikely to be influenced by moulting and breeding. Lastly, trips that transitioned between haulouts in different habitat association regions were excluded (49 grey seal trips; Appendix S1). The final dataset comprised 12,488 trips from 236 grey seals and 34,785 trips from 606 harbour seals. All capture, handling and associated procedures were carried out with the appropriate licences and site-specific approvals (see Section 2.7).

2.3 | Habitat association modelling

Methods followed the regional use-availability habitat association approach described by Carter et al. (2022), whereby each "used point" (regularised seal location; representing the habitat used by the seals) was matched to a set of "control points" (a random sample of locations generated within an accessibility polygon; available habitat that is accessible to the individual). Used and control points were modelled per species-region combination as a binary response term (1/0) in generalised additive mixed models (GAMMs) as a function of environmental covariates (distance to haulout, distance to coast, seabed substrate type, geomorphology, and, for grey seals, summer mean potential energy anomaly [relating to water column stratification]). An individual seal identifier was included as a random intercept term. Control points were weighted in the models such that each set contributed equally to one used point. There were a number of key modifications to the methods of Carter et al. (2022): (i) the radius of accessibility polygons was defined on a species-region (rather than species) basis to account for differing scales of movement among the species-region groups; (ii) GAMMs were fitted using the "bam" function in the "mgcv" package (version 1.9-1) (Wood, 2017) in R (R Core Team, 2023) to leverage the faster restricted maximum likelihood (fREML) functionality compared to REML in "gam", and the ability to fit a correlation structure (AR1 for used points) rather than thinning the data; and (iii) no model selection was undertaken since the primary aim was to maximise predictive ability and the use of shrinkage splines for smoothed terms reduced the impact of non-informative terms on the resulting distribution estimates. Further detail on model structure, validation and environmental covariates is given in Appendix S1.

2.4 | Haulout count data

Counts of grey and harbour seals on haulouts (conducted during harbour seal moult in August) were collated from multiple sources (see Appendix S1) (Figure 2c,d). Counts were aggregated to cells in the 5 km prediction grid (see Section 2.5). For each haulout cell, the most

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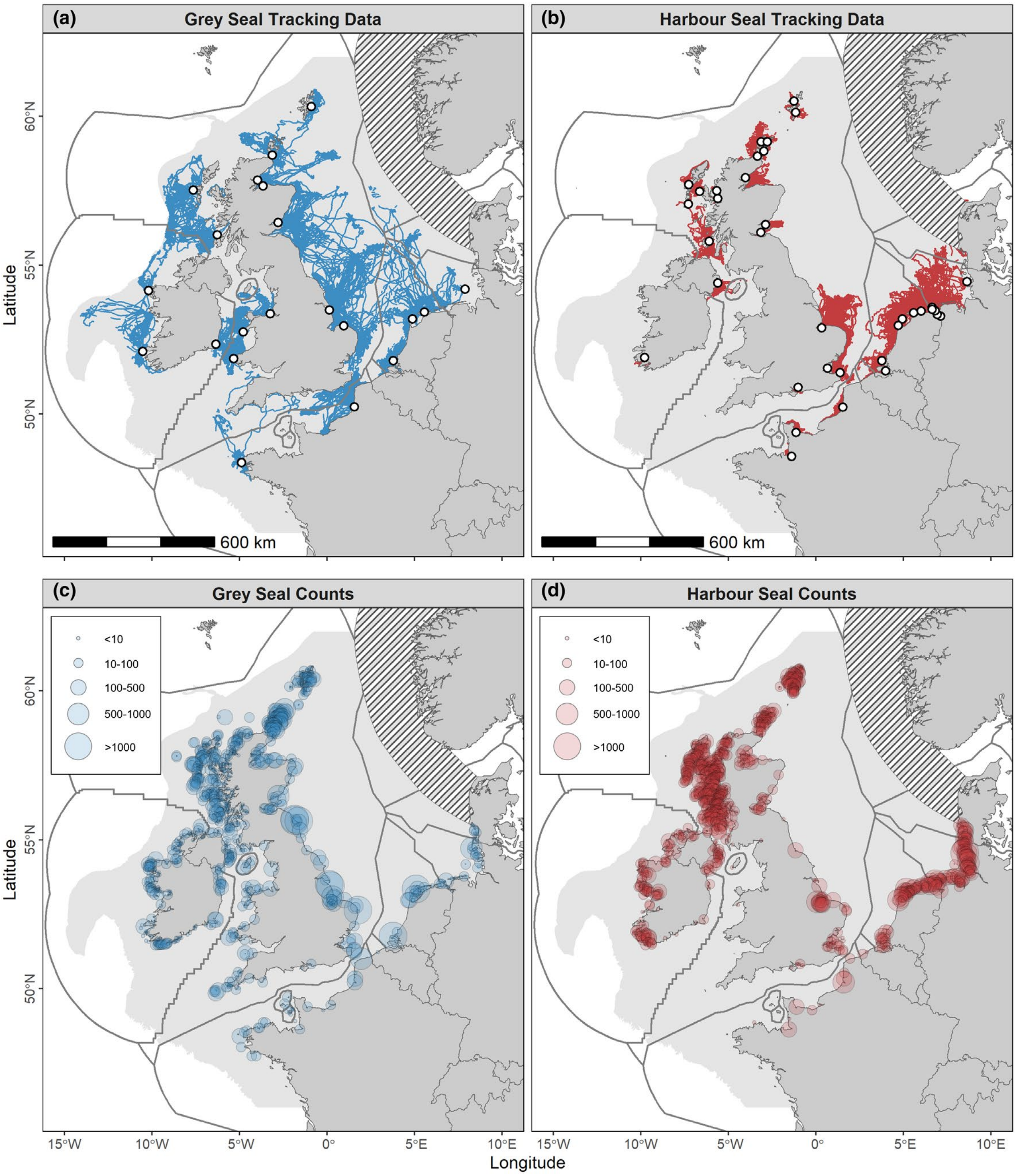

FIGURE 2 Tracking and haulout count data. Tracking data from (a) 236 grey and (b) 606 harbour seals. White dots show capture locations. Haulout count data taken from most recent available August surveys for (c) grey and (d) harbour seals (see Section 2.4). Light grey shading shows the study area, hatching shows excluded areas, and grey lines denote Exclusive Economic Zone (EEZ) boundaries.

recent available count was used up to 2024 (~98% of counts from 2017 onwards; Appendix S1) to scale predictions of at-sea distribution. Where multiple surveys were conducted in a year, the mean of individual counts was used.

2.5 | Predicted distributions

Following Carter et al. (2022), predictions of at-sea distribution were generated on a 5 km grid in a Universal Transverse Mercator (UTM) 30 N projection for the study season. Briefly, for each country, spatial predictions were made emanating from each haulout cell using the corresponding species-region model, weighted by the number of individuals counted on the most recent survey and summed into one country-specific surface per species. Values were standardised to relative density (mean percentage of the component of overall abundance at sea at any one time, hereafter "at-sea population") per cell. Cell-wise 95% confidence intervals (CIs) around the mean values were generated using a posterior simulation approach from the habitat association models, reflecting uncertainty in the habitat association relationships (Carter et al., 2022). Relative values were converted to absolute density (mean number of individuals) for 2023 using two scalars: (1) the proportion of the overall population hauled out and thus available to count during the August survey window and (2) the proportion of time seals spend at sea on average during the study season. Scalar 2 is averaged across the tidal cycle, but seals are more likely to be at sea at high tide; thus absolute estimates were also generated using a value of 1 for Scalar 2 (i.e. assuming all seals are at sea), providing estimates that would sum to the total population. Country-specific surfaces were then summed into one layer for the NWES. Further detail on spatial predictions, scalars and uncertainty estimation is given in Appendix S1. A 5 km grid resolution was used to match the temporal resolution of the tracking data and spatial resolution of environmental covariates, providing consistency with previous work (e.g. Carter et al. 2022). Based on the regularised telemetry data, the maximum distance we expect a seal to cover in any 30 min time interval is ~3.6 km. A grid resolution much finer than 5 km (e.g. 1 km) would therefore result in a mismatch with the telemetry data, alongside large increases in computation time. Similarly, coarser resolutions (e.g. 10 km) would reduce the utility of the outputs for real-world applications.

2.6 | Transboundary analysis

For each country-specific prediction (hereafter "haulout country") per species, the total number of seals estimated to be present at sea at any one time within the EEZ of other countries (hereafter "at-sea country") was calculated. The analysis was repeated with the distinction of constituent nations and dependencies of the UK (results shown in Appendix S2). To demonstrate the utility of the distribution estimates for transboundary conservation and management, the estimated number of grey seals within the three MPAs designated in UK, Dutch and German jurisdictions on the Dogger Bank was apportioned to their haulout countries.

2.7 | Ethical approval and permissions

Ethical approval for this study was given by the University of St Andrews School of Biology Ethics Committee (approval numbers: BL17759 and BL17766). All capture, handling and other licenced procedures in the UK were carried out under UK Home Office project licence PF84B63DE (and previous iterations: 60/2589, 60/3303, 60/4009 and 70/7806) under the Animals (Scientific Procedures) Act 1986, with specific licences from the Scottish Government Marine Directorate, the Marine Management Organisation and Natural Resources Wales. In Ireland, work was conducted under licence from the National Parks and Wildlife Service, with additional licences from the Irish Health Products Regulatory Authority. In France, work was conducted under licence from the Ministère de l'Enseignement Supérieur et de la Recherche, with project-specific approvals from the Ministère de la Transition Écologique. In Germany, work was conducted under ethical permit numbers for the federal states Schleswig-Holstein: AZ V312-72241.121-19 (70-6/07), V244-3986/2017 (17/14) and V241-64499/2018 (11-2/19), with site-specific approvals from the Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation (LKN) and Schleswig-Holstein's Agency for Agriculture, Environment and Rural Areas (LLUR). In the Netherlands, work was conducted after approval by national ethical committees (KNAW, later WUR) and where required, appropriate site-specific approvals were obtained relating to protected areas and species ("NB-wet" and "Flora en Fauna wet"). Any associated mitigation measures were observed for designated sites.

Whilst a recent study demonstrated that drag effects from SMRU Instrumentation GPS-GSM tags can influence dive behaviour of seals (McKnight et al., 2024), we do not anticipate any tag effects to be evident at the data resolution considered in this study. Here we combine data from the first generation of SMRU Instrumentation GPS-GSM tags with deployments of the newer, more hydrodynamic generation (McKnight et al., 2024). As well as minimising the impact on individuals tagged, our study supports the 3Rs principle (Replacement, Reduction, Refinement) by collaborating widely and utilising data collected for various specific projects.

3 | RESULTS

3.1 | At-Sea distribution estimates

Distribution estimates for grey seals (summer) revealed large concentrations in coastal waters adjacent to major haulout areas, but also showed substantial numbers of individuals in offshore areas (Figure 3). Estimates for harbour seals (autumn-winter–spring) also revealed the largest concentrations in coastal waters around major haulout areas, but with a tighter coastal distribution than for grey seals (Figure 3). Distribution estimates emanating from haulouts in Southeast England and the Wadden Sea extend further offshore than those in the rest of the study area, as observed in the movements of tracked harbour seals (Figure 2b).

Data layers of at-sea distribution for grey and harbour seals on the NWES are provided for download (https://doi.org/10.17630/00334852-4f8c-4799-a418-664c8104d68f; Carter et al., 2025). The layers include shelf-wide and country-specific estimates as both relative density and absolute density for 2023 (see Appendix S1 for interpretation guidelines). Country-specific distribution maps are shown in Figures 4 and 5. Additional resources are provided for the UK, including estimates for constituent nations and dependencies, Seal Monitoring Units (SMUs) and Special Areas of Conservation (SACs). Fitted relationships from the underlying habitat association models, as well as maps of relative density, cell-wise uncertainty and absolute estimates for high tide (summing to total population), are shown in Appendix S2.

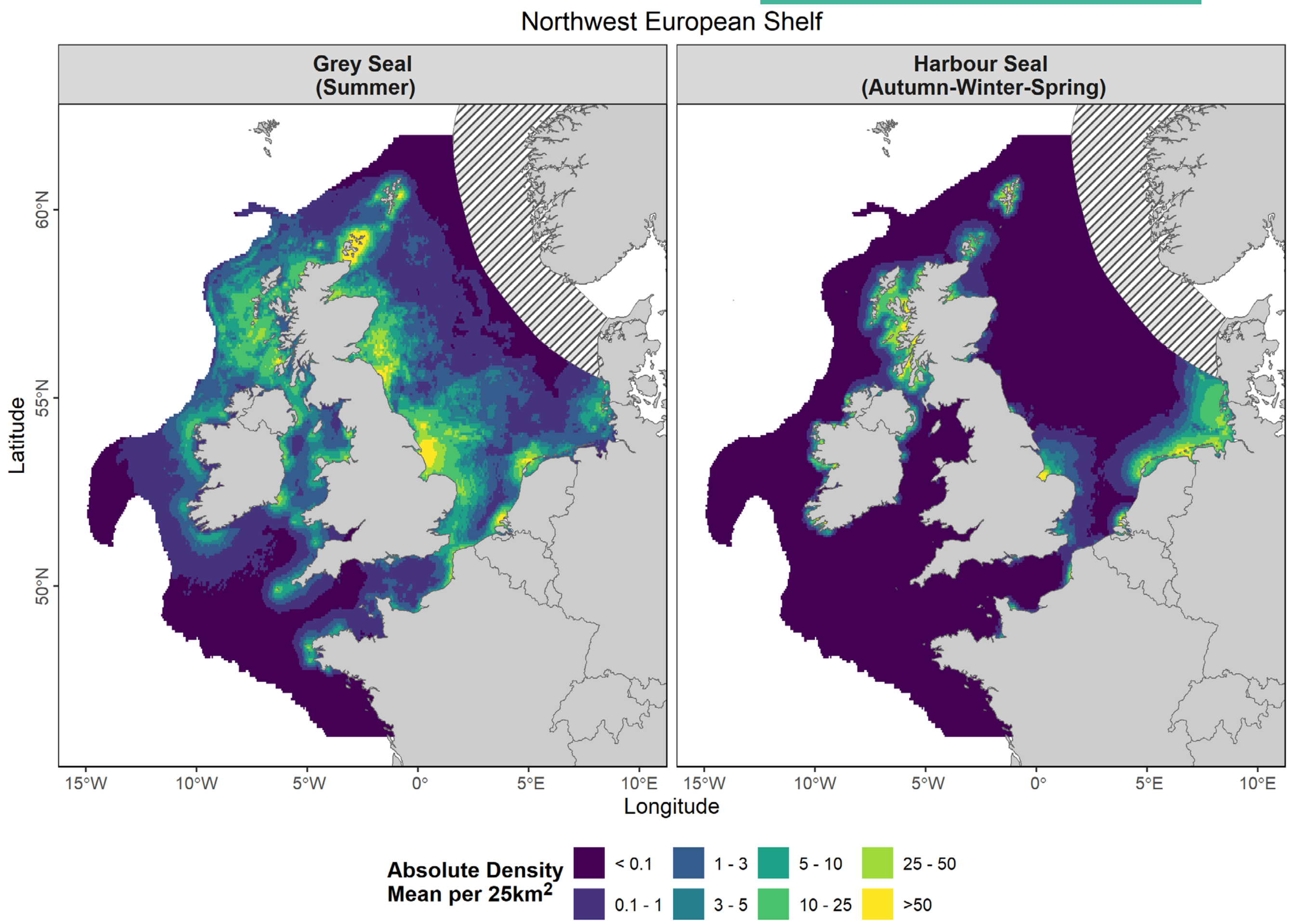

FIGURE 3 At-sea distribution of grey and harbour seals on the NWES during the study season. Values show the mean estimate, scaled to absolute density (number of individuals averaged across the tidal cycle) per 5 km cell, based on the estimated at-sea population size in 2023. Hatching shows excluded areas. Cell-wise uncertainty and high tide estimates are shown in Appendix S2.

3.2 | Transboundary distribution of seals

Transboundary distribution analysis revealed that large numbers of seals present in the EEZ of a given country at any one time are apportionable to haulouts in other countries (Figure 6). This was especially the case for grey seals. For example, of the grey seals present at sea in the French and Dutch EEZs at any one time, >3000 (>15%) are apportionable to haulouts in other countries, with the vast majority apportionable to the UK. Grey seals undertaking trips from haulouts in all seven countries are estimated to be present in UK waters, whilst Dutch waters host seals from all countries except Ireland.

The degree of transboundary exchange was lower for harbour seals, except for the Wadden Sea countries of the Netherlands, Germany and Denmark. Of the harbour seals present at sea in the German EEZ at any one time, >1600 (~12%) are apportionable to haulouts in the Netherlands. Similarly, of the harbour seals making trips from haulouts in Germany (Helgoland and the German Wadden Sea), >1000 (~9%) are estimated to be present in the Danish EEZ at any one time. This number is comparable to the number of individuals in the Danish EEZ apportionable to haulouts in the Danish Wadden Sea. Of the harbour seals making trips from haulouts in the Danish Wadden Sea, >600 (~32%) are estimated to be present in the German EEZ at any one time. Relative values for transboundary analysis are shown in Appendix S2.

3.3 | Case study: Distribution of seals in Dogger Bank MPAs

Grey seals apportionable to haulouts in the UK, Netherlands and Germany are estimated to be present in all three MPAs designated on the Dogger Bank during summer (Table 1; Figure 7). Grey seals apportionable to haulouts in the UK accounted for the majority of predicted density in each of the MPAs. Indeed, ~91% of seals in the Dutch MPA and ~82% of those in the German MPA at any one time were apportionable to UK haulouts.

4 | DISCUSSION

This study addresses the spatial mismatch between local or regional population monitoring and the broader transboundary scale of

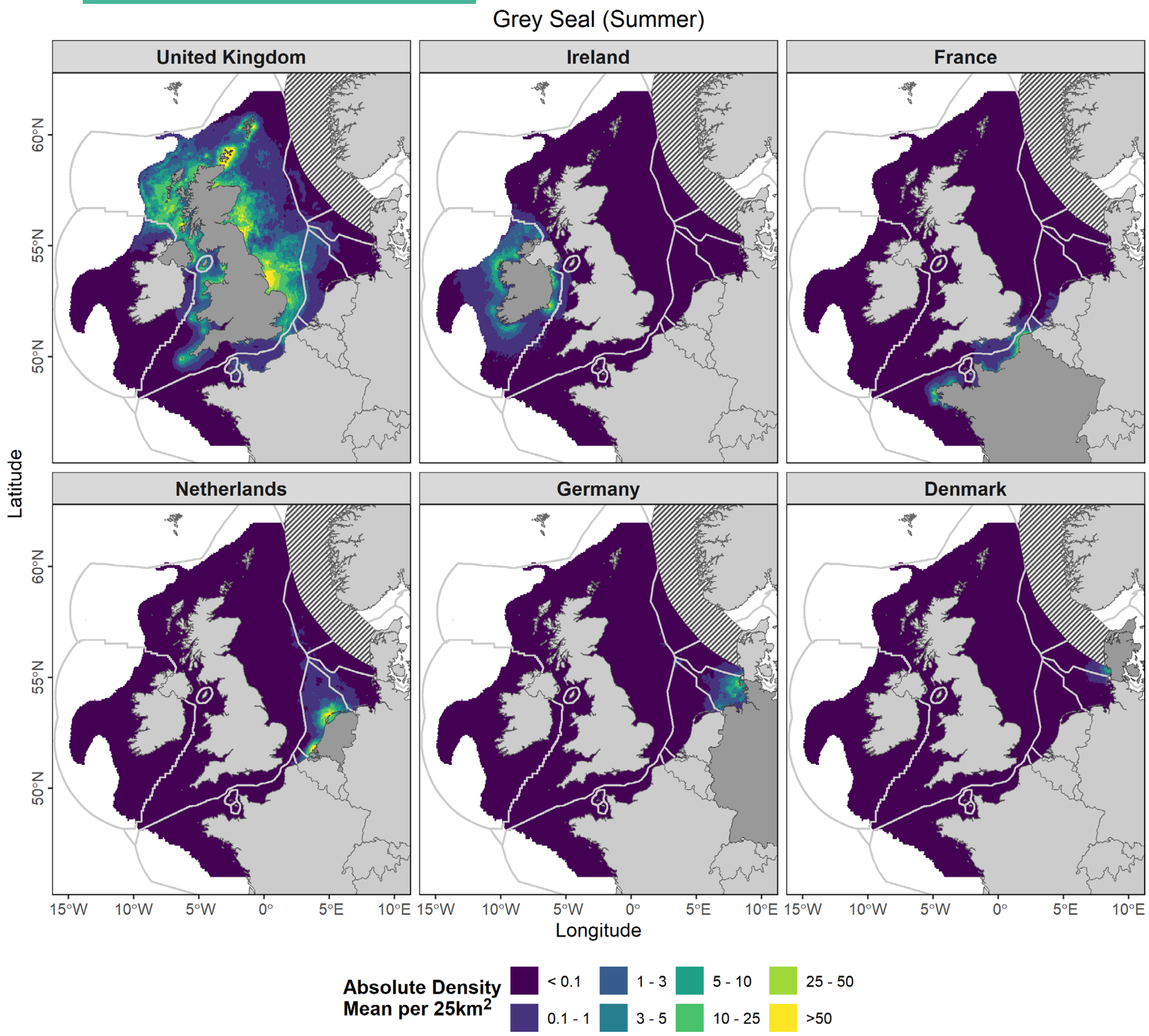

FIGURE 4 At-sea distribution of grey seals per haulout country during the study season. Values show the mean estimate, scaled to absolute density (number of individuals averaged across the tidal cycle) per 5 km cell, based on the estimated at-sea population size in 2023. Light grey lines show the EEZ boundaries, dark grey polygons indicate the haulout country, hatching shows excluded areas. Estimates for Belgium are shown in Appendix S2.

pinniped at-sea movements. By linking tracking and abundance data in regional habitat association models, we produced the first transboundary distribution estimates for pinnipeds across the NWES, encapsulating globally important study populations of >200,000 grey and >75,000 harbour seals (SCOS, 2024). These estimates fill an important data gap, improving the robustness of impact assessments and ecosystem models. The framework is broadly applicable to systems where movements of wide-ranging species can be linked to abundance data from breeding or resting sites, including migratory species such as marine turtles, large herbivores and songbirds, as well as central-place foragers such as denning carnivores and breeding seabirds. Quantifying transboundary distribution for these taxa is vital to understanding ecological connectivity and informing cohesive international conservation.

In addition to the NWES-wide estimates, our study allows apportioning of seal numbers at sea to seven European countries. These outputs show that country-specific estimates (e.g. Carter et al., 2022) may underrepresent total seal numbers in offshore waters by overlooking individuals foraging from haulouts in other jurisdictions. Indeed, our Dogger Bank case study illustrates that, where total density is required, overlooking transboundary distribution in a given area (e.g. MPA or development zone) can underrepresent numbers by an order of magnitude (Table 1). Given that grey seals in the NWES likely represent a single metapopulation (McCarthy et al. 2025), and harbour seals likely comprise

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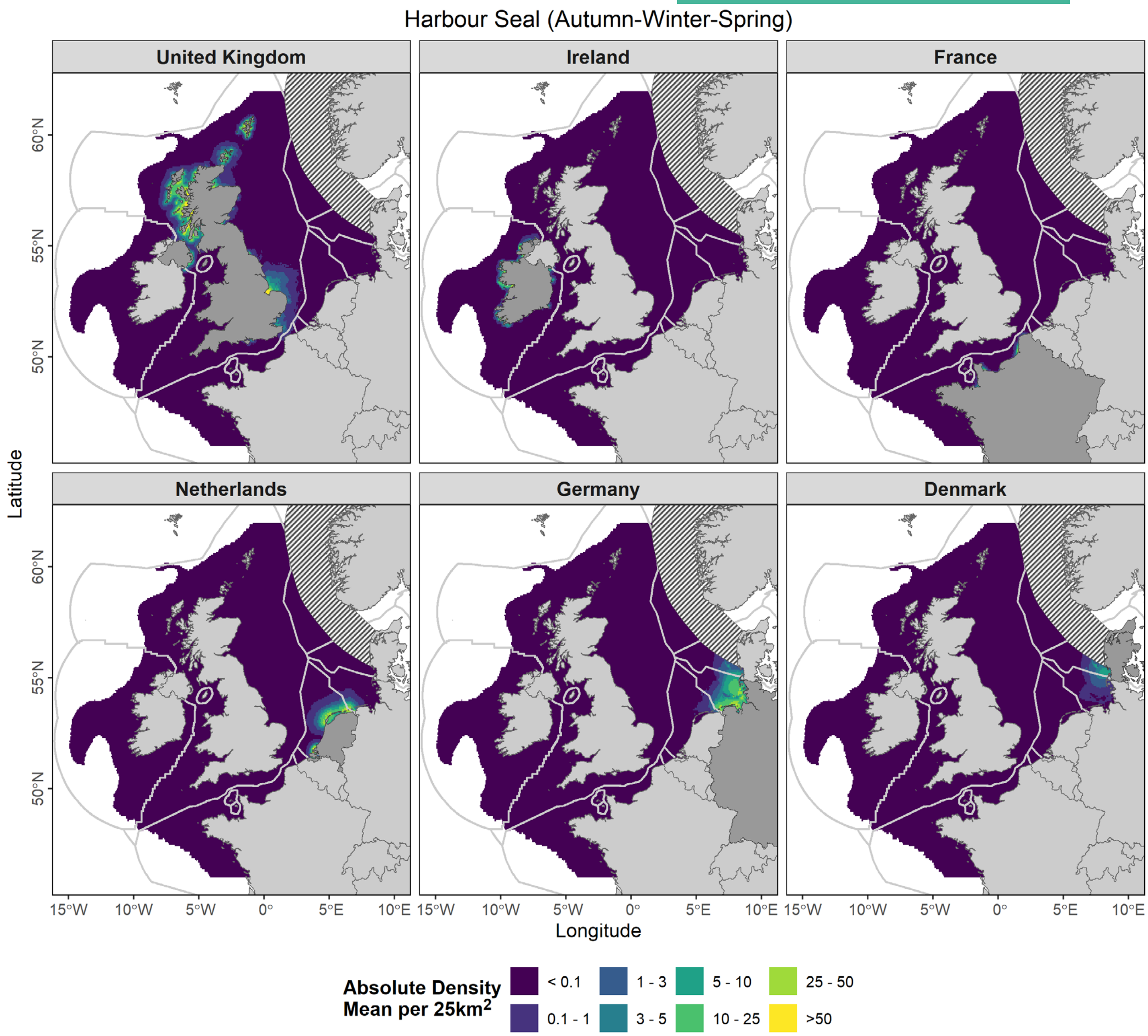

FIGURE 5 At-sea distribution of harbour seals per haulout country during the study season. Values show the mean estimate, scaled to absolute density (number of individuals averaged across the tidal cycle) per 5 km cell, based on the estimated at-sea population size in 2023. Light grey lines show the EEZ boundaries, dark grey polygons indicate the haulout country, hatching shows excluded areas. Estimates for Belgium are shown in Appendix S2.

at least two discrete metapopulations: one centred in Scotland, and another spanning Southeast England and the European continent (Carroll et al., 2020), impacts occurring at sea in one country may influence population trends observed across Europe. Transboundary exchange is particularly high for grey seals, partly reflecting their broader foraging range compared to harbour seals. However, there was evidence of substantial connectivity across national boundaries for harbour seals within the Wadden Sea (Figure 6b) where seals ranged further offshore and borders converge in a relatively small area. Overlooking transboundary distribution therefore risks suboptimal management and undermines legislative frameworks such as the OSPAR (OSPAR Commission, 1992) and Espoo Conventions (UNECE, 1991).

The scale of transboundary exchange for seals in the NWES exemplifies the need for international alignment in monitoring and conservation of wide-ranging species. Whilst international legislative frameworks like RSCs promote cohesive biodiversity management, effective enforcement depends on understanding ecological connectivity. For migratory species such as sea turtles, many historically exploited populations have failed to recover or continue to decline despite long-standing protection at breeding sites (Nel et al., 2013). Satellite tracking can reveal cryptic drivers of population trends. For example, Witt et al. (2011) showed that critically endangered leatherback turtles (*Dermochelys coriacea*) breeding in Gabon disperse widely into areas of intensive longline fishing, requiring cooperation of at least 11 nations for effective

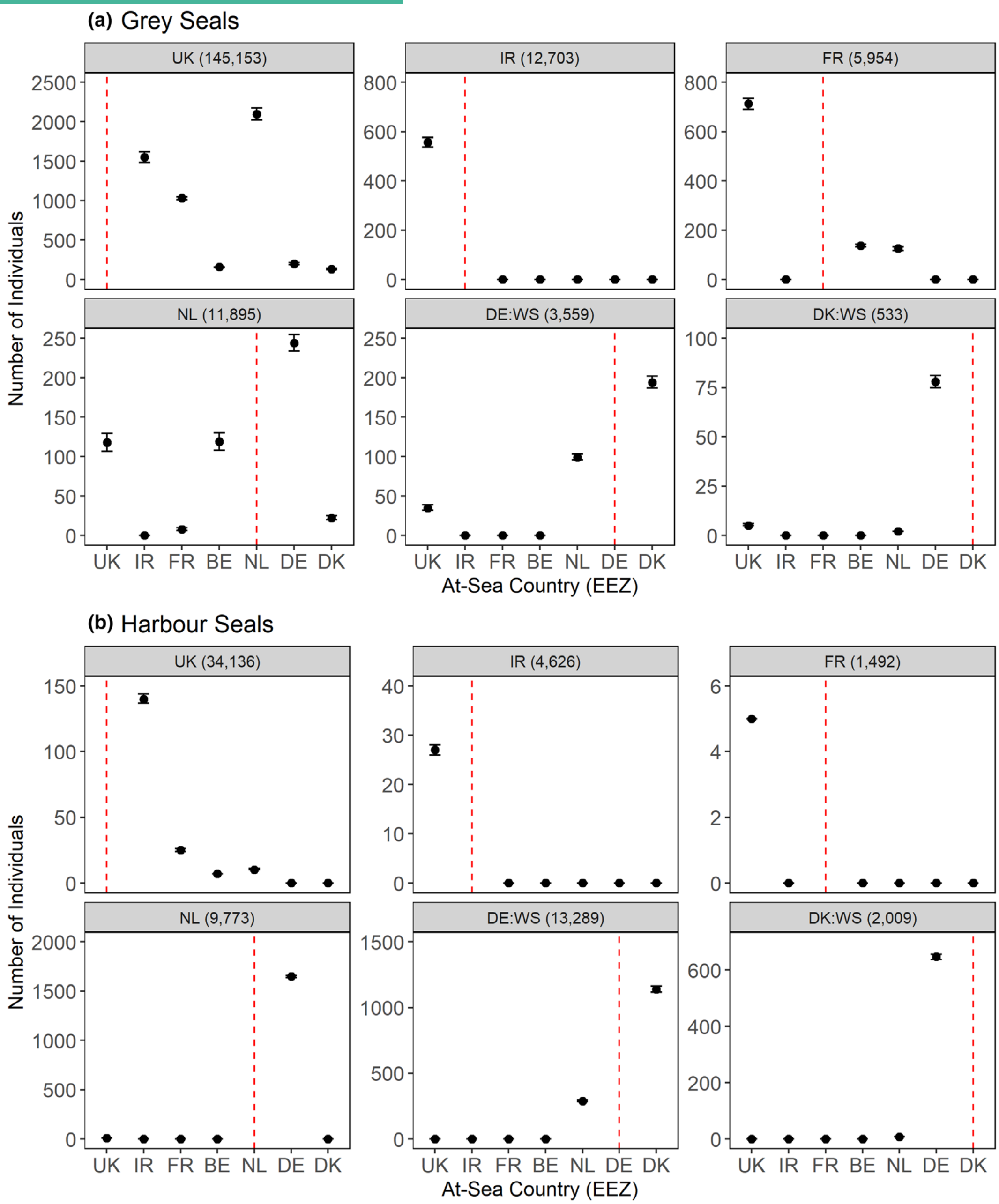

FIGURE 6 Transboundary analysis of seal distribution for (a) grey and (b) harbour seals during foraging trips. Values show the mean with 95% area-based CIs of the estimated number of individuals from haulout countries present in different at-sea countries at any given time in the study season. Panels show the haulout country, approximate size of the at-sea population in 2023 is shown in parentheses. Dashed red lines indicate the haulout and at-sea country is the same. Values apportionable to Germany and Denmark relate only to haulouts on Helgoland and the Wadden Sea coast (WS). For estimates from haulouts in Belgium, see Appendix S2.

conservation. Applying our modelling framework to such tracking datasets could help scale up individual movements to population-level distribution estimates, supporting targeted multinational conservation strategies.

Our analysis of transboundary exchange reveals the potential for mismatches in the relative importance of countries for central-place foragers, based on terrestrial versus at-sea habitat use. For example, grey seals are 80 times more abundant in Belgian waters than haulout counts suggest (Appendix S2, Table A2.3). This mismatch may pose complex management problems. A recent study reported relatively large numbers of stranded seals on the Belgian coast with suspected bycatch injuries, likely originating from haulouts outside Belgium (Haelters et al., 2022). This underscores the need for harmonised management of wide-ranging taxa across metapopulation ranges, rather than administrative units. Our distribution estimates could help probabilistically apportion bycaught seals to source haulouts. However, the estimates likely do not apply to young-of-the-year seals, which are particularly vulnerable to bycatch (Baker et al., 1998). Young-of-the-year seals were excluded due to high early-life mortality (their contribution to total abundance varies

TABLE 1 Apportioning of grey seals within MPAs on the Dogger Bank. Values show the mean number of individuals apportionable to haulouts in a given country present at sea in the different MPAs on the Dogger Bank whilst making foraging trips during summer, scaled to absolute values for 2023. Predictions for Germany and Denmark are seals from haulouts on Helgoland and the Wadden Sea coast only. 95% area-based CIs around the mean are shown in brackets, reflecting uncertainty in the habitat association relationships, but not uncertainty in population size or the proportion of the population expected to be at sea at any one time.

		MPA jurisdiction		
		UK	Netherlands	Germany
Haulout Country	UK	1948 (1848–2055)	392 (368–415)	72 (67–78)
	Netherlands	13 (11–14)	34 (30–39)	11 (10–13)
	Germany	2 (2–3)	6 (5–7)	4 (3–4)
	Denmark	0	1 (1–1)	1 (1–1)
Total		1963 (1861–2072)	433 (404–462)	88 (81–96)

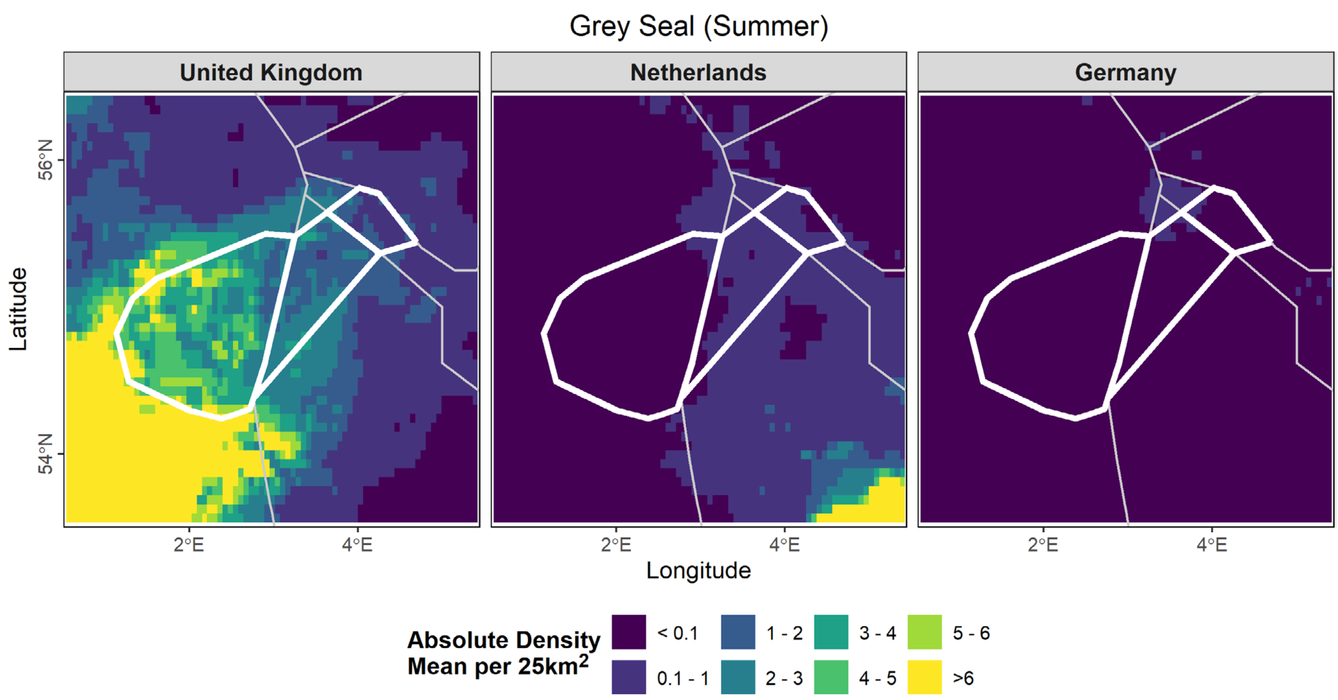

FIGURE 7 Distribution of grey seals apportionable to haulouts in different European countries within Dogger Bank MPAs (white polygons; left–right: UK, Dutch, German) during summer. Panels show the mean number of individuals apportionable to each haulout country per 5 km cell. Grey lines delimit the EEZ boundaries.

markedly throughout the year) (Thomas et al., 2019) and highly dispersive behaviour (Carter et al., 2017). Juveniles are largely under-represented in species distribution modelling due to the complexity of observing highly dispersive individuals and modelling habitat associations that may be poorly formed or undergo ontogenetic change (Robinson et al., 2011). As technological advances facilitate tracking larger numbers of juveniles from more diverse taxa (Hazen et al., 2012), future work should develop frameworks to predict juvenile distributions from emerging datasets.

This study represents a collaborative effort across Europe to provide the most comprehensive seal distribution estimates for the NWES. Given the scale, some limitations common to large-scale modelling studies apply, and users should consider these when interpreting the outputs. First, models were fitted using environmental covariates available across the study area, meaning optimal covariates were not necessarily used in all regions. Whilst the outputs are appropriate for most applications, location-specific studies (e.g. Aarts et al., 2016) may be more suitable where fine-scale understanding is needed.

Second, pooling data across time and space is often necessary in large-scale distribution models to achieve broad coverage, but may obscure temporal shifts in habitat use. Here, tracking data were combined from the past two decades (Appendix S1), during which changes to habitat (e.g. anthropogenic developments, prey redistribution, climate change) and population size may have influenced seal distribution. Further, the modelled data excluded trips transiting between countries that fall in different habitat association regions during the study season (49 grey seal trips: Appendix S1). Given that this is a relatively small percentage of all trips (<0.4%), it is unlikely to affect results. Some NWES areas hosting seals were excluded due to lack of comparable tracking data and/or haulout surveys or because they host relatively small numbers with likely unique habitat associations. However, these excluded seals represent a small proportion of total NWES numbers. Future GPS-GSM tag deployments in areas where tracking data are lacking, incomparable or outdated (e.g. Northwest Denmark and Norway) will help to provide a more complete picture of seal distribution on the NWES. Moreover, as more data become available in the study area, future studies should examine the potential for temporal distribution shifts.

Third, species distribution estimates are often provided as absolute values for ease of interpretation, but these depend on population size, which may change through time. We show maps of absolute density for 2023, but recommend using relative density wherever possible (see Appendix S2) since it is somewhat robust to temporal changes in abundance (provided the distribution of the population remains the same proportionally among haulouts and the at-sea environment does not change). Absolute estimates were generated using published scalars from UK telemetry studies (see Appendix S1), but their application to other regions requires further validation. Moreover, there are sources of uncertainty in these scalars that are not propagated through to the confidence intervals around the mean estimates. Confidence intervals therefore reflect model-based uncertainty in mean habitat associations only and do not capture uncertainty in population size or temporal variation in haulout use. Haulout counts were used from August (during harbour seal moult), since these were available for the entire study area (grey seal moult surveys are not conducted for the majority of UK and Ireland haulouts and breeding surveys may be unrepresentative due to seasonal redistribution; Carter et al., 2022; Russell et al., 2013). Therefore, for grey seals, counts represent a snapshot of individuals that are hauled out between foraging trips, and there may be some sources of local variability (e.g. disturbance, weather conditions) in how this snapshot relates to the overall population size (Scalar 1) that are difficult or impossible to quantify (Russell & Carter, 2021). The proportion of the harbour seal population hauled out is likely to be more consistent as individuals favour being on land during the moult (Lonergan et al., 2013).

Scalar 2 estimates the at-sea population size based on average time spent at sea during the study season, which varies throughout the tidal cycle since seals are more likely to be hauled out at low tide. This scalar is averaged across the tidal cycle, and therefore, such variation is not captured in the estimates. For some applications, high tide density estimates may be more appropriate. To address this, density maps based on the total population (rather than the average at-sea abundance) were generated (see Appendix S2, Figure A2.27). Even so, these high tide density estimates should not be viewed as upper bounds because of the lack of repeat haulout counts, and the use of a single value to scale counts to population size. Future work should focus on refining uncertainty estimation for these scalars to capture temporal and geographic variation in abundance and time spent at sea.

Lastly, some seals redistribute outside the study seasons on both local and inter-regional scales, using different haulout sites for foraging and breeding (Brasseur, 2017; Brasseur et al., 2015; Carter et al., 2022; Russell et al., 2013). For example, grey seals hauling out in the Netherlands during the summer but breeding in the UK may be considered part of the Dutch or UK national population depending on the season (Brasseur et al., 2015). Similarly, some harbour seals undertaking foraging trips from haulouts in the Netherlands are observed to breed in Germany (Brasseur, 2017). More local redistribution also occurs between foraging and moult seasons. Since harbour seal surveys are typically limited to breeding and moulting seasons, any impact of redistribution between moulting and foraging on the estimates is impossible to quantify. However, distribution estimates for grey seals in the Wadden Sea generated with moult (March/April) rather than foraging season (August) counts revealed significant coastal redistribution, although offshore patterns remained comparable (Appendix S2). Users should therefore be mindful of the seasonality of estimates, particularly in coastal areas.

Like most species distribution estimates, the maps presented here represent a snapshot of mean density. Such estimates are widely used in marine and terrestrial systems for various applications, including EIAs, potential biological removal (PBR) thresholds (Taylor et al., 2022), biodiversity indicator assessments (e.g. OSPAR—Banga et al., 2022), ecosystem models (Trifonova & Scott, 2024) and spatial conservation initiatives (e.g. Important Marine Mammal Areas [IMMAs]—Tetley et al., 2022). However, they do not capture temporal dynamics such as tidal, daily or seasonal variation in density or the turnover of individuals within an area. Turnover rates will vary across cells depending on various factors including their primary use (e.g. foraging vs. travelling); seals may traverse a 5 km grid cell in <2 h whilst travelling, but can remain in foraging areas for days. As anthropogenic pressures on biodiversity grow in most of Earth's ecosystems, tools such as Population Consequences of Disturbance (PCoD) models (Keen et al., 2021) hold great promise for quantifying the extent of such impacts and informing effective conservation management. However, making this step from a snapshot to a dynamic understanding of distribution is a key challenge that will be critical to their success. This study provides a foundation for integrating distribution estimates with mechanistic information on individual-level movements and habitat use to support that transition.

5 | CONCLUSIONS

Our study provides the first comprehensive distribution estimates for pinnipeds on the NWES, alongside estimates for seven constituent countries and additional resources for UK Seal Monitoring Units and Special Areas of Conservation. These resources will help developers and conservation managers improve estimates of the potential transboundary impacts of anthropogenic stressors on pinnipeds, facilitating environmentally sensitive marine spatial planning and fulfillment of environmental protection legislation. More broadly, this study highlights the importance of incorporating transboundary distributions into ecological assessments and management plans for wide-ranging species. Whether in marine or terrestrial systems, overlooking ecological connectivity across borders risks underestimating impacts and undermining conservation outcomes.

AUTHOR CONTRIBUTIONS

Matt I. D. Carter: conceptualisation (supporting); methodology (co-lead); formal analysis (lead); validation; data curation (co-lead) and visualisation; writing—original draft (lead), reviewing and editing (lead); funding acquisition (supporting). Debbie J. F. Russell: conceptualisation (lead); methodology (co-lead); resources (equal); data curation (co-lead); writing—original draft (supporting), reviewing and editing (equal); supervision; project administration; funding acquisition (lead). Geert Aarts: methodology (supporting); resources (equal); writing—review and editing (equal). Floris M. van Beest: resources (equal); writing—review and editing (equal). Matt Bivins: investigation (supporting); writing—review and editing (equal). Sophie M. J. M. Brasseur: resources (equal); writing—review and editing (equal). Rune Dietz: resources (equal); writing—review and editing (equal). Callan D. Duck: data curation (supporting); resources (equal); writing—review and editing (equal). Anders Galatius: resources (equal); writing—review and editing (equal). Anita Gilles: resources (equal); writing—review and editing (equal). Jan Haelters: resources (equal); writing—review and editing (equal). Gordon D. Hastie: resources (equal); writing—review and editing (equal); funding acquisition (supporting). Mark Jessopp: resources (equal); writing—review and editing (equal). Chris D. Morris: data curation (supporting); resources (equal); writing—review and editing (equal). Simon E. W. Moss: investigation (lead); writing—review and editing (equal). Jacob Nabe-Nielsen: resources (equal); writing—review and editing (equal). Dominik A. Nachtsheim: resources (equal); writing—review and editing (equal). Tobias Schaffeld: resources (equal); writing—review and editing (equal). Jessica Schop: resources (equal); writing—review and editing (equal). Ursula Siebert: resources (equal); writing—review and editing (equal). Jonas Teilmann: resources (equal); writing—review and editing (equal). Dave Thompson: resources (equal); writing—review and editing (equal). Paul M. Thompson: resources (equal); writing—review and editing (equal). Cecile Vincent: resources (equal); writing—review and editing (equal). All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest, financial or otherwise. Debbie J. F. Russell is an Associate Editor of the Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

The datasets generated in this study are freely available at https://doi.org/10.17630/00334852-4f8c-4799-a418-664c8104d68f (Carter et al., 2025).

STATEMENT ON INCLUSION

Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

ORCID

Matt I. D. Carter https://orcid.org/0000-0002-5481-6254
Geert Aarts https://orcid.org/0000-0003-3196-4235
Floris M. van Beest https://orcid.org/0000-0002-5701-4927
Sophie M. J. M. Brasseur https://orcid.org/0000-0002-9245-6990
Rune Dietz https://orcid.org/0009-0008-9702-9737
Anders Galatius https://orcid.org/0000-0003-1237-2066
Anita Gilles https://orcid.org/0000-0001-7234-8645
Jan Haelters https://orcid.org/0009-0005-3177-4863
Gordon D. Hastie https://orcid.org/0000-0002-9773-2755
Mark Jessopp https://orcid.org/0000-0002-2692-3730
Chris D. Morris https://orcid.org/0000-0003-2070-4251
Simon E. W. Moss https://orcid.org/0000-0001-5378-7773
Jacob Nabe-Nielsen https://orcid.org/0000-0002-0716-9525
Dominik A. Nachtsheim https://orcid.org/0000-0002-1010-3527
Tobias Schaffeld https://orcid.org/0000-0002-2576-6534
Ursula Siebert https://orcid.org/0000-0002-2556-3948
Jonas Teilmann https://orcid.org/0000-0002-4376-4700
Dave Thompson https://orcid.org/0000-0003-1546-2876
Paul M. Thompson https://orcid.org/0000-0001-6195-3284
Cécile Vincent https://orcid.org/0000-0002-5224-0757
Debbie J. F. Russell https://orcid.org/0000-0002-1969-102X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. (A1) supplementary methods, (A2) supplementary results and discussion, and (A3) supplementary acknowledgements and funding information.

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