Postbus 68 | 1970 AB IJmuiden

Ministerie van Infrastructuur en Waterstaat
Rijkswaterstaat Water, Verkeer en Leefomgeving
T.a.v. Jakob Asjes en Rens Cronau
Griffioenlaan 2
3526 LA Utrecht

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POSTAL ADDRESS
Postbus 68
1970 AB IJmuiden

VISITORS' ADDRESS
Haringkade 1
1976 CP IJmuiden

INTERNET
www.wur.nl/marine-research

CoC NUMBER
09098104

HANDLED BY
Geert Aarts

TELEPHONE
+31 (0) 6 30462385

EMAIL
geert.aarts@wur.nl

Authors: Geert Aarts, Sophie Brasseur & Jessica Schop

Hinterland analysis: Is the onshore distribution of harbour seals regulated by offshore habitat quality?

This report represents a summary of the key results and conclusions. Additional details can be found in the appendix and supplementary material. The appendix includes a more technical scientific manuscript intended for publication in a peer-reviewed academic journal. The supplementary material includes the R-code used for the analysis and habitat-based distribution maps used for the Hinterland analysis.

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Uitgebreide Nederlandse samenvatting

Zeezoogdieren zijn van groot belang in de Noordzee, aangezien ze als roofdieren aan de top van de voedselketen staan. Eén van de onderzoeksvragen binnen het MONS-programma is daarom ook om te achterhalen in hoeverre de toenemende menselijke activiteiten op zee kunnen leiden tot een verandering van de ecologische draagkracht en zo de populatieomvang van zeezoogdieren kan beïnvloeden. De vraag is echter óf de beschikbaarheid en kwaliteit van foerageergebieden een directe invloed heeft op de populaties van de verschillende soorten en op welke manier? Het doel van dit onderzoek is om beter te begrijpen in hoeverre de aantallen gewone en grijze zeehonden worden beïnvloed door de beschikbaarheid en kwaliteit van geschikt foerageergebied. Als deze relatie namelijk kan worden vastgesteld, kan deze in de toekomst gebruikt worden om te onderzoeken in welke mate menselijke activiteiten op de Noordzee de kwaliteit van foerageergebieden, en daarmee de draagkracht voor de verschillende soorten beïnvloeden.

Voor dit onderzoek wordt de verspreiding van de gewone en grijze zeehonden op zee bepaald op basis GPS-zenderdata gemodelleerd als functie van omgevingsvariabelen afstand tot de ligplaats, diepte, sediment samenstelling en topografische kenmerken, zoals zandruggen en geulen in de Noordzee. Tevens wordt onderzocht in welke mate zeehonden foerageren binnen dat gebied wat het dichts bij hun vertrek- en aankomstligplaats ligt (de 'Hinterland' horende bij hun ligplaats), of dat ze ook de hinterlandgrenzen oversteken en dichter in de buurt van andere ligplaatsen foerageren. Vervolgens wordt dit habitatmodel gebruikt om voor elke plek op zee te bepalen wat de relatieve kwaliteit is van dat gebied en hoeveel zeehonden zich daar gemiddeld bevinden, en wordt met deze geschatte dichtheid een voorspelling gemaakt van het aantal zeehonden op de nabijgelegen ligplaatsen. Deze voorspellingen van aantallen op de ligplaatsen worden vervolgens vergeleken met vliegtuigtellingen uit de internationale Waddenzee en de Delta in het zuiden van Nederland.

De resultaten laten een significante correlatie zien tussen de voorspelde aantallen en de getelde aantallen voor zowel grijze als gewone zeehonden. Toch zijn er enkele interessante afwijkingen. Op de locaties die bekend zijn als belangrijke geboortegebieden voor gewone zeehonden, zoals het grensgebied tussen de Nederlandse en Duitse Waddenzee en Schleswig-Holstein, worden veel meer dieren geteld dan verwacht op basis van het habitatmodel. Tijdens de voortplanting migreren dieren naar die gebieden toe en het is aannemelijk dat ze zich pas na de verharing in augustus herverdelen conform de beschikbaarheid van foerageergebieden. Ook zijn er plekken waar minder dieren worden waargenomen dan voorspeld, zoals met name in het Deltagebied. De gewone zeehonden in dit gebied waren rond 1990 nagenoeg verdwenen en hun aantal groeit nog steeds. Waarschijnlijk hebben de gewone zeehonden de beschikbare foerageergebieden nog niet helemaal opgevuld. Voor grijze zeehonden is er ook een significante relatie tussen de vliegtuigtellingen en de voorspellingen op basis van het habitatmodel. Echter grijze zeehonden zijn veel meer geclusterd op een beperkt aantal ligplaatsen, vooral in de Nederlandse wateren, terwijl het model voorspelt dat er ook veel grijze zeehonden in de andere delen van de Waddenzee zouden moeten bevinden. Ook voor de grijze zeehond kan het zijn dat de beschikbare foerageergebieden nog niet helemaal zijn opgevuld. Mogelijk komt dit door de nabijheid van deze gebieden t.o.v. het Verenigd Koninkrijk, waar de bronpopulatie zicht bevindt. Verder onderzoek zou kunnen uitwijzen of competitie tussen de grijze en de gewone zeehonden hier ook een rol speelt.

Wanneer voor ieder deelgebied (de Delta, Nederland, Niedersachsen, Schleswig-Holstein en Denemarken) de aantallen bij elkaar worden opgeteld, dan kan men de draagkracht op basis van het habitatmodel schatten. Deze komt redelijk overeen met het maximaal aantal getelde dieren per deelgebied. Echter, dit wijkt af voor Schleswig-Holstein waar relatief veel jongen geboren worden. Zoals hierboven geschetst wordt, kan het zijn dat de dieren tijdens de telling in augustus nog niet zijn terug gemigreerd. Voor het Deltagebied is de geschatte draagkracht juist veel hoger dan de augustus tellingen. Deze populatie groeit echter nog steeds. Daarnaast worden hier juist relatief weinig jongen geboren. Een deel van de dieren is mogelijk in augustus nog in de Waddenzee. Ook is dit gebied, in de nabijheid van de haven van Rotterdam, een van de drukste gebieden van de Noordzee, en zou verstoring door menselijke activiteiten een rol kunnen spelen.

Als voorlopige conclusie kan worden gesteld dat het haalbaar is om, op basis van de verspreiding van habitattypes op zee, de aantallen zeehonden op het land en hun lokale verspreiding te voorspellen. Daarmee kunnen tevens voorzichtige uitspraken worden gedaan over regionale draagkracht voor zeehonden. Desalniettemin zijn er nog steeds aanzienlijke regionale afwijkingen tussen de voorspelde en waargenomen aantallen. Deze afwijkingen bieden interessante aanknopingspunten voor toekomstig onderzoek. Bijvoorbeeld, wanneer tellingsgegevens uit de foerageerperiodes worden verzameld (voor de gewone zeehonden de wintermaanden, in plaats van de huidige augustus - rui tellingen), blijken dan dat de voorspellingen minder af te wijken van de waargenomen aantallen? Kan men dan stellen dat dieren zich na de rui in augustus andere ligplaatsen kiezen en zich verder verdelen over het beschikbare foerageergebied? Wordt de waargenomen verdeling van gewone zeehonden lokaal mede beïnvloed door competitie met grijze zeehonden, of bruinvissen?

Het huidige model is gebaseerd op omgevingsfactoren zoals bodemtype en diepte. De analyse kan in de toekomst worden uitgebreid door effecten van menselijke activiteiten op de verspreiding mee te nemen. Dit creëert mogelijkheden om te schatten wat de invloed van deze activiteiten is op de kwaliteit van foerageergebieden en hoe zich dat door zou kunnen vertalen op de omvang van de populatie. Daarnaast is het mogelijk om scenario's te simuleren waarbij de hier genoemde methode kan worden toegepast om vast te stellen waar menselijke activiteiten de grootste invloed hebben op de zeehondenpopulatie.

Briefing report

Marine mammals play a critical role in the North Sea ecosystem. The most abundant marine mammal species in these waters are the harbour seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*) and harbour porpoise (*Phocoena phocoena*). These species occupy the top of the food chain and thus exert an important influence on the abundance and distribution of lower-trophic-level species within the North Sea food web. However, the rise in human activities in the North Sea, including the construction of offshore wind farms and shipping, may compromise the regulatory role of marine mammals by changing both the overall availability and the quality of their foraging areas. One of the research questions within the MONS program is to determine the extent to which increasing human activities at sea can lead to a change in the ecological carrying capacity and population size of marine mammals. To address this question, it is first necessary to determine if the availability and quality of foraging areas at-sea is a driving factor of population size. Once this relationship can be established, it could potentially be employed in the future to investigate if natural or human-driven changes of habitats in the North Sea, may lead to changes in the carrying capacity of the different species.

Within Dutch coastal waters, well studied marine mammal species are the harbour seal and grey seal. A large amount of historical transmitter data is available that can be used to map the at-sea distribution of these species. In addition, systematic counts of numbers on land have been carried out since the 1960s, which have not only provided insights into the historical development of population size, but these data can also be used to identify where most individuals can be found resting in the Wadden Sea. The aim of this research project is to determine the habitat quality of various areas in the North Sea, and then to investigate to what extent the location, surface area and quality of these foraging areas influence the number of animals observed on land and the size of the population in the various sub-areas of the Dutch Delta and the international Wadden Sea.

For this study, GPS tracking data were used to model the density of harbour seals (Fig. 1, left) and grey seals (Fig. 1, right) at sea as a function of environmental variables such as distance to the haul-out, depth (Fig. 2, left), sediment composition and topographic features, such as sand ridges and channels (Fig. 2, right). We also investigated to what extent seals forage exclusively within the 'Hinterland' (i.e. the area of space closest to a specific haul-out site), or whether they also cross Hinterland borders and forage closer to other haul-out sites. The fitted habitat model and estimated degree of spatial segregation was then used to determine the relative quality of each location at-sea, and the estimated density of seals was subsequently distributed over the nearby haul-out sites.

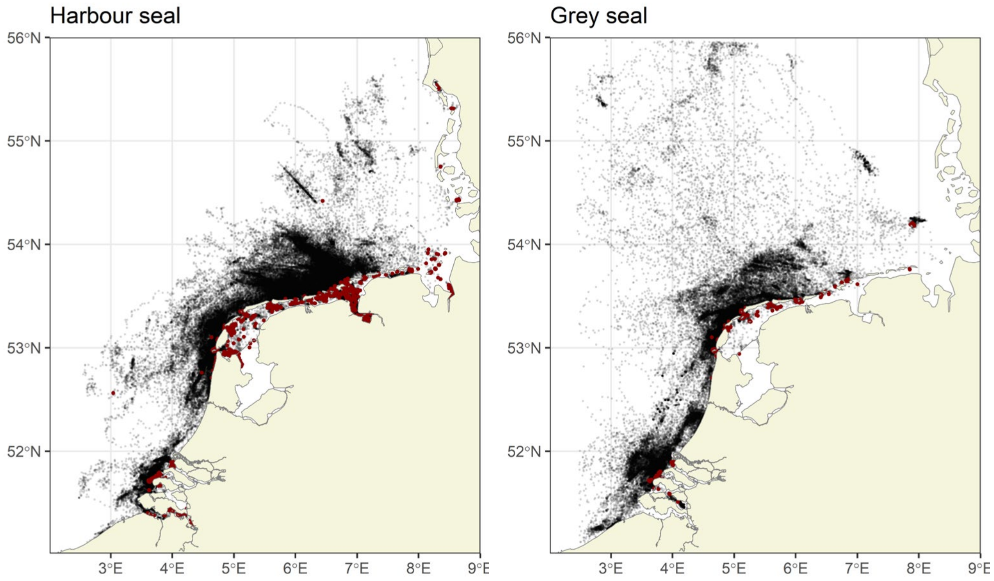

Figure 1. *The GPS transmitter data (black) used in this analysis. Haul-out locations are shown in dark red.*

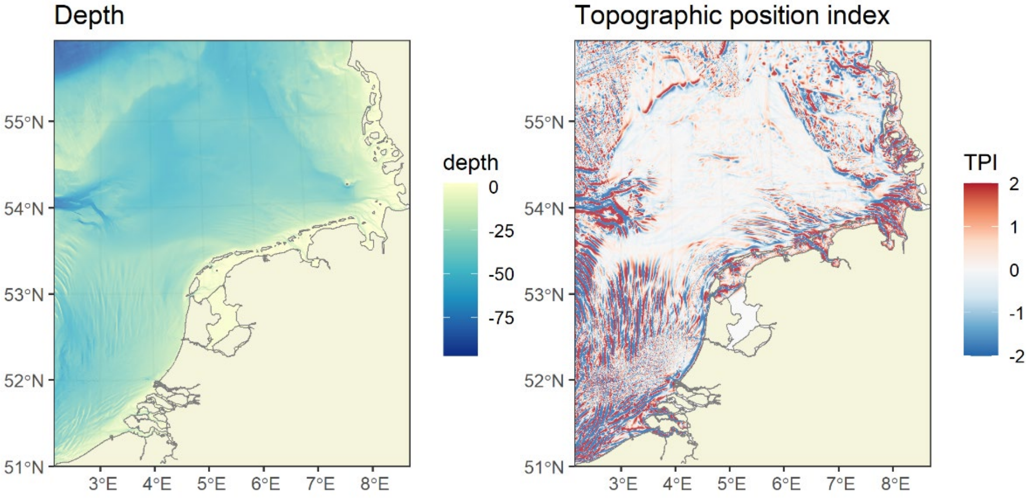

Figure 2. *Two environmental variables used in this study. Left: Depth (in m). Right: Topographic position index. Values greater than 0 refer to ridges or peaks in the underwater landscape. Values less than 0 refer to troughs or channels.*

The habitat-model derived from GPS tracking data can be used to predict the number of seals at the different haul-out sites. Aerial survey count data were used to compare with the model predictions. Here, counts were used from the entire international Wadden Sea, which encompasses the Netherlands, Lower Saxony and Schleswig-Holstein in Germany, and Denmark. Additionally, we obtained count data from the Dutch province Zeeland (Fig. 3). If data were available for multiple years, we used the average of the moult counts collected in the past 10 years (2014-2023). For Denmark, the only moult count at the haul-out level that is currently available was from 2017.

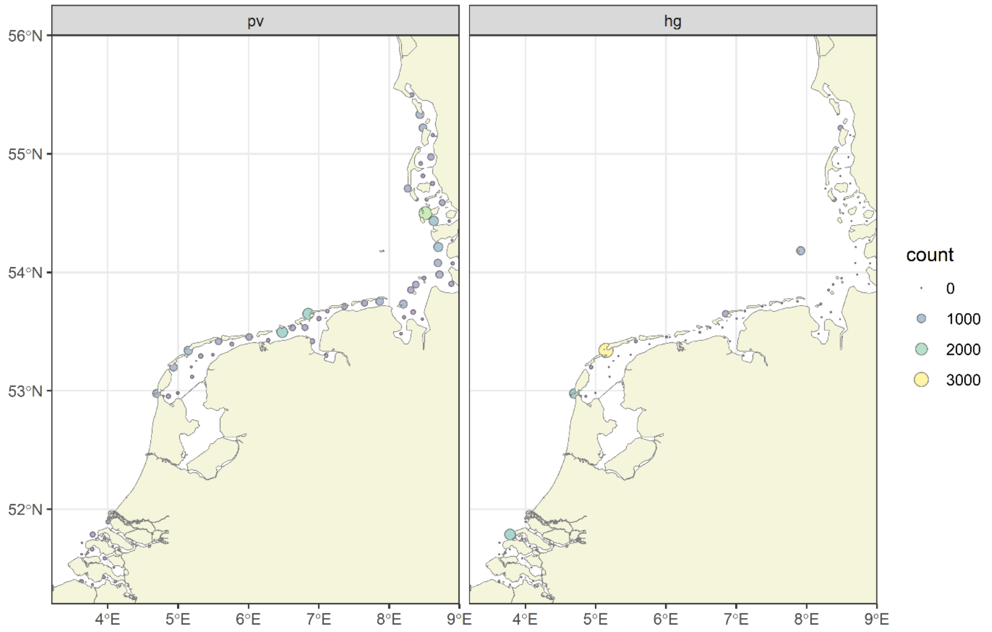

Figure 3. *Distribution on land of the number of harbour seals (pv) in August (left) as well as the number of grey seals (hg) in March and April (right). The numbers counted on nearby haul-out sites are clustered to limit overlap in the symbols.*

The habitat model that was developed using transmitter data shows that harbour seals exhibit a strong preference for areas that are relatively close to their resting places. This can be attributed to the fact that foraging habitats closer to the haul-out require less travel time, as well as the fact seals must always cross nearby areas in order to reach foraging habitats further offshore. Harbour seals also show a preference for foraging areas that are located at a depth of less than 20 meters, and they are less likely to be found in areas that are much deeper. Furthermore, they often choose areas that contain a low mud fraction and exhibit a slight preference for areas that are situated within channels and gullies, or on ridges and peaks. Areas that are flat are less likely to be used. Grey seals exhibit a similar preferential selection for environmental variables to harbour seals, although they occasionally make longer and more distant foraging trips and their preference for peaks and ridges is more pronounced. This model can be used to determine the habitat suitability for each location at sea and to estimate the density of seals at sea (shown for harbour seals in Fig. 4).

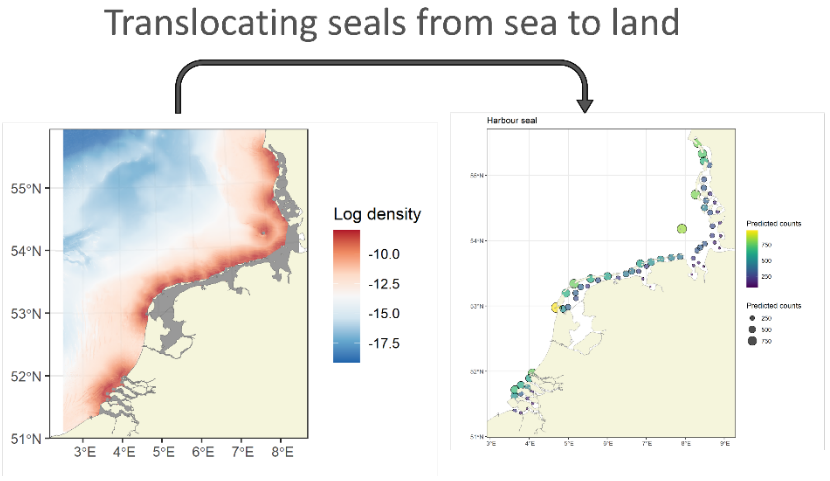

Figure 4. *The relative distribution of harbour seals based on distance to the nearest haul-out site (left), used to translocate seals onto the known haul-out sites*

The habitat model allows for an estimation of the numbers of resting seals across the available haul-out sites, revealing a significant correlation between predicted and observed numbers of harbour seal (Fig. 5).

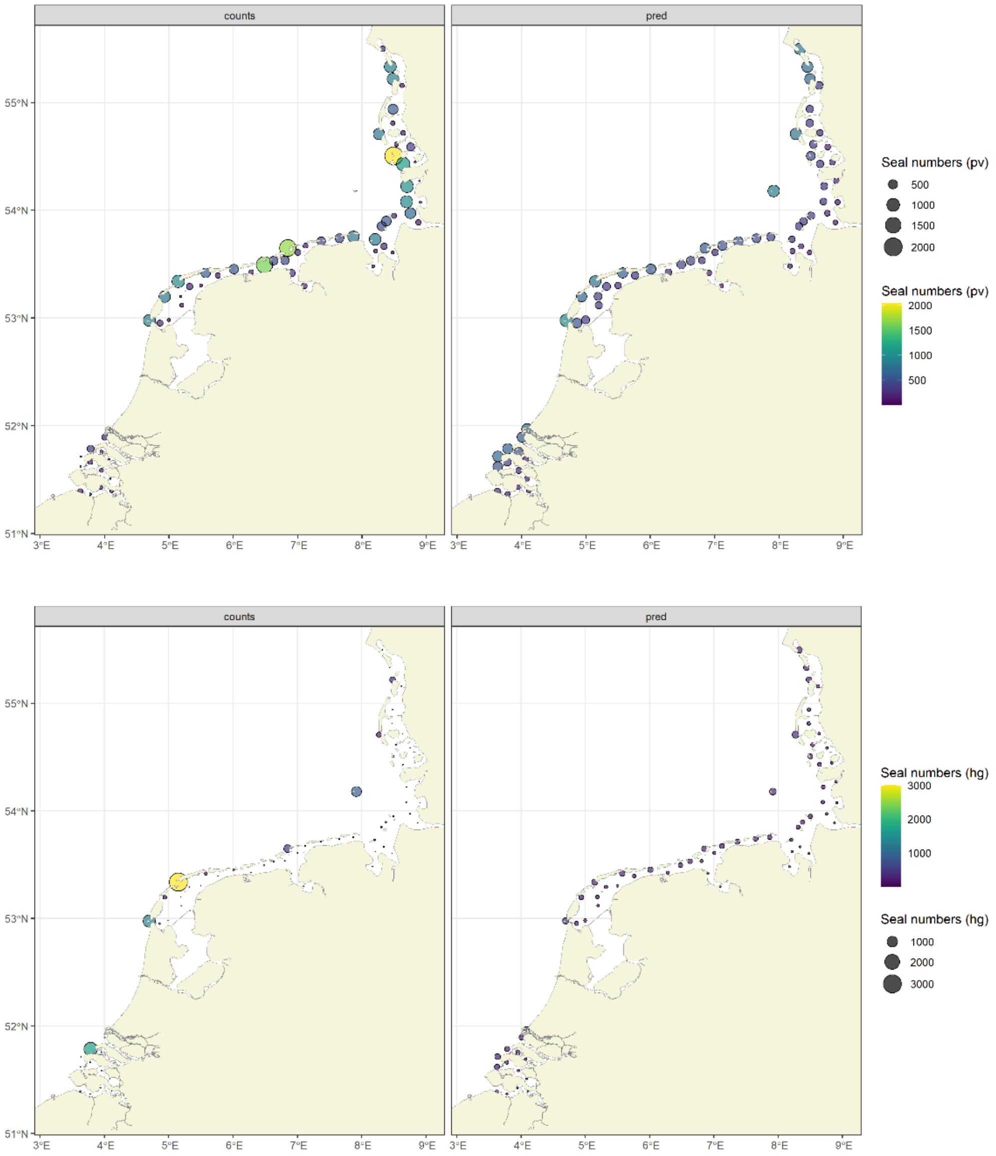

Figure 5. Observed numbers of harbour seals (top panels) and grey seals (bottom panels) based on aircraft counts (left panels) and predicted numbers of the habitat model (right panels).

Notably, there are some interesting deviations (Fig. 6 and Fig. 7). In key breeding regions, such as the border area between the Dutch and German Wadden Sea and Schleswig-Holstein, observed harbour seal counts exceed model predictions. It is plausible that the distribution of harbour seals observed during the moult counts in August may not yet be completely aligned with their haul-out distribution during the foraging season. In other regions, such as the Dutch Delta region in Zeeland, the model predictions exceed the aerial survey counts. The population of harbour seals in this region is still growing, and it is likely that the population has not fully occupied the available foraging areas. Additionally, competition may exist with other predators, particularly among other marine mammal species like grey seals and harbour porpoises. Competition may also explain the under-representation of harbour seals on Helgoland.

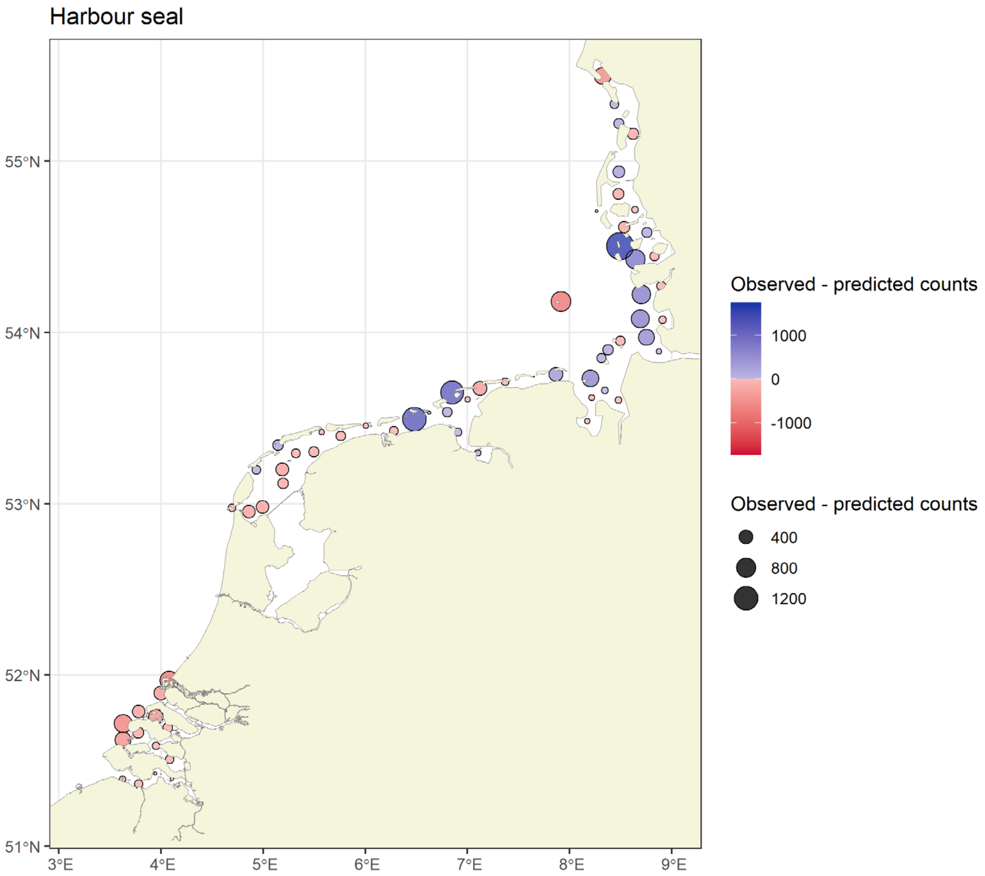

Figure 6. *The discrepancy between the observed counts of harbour seals during aerial surveys and the predicted numbers derived from the habitat model. Blue points are clusters of resting places where relatively more animals are observed than predicted based on the habitat model, and at the pink points fewer animals are observed than predicted.*

For grey seals, a significant correlation also exists between the predicted counts from the habitat model and the observed counts recorded during the aerial surveys. Haul-out sites predicted to have highest numbers of grey seal typically also host the largest groups of these animals. Compared to harbour seals, grey seals exhibit a higher degree of clustering at a limited number of haul-out sites, predominantly located in the Dutch Wadden Sea (Fig. 7).

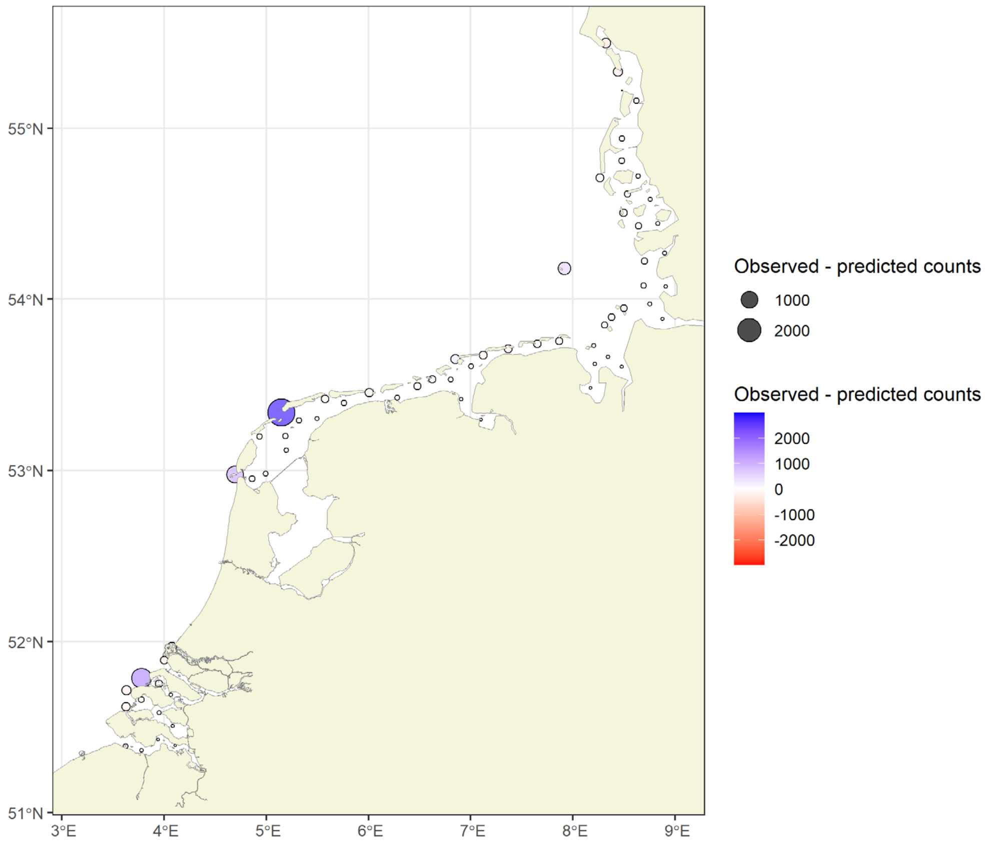

Figure 7. *The discrepancy between the observed counts of grey seals during aerial surveys and the predicted numbers derived from the habitat model. See Fig. 6 for more details.*

When aggregating the numbers of harbour seals for each sub-area (the Dutch Delta in Zeeland (ZE), the Dutch Wadden Sea (NL), Lower Saxony (LS), Schleswig-Holstein (SH) and Denmark (DK)), the estimated carrying capacity derived from the habitat model aligns with the maximum counts recorded for each sub-area (Fig. 8). In Schleswig-Holstein, the number of animals observed during the moult markedly exceeds the estimates derived from the habitat model. Many pups are born in this region, and it is likely that both the immature and the reproductive individuals have not completely dispersed throughout the area by August. For the Dutch Delta area near Zeeland, the estimated carrying capacity significantly exceeds the August counts. This population is still growing, despite a limited number of young individuals being born in this region. Later in the year, during the more intensive foraging season, harbour seals from the Wadden Sea may use this area to feed. The population of grey seals is also comparatively high in the Dutch Delta region in Zeeland, which may lead to some level of competition. The Dutch Delta region is also adjacent to the international port of Rotterdam, one of the busiest shipping areas in the North Sea, which may negatively impact the quality of foraging habitats in the area. Future population monitoring data may indicate whether harbour seal numbers persist below the estimated carrying capacity.

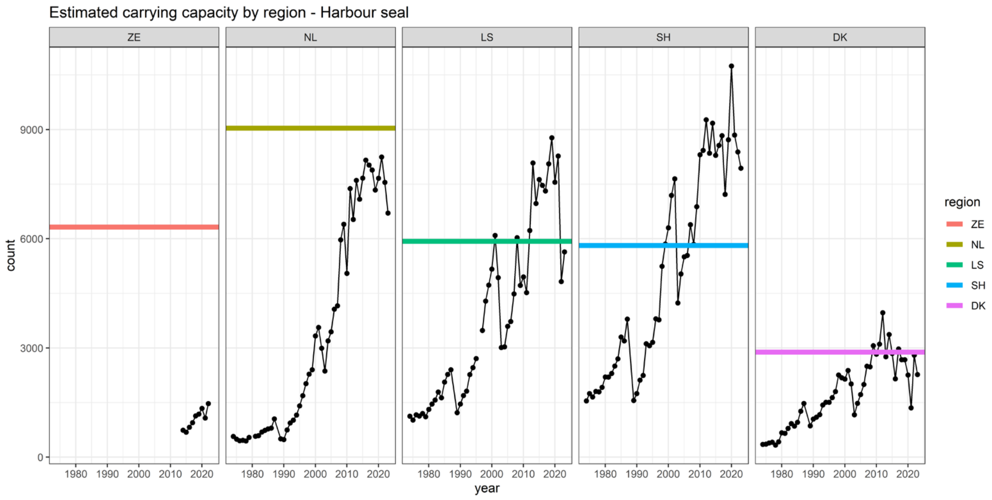

Figure 8. *Maximum moult counts (black line) of harbour seals in the different sub-areas (ZE = Dutch Delta near Zeeland, NL = Dutch Wadden Sea, LS = Lower Saxony, SH = Schleswig-Holstein, DK = Denmark) and the estimated carrying capacity derived from the habitat model.*

A similar analysis has been performed for grey seals. While the habitat model predicts the highest grey seal numbers in the Dutch Wadden Sea, the actual number of seals observed far exceeds the predictions. This could be because the Netherlands is closest to the UK, the source population from which most grey seal immigrants originate. Furthermore, compared to harbour seals, grey seals appear to have a stronger tendency to form large groups at a limited number of haul-out sites.

In conclusion, the distribution of habitat types at sea significantly explains some of the observed variation in seal numbers at the haul-out sites, allowing for cautious statements regarding regional carrying capacity. The explanatory capability of the habitat model is heavily influenced by the granularity of the haul-out site clustering used. A finer clustering implies smaller travel distances between haul-out clusters. When seals choose to travel slightly further to rest at more suitable haul-out locations (e.g., due to lower exposure or conspecific attraction or intraspecific repulsion), a finer clustering will likely lead to a lower predictive performance. However, when seal numbers from haul-out clusters are combined to estimate regional carrying capacity, the influence of such finer scale processes diminishes, although the effects of larger-scale processes, like delays in population redistributions, may become more prevalent.

While a correlation exists between the predicted and observed seal numbers, considerable discrepancies remain. These deviations offer valuable opportunities for future research. For instance, when count data from the foraging periods, specifically the winter months for harbour seals, are collected, is there a more robust correlation between the numbers predicted by the habitat model and the aerial survey counts? Or can the observed differences be partially attributed to the presence of grey seals, suggesting competition for space or resources? Is there potential competition with harbour porpoises, currently the most abundant marine mammal species in the North Sea? Which research question to tackle and which improvements to make likely depends on the research objective. Two research lines can be proposed:

1) Inclusion of population dynamical processes, which includes both model improvement and additional survey data outside the moulting and pupping season.
2) Improving the habitat model by including other environmental variables, such as those related to human activities or the presence of natural competitors, like grey seals

Inclusion of population dynamic processes

One implicit assumptions of the method used in this study is that each cluster of haul-out sites has reached its carrying capacity. This assumption may not be valid. The seal population in the Dutch Delta continues to grow and may continue to do so since in the coming years. Also, the Dutch part of the Wadden Sea may not yet be fully saturated with harbour seals, as suggested by figure 13, which shows negative residuals. The modelling of observed counts as a function of the habitat-based predicted counts fails to account for transients in population size and other population dynamic processes. Instead, one could model the regional population growth rate as a density dependent process, with the availability and quality of habitats explicitly included into the carrying capacity component of the model.

Habitat model improvement
The proposed analysis can be extended to include the effects of human activities. When there is sufficient support in the seal tracking data to estimate the effect of human-related variables on seal density, it might be possible to estimate how this translates into population consequences. In some cases, the effect of human activities could be temporary, such as the avoidance during pile driving. For those activities, more complex individual-based models might be required to derive the population-level consequences. When the effects become more permanent, such as a permanent partial or complete exclusion of seals, the approach presented here may be used to determine how this translates into regional declines in carrying capacity, reflected in changes seal numbers. For example, the habitat model could be used to investigate whether the construction and operation of windfarms affects seal distribution at sea, for example by including the distance to an operational windfarm as a covariate. Shipping activity may also deter seals or their prey, and shipping density maps for different vessel types (including fishing vessels) derived from AIS data could be included as a covariate in the habitat model. Since the effect of shipping may propagate over larger distances, the shipping density is spatially smoothed (using variable band widths) to capture possible effects over larger distances. After estimating the influence of the various human-related variables on seal distribution, the methodology proposed in this study could be used to predict regional population sizes both with and without these anthropogenic covariates. The initial focus will be on examining variations in seal density related to human activities. Future considerations may encompass alterations in foraging efficiency, including changes in prey capture ability. Once changes in density and foraging efficiency are fully quantified, this could theoretically be used to predict population-level consequences of human activities and infrastructure. Similarly, also the potential influence of competition with natural predators, could be considered by including density of the other seal species as a model covariate.

The proposed model improvements could potentially enable the direct estimation of the impact of these activities on the quality of foraging habitats and how this may translate into changes in population size. Furthermore, scenarios can be simulated using the methodology proposed here, to determine where human activities have the greatest or least impact on the seal population. Finally, the method presented may also serve as a conservation tool by estimating the anticipated number of seals on current or newly established resting sites (e.g., beach closures).

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Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

Justification

Project Number: 4315100228

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved:	Dr J.M. Ransijn Researcher
Signature:	
Date:	15 May 2025

Approved:	Maarten Mouissie Business Manager
Signature:	
Date:	15 May 2025

The regulation of colony size by offshore habitat quality: Extending the hinterland model

Aarts, Geert[1,2,*], Brasseur, Sophie[1], Schop, Jessica[1], Ransijn, Janneke[1]

[1] Wageningen Marine Research, Wageningen University & Research – Den Helder, The Netherlands
[2] Wildlife Ecology and Conservation, Wageningen University & Research – Wageningen, The Netherlands

*Corresponding author
Correspondence: geert.aarts@wur.nl

ABSTRACT

The regulation of colony sizes in central-place foragers, such as seabirds and pinnipeds, is intricately linked to the surrounding seascape. In a rapidly changing world, understanding this link is vital to predict how environmental changes at sea will impact the population dynamics of these predators. Typically, those colonies with a large hinterland (defined as the total region of space that is closest to a specific colony) tend to have more individuals. Currently, this approach often ignores variation in habitat suitability within the hinterland. Here we extend the hinterland model by incorporating spatial heterogeneity to predict harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) group sizes and distributions along the coast of the southern North Sea. Using GPS tracking data from more than 300 harbour and grey seals, tagged between 2007 and 2023, we developed a species-habitat-association model to quantify seal density as a function of environmental variables, including depth, sediment type, and topographic position index. Subsequently, model-based predictions of their at-sea distribution were allocated to the surrounding haul-out sites based on distance, and the estimated regional population sizes were compared to numbers observed during aerial surveys. The habitat model revealed a strong correlation between habitat features and seal density, with seals favouring relative shallow waters of around ~20m depth with low mud content and presence of gullies. However, the distance between the haul-out site and these habitat types was by far the most important environmental variable explaining seal distribution, indicating seals density is on average higher in areas closer to their haul-out site. Predictions of the number of individuals on the haul-out site based on the habitat model were significantly correlated with the numbers observed during the aerial surveys. However, large discrepancies between observed and predicted haul-out numbers often existed, most likely caused by both small- and large-scale processes. Small scale processes include differences in preference for specific haul-outs sites, for example their exposure to waves or anthropogenic disturbances, which were not included in the model. Large scale processes may include delays in redistribution following breeding and moulting, potential interspecific competition with other predators, including interactions between seal species, and influences form human activities. Nevertheless, these findings suggest that on average the availability and quality of foraging habitats at sea can explain where seals can be found on land and in what numbers. These findings also suggest that aerial survey counts of seals on haul-out sites, particularly outside the pupping and moulting seasons, could serve as indicators of regional marine habitat quality for seals and changes therein. The approach has implications for marine spatial planning, including the mitigation of human impacts such as the construction offshore wind farms. This methodology also offers a framework for assessing habitat suitability and carrying capacities for other central-place foraging species. Future research should include inter- and intraspecific competition and facilitation, variations in prey abundance and anthropogenic factors to improve predictive performance and support conservation applications.

Keywords: *Species distribution model, habitat selection, optimal foraging, ideal-free distribution, animal aggregations, marine predators, central-place foragers, environmental impact assessments.*

Introduction

Many central-place foraging species across the globe aggregate in groups to form colonies. These animal aggregations can vary greatly in size, and some may contain millions of individuals (Brown, 2016). This variation in group size has intrigued ecologists for decades, and has instigated investigations into the underlying mechanisms (Cairns, 1989, p. 19; Gaston et al., 2007; Jovani et al., 2016; Santora et al., 2020). Several studies have shown that (maximum) group size is often regulated by the size of the foraging area in the surrounding landscape. For example, those species with larger maximum foraging ranges tend to aggregate into larger groups (Patterson et al., 2022). More specifically, (Jovani et al., 2016) found that the square of the maximum foraging range is linearly correlated with colony size. While this linear relationship may hold when central-place foragers can freely radiate out away from the colony, density-dependent competition may cause spatial segregation between the foraging distribution when individuals from neighbouring colonies compete for the same resources, (Aarts et al., 2021; Bolton et al., 2018; Grémillet et al., 2004; Wakefield et al., 2013). Such spatial segregation may severely reduce the foraging area available to individual members of a specific aggregation.

The most simplistic model that accounts for the effect of spatial segregation on the distribution and size of colonial animal aggregations is the Hinterland model (Cairns, 1989), where the Hinterland is the region of space that is in closer proximity to a particular colony than any other colony. Under this model, foraging animals are assumed to always return to the nearest colony, which leads to equidistant boundaries between neighbouring colonies (i.e., a Voronoi tessellation of space). The size of these colony-specific Hinterlands will dictate colony size (Cairns, 1989; Wakefield et al., 2014). For example, colonies that are surrounded by other colonies will have smaller Hinterlands and are expected to contain fewer individuals than colonies located in isolation. There are, however, two main shortcomings to the use of Hinterland areas to explain colony size. First, in nature the boundaries between hinterlands are not absolute and impermeable, and the foraging distribution of animals from neighbouring colonies may be mixed across these boundaries. Second, habitat quality will vary across the landscape; as a result, certain Hinterlands may contain more profitable foraging habitats than others. For example, a particular Hinterland may have large foraging areas of high quality that are in close proximity to the colony. The latter aspect, the importance of habitat in shaping colony size, has been studied by Wakefield et al. (2014). They used prior information on habitats suitability for black-browed albatross and used this to remove unsuitable habitat from each Hinterland. This led to a strong and significant correlation between the observed colony size and the size of this habitat-filtered Hinterland. While this approach may work well for species with clear discrete partitioning between suitable and unsuitable habitat, several species may perceive habitat suitability on a more continuous scale, with some areas more suitable compared to others. This is especially true for marine top predators that rely on mobile and variable prey.

Species-habitat association models can be used to determine this gradient in habitat suitability and assess the degree to which habitats within the foraging range are preferentially selected. When the individuals are aware of the quality of each patch and free to enter any patch (known as the ideal-free distribution - (Fretwell & Lucas, 1969)), they are expected to feed in the most profitable patch. When a species population is at carrying capacity and all available habitats are saturated, species density will be proportional to habitat quality (Matthiopoulos et al., 2020). Therefore, by linking variation in species densities to environmental variables, habitat selection and thus habitat quality can be derived. This idea has led to the development of a large variety of habitat selection models, many of which have been fitted to either line- or point-transect survey (Buckland et al., 2001; Gilles et al., 2016) or tracking data (Aarts et al., 2008).

The objective of this study is to predict the distribution and size of colonies based on the quality and availability of foraging habitat types in the surrounding landscape based on an improved version of the Hinterland model which also incorporates the influence of spatial habitat heterogeneity. This approach will be explored for both harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), the only two resident seal species of the North Sea. The harbour seal is the most prevalent seal species in the coastal waters of continental Europe. For example, following a rapid recovery, an estimated 35,000 individual harbour seals are currently present in the Wadden Sea (Galatius et al., 2024). However, population size has remained stable since approximately 2011 (Brasseur et al., 2018), and in recent years, it has decreased (Galatius et al 2024). One possible hypothesis is that the population has reached carrying capacity, which may have been reduced in recent years as a result of natural or human-related processes within their foraging range. When they are not at-sea, harbour seals haul-out on sandbanks or edges of intertidal flats. During the pupping (June-July) and moulting (July-September) seasons in the Wadden Sea, a substantial portion of the population is found on land. Hence most surveys assessing population size and pup production are carried out during these periods (Cowles et al., 2013; Meesters et al., 2007; Teilmann et al., 2010; Thompson et al., 1997). However, harbour seals also utilize haul-out sites throughout the rest of the year, and during those periods, their haul-out is likely more closely linked to the distribution of high-quality foraging habitats at sea. From the haul-out sites, harbour seals undertake regular foraging trips to sea. Harbour seals mostly feed near the bottom on a variety of relatively small prey species (i.e. 10-30cm (Tollit et al., 1997; Wilson & Hammond, 2016), e.g. flounder, plaice, sole, sandeel, dragonet (unpublished data from Dutch diet studies, Aarts et al. 2019). Although harbour seals can make trips of tens to hundreds of kilometres, in the southern North Sea they mostly forage within 50km from their haul-out site, in relatively shallow waters (10-50m) characterized by sandy substrates (Bailey et al., 2014; Jones et al., 2015; Sharples et al., 2012; Tollit et al., 1998).

Grey seals were virtually absent in the southern North Sea, near the coast of continental Europe (Reijnders et al., 1995). However, following a few incidental sightings in the early 1980s, the number of grey seals has increased exponentially at a rate of approximately 15% per year (Brasseur et al., 2015). Immigration, particularly of juveniles from UK waters, is likely responsible for the initial growth. In addition, it assumed that a significant number of grey seals that breed in the UK continue to migrate to the southern North Sea to forage and potentially moult, particularly during the early spring and summer (Brasseur et al., 2015). As a result, during the moult surveys conducted in March and April in recent years, a total of 3,437 (2023) grey seals were counted in the Dutch Delta region and 11,515 (2024) grey seals were counted in the Wadden Sea and Helgoland (Hoekstein et al., 2024; Schop et al., 2024). The vast majority of these seals reside in Dutch waters. In contrast to harbour seals, grey seals are more frequently found in large and dense groups (Hoekendijk et al., 2023) on sand banks that remain dry during high tide, from which they make trips to sea. Although grey seals also feed in close proximity to their haul-out sites and near the shore, they typically embark on foraging trips that are longer and more distant, occasionally travelling as far as the Dogger Bank, which is approximately 300km away. Grey seals, like harbour seals, are primarily benthic foragers, feeding a diverse array of prey species, with different flatfish species and sandeel being the important prey species in the North Sea (Damseaux et al., 2021).

Grey seals are known to favour regions with coarse substrate (Aarts et al., 2008; McConnell et al., 1999).

In this study, we will utilize an extensive data set of 257 tracked harbour seals (2007-2023) and 94 tracked grey seals (2005-2019) and fit a species-habitat association (SHA) model to study their distribution at sea and its relationship with environmental variables (e.g., depth-related variables, seafloor sediment type and accessibility). This SHA model is then used to predict the at-sea distribution for all harbour and grey seals in the North Sea hauling-out in the Netherlands, Germany, and Denmark. The predicted at-sea distribution is subsequently allocated to the nearest cluster of haul-out sites to estimate the expected number of seals found on those haul-out sites.

Methods

Seal GPS tracking.

This study was based on previously collected data from animal-borne GPS data loggers (Brasseur et al., 2009a, 2009b, 2010, 2011; Brasseur & Kirkwood, 2015; R. Kirkwood et al., 2014; R. L. Kirkwood et al., 2015). Between 2006 and 2023 a total of 257 harbour seals and 94 grey seals were fitted with tracking devices. Most individuals (i.e., 142) were tagged in the Ems estuary, between 2009 and 2011. GPS tagging mostly took place in March (N=123) and September (N=104), and most GPS location data were collected during the first months following tagging. The seals were caught on the haul-out site with a large seine net, and tagging details can be found in (Aarts et al., 2019; Brasseur, 2017). Because the data loggers were glued to the seals' fur, most would become dislodge after several months, but certainly before August for harbour seals and March/April for grey seals, when they moult, and their fur is shed.

The Fastloc GPS data loggers (Sea Mammal Research Unit, UK) were set to collect and store GPS locations every 10-20 min (depending on the research project). Data from a depth sensor (precision of 0.5 m) and a submergence sensor were used to determine the activity of the seal: "diving" (defined as deeper than 1 m for at least 4 s), "at surface" (no dives for 180 s) or "hauled out" (continuously dry for at least 600 s until wet for 40 s) (Vincent et al., 2010). Locations, dive, haul-out, and summary records were stored, and the Fastloc GPS data loggers transmitted the data via the Global System for Mobile Communications (GSM) phone network, when in contact with a GSM base.

Aerial survey haul-out counts.

In the international Wadden Sea bordering the Netherlands, Germany (Lower Saxony and Schleswig-Holstein) and Denmark aerial surveys were conducted to count harbour and grey seals, (Brasseur et al., 2015, 2018; Reijnders et al., 1997). For both species, 5 aerial surveys were carried out each year, 3 during pupping periods (Jun. – Jul. for harbour seals; Nov. – Jan. for grey seals) and 2 during moulting period (Aug. for harbour seals; Mar. – Apr. for grey seals). In the Dutch Delta area aerial surveys were conducted on a monthly basis (Hoekstein et al., 2024).

Harbour seals are typically more widespread over numerous haul out sites, while grey seals tend to concentrate on fewer higher grounds mostly in the western part of the Wadden Sea. Therefore, the focal harbour seal pup and moult surveys cover all seal haul-out sites, while grey seal pup and moult surveys might not cover all harbour seal haul outs. Only the survey dates that covered at least 90% of the haul outs were selected.

Aerial surveys were carried out from a fixed-wing, single engine aircraft. Surveys were conducted around low-tide and only in optimal weather conditions (Brasseur et al., 2018; Reijnders et al., 2003). The flight route was recorded using GPS. In all regions, except Lower Saxony, all seals observed were photographed, from which animals were counted, separating species and, when applicable, pups from adults. In Lower Saxony seals were counted directly during the flight.

For the Delta region and the Wadden Sea areas of the Netherlands and Lower Saxony, we used the average counts from a 10-year period (2014-2023) of aerial survey data collected during the moult season. For the Wadden Sea areas in Denmark, we only used data from 2017 as multi-year or more recent data are currently not available.

Telemetry data pre-processing and trip definition

First, we removed records of haul-out periods that did not result in a subsequent trip to sea. These occurrences were presumed to be the result of tags falling off on land, primarily during the moult. Also, data during the first 10 days of tracking data were removed due to the possibility that seals may exhibit aberrant behaviour immediately following the tagging event. To predict absolute densities at sea for the entire population using aerial survey haul-out counts, it was necessary to model the spatial distribution of tracked seals in relation to the haul-out sites from which they performed trips. To achieve this, each trip to sea was linked to the corresponding start and end haul-out in the following manner. A GPS wet-dry sensor on the tag record the start and end of each haul-out event and all GPS locations outside these haul-out events were considered at-sea locations, and within these haul-out events the seal was assumed to be resting on land. The location of a haul-out event was estimated as the average location of all GPS-fixes during that haul-out event. In some cases, no GPS location fix was obtained during a haul-out event. In that case, we first estimated all true haul-out locations, which were defined as any GPS location during any haul-out event which lasted at least 3 hours. Next, the GPS location fix closest in time before or after the haul-out event with missing GPS fixes was linked to the nearest true haul-out locations. The coordinate of that true location was used as the coordinate of that haul-out event. For all GPS locations it was then possible to estimate the start and end time and location of a trip. In theory, if the start and end location of a trip was exactly the same (return trip), that haul-out location was defined as the “trip haul-out”. However, in practice, the start and end haul-out location were almost always different (transitory trips), and all locations prior to the midpoint (in time) of the trip were allocated to the start haul-out, and those after the midpoint to the end haul-out. Locations with no “trip haul-out”, e.g. those at the beginning or end of the deployment period, were removed from the analysis.

Location fixes could be obtained every 10-20 minutes, but the time window between fixes could also be several hours if a seal stayed at the surface only briefly. To reduce the number of data points and achieve some regularity in the tracking locations, a regular sequence of two-hour time points was generated within the deployment period for each individual and only those GPS locations were retained which were closest to one of those two-hour time point. This way we reduced the number of data points, without losing too much information: several of the points close in time will be removed, while the less frequent GPS location fixes were retained.

Explanatory environmental variables used for habitat modelling.

Seals are central-place foragers, feeding predominantly near the bottom on benthic prey species. Studies have shown that harbour and grey seals use areas that are relatively shallow and characterized by sandy substrate (Bailey et al., 2014; Jones et al., 2015; Sharples et al., 2012; Tollit et al., 1998). Therefore, the covariates, distance to haul-out, depth, topographic position index (TPI) and sediment type (%mud) were used (see sections below for more details). The study did not use fish surveys to estimate environmental variables describing the distribution of prey because of the very low sampling effort within the foraging range (Aarts et al., 2019) and the lack of resolution required to capture the fine scale variations in seal distribution..

Distance to haul-out

Foraging sites closer to haul-out sites are more easily accessible. Even if they select areas further offshore to forage, they always must cross the intermediate areas. Consequently, habitat use is expected to be negatively correlated with distance to the haul-out site. Because seals circumvent all land or shallow areas, the shortest at-sea path between each haul-out site and point at-sea was derived. Shortest path calculation was based on a regular grid with varying spatial resolution; a higher resolution (i.e., a point every 200m) in coastal waters (<10km from land), and a coarser resolution (i.e., a point every1 km) offshore in the North Sea, which would reduce the computational cost, but maintain the level of detail where needed. For each grid point, links were created with the 16 nearest neighbours (function nn2, R package RANN (Arya et al., 2019)). Any link with a land-based point was removed. Based on this, a graph object was created (function graph.data.frame, R package igraph (Csardi & Nepusz, 2006)). The graph object can subsequently be used to calculate the path (and distance) of any grid point within the landscape to a haul-out site. Each trip's haul-out event location may be regarded as a distinct haul-out site. To minimise the computation time required for calculating the at-sea distance, the locations of the haul-out events were grouped into a limited number of haul-out clusters. This was achieved by applying hierarchical clustering to the distances between all pairs of haul-out locations using the function `hclust` (R package = stats, method =”average”) and `cutree`, with cut-off distance of d=2.5km. Next, for each cluster, the distance between the haul-out cluster *c* and each point at sea (taking land obstacles into account) was calculated.

Nearest distance ratio

Previous studies have revealed that the at-sea distributions of seals making foraging trips from neighbouring haul-out sites tends to be spatially segregated, which leads to a more channelled and outward distribution, rather than seals radiating out equally in all directions (Aarts et al 2019). This spatial segregation is most likely caused by a combination of foraging efficiency (i.e. choosing a haul-out site which is closest to the foraging site) and density dependent competition. As a result, it is less likely for seals to forage in the direct vicinity of a neighbouring colony. To capture this aspect, we calculated for each cell in space the distance to the seal's trip haul-out and divided this by the distance to the nearest haul-out site. This ratio is equal to 1 when the cell is (just) closest to the seals' trip haul-out cluster, and almost zero when the seal is foraging near another neighbouring haul-cluster, far from its original trip haul-out cluster.

Sediment

To describe sediment type in this study, we used the relative proportion of the grain size fraction < 63 μm (% mud - Fig. 1a, b). Sediment data was obtained from a combination of two data sources. For the Dutch EEZ data, details can be found at http://www.emodnet-seabedhabitats.eu/pdf/Imares_Dutch_Marine_landscape_Map.pdf. For other areas in the North Sea, we used maps created by Helmholtz-Zentrum Geesthacht (HZG) as part of the NOAH project (https://www.noah-project.de/habitatatlas/substrate/index.php.de).

Depth

Bathymetry data were extracted from the harmonized EMODnet Digital Terrain Model (DTM, see http://www.emodnet-hydrography.eu/), which is based on regional DTMs, and gaps with no data coverage were completed by integrating the GEBCO Digital Bathymetry (Fig. 1). The measurements were continuous, and the spatial resolution was approximately 100m x 100m in a WGS84 geographical projection but converted to a regular 200m x 200m grid in UTM 31N projection.

Topographic position index

The topographic position index (TPI, function tpi, package spatialEco (Evans, 2020)) is defined as the height of each pixel relative to the average height of pixels within a prespecified radius. TPI values >0 characterize peaks and ridges, while low TPI values <0 characterize gullies or troughs. Here TPI was calculated for a radius of 5km, describing intermediate-scale topographic features, respectively.

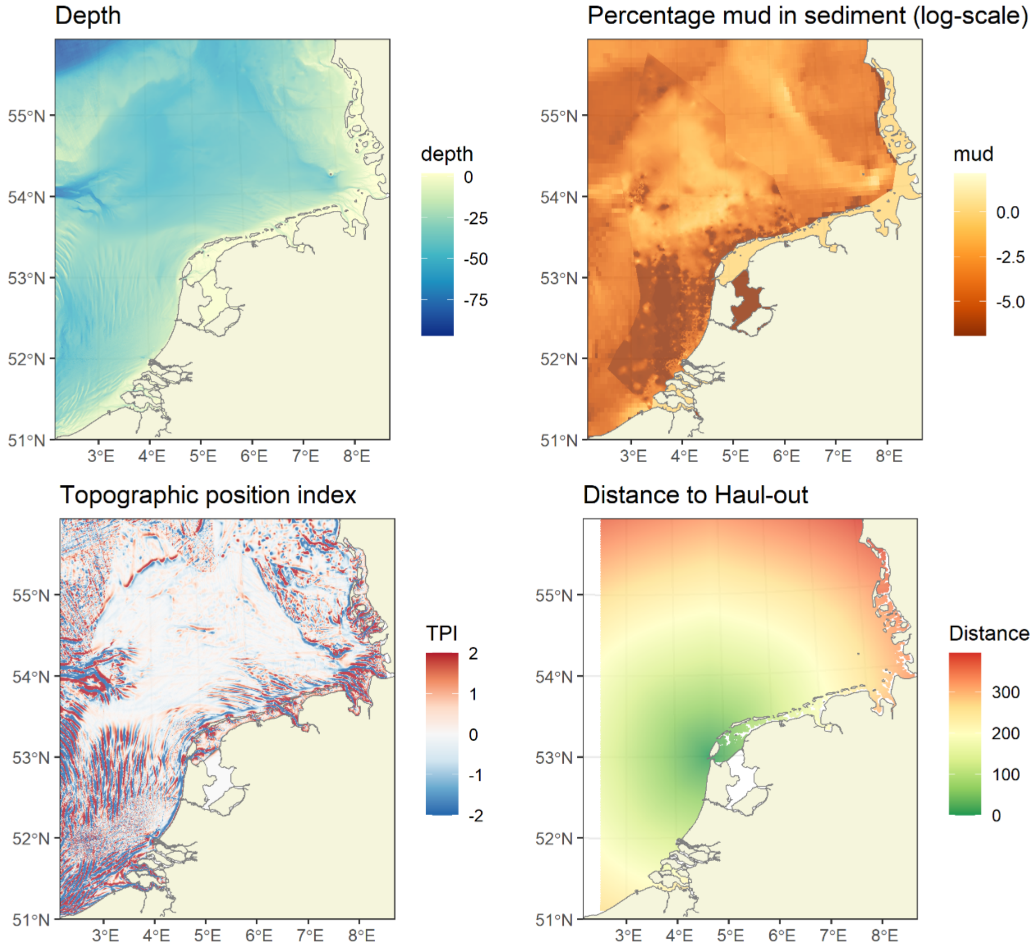

Figure 1 Maps of the explanatory variable Depth (m), %mud in the sediment, topographic position index (5km circle), and distance to one haul-out (km) (here Razende bol as an example).

Use availability design and Poisson point process likelihood.

We aim to estimate a Species-Habitat Association (SHA) model $w(X)$ that quantifies seal density as a function of environmental variables X. To achieve this, one could discretize space into grid cells, calculate the number of seal GPS locations within each cell and model the corresponding counts using a Generalized Linear Model (GLM) with a Poisson likelihood. Alternatively, the SHA model can be fitted using a use-availability design, in which the GPS locations ('used' points) are contrasted with a set of random points in space ('availability' points) and fitting the model using an Inhomogeneous Poisson point process (IPP) likelihood function. As the IPP likelihood is generally not available in most GLM-fitting software, infinitely weighted logistic regression (IWLR) can be used instead. In this case a binomial model is fitted to the data, where the GPS locations have a response value of 1 and the availability points a response value of 0. These availability points receive a large likelihood weight (1000 in our case), which can be specified by the 'weight' argument. Under such a IWLR framework, the exponential of the linear predictor will be proportional to the Species-Habitat Association (SHA) model $w(X)$.

To approximate the integral of the IPP likelihood, for each GPS location, more availability points lead to more precise estimates. Due to computational limits, we generated 2 availability points for each used point, with sampling weights of 1/distance^2. Since the vast majority of the tracking data was within 150km from the haul-out for harbour seals and 200km for grey seals, and to reduce the computation time, we constrained the used and availability points to this range. For each sampled point, the total area represented by all nearest points (sampled and unsampled) was calculated and used as quadrature weights q_n. This will lead to an unbiased sampling design, but higher resolution near those places heavily used by seals. Another factor to take into consideration is that the GPS locations are serially correlated, with locations close in time being also more likely to be close in space. Since most environmental variables are also spatially correlated, successive GPS locations will also tend to have similar values for the environmental variables. This would lead to an artificial inflation of the degrees of freedom. Instead of resampling and removing GPS observations, we downweigh (r) the observation in the likelihood function based on the time between successive observations expressed as fraction of two hour, a time window commonly used in other seal habitat studies (Carter et al. in prep). Finally, although 2 random locations were generated for each GPS locations, some of those might be removed when they did not contain the necessary environmental data. Since this might lead to fewer availability points, each availability point received a weight which was the inverse of the number of availability points (a) per GPS observation. The product of all three observation specific weight factors (i.e. quadrature weights *q*, time-interval weights *r* and removal-correction weights a) was included as model weights for the availability points and the time-interval weights were included as model weights for the used/telemetry points.

Species habitat-association model structure and fitting

The spatial distribution of the observed animal locations in geographical space can be treated as realization of an IPP with a rate $w(X)$. This rate $w(X)$ describes the animals' preference for being at a point in space with environmental conditions *X*. In accordance with count models, we assume that w is the exponent of the linear predictor η.

(1) $$w(X) = e^{\eta}$$

The simplest form of the linear predictor is to assume that it is a linear function of the environmental variables $x_1 - x_J$. However, animals often respond non-linearly to environmental variables, e.g., they might have a peak preference for a particular explanatory variable. This non-linearity was included in the model by including smooth functions of *x*

(2) $$\eta = \beta_0 + s(x_1) \cdots + s(x_j) \cdots + s(x_J)$$

Since individual animals may differ in how they respond to different environmental variables, these smooth functions were allowed to differ by individual, which was enabled by including a factor level smoother:

(3) $$s(x_j, m = 2) + s(x_j, ID, m = 2, bs = "fs"),$$

where m=2 implies the model penalizes the second derivative of the smooth function and ID refers to each unique individual. This is an additional penalty that helps to avoid overfitting by allowing the parameters estimates to 'shrink' towards zero. The above formulation essentially corresponds to a Generalized Additive Mixed Model, consisting of a global smoother (first term) plus group-level smoothers with a shared penalty (second term) (Pedersen et al., 2019).

Additionally, a spatially autocorrelated error structure was included. For this, a spatial mesh was created based on all the model data (use and availability points) with a maximum edge length of 50km in the core area and 100km in the boundary area and a cut off of 5km (function inla.mesh.2d). Based on the mesh, a Matern SPDE model, with spatial scale parameter κ(u) and variance rescaling parameter τ(u) is estimated (function inla.spde2.matern). In addition to this 'global' spatial latent field, individual-specific spatial latent fields were also estimated, which captures individual-specific selection of spatial regions that cannot be explained by the environmental variables included. Furthermore, since temporal correlation between successive telemetry locations will also manifests itself as more clustered locations in space, this individual-specific latent field should not only absorb spatial correlation, but also (part) of the temporal correlation.

Model fitting was done in sdmTMB. Individual was included as factor level, to absorb any difference in the relative ratio between used and availability points. The environmental variables distance to haul-out, distance ratio, depth and TPI were included as model-covariate. Both distance to coast and %mud was excluded due to model convergence problems. For each covariate, global and individual-level smoothers (see eq. 3) were included. A global spatial latent field was included (spatial = on), and individual-level latent field were included by including 'time'-varying spatial latent field, where 'time' is redefined as to represent an individual animal in this case (time=ID) and an IDD error structure (spatiotemporal = "IDD").

Habitat-based prediction of numbers at the haul-out sites

To establish a connection between the at-sea distribution of seals to a particular haul-out site on land, the individual seals counted during the survey needed to be clustered. Similar to the clustering of haul-out locations from tracking data, hierarchical clustering was applied to the distances between all pairs of counts (photographs for the Dutch Wadden Sea data and grouped counts for the other regions) using the function `hclust` (method ="average") and `cutree`, applying a cut-off distance of d=10km. Next, the SHA (with distance to the haul-out cluster) was used to predict for each haul-out cluster the usage for each cell in space. Here, we first assumed seals behave as ideal-free foragers: they select habitats in accordance with habitat quality (as defined by the SHA model) and only return to the haul-out site nearest to its foraging location (in accordance with the Hinterland-model). While the SHA model was fitted using the covariate 'distance to the trip haul-out site', under the ideal-free null-model, this covariate can be replaced by a single covariate 'distance to the nearest haul-out site'. This results in a single usage map for the entire study area. Next, the usage within each cell needs to be distributed over all the different haul-outs clusters. One approach is to use the Hinterland-model, which would allocate the usage within each cell to the nearest haul-out site only. However, one the shortcomings of this Hinterland-model and assumed ideal-free distribution is that if a cell is almost equally close to two haul-out sites, all of its usage is allocated to only the nearest haul-out site. To allow mixing across and thus making the Hinterland boundaries more diffuse, we use the estimated effect of the ratio between the distance to the nearest haul-out and distance to the trip haul-out to divide the usage of each cell among the surrounding haul-out sites. For each cell in space, this results in a cluster-specific usage estimate, which was used to estimate the relative contribution of usage from each cluster.

Results

Seal tracking

Out of 259 harbour seals tagged, 202 individuals contained sufficient data (>10 days) within the study region (Fig. 2) for the analysis. To reduce computational time, we only selected those individuals with at least 200 GPS observations in the prepared data frame used for model fitting, resulting in a total of 164 harbour seals. Among the 94 grey seals tagged, 69 individuals provided a minimum of 200 GPS locations for the final model. The distribution of these GPS locations is heavily influenced by where seals were tagged. For example, the high number of GPS locations offshore along the Dutch and German border, North of the Ems Estuary is heavily influenced high tracking effort (i.e. 148 tagged harbour seals) in that region. The tracking data also occasionally reveals systematic clustering, e.g. in lines or clusters, which are often due to the presence of hard substructures like pipelines, windmills or oil and gas platforms (Russell et al., 2014).

In total the data comprised of ~ 909 thousand GPS locations. Approximately 87 thousand locations remained after subsampling at 2-hour intervals, and after data were selected to correspond with the available environmental data (see Fig. 1), excluding the Wadden Sea and inner-Delta region, and excluding locations less than 3km of any haul-out cluster or during haul-out. The majority of these haul-outs (shown by red dots in Fig. 2a) were located near known haul-out sites, which are typically sandbanks that become exposed during low-tide and are easily accessible from the sea. None of the tracked seals hauled-out along the west coast of the Dutch mainland, but one individual hauled-out on the coast of the island of Texel. Some apparent haul-out events are located far into land or out at-sea, either due to erroneous location estimates or because seals may occasionally spend long times at the water surface which can be perceived as haul-out events. For each individual foraging trip, a set of availability locations were generated (shown in Fig. 2b).

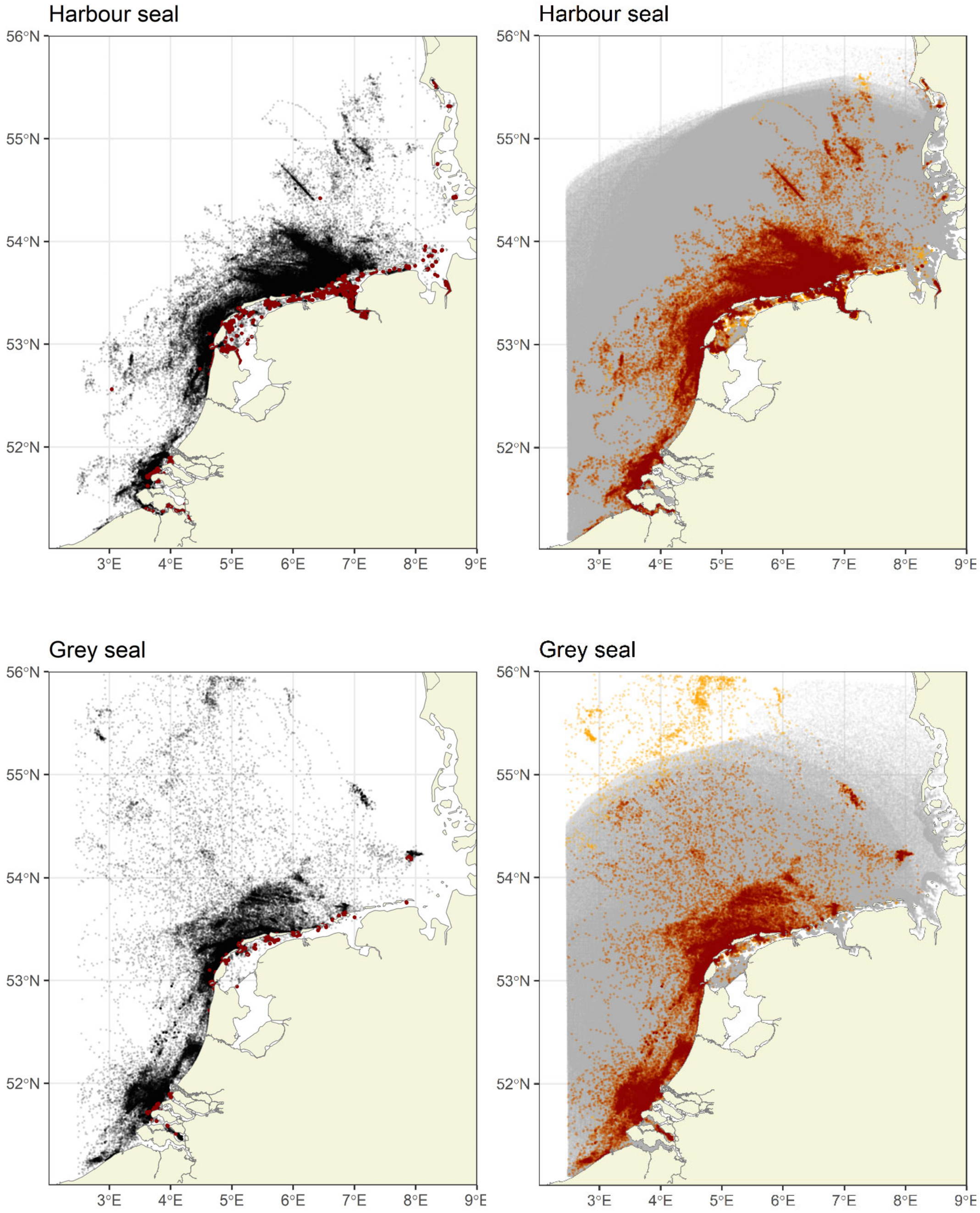

Figure 2. Left figure: The distribution of seal GPS (black dots) and estimated locations of the haul-out events (red dots). Note that during some haul-out events no GPS locations were obtained, and instead the nearest GPS location was used, leading to erroneous locations. Right figure: The distribution of all 'used' locations (i.e. GPS locations) and 'availability' locations. The orange points represent all GPS locations, and the red points those used in the analysis (sub-sampled at 2hr interval and within 150km (harbour seals) and 200km (grey seals) from the trip haul-out site). The grey points represent the availability points.

Distribution and abundance of harbour and grey seals on the haul-out sites

The distribution of sampling effort in time is shown in Appendix A, Fig. A2. All counts were grouped into clusters representing haul-out areas as shown in Fig. 3. Although harbour seals are found to haul-out throughout the international Wadden Sea, there are a few haul-out clusters that contain substantially more individuals. These includes the Japsand, Norderoogsand and Süderoogsand region in Schleswig-Holstein, the Kachelotplatte in Lower Saxony and the Rottumerplaat and Rottumeroog region in the Netherlands. In contrast to harbour seals, grey seals are much more clustered into fewer colonies. During the grey seal moult season, aggregations are found on Engelschhoek and the Razende Bol in the Dutch Wadden Sea, the Aardappelbult in Zeeland and on the island of Helgoland.

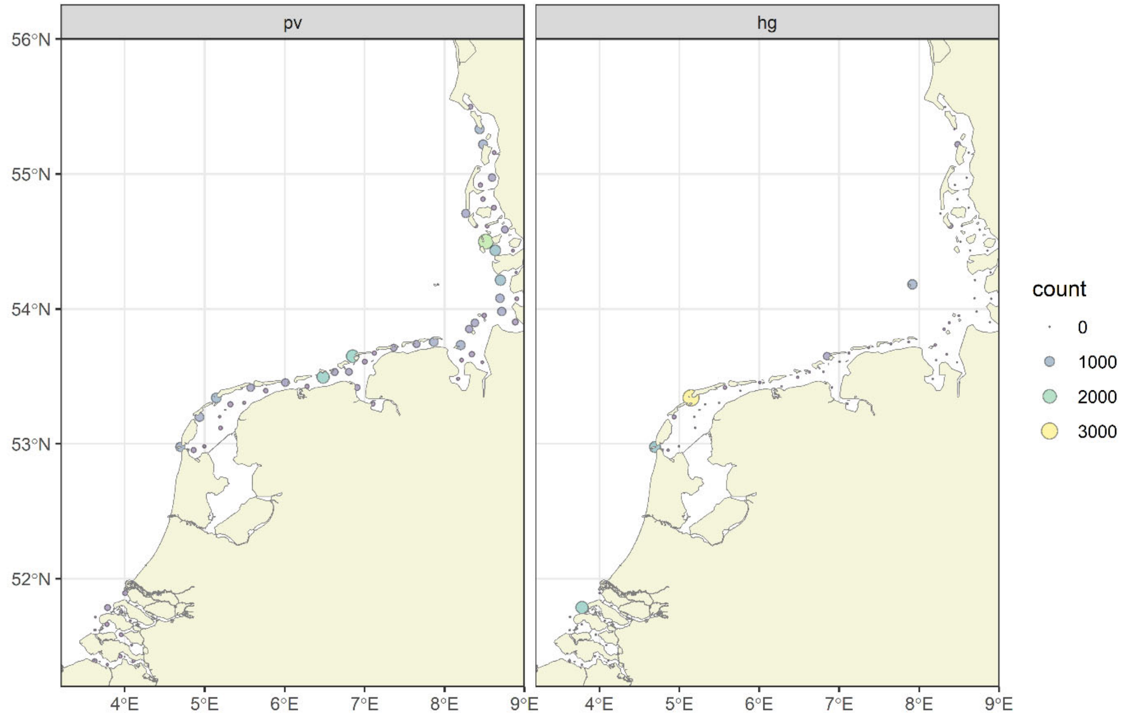

Figure 3. Land-based distribution of harbour seals (left) and grey seals (right) counted during aerial surveys of the haul-out sites located in Dutch Delta region in the south (Netherlands) and the international Wadden Sea (Netherlands, Germany, and Denmark).

Averaging the August counts from 2014-2023 for the Dutch Delta region (1126), Dutch Wadden Sea (7325), and Lower Saxony (7017), along with the 2017 counts for Schleswig-Holstein (8250) and Denmark (2490, from 2017 only), a total of 26208 harbour seals were counted. Note that these numbers deviate from the internationally coordinated trilateral counts (Galatius et al., 2024), since here, we calculate the average over multiple years, while the trilateral counts derive maximum estimates for each given year and estimate the total population size. We used the haul-out probability of 68% (Ries et al., 1998), to correct for the number of seals in the water during the survey counts, resulting in an estimated average total population size of 38541 harbour seals.

For grey seals, the ten-year averages in various regions were as follows: 1665 in the Dutch Delta region, 4559 in the Dutch Wadden Sea, 593 in Lower Saxony, and 1092 in Schleswig-Holstein and Helgoland. In 2017, a total of 267 grey seals were recorded in Denmark. This results in a total of 8,176 grey seals. Presently, there is no correction factor for the haul-out probability of grey seals.

Preferential selection of environmental variables

As expected from the seal GPS data, the harbour seal habitat model estimated a strong decline in habitat use as a function of distance to the haul-out site (Fig. 4a). In relation to depth, the model showed that on average seals preferred regions of up to ~20 m depth and have a lower preference for deeper areas (Fig. 4b). Harbour seals generally seem to prefer areas with either low or high TPI values (Fig. 4c). Although the effect size was relatively small, this relationship suggests that harbour seals tend to preferentially select the holes and trenches, and the peaks and ridges, more than the flat areas or slopes of the seabed. Finally, there is a positive relationship between seal density and the “distance ratio” (Fig. 4d), with seals being more likely to select those points in space which are closest to their trip-haul-out (i.e. distance ratios of 1).

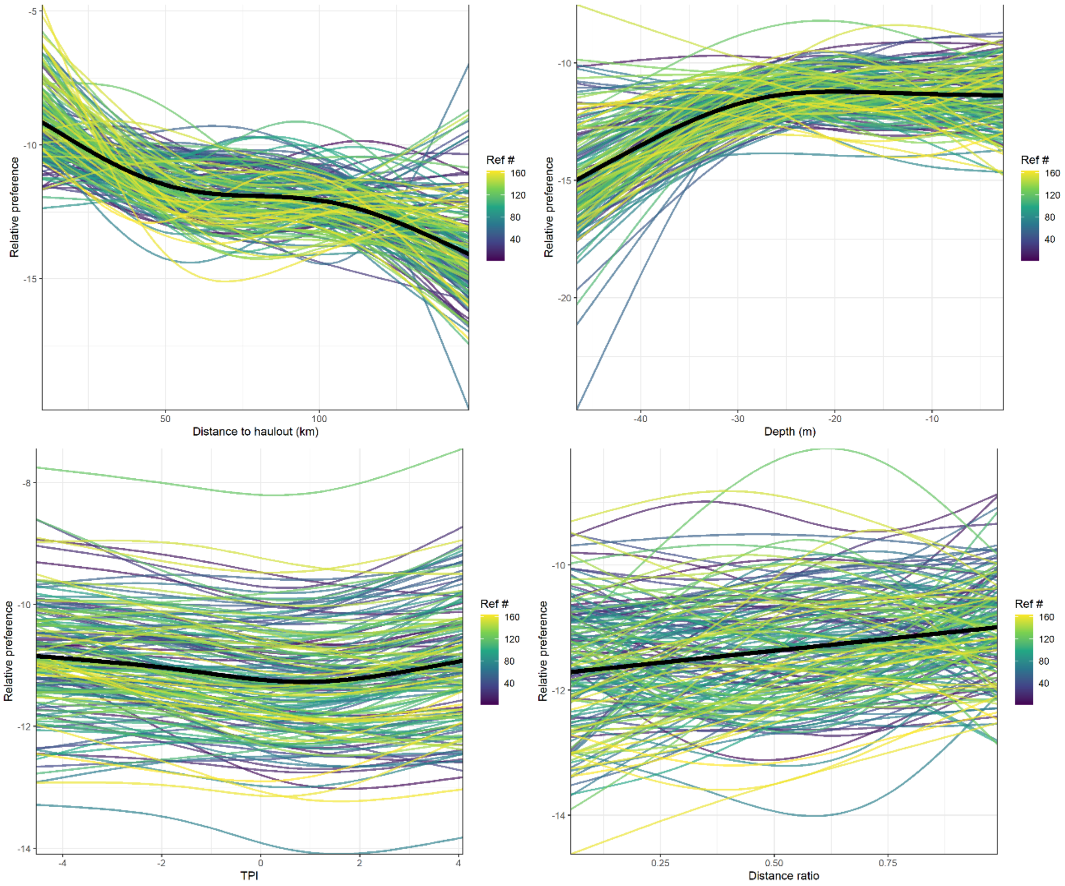

Figure 4. Variation in harbour seal density as function of the explanatory variable distance to the haul-out in km (**a**), depth in m (**b**), topographic position index (TPI) (**c**), and the ratio between each grid cell’s distance to the nearest haul-out site and the distance to start haul-out site from which the seal is departing (or returning to) (distance ratio) (**d**).

For grey seals, the relationship between relative density and the environmental covariates is fairly similar to that of harbour seals (Fig. 5). Grey seals also generally prefer areas closer but make further trips from their haul-out sites (Fig. 5a). They also prefer areas which are shallower (Fig. 5b). However, there is a risk that some collinearity between distance to the haul-out and depth (Pearson's product-moment correlation of the GPS-points = -0.548) may complicate the ability to differentiate between the effect of these two correlated variables. Overall, grey seals have a slight preference for areas with high TPI values (peaks and ridges), however the estimated effect size is small and is characterized by large variation between-individuals (Fig. 5c). Similarly to harbour seals, there is a weak positive relationship between seal density and the “distance ratio” (Fig. 5d).

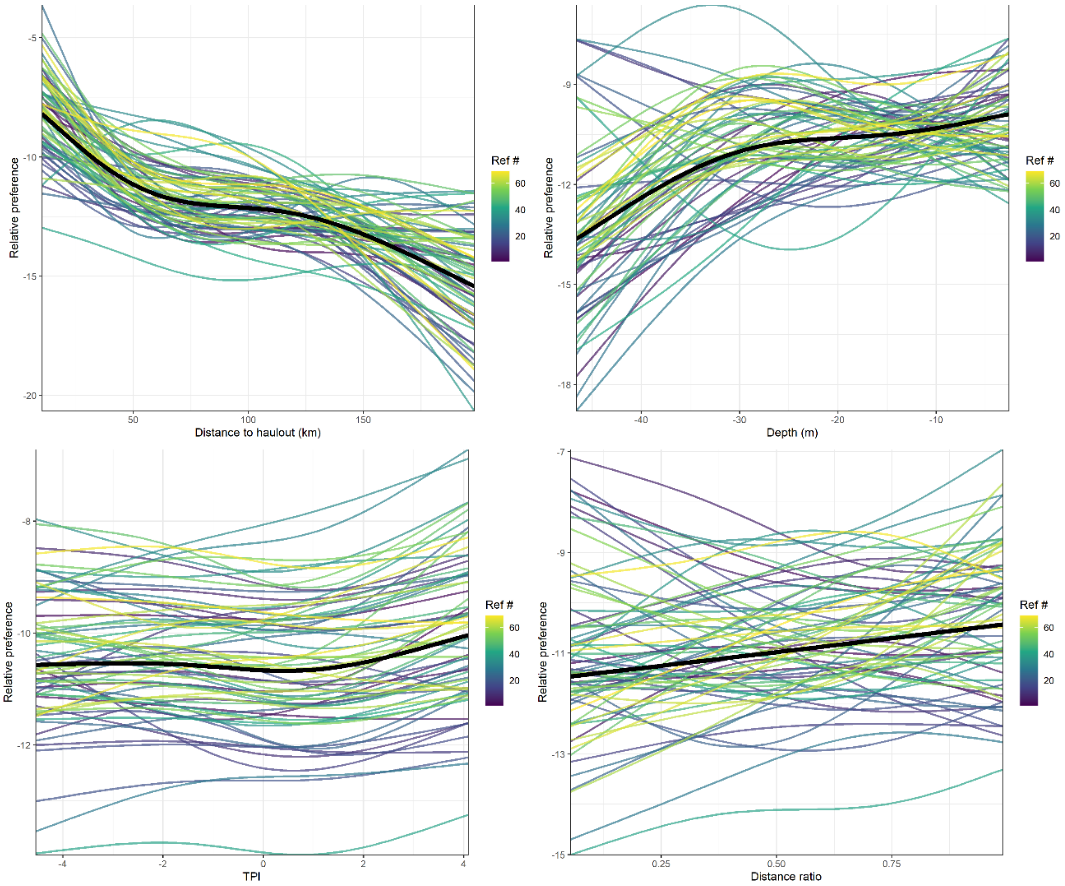

Figure 5. Variation in grey seal density as function of the explanatory variable distance to the haul-out in km (**a**), depth in m (**b**), topographic position index (TPI) (**c**), and the ratio between each grid cell’s distance to the nearest haul-out site and the distance to start haul-out site from which the seal is departing (or returning to) (distance ratio) (**d**).

Unexplained spatial variation: Residual latent fields

While a large part of the spatial variation in seal density can be explained by the environmental variables (see also Fig. 6a, c), the global and individual-specific latent fields also absorb a large part of the variation. For example, for harbour seals the global latent field (Fig. 6b) shows high density in the South near the Delta region, along the northern part of the Dutch mainland coast, and the region North of the Ems estuary along the border between the Netherlands and Germany. For grey seals, the latent field shows relative higher density along the central part of the Dutch mainland coast, and slightly higher density northwards, but otherwise, no large discrepancies elsewhere.

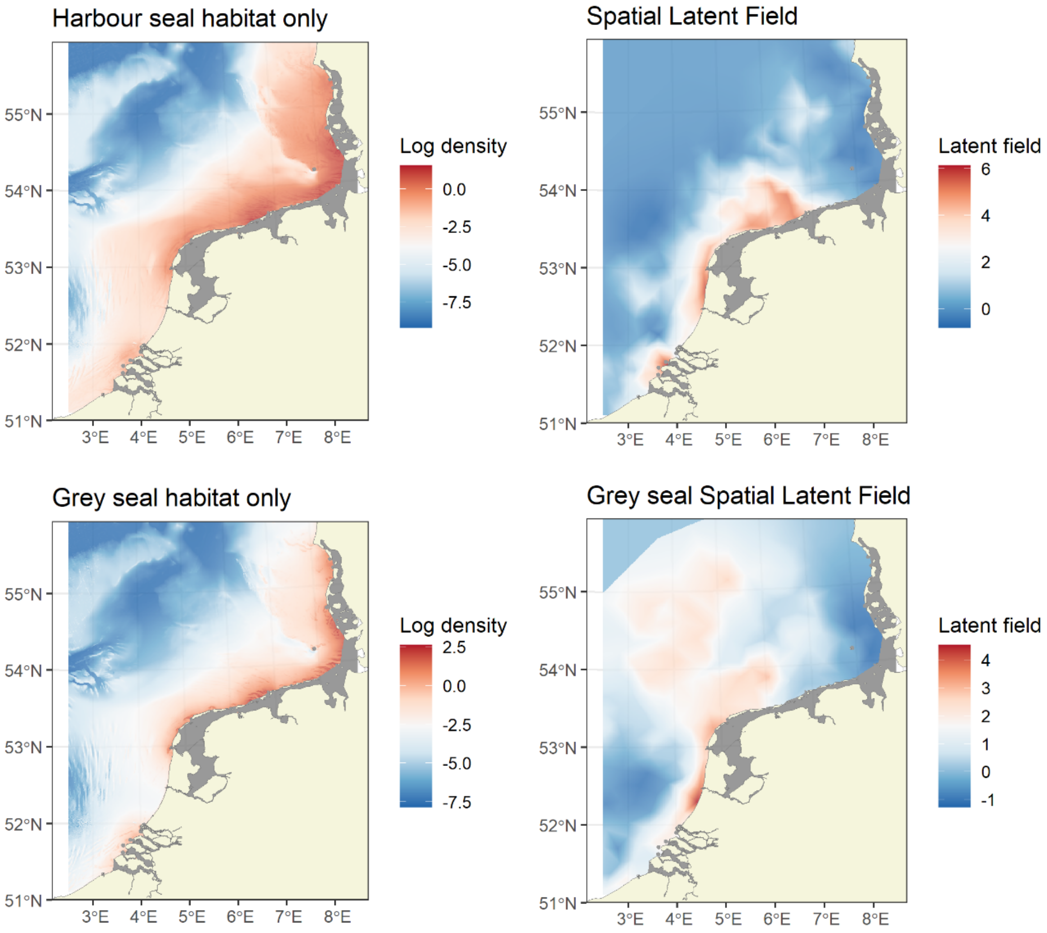

Figure 6. The estimated density of seals consists of the modelled density based on environmental variables (left column) and the unexplained spatial variation as captured by the spatial latent field (right column).

In addition to the global latent field, individual-specific latent fields also account for considerable unexplained variation in seal density (Fig. 7 and 8). As expected, there is considerable variation among individuals, with some regions being used more intensively than predicted by the habitat model, while others are underutilized in relation to the habitat model.

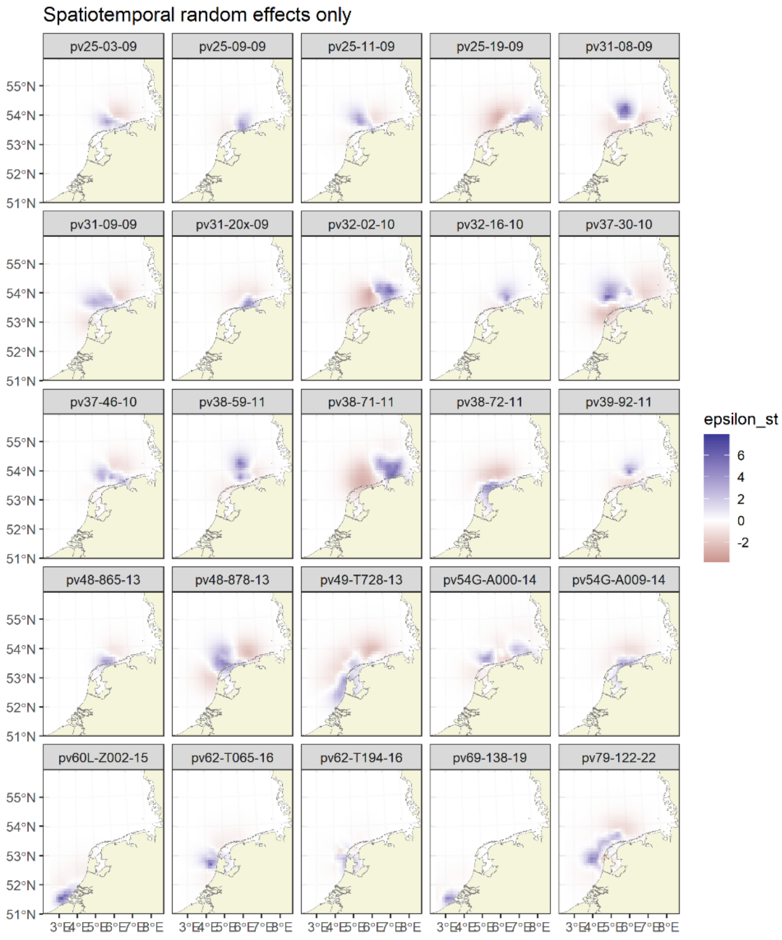

Figure 7. Individual-specific latent fields of a random selection of 25 individual harbour seals (individual IDs are shown in panel title).

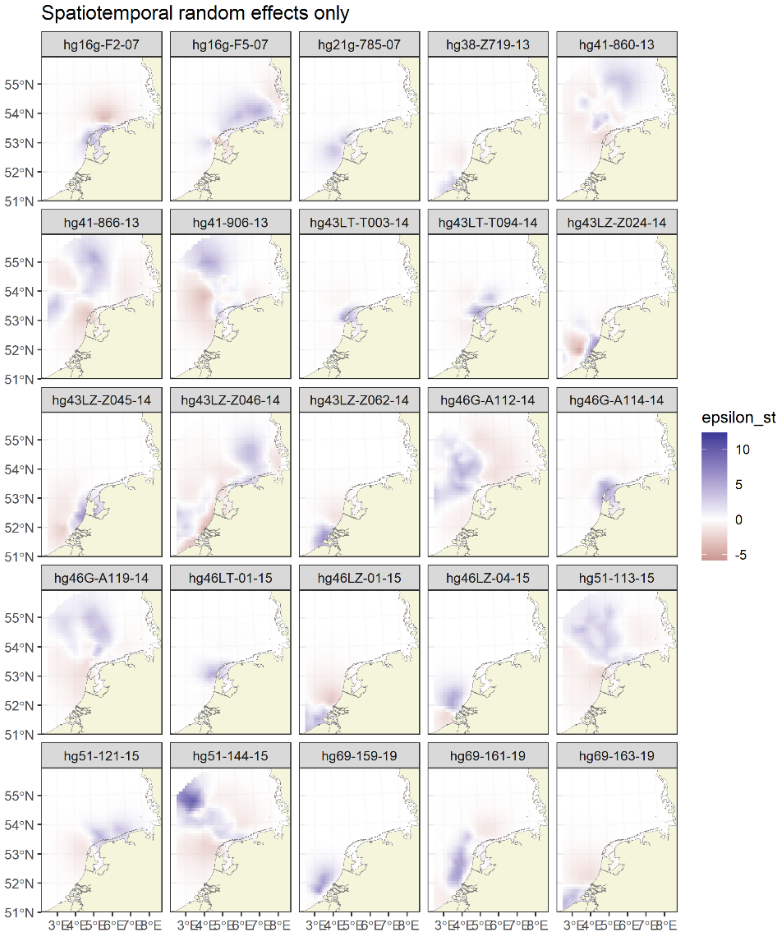

Figure 8. Individual-specific latent fields for of a random selection of 25 individual grey seals (individual IDs are shown in panel title).

Predicted Spatial distribution.

The predicted distribution of seals at sea, which takes into account the observed number of seals on the haul-out site is shown in Fig. 9 (for harbour seals) and Fig. 10 (for grey seal). These distribution maps have a 200 x 200m resolution and reflect seal density (i.e. number of seals per km^2). As an example, Appendix A, Fig. A3 shows those predictions for two arbitrarily selected haul-out sites. The estimated density consists of two components; the predicted density derived from the global estimates of the habitat model (indicated by the thick black lines in Fig. 4 and 5, and used for spatial prediction in Fig. 6a and 6c) and the global spatial latent field (shown in Fig. 6b and 6d). The density of harbour and grey seals was highest near the haul-out sites. It is important to note, however, that in the Danish and German region, the predicted density was more uniformly distributed within the foraging range, in contrast to the Dutch area, for which tracking data were available. The variation in the latent field estimates accounts for part of this regional difference, as these latent field estimates can only be derived for regions with available tracking data. Beyond a specific depth (~30-40m), there is a considerable decline in seal density, which is also reflected in the preferential selection curves presented in Fig. 4 and 5.

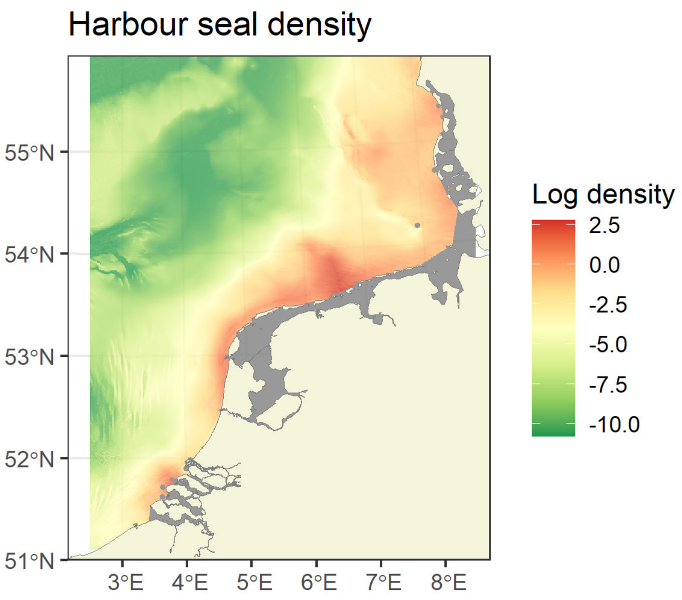

Figure 9. The estimated population density (on log-scale) of harbour seals based on the habitat model and global latent field, also taking into account the average numbers of seals on the haul-out sites observed during the moult season (August).

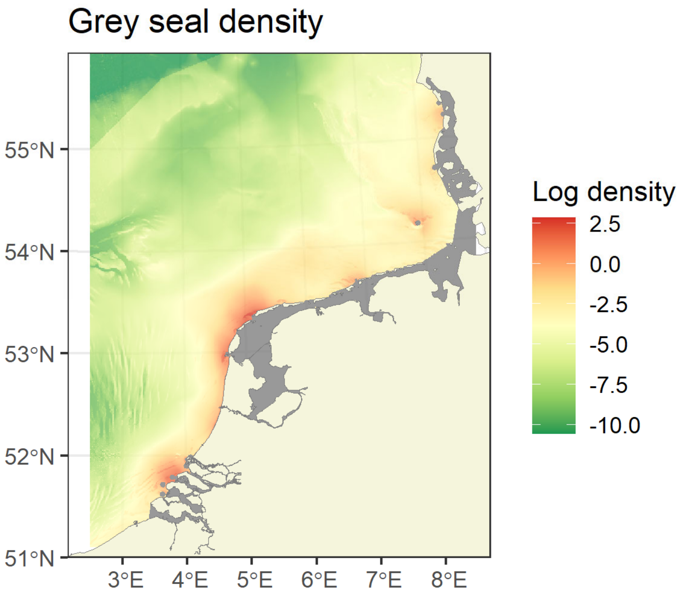

Figure 10. The estimated population density (on log-scale) of grey seals based on the habitat model and global latent field, also taking into account the average numbers of seals on the haul-out sites observed during the moult season (March/April).

Habitat-based predictions of colony size

Replacing the variable “distance to the trip haul-out” with “distance to the nearest haul-out” allows for the creation of a single usage map of seal distribution for the entire study area (independent of the location of haul-out sites). Subsequently, the seal usage in each cell can be distributed among the haul-out clusters. The habitat-based predictions of the number of seals at each cluster were significantly correlated with the observed counts for both harbour seals (Fig. 11a and 11b) and grey seals (Fig.11c and 11d). The p-values of the slope parameter relating these predicted counts with observed counts were 3.4e-05 and < 2e-16, respectively. Also note that the slope coefficients were close to 1 for harbour seals (0.9308), but substantially higher for grey seals (3.40). In comparison to the predictions, the observed counts show considerable over-dispersed, indicating that seals tend to cluster in larger groups. For example, the highest prediction for harbour seals is just under 1000, whereas the observed counts surpassed this value at several haul-out clusters, with one specific haul-out cluster exceeding 2000. The observed grouping of grey seals was even more pronounced; the highest prediction was 365 individuals, whereas the largest observed haul-out count reach 3000 individuals, tenfold higher.

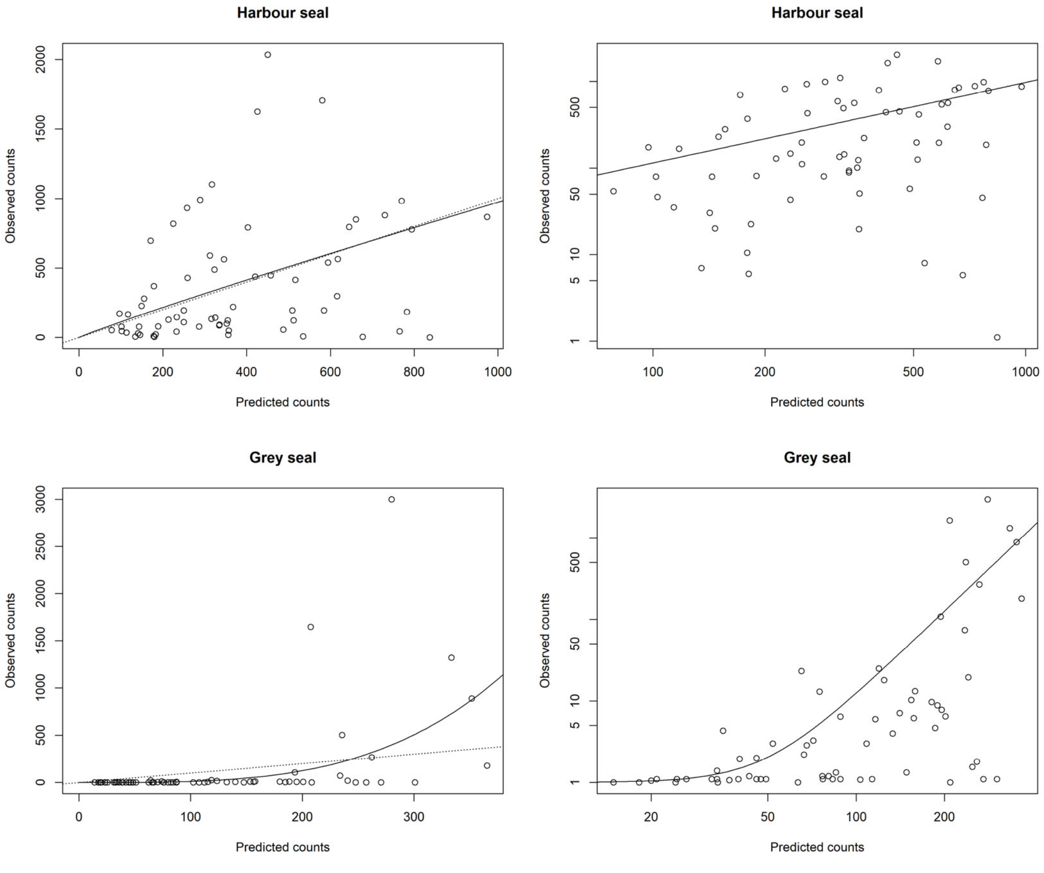

Figure 11. The relationship between predicted counts on haul-out clusters (derived from the habitat model) and the observed counts for each haul-out cluster. The left and right figures are identical, with the exception that the x and y axes in the right figures, are represented on a logarithmic scale. The solid black line reflects the slope of the generalized linear model fitted to the data points. The dotted line represents

a 45°-degree line (e.g. slope of 1) through 0. Note, for harbour seals (top figures) this line is almost identical to the fitted curve.

Fig. 10a and 11c show the observed distribution of seals on land (based on 10km maximum distance clustering) and Fig. 10b and10d the predicted number of seals on each haul-out site. For both harbour and grey seals, the model predicts a more uniform distribution of animals across the haul-out clusters than was observed in the data. And as expected, the highest numbers of seals are predicted to occur on the haul-out sites bordering the Wadden Sea, rather than further inside the Wadden Sea bordering the mainland coast. This is also observed in the count data. Peak predictions occur on those haul-out sites with a large Hinterland, such as the Razende Bol (a sand bank between the most western Wadden Sea island and the mainland) Helgoland (the only island offshore in the German Bight).

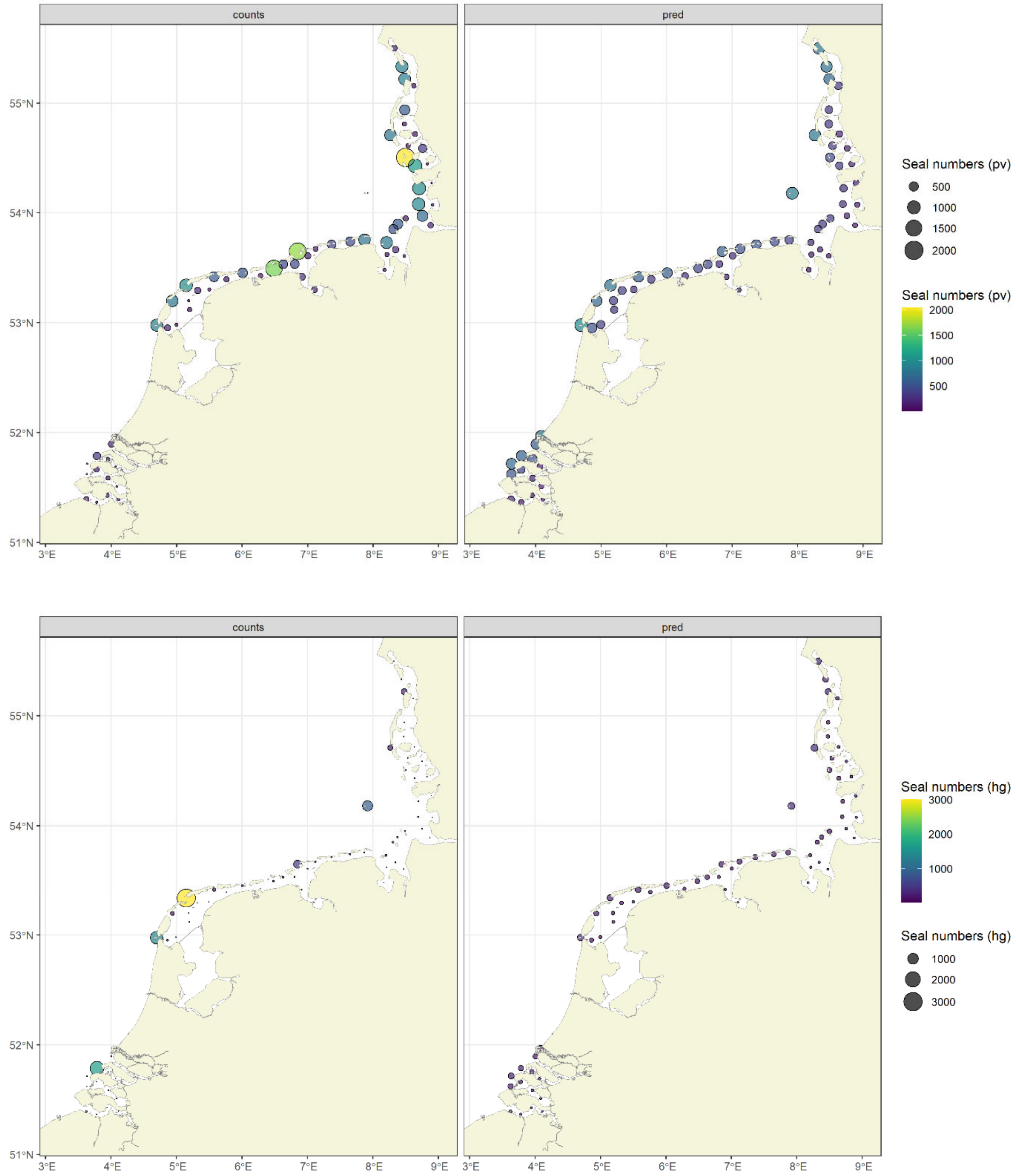

Figure 12. Left panels: The observed number of seals for each haul-out cluster (10 km maximum distance clustering) (a) for harbour and (c) for grey. Right panels: The predicted number of seals on each haul-out cluster based on the habitat model (b) for harbour and (d) for grey.

When we compare the observed versus predicted seal distribution, a pattern emerges. Some haul-out clusters are used by substantially more seals than predicted (i.e. blue coloured circles, Fig. 13). In the eastern Wadden Sea, the observed numbers of Harbour seals exceed the predictions made by the model. In comparison to the model predictions, Schleswig-Holstein as well as the region surrounding the Ems Estuary at the Dutch-German border, contains substantially more harbour seals. These regions are characterized by relative high number of pups observed during the breeding season. Helgoland, the rocky island offshore in the German Bight of the North Sea, has substantially less seals than predicted by the model (red/pink coloured circles). Another region with far fewer seals than predicted by the model is the Delta area in the South of the Netherlands. All haul-out sites contain fewer seals than predicted by the model. Population survey data show that harbour seal numbers continue to increase in this region.

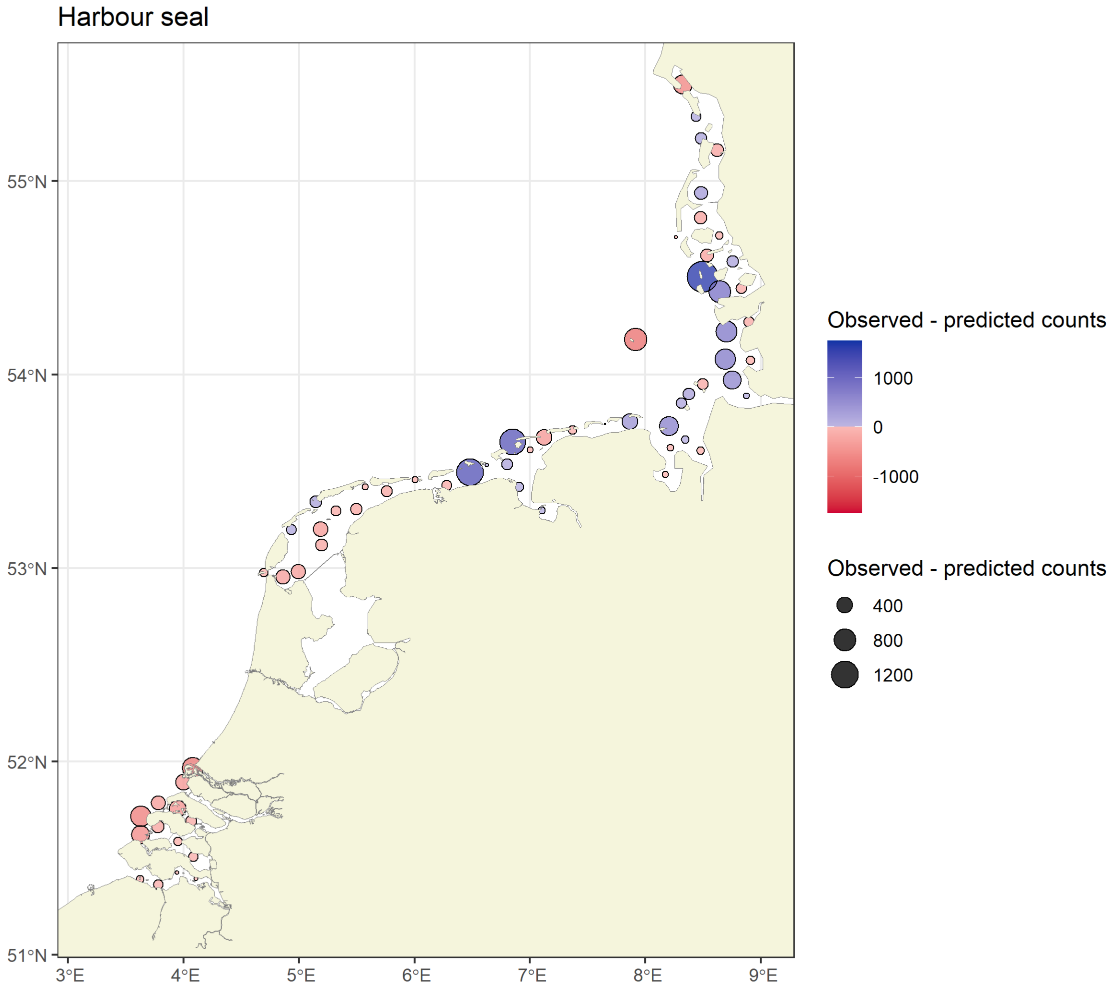

Figure 13. Absolute difference between the observed and predicted number of harbour seals. Blue dots represent haul-out sites where more seals are observed than predicted by the model. Red dots are haul-out sites with fewer observed seals than predicted.

In comparison to harbour seals, grey seals are even more confined to a limited number of confined haul-out sites, with the majority of these sites situated along the outer edges of the Wadden Sea or Dutch Delta area. Seals are observed in significantly lower numbers than predicted by the model at all haul-out sites within the inner Wadden Sea. The highest positive residual can be observed near the “Engelschhoek”, situated between the Wadden Sea islands of Vlieland and Terschelling.

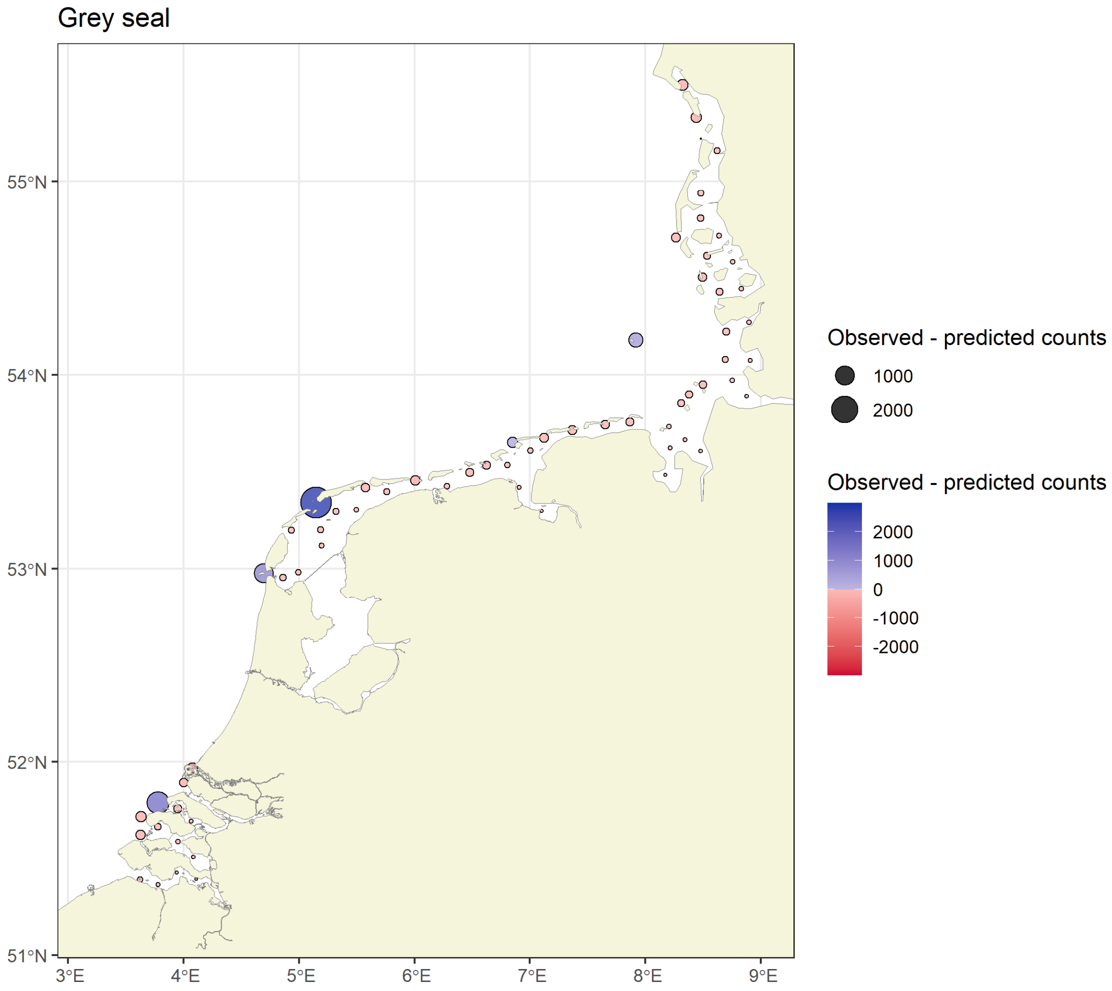

Figure 14. Absolute difference between the observed and predicted number of grey seals. Blue dots represent haul-out sites where more seals are observed than predicted by the model. Red dots are haul-out sites with fewer observed seals than predicted.

Based on the predictions as shown in Fig. 12, it is possible to aggregate the counts by region. Note that we assume that the total predicted number of seals for the entire Wadden sea (i.e. the Delta region excluded) are equal to the total observed number of seals, and those predicted numbers were rescaled accordingly. The implicit assumption is that seal population size has reached a carrying capacity. For the Netherlands (NL), Lower Saxony (LS) and Denmark (DK) the predicted number of harbour seals (coloured horizontal line in Fig. 15) are remarkedly similar to the maximum counts observed in the different regions in the most recent years (Fig. 15). However, in Schleswig-Holstein (SH), substantially more harbour seals were observed during the moult season than predicted by the model. Schleswig-Holstein is characterized by the highest pup production of all regions. For the Delta region (ZE), the current counts are substantially lower than the habitat-based estimate of harbour seals. This is also reflected in Fig. 12, which shows far fewer observed seals than predicted by the model for this region.

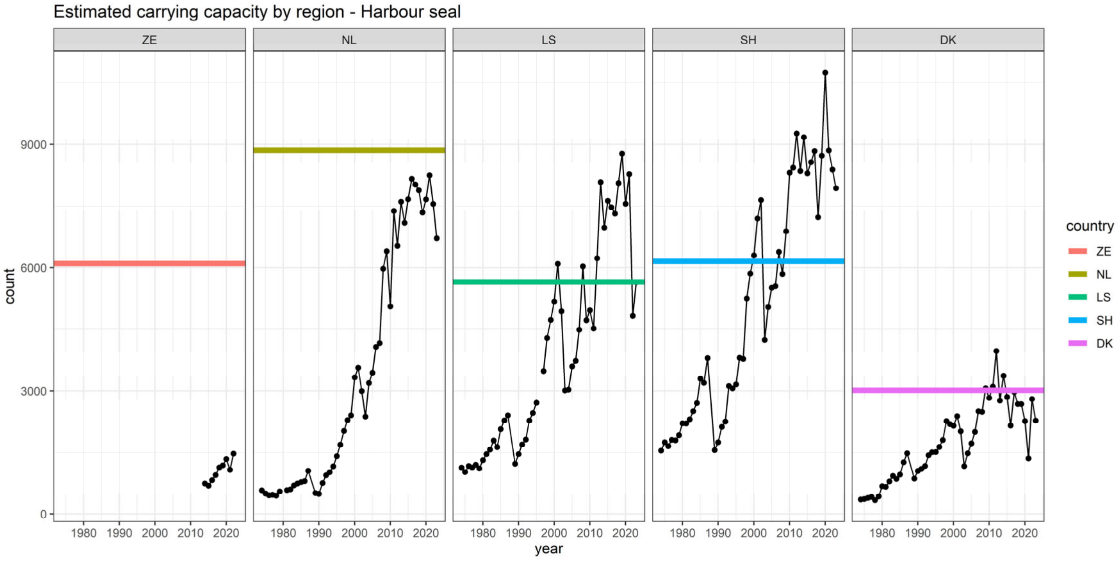

Figure 15. Trends in harbour seal moult counts (black lines) for each of the five regions, and carrying capacity as estimated by the habitat model (coloured lines). The five regions are the Delta area (ZE) and in the Wadden Sea: the Netherlands (NL), Lower Saxony (LS), Schleswig-Holstein (SH) and Denmark (DK).

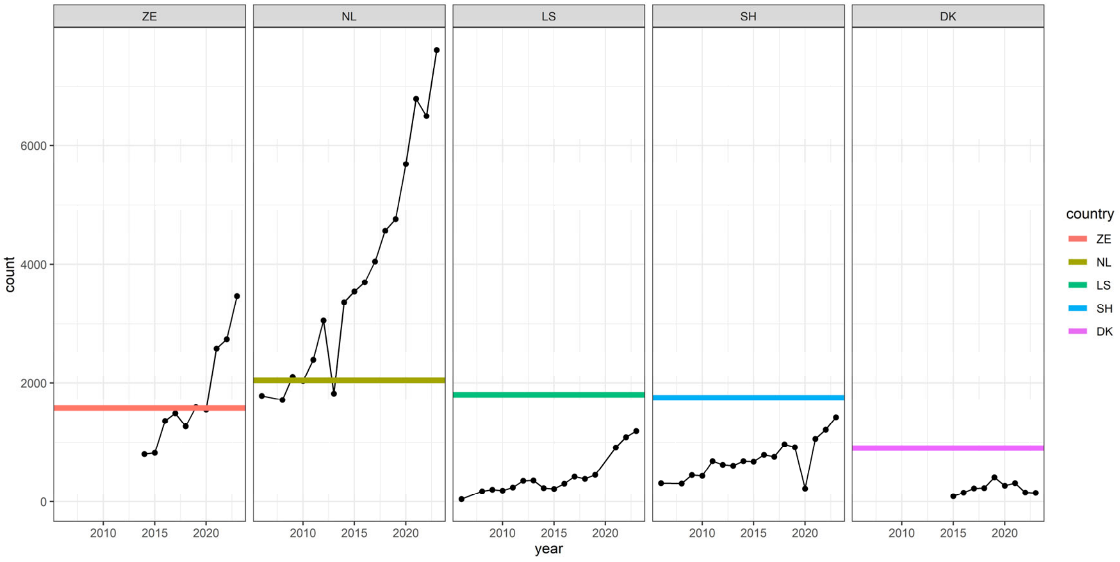

Figure 16. Trends in grey seal moult counts (black lines) for each of the five regions, and carrying capacity as estimated by the habitat model (coloured lines). The five regions are the Delta area (ZE) and in the Wadden Sea: the Netherlands (NL), Lower Saxony (LS), Schleswig-Holstein (SH) and Denmark (DK).

Discussion

This study's primary objective was to determine whether the abundance and distribution of harbour or grey seals on land could be explained by the quality and availability of foraging habitat types at sea. If so, this relationship could be utilized to estimate the carrying capacity of a population. Indeed, the number of seals predicted by the habitat model was significantly correlated with the number of seals found on land during the aerial surveys for both species. When these predicted counts for harbour seals within each of the survey regions were aggregated, serving as a proxy for a regional carrying capacity, overall, those estimates showed resemblance with the maximum moult counts observed for most regions. These are promising findings, as they demonstrate that the quality of habitat at sea can provide valuable information regarding the distribution and population size of seals on land. Furthermore, it also implies that the land-based aerial survey counts could potentially serve as valuable indicators of the quality and availability of habitats in the surrounding seascape and changes that might occur. However, there are also considerable discrepancies between the observed and predicted numbers at the different haul-out sites, which could potentially be explained by anthropogenic disturbances, intraspecific competition or facilitation and food availability, and these effects should be included in future studies.

Habitat selection

The habitat model was fitted to the GPS locations, capturing the variations in seal density as a function of environmental variables. This dependence was used for spatial predictions of at-sea density for the part of the North Sea bordering the Dutch, German and Danish coastline. The model showed that, by far, most variation in density at sea could be explained by the distance to the haul-out site. Furthermore, the residual variation in seal density showed a peak preference for regions of ~20 m depth, a preference for areas with low mud-content and areas with a low TPI for both species (e.g. gullies, trenches, and holes and also high TPI for harbour seals (e.g. peaks and ridges).

The strong tendency of seals to stay closer to the haul-out sites may be explained by their attempt to minimize travelling costs (Matthiopoulos, 2003). Since most trips were observed to be relatively short (<20h) and the seal's cruising speed is relatively slow (~1 m/s), most feeding trips are expected to be within 36 km from the haul-out site, or even closer, to leave sufficient time to forage (although they may also search for prey while travelling (Vance et al., 2021)). However, heterogeneity in habitat quality may cause some patches further offshore to be more profitable, forcing them to make longer and further foraging trips. Also, seals may deplete prey resources in the vicinity of the colony, forcing animals to go further away. This process is known as density dependent competition and has been observed for other species (e.g. for northern gannets (*Morus bassanus*), see (Wakefield et al., 2013)). Depth also proved to be an important explanatory variable, suggesting that seals tracked in this area have a strong preference for depths ~20m, and making less use of areas that are deeper. Apparently, those areas provided sufficient prey for seals, making it unnecessary to dive deeper. Although seals could easily dive to greater depth (i.e. harbour seals 480m, (Eguchi & Harvey, 2005) and 477 for grey seals (Boehme et al., 2012)), any time spend diving is potentially deducted from the available foraging time near the bottom, and this might explain the avoidance of deeper depths. Why seals avoid more shallow waters is unclear, but this could possibly be because of prey preference or competition with other air-breeding species (e.g. diving birds, like cormorants (*Phalacrocorax carbo*)) or smaller-sized conspecifics (e.g. juvenile (0-year-olds) seals that are not tagged). However, it might also be caused by collinearity with other environmental variables not included in the model, such as wave-related bottom sheer-stress or human use. Finally, seals are also more likely to be found in areas with high TPI (i.e. places that peaks and ridges) and for harbour seals also low TPI (i.e. gullies and trenches). These geomorphological features may serve as prey aggregation sites and/or enhance prey capture success (Wyles et al., 2022). The estimated effect of these environmental variables on seal distribution is however substantially smaller than the effect of distance to the haul-out and depth. Finally, the ratio between the distance to the nearest haul-out site and the distance to the start haul-out site shows that seals are more likely to stay within their ‘Hinterland’ and as a result create spatial segregation between neighbouring colonies. This is an important result, because it indicates the possibility of designating particular marine areas and their associated foraging habitats to terrestrial haul-out sites, and this could be a valuable tool for designation of protected areas on land or at sea.

Delays in redistribution: non-ideal and non-free distribution

While the habitat model is capable of predicting the number of seals found ashore during the aerial surveys, there are still substantial discrepancies between the predictions and observations. Part of this could be because of a misspecification of the habitat model. Environmental variables that may change over time for example changes in prey availability, inter- and intraspecific competition, and human activities (e.g., shipping, seismic surveys, and the construction of wind farms) are currently not included in our model. For example, during construction of offshore wind-farms pile-driving was shown to deter both grey and harbour seals up to a distance of 40km (Aarts et al., 2018; Russell et al., 2016). Similarly, operational wind farms, shipping noise, explosions at sea and seismic surveys may also deter seals (Jansen et al., 2010; Jones et al., 2017; Tougaard et al., 2009). Similar impacts have been found for other species, like harbour porpoises (*Phocoena phocoena*) (Aarts et al., 2016; Thompson et al., 2013; von Benda-Beckmann et al., 2015), and ringed seals (*Pusa hispida*) (Harris et al., 2001). Adding these anthropogenic factors into the model in future studies might improve explaining current seal distribution.

It seems that the largest discrepancies between observed and predicted numbers are caused by delays in redistribution (Fig. 11). These delays may be the result of both seasonal and interannual movements. Some regions in the Wadden Sea take up a much larger share of the total reproduction. For example, the majority of harbour seal pups are born in Schleswig-Holstein, which was also historically the population stronghold prior to its recovery (Brasseur et al., 2018). (Brasseur, 2017) showed that many individuals, mostly adult females, move from the Netherlands, as far as the Delta region, to the German Wadden Sea to pup. After the breeding season, individuals tagged in the eastern Dutch Wadden Sea move on average more in western direction, presumably to return to feed in more suitable foraging areas. In this study we relied on August counts for harbour seals, when many individuals might still reside close to the breeding areas, creating a mismatch between the distribution of high-quality foraging areas and the distribution of seals on land. If we would have been able to rely on international Wadden Sea counts collected later in the year (e.g. the winter months), it is expected that there would be a more accurate correspondence between the predicted and observed haul-out counts.

In addition to seasonal delays, there might also be multi-year delays. The harbour seal population declined due to hunting until the 1970’s. After the ban, the population was also affected by disease (i.e. Phocine morbillivirus, formerly known as phocine distemper virus (PDV)) and pollution (i.e. contamination of polychlorinated biphenyls (PBC's)) but overall recovered over the following decades. The numbers in the Delta are still increasing, while numbers in all Wadden Sea regions have now levelled off (or are even in decline). The estimated carrying capacity based on the habitat model suggests that harbour seal numbers in the Dutch Delta might still increase to more than five thousand individuals. Interestingly, this estimate corroborates the figure of 4000 animals estimated by (Reijnders, 1994), which was derived from hunting statistics.

The estimated carrying capacity for harbour seals, however, does not take other predators into account, such as grey seals or harbour porpoises. Grey and harbour seal may compete for haul-out space, and they, but also porpoises, show overlap in diet. The largest proportion of grey seals in the Southeastern North Sea are observed on haul-out sites in the Netherlands, both in the Wadden Sea, and the Delta region (Fig. 10). In addition, approximately 40,000 harbour porpoises are estimated to reside in Dutch waters (Geelhoed et al., 2020). Grey seals have higher food intake than harbour seals but might also target fish that are less accessible to harbour seals, for example by selecting foraging areas further offshore. In lack of data, it is difficult to assess effects of porpoises, but elaborating our models by including grey seals might help explaining the current distribution of harbour seals. Incorporating grey seal numbers into the calculation may improve the estimate for both the Netherlands (Wadden Sea and Delta) and Schleswig-Holstein, which currently appears inconsistent with the counts (Fig. 15). Most grey seals are found in Dutch Waters, and this may explain part of the overprediction in this region, while in Schleswig-Holstein contains fewer grey seals. In this region, the model underpredicts the harbour seal numbers. An overall rescaling of the carrying capacity estimate may yield a more accurate prediction of seal numbers in accordance with the habitat model for that region.

In summary, one of the core assumptions of the approach used is that seals have an ideal-free distribution. This implies that they have perfect information about the distribution and quality of all habitats and select them accordingly (i.e. their distribution is ‘ideal’) and that they have the ability to enter all habitats equally (i.e. they are ‘free’). Both assumptions are questionable, and particularly the latter one. The current harbour seal distribution is potentially affected by natural factors like the distribution of prey or other predators and might still be affected by historical human activities (hunt and pollution) or even more recent growth in human use of the area. Nevertheless, the ideal-free distribution and the method used in this study can be a valuable null model, which can be used to detect discrepancies, which can be informative about the underlying biological processes, like the delays in redistribution and inter-specific competition.

Implications and applications:

While the model is capable of predicting the number of seals on the haul-out sites based on the availability of suitable habitat within the surrounding waters, there are considerable discrepancies. One valuable application is that large discrepancies between the model and count data could also serve as indicators, signalling areas where other processes might be ongoing and further investigation is needed. For example, this analysis only incorporated natural and fixed environmental variables to explain the distribution of seals and predict their onshore abundance. In the future this could be extended by including anthropogenic structures or activities and changes in these over time. Potentially, human activities could affect the suitability or accessibility of habitat and resources. Throughout the past decade there has been a significant rise in human use of the area used by seals (Martins et al., 2023; Robbins et al., 2022; Xu et al., 2020). For a large part, current seal tracking data used for this study, preceded these changes.

When there is sufficient support in the seal tracking data to estimate the effect of these human-related variables on seal density, it is possible to estimate how this could translate into population consequences. In some cases, these population-level effects could be temporary, in which case more complex individual-based on dynamic population model might be additionally required to derive the population consequences. However, when the effects are more permanent, like a permanent partial or complete exclusion, it would be possible to use the approach presented here derive how this would translate in (regional) declines in carrying capacity, reflected in changes in number of seals. This analysis could be achieved by incorporating explanatory variables related to those anthropogenic variables into the species-habitat-association model. Those anthropogenic variables could include the proximity to the nearest hard structure, such as rocks, wrecks, pipelines, oil- and gas platforms, and windmills (Martins et al., 2023; Russell et al., 2014). Hard structures typically lead to increased turbulence in their wake (Schultze et al., 2020), causing reduced mud concentrations and higher median grain sizes in the surrounding areas; these habitat conditions are generally favoured by grey and harbour seals. The impact of offshore wind farm construction and operation could also be investigated. It has been demonstrated that pile-driving during construction can result in changes in dive behaviour and movement (Aarts et al., 2018; Russell et al., 2016), as well as the avoidance of the construction area (Russell et al., 2016). Seals may also be deterred by the visual rotation of the blades and the underwater sound produced by the rotation, as well as maintenance activities. To capture these effects, the distance to wind farm under construction or the distance to a windfarm in operation could be included as a covariate. Also shipping activity may deter seals (Jones et al., 2017). Shipping density maps are derived from AIS data, and monthly estimates grouped by vessel type are (freely) available from EMODnet for the years 2017-2023. Fishing intensity, defined as fishing vessel density by gear type and the average surface or sub-surface swept area ratio, can also be incorporated as a model covariate. Care must be taken in interpretation, as fishing acitivities influence fish abundance; however, their distribution is also closely linked to biotic and abiotic habitat characteristics, such as sediment composition and fish density. Finally, the proximity to seismic surveys and detonations of unexploded ordnance (UXO) could also be included into the species-habitat relationship model. The seismic surveys appear to have little overlap with the seal tracking and the data may be insufficient to derive their association. For the detonations, detailed information on the exact timing of the detonations is available for a number of years (Aarts et al., 2016; von Benda-Beckmann et al., 2015). An interaction smooth term between distance and time to the detonation could be included as covariate to capture persisting avoidance of regions where seals were exposed, however, more detailed analysis of individual tracking data and behavioural responses might be required. After estimating the impact of the various human-related variables on seal distribution, the methodology proposed in this study can be used to predict regional population sizes both with and without these anthropogenic covariates. Once fully developed, this could in theory be used to predict population-level consequences of human activities and infrastructure.

Another application of the method is to estimate other potential suitable haul-out sites. Currently, the entire beach along the west-coast of the Netherlands is accessible to the public, and this is assumingly why seals only rarely haul-out on this stretch of the coast. As a consequence, seals foraging off the coast have to haul-out either in the Wadden Sea in the North (like the Razende Bol) or in the Delta in the South. If seals are able to haul-out in closer proximity to their feeding grounds, this could vastly reduce their energetic costs. As a consequence, the method proposed here could help decide where to locate a permanent closure of the beach closure or an artificial haul-out off the west coast and as a result, increase harbour seal population size.

Future model improvements

An implicit assumption of the method used in this study is that each cluster of haul-out sites has reached its carrying capacity. This assumption may not be valid. For example, the seal population in the Dutch Delta continues to increase and may continue to do so in the years to come since the estimated carrying capacity is substantially higher than the regional counts. Also, the Dutch part of the Wadden Sea might not yet be fully saturated by harbour seals, as suggested by figure 13 (negative residuals). By modelling the observed counts as function of the habitat-based predicted counts, transients in population size and other population dynamic processes are not captured. Instead, one could model the regional population *growth rate* as function of the availability and quality of habitats (Matthiopoulos et al., 2015). This approach has, for example, been applied to house sparrows (Matthiopoulos et al., 2019). In addition, habitat selection itself may change as function of population size (Avgar et al., 2020), known as functional response in habitat use (Aarts et al., 2013; Matthiopoulos et al., 2011). To capture this aspect, one could include a (smooth) interaction term between an environmental variable and regional population size.

Another feature of the method that could be improved is the estimation of the Hinterland. The traditional approach is to define the Hinterland as equidistant Voronoi tessellations. This, however, assumes that individuals from neighbouring colonies do not overlap in their foraging distribution. This is unlikely, particularly when the difference in distance between a foraging location and two or more colonies/haul-out sites is neglectable. In the current model, overlap in foraging distribution is partly captured by modelling the ratio between the nearest haul-out and the trip haul-out. This is however, a relative simplistic formulation, and does not include differences in colony size and the resulting difference in density dependent competition which may ‘push’ and ‘pull’ foraging distributions of neighbouring colonies (Aarts et al., 2021; Riotte-Lambert et al., 2015; Wakefield et al., 2013). An alternative approach would be to include individual-based models, or fit a more mechanistic dispersion model to tracking data, as proposed by (Niven et al., n.d.). Including more realistic and accurate estimates of the Hinterland and incorporating population dynamic processes in the approach may lead to a closer correspondence between the observed and predicted distribution, and more reliable estimates of the population potential of each haul-out site.

Appendix A

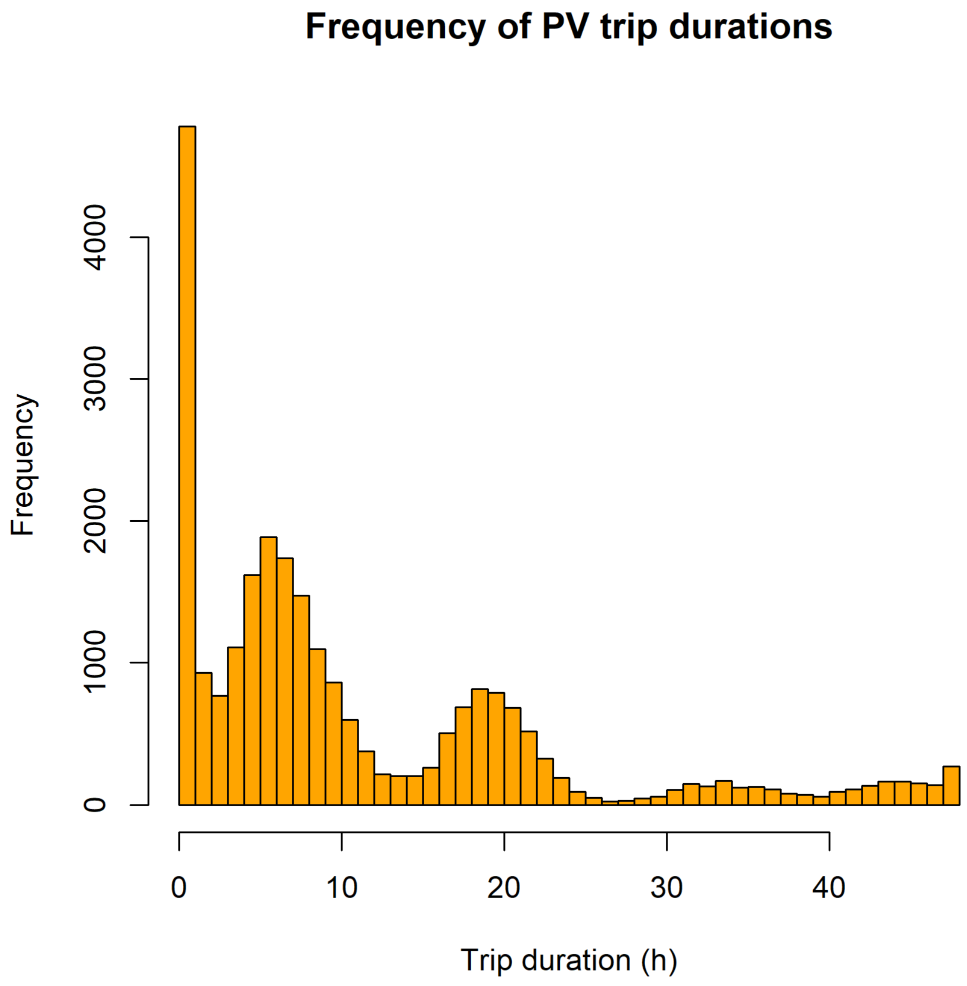

Figure S1. Frequency distribution of trip duration based on the harbour seal tracking data used in this study.

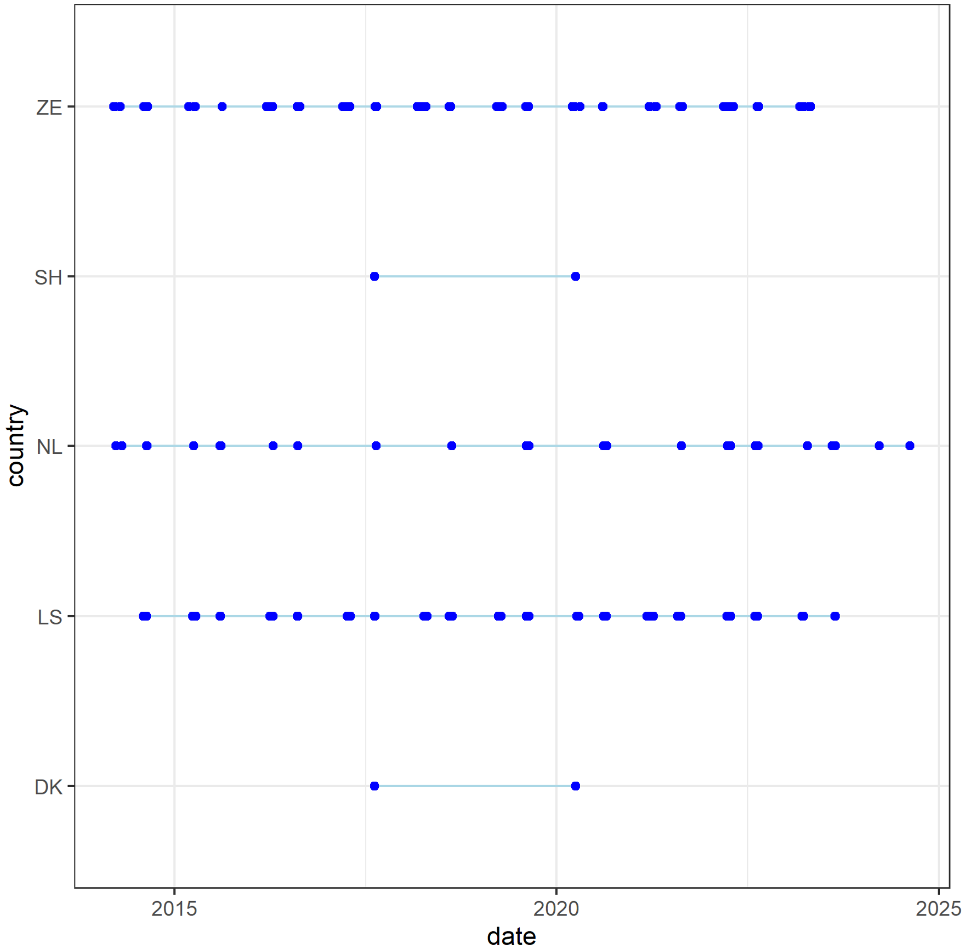

Figure S2. Yearly and regional availability of survey data used in this study

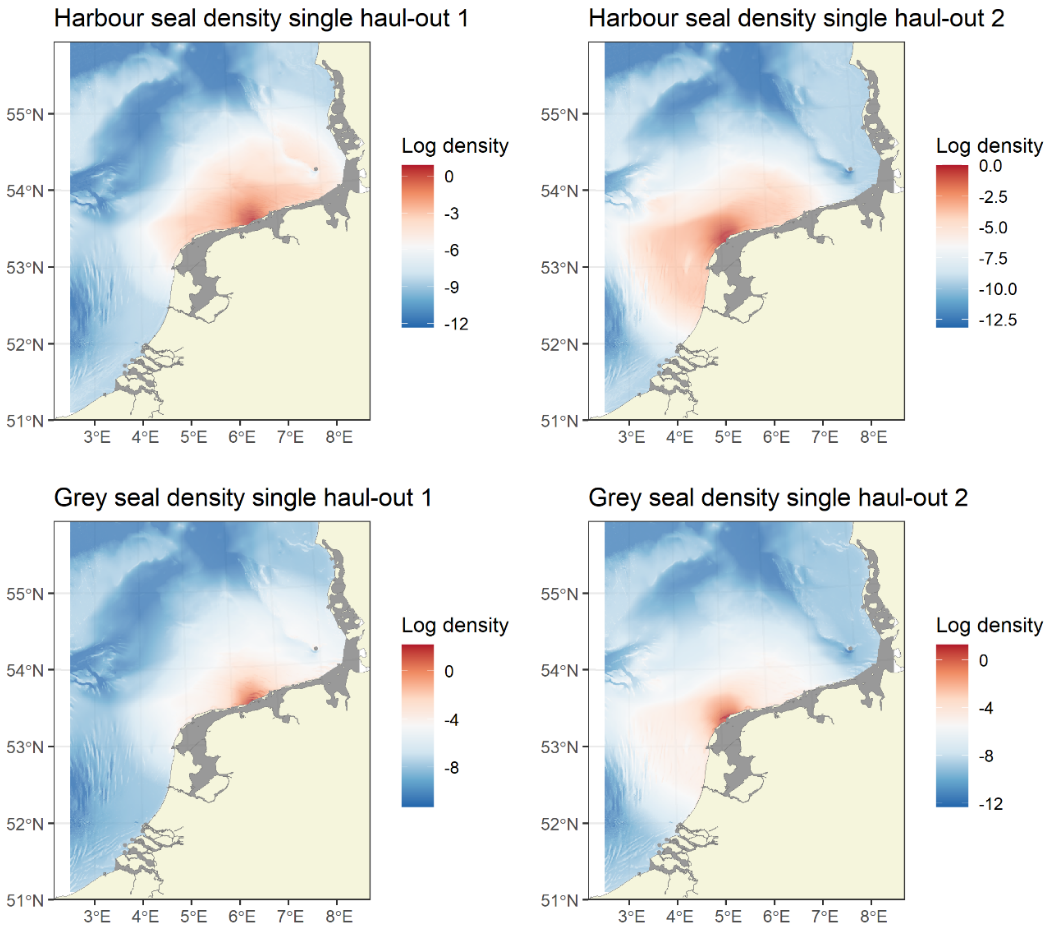

Figure S3. Predicted density (on log-scale) **of** two colonies; the Razende Bol (left figure) and near Rottumeroog/Rottumerplaat (right figure).

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Conflict of interest disclosure

The authors declare that they have no financial conflicts of interest in relation to the content of the article.

Data, scripts, code, and supplementary information availability

Example data are available online: https://wozep.nl/git/wozep/04_marine_mammals/-tree/master/tagging_seals/raw_data

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