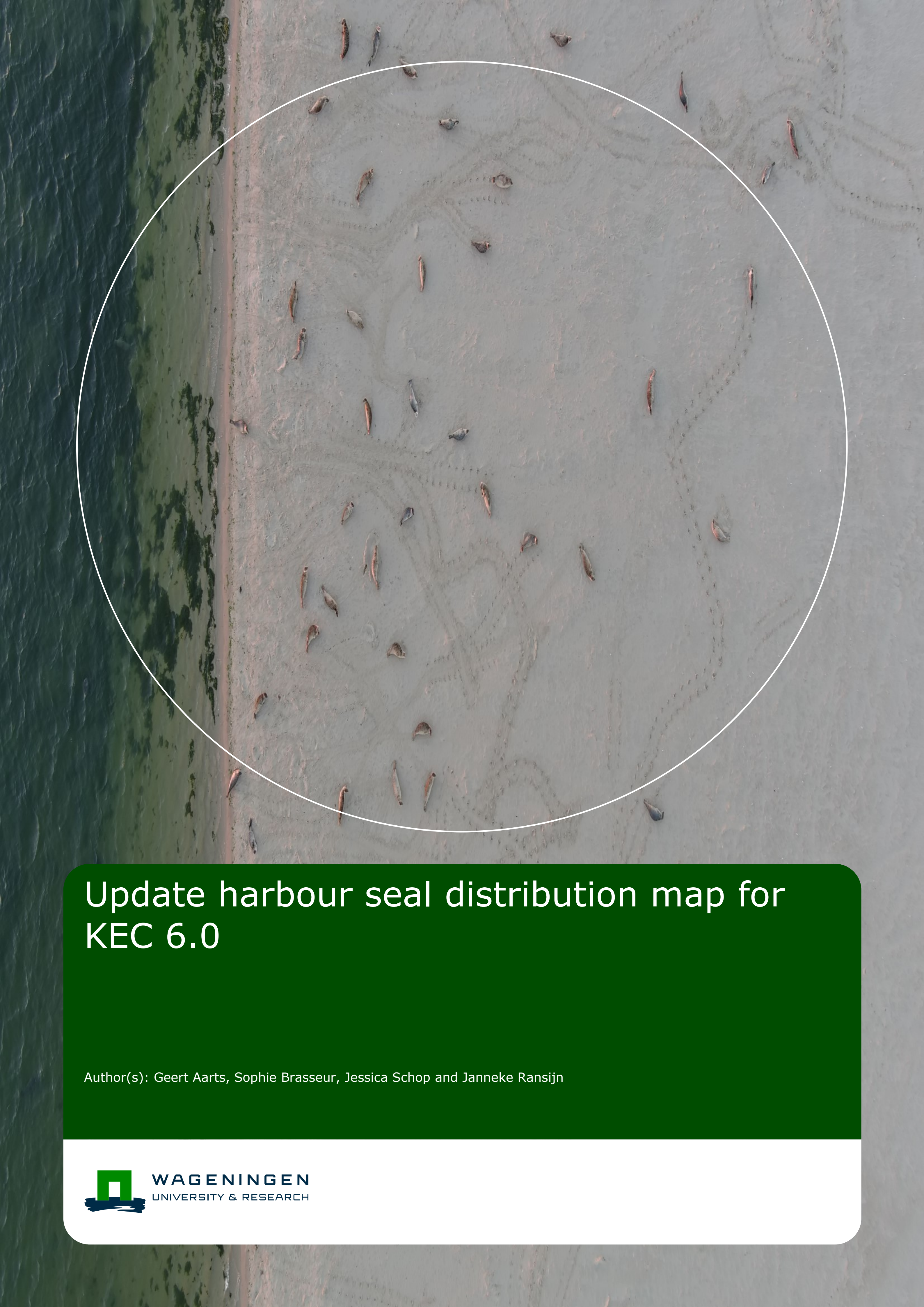

Update harbour seal distribution map for KEC 6.0

Author(s): Geert Aarts, Sophie Brasseur, Jessica Schop and Janneke Ransijn

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Wageningen Marine Research
Den Helder, June 2026

Report C048/26

Geert Aarts, Sophie Brasseur, Jessica Schop and Janneke Ransijn, 2026. 25.43.101 Update harbour seal distribution map for KEC 6.0; Wageningen, Wageningen Marine Research, Report C048/26.

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Wageningen Marine Research Report

Photo cover: Geert Aarts

Contents

Summary

To assess the cumulative impacts of offshore wind farms on protected species, detailed information on their spatial distribution is required. To update the estimates of harbour seal distribution, particularly of 0-year-old individuals, 28 new GPS trackers were deployed in 2025. The aims of this study are to (i) investigate variation in trip characteristics (duration and distance to haul-out) in relation to age class, sex, and season, and (ii) use this information to refine a habitat model for population-level distribution estimates, originally developed for KEC 4.0.

Trip analyses revealed substantial individual-level variation in both trip duration and distance. Nevertheless, consistent patterns emerged: harbour seals undertook longer trips and travelled further from haul-out sites during winter. The intermediate and largest sized individuals exhibited greater trip duration and distance than smaller individuals, suggesting relatively higher offshore usage. However, significant interannual variation in trip characteristics was observed, with the 2025 deployment showing the greatest average trip duration and travel distance. Because a relatively large number of 0-year-olds were tagged during this deployment, the effects of year and age may be confounded. Interpretation of observed time effects is complicated by spatial bias in tagging effort, as deployments were unevenly distributed across locations and years.

Insights from the trip analysis were used to improve the habitat model. Extensions included interactions between distance to haul-out and body length, and between distance to haul-out and season. While the effect of body length was modest, seasonal variation was pronounced and consistent with the trip analyses, indicating increased offshore foraging during winter. Seals are most often observed in relatively shallow areas (~20 m), coarser sediments, and areas with distinct seabed features such as ridges and troughs. The model was further improved by incorporating both individual-level latent fields and a global latent field, which capture unexplained spatial variation in distribution beyond that accounted for by the environmental covariates for each individual separately and for all individuals combined. In particular, the global latent field revealed substantially higher seal use along the west coast of the Dutch mainland than predicted by the environmental covariates in the habitat model. One possible explanation is that density-dependent competition pushes individuals farther from the central place. North of the Wadden Sea islands, such movements may be constrained by water depth or shipping lanes, whose effects could be absorbed by the variable “distance to the haul-out”, leading to underprediction in the shallow regions off the west coast of the Dutch mainland farther south.

The final model was used to predict the absolute number of seals per km^2 for harbour seals making foraging trips to the North Sea from the Delta area, the Dutch Wadden Sea, and Lower Saxony in Germany, incorporating haul-out counts from aerial surveys. Predictions were generated for two seasons: summer (September) and winter (February), corresponding to the months with the lowest and highest use of far offshore areas, respectively. Although the model can generate monthly predictions, its accuracy is constrained by limited data on haul-out distribution. Typically, most surveys of harbour seals are carried out in summer during breeding and moult, while peak offshore foraging occurs outside these periods in winter. Despite these limitations, the results provide valuable new insights into the spatial and temporal distribution of harbour seals. Future work could incorporate additional covariates and more complex interaction structures to investigate the seals’ preference for natural and anthropogenic habitat variables, and how these relationships vary by sex, age, and season.

1 Background

In 2016, the Dutch Ministry of Economic Affairs commissioned Rijkswaterstaat (RWS) to establish an integrated research program aimed at reducing knowledge gaps concerning the effects of offshore wind farms on the North Sea ecosystem: the Offshore Wind Ecological Programme (Wozep). The results generated within Wozep are incorporated into the Framework for Ecology and Cumulative Effects (KEC), where the cumulative impacts of offshore wind farms on species protected under nature conservation legislation are assessed.

RWS subsequently commissioned Wageningen Marine Research (WMR) to build upon KEC 4.0 through a multi-year assignment. The objective is to incorporate newly acquired knowledge and further develop and refine the methodology, resulting in KEC 5.0 and subsequently KEC 6.0. In the forthcoming KEC 6.0, cumulative effects on populations of seabirds, seals, and porpoises associated with wind farms planned up to 2040 will be assessed.

Implementation of the KEC requires the development of distribution maps for selected seabird species, seal species, and porpoises. This report focusses on harbour seals (*Phoca vitulina*). For seals, the existing tracking data (collected between 2006 and 2019) used to generate these maps had become outdated, and especially individuals in their first year of life were underrepresented. To address this limitation, 28 harbour seals were tagged in 2025, during both spring (March) and autumn (October/November). Ten of these were 0-year-olds. Previous studies have shown that tracking devices deployed in November can remain operational until June, and at least until April. Consequently, tracking data from seals tagged in autumn 2025 continue to be collected during the months leading up to this report. A balance was therefore sought between ensuring sufficient data availability and meeting the project timeline. For this reason, the distribution maps for harbour seals presented in this report are based on tracking data collected up to 2 March 2026.

2 Aim

RWS has tasked Wageningen Marine Research with updating existing distribution maps, or creating new ones where possible, for seabirds, seals, and porpoises to support KEC 6.0, based on the currently available data. No new data are available for grey seals (*Halichoerus grypus*); therefore, no updated distribution maps will be produced for this species. Instead, the maps developed for KEC 4.0 will be reused in KEC 6.0. In contrast, since new harbour seal tracking data have been collected, RWS commissioned WMR to update the harbour seal distribution maps as described in Aarts *et al.* (2021) and improve the methodology and habitat model where needed. The update of the maps is based on existing tracking data and those tracking data collected during the Wozep harbour seal tagging campaign conducted in 2025.

3 Assignment

1. Updating distribution maps for harbour seals, based on WOZEP tagging data collected in 2025, including transmitter data up to 2 March 2026.
2. Preparing a technical memo describing: (i) the methodology used to generate the maps; (ii) the selection and processing of data used for model fitting; (iii) additional supporting analyses, such as trip analysis, informing the development of the habitat model; and (iv) a description of how the newly acquired knowledge has been incorporated into the maps.

Since no new tracking data are available for grey seals, no updated distribution maps are produced. Consequently, the distribution maps developed for KEC 4.0 will be reused in KEC 6.0.

A description of the methods (as described in point 2), can be found in the annex. In the following, we present the main results of the analysis and distribution maps and discuss the findings.

4 Results

4.1 Distribution of seal tracking data

Figure 1 shows the distribution of all harbour seals tracked with GPS-trackers between 2006 and 2026. More details on the latest tracking data collected in 2025-2026 can be found in Brasseur & Aarts (2026). For the seal distribution estimates based on the habitat model, only tracking data collected from 2013 onwards were used. This excluded the Ems estuary dataset, which would otherwise have exerted a disproportionate influence on the resulting distribution estimates.

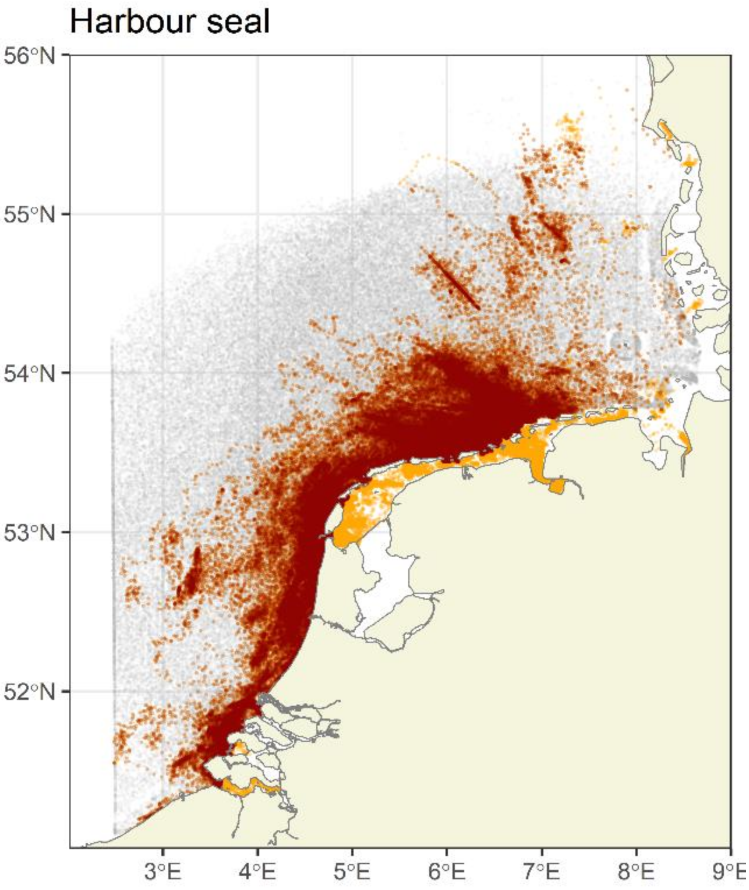

Figure 1. *Data used for model fitting. Red points represent GPS locations included in the model. Since the model was developed to derive the seal's habitat preference and spatial distribution in the North Sea only, all GPS locations in the Wadden Sea, estuaries in the Delta region, or within 3 km of a haul-out site were excluded (orange points). Grey points denote randomly generated availability locations (i.e. reflecting locations that seals could potentially have used) included in the model. To limit the number of used and availability points—and thereby reduce computational demands—only locations within the defined study area (i.e. boundaries of the map shown above) and within 200 km of haul-out sites were included.*

4.2 New tracking data (2025-2026)

In 2025, an additional 28 harbour seals were tracked, including 6 individuals in March and 22 in October/November. Less individuals were tagged in March due to difficulties of catching sufficient individuals. Notably, these data comprise a relatively high proportion of 0-year-olds (10 individuals). Further details can be found in the report describing the 2025 tagging campaign (Brasseur & Aarts, 2026). Below in figure 2-5 we provide an overview of those tracking data.

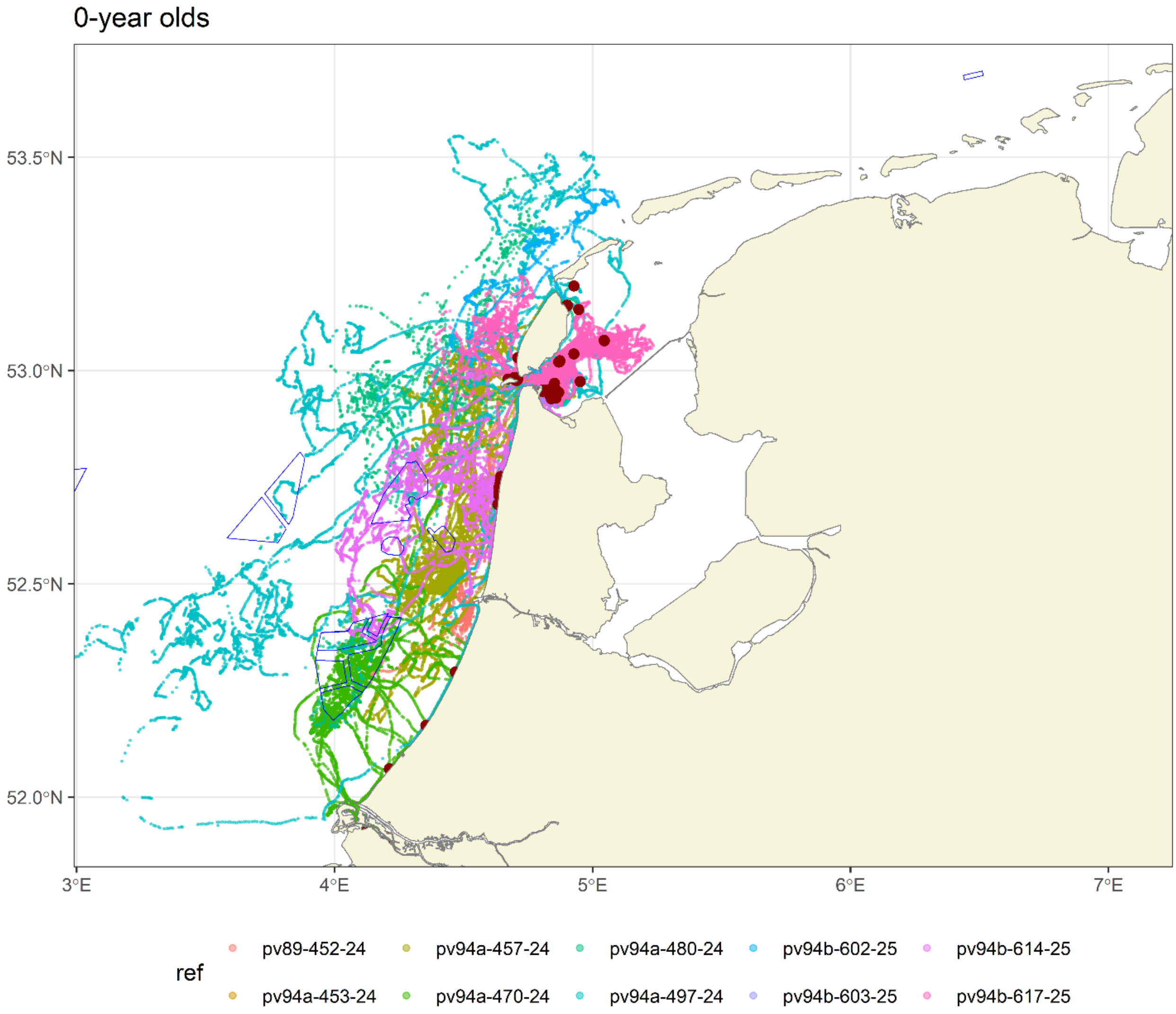

Figure 2. *Movement tracks of 10 individual harbour seals (represented by the different colours) assumed to be 0-year-olds (2025-2026). Tags were deployed on seals caught near Balgzand, east of Den Helder, in March (N=1) or October/November 2025 (N=9). Maps include GPS locations received up to March 2, 2026. For more details, and maps of individual animals, see Brasseur & Aarts (2026). Dark red dots indicate locations where tracked seals hauled out, which are mainly located on intertidal haul-out sites in the Wadden Sea or Delta region, however seals occasionally also haul-out on other locations, like the beaches along the mainland coast. The blue polygons represent offshore wind farms.*

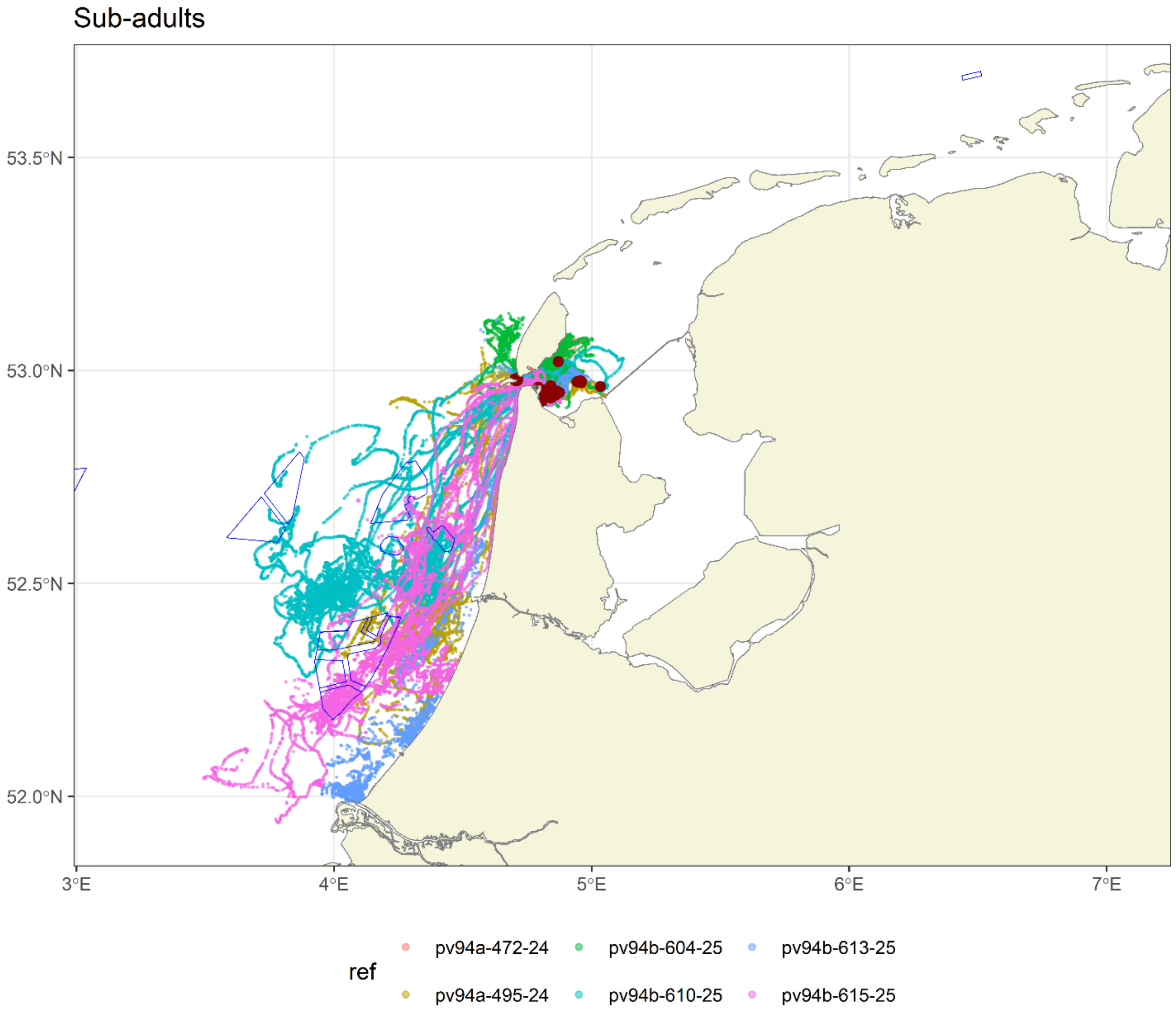

Figure 3. *Movement tracks of 6 harbour seals (3 males and 3 females, represented by the different colours) assumed to be sub-adults tracked from October/November 2025 onwards. For more details, see Figure 2 legend and Brasseur & Aarts (2026).*

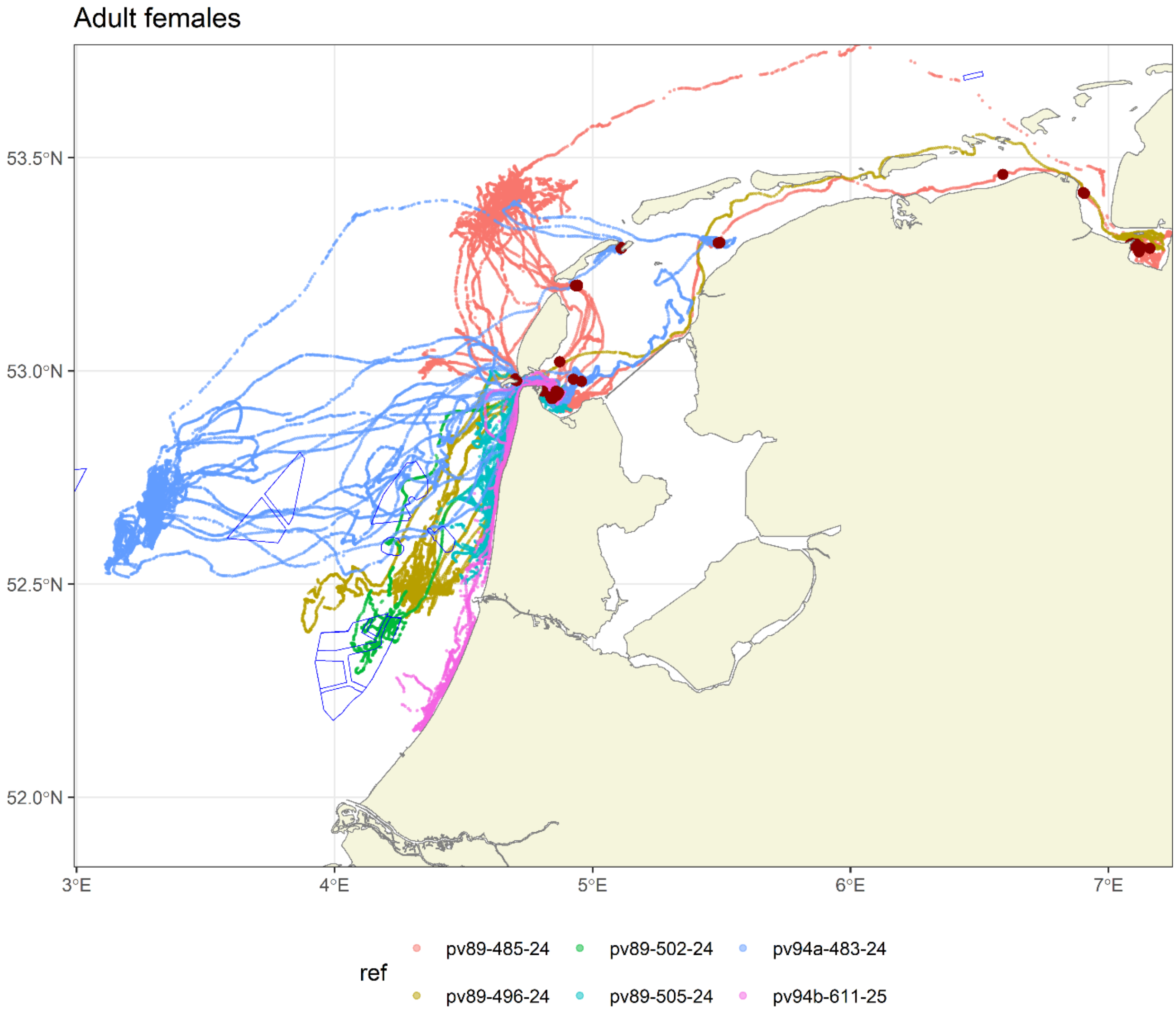

Figure 4. *Movement tracks of 6 adult females tracked in March (N=4) and October/November 2025 (N=2). For more details, see Figure 2 and Brasseur & Aarts (2026).*

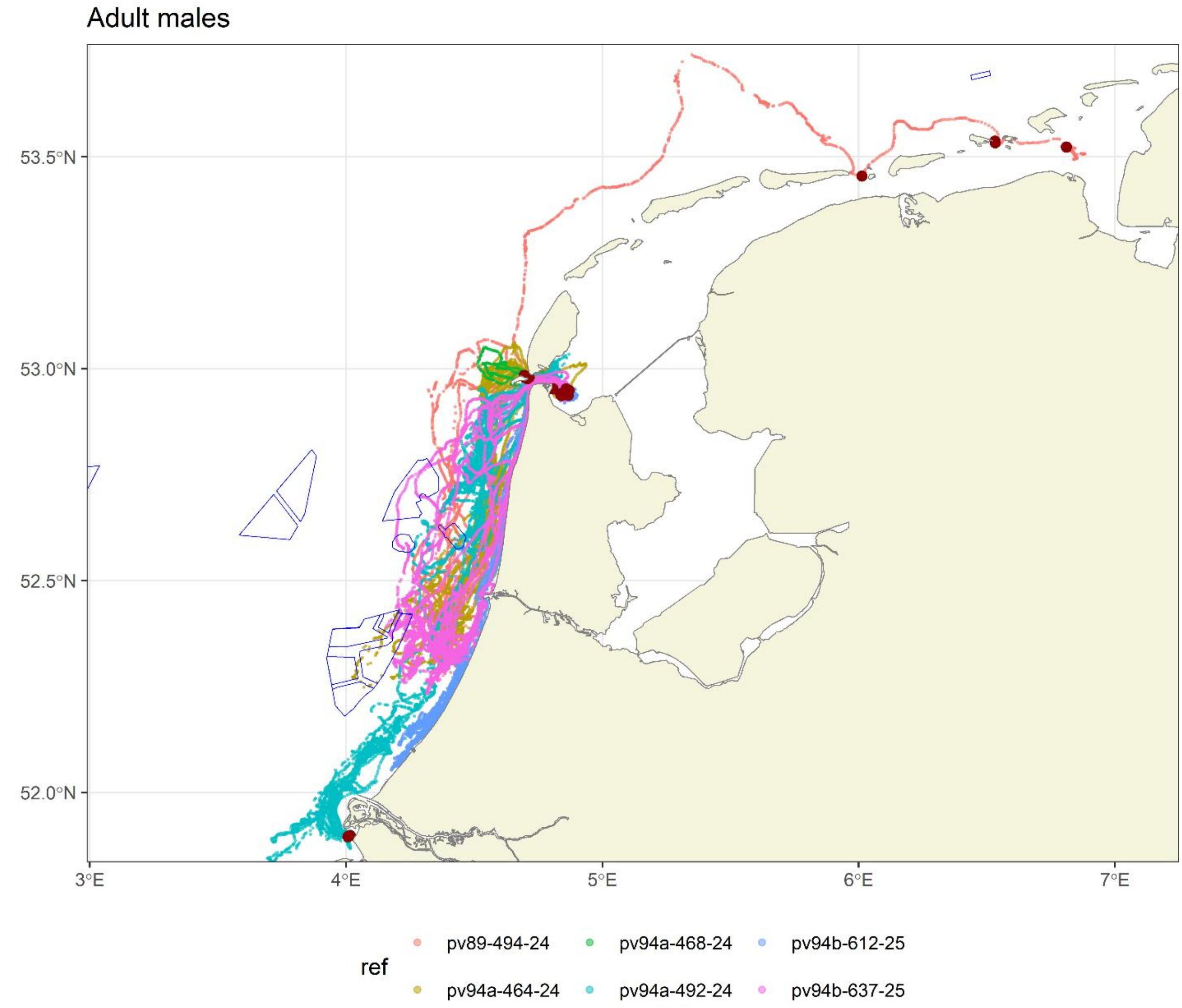

Figure 5. *Movement tracks of 6 adult males tracked in March 2025 (N=1) and October/November 2025 (N=5). For more details, see Figure 2 and Brasseur & Aarts (2026).*

4.3 Harbour seal haul-out counts

Aerial survey data from the Dutch Wadden Sea were extracted for the period 2020–2025 during the annual harbour seal moult in August. In total, 10 trilaterally coordinated surveys were conducted. The mean of these annual maxima was 7,400 individuals (Table 1). Applying a haul-out correction factor of 0.68 (Ries et al., 1998) results in an estimated total population size of 10,882 harbour seals in the Dutch Wadden Sea. For Zeeland, four surveys were conducted during the August moult between 2020 and 2023, while for Lower Saxony, ten surveys were carried out between 2020 and 2025 (Table 1). The average number of seals observed on each haul-out cluster is shown in figure 6.

In the Dutch Wadden Sea, four aerial surveys conducted in March or April covered at least 90% of known harbour seal haul-out sites. These surveys yielded an average count of 4,639 individuals. Assuming the total population size is comparable to the August estimate, this corresponds to a haul-out fraction of 0.43 (4,639 / 10,882), which is substantially lower than the 0.68 correction factor used for moult surveys. In Zeeland, eight surveys were conducted in March and April between 2021 and 2024. No comparable survey data were available for Lower Saxony during this period; for figure 7 for this region, the relative spatial distribution observed during the August surveys was assumed to apply.

Due to the lack of March and April data for Lower Saxony, combined with the generally lower counts and high variability between surveys during this period in the other regions, August moult counts were used to predict seal distribution at sea. See the Discussion section for a more detailed consideration of this decision.

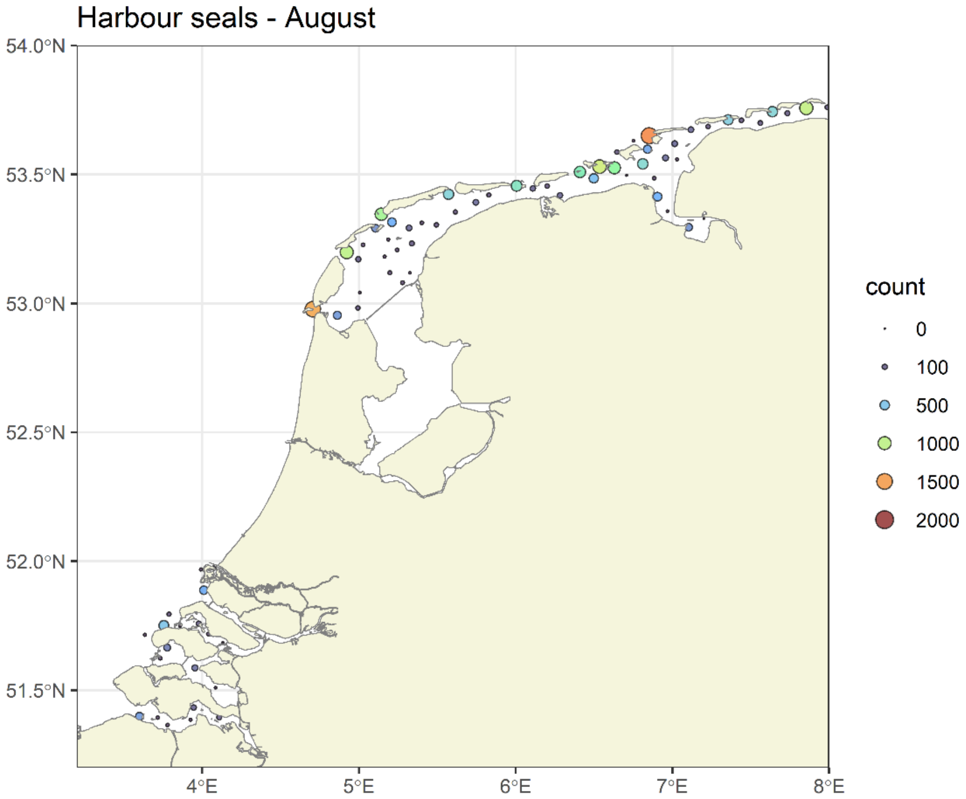

Figure 6. *Average aerial survey counts in August (2020–2025) for each haul-out. Each point represents a haul-out cluster (cut-off distance = 10 km), with seal counts allocated to the nearest cluster based on its location.*

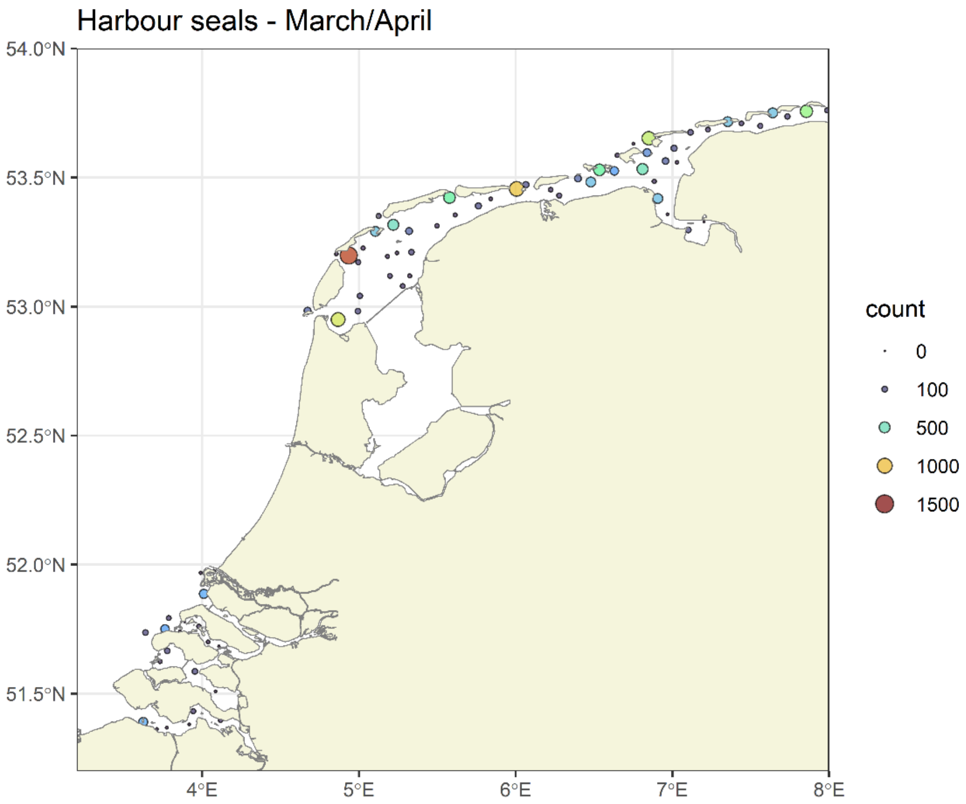

Figure 7. *Average aerial survey counts in March and April (2020–2025) for each haul-out cluster. Each point represents a haul-out cluster (cut-off distance = 10 km), with seal counts allocated to the nearest cluster based on its location. Note that for the Dutch Wadden Sea, these estimates are based on four surveys aimed to count (moulting) grey seal, but during which most known harbour seal haul-out locations were also visited and counted. For Lower Saxony, no harbour seal survey data were available for March/April. Instead, the relative distribution was assumed to be equal to that observed in August.*

Table 1. *Overview of survey counts conducted in August from 2020–2025 and estimated total number, based on a correction factor of 0.68 (Ries et al., 1998) (subject to data availability) across the different regions: Lower Saxony (LS), the Netherlands (NL), and Zeeland (ZE).*

date	country	count	pop.size	date	country	count	pop.size	date	country	count	pop.size
12/08/2020	LS	7553	11107	12/08/2020	NL	7661	11266	10/08/2020	ZE	1435	2110
25/08/2020	LS	7833	11519	17/08/2020	NL	7555	11110	25/08/2021	ZE	1162	1709
02/08/2021	LS	8244	12124	19/08/2021	NL	8245	12125	16/08/2022	ZE	1528	2247
16/08/2021	LS	7766	11421	07/08/2022	NL	7721	11354	23/08/2023	ZE	1738	2556
04/08/2022	LS	4748	6982	20/08/2022	NL	7550	11103		**mean**	**1466**	**2156**
18/08/2022	LS	4822	7091	09/08/2023	NL	7211	10604				
23/08/2023	LS	4063	5975	24/08/2023	NL	6706	9862				
13/08/2024	LS	6115	8993	15/08/2024	NL	7475	10993				
06/08/2025	LS	7296	10729	04/08/2025	NL	7287	10716				
18/08/2025	LS	7246	10656	17/08/2025	NL	6589	9690				
	mean	**6569**	**9660**		**mean**	**7400**	**10882**				

4.4 Trip duration and distance analysis results

4.4.1 Trip duration

For the trip analysis, we used all available GPS tracking data, starting with the first major deployment in 2007. Preliminary inspection of the most recent tracks (Figure 2-5) suggested that harbour seals, particularly 0-year-old individuals, may currently exhibit a more widespread distribution compared to tracks from harbour seals collected in previous years, which predominantly included older individuals. It is anticipated that this pattern would also be reflected in trip duration and trip distance to the haulout site. The aim of this analysis is to investigate which variables (e.g. age, sex, year, and season) influence these trip characteristics and spatial distribution. This information can subsequently be used to improve the distribution estimates by incorporating these variables into the habitat model.

For both trip duration and trip distance to the haul-out (for which we used the maximum distance), we fitted a model that included an intercept, sex as a factor variable, and individual and year as random effects, as well as smooth terms for day of year and body length, which were allowed to vary by sex.

Variation in trip duration was described by a GAMM with a Gamma error distribution (link = log), including individual and year as a random effect and smooth terms for body length and day-of-year (Here, a value ‘1' for day-of-year corresponds to 1 September, immediately following the breeding and moulting season, when tracking commenced). For the full model, the deviance explained was approximately 36% (Table 2), which suggests that a substantial proportion in the observed variation in trip duration can be explained by the variables included in the model. Individual (as random effect) explained the largest proportion of variance, confirming that between-individual differences dominate trip duration variability. Effect of the factor sex on trip duration was not significant ($p = 0.28$), though females tended toward longer trip durations than males (estimate: −0.06 on the log scale), an effect that should be interpreted cautiously given its borderline significance. Body length had a modest but significant effect on trip duration, with both medium and large animals undertaking slightly longer foraging trips, though variation was larger at smaller size classes (Figure 8). The seasonal pattern was the strongest fixed effect, with trip duration peaking in December–January and reaching a minimum in June–Juli. Females showed a significantly distinct seasonal pattern in trip duration ($p = 0.027$, edf = 2.68), with markedly higher predicted durations in midwinter compared to males, while the male-specific seasonal smooth was near-zero ($p = 0.008$, edf = 0.001) (Figure 9). Note that, due to the annual moult, data collected during the end of the breeding season and moult (July-August) was limited, or for some regions almost absent. The interaction between body length and day-of-year was statistically significant ($p < 0.05$), indicating that there was evidence of a general effect of body size on trip duration varying throughout the year, with medium sized seals undertaking longer trips in winter (Figure 11). Trip duration varied across the years, with a jump in recent years (Figure 10).

4.4.2 Trip distance

Model selection for trip distance to the haul-out followed the same procedure as for trip duration (Table 2). Both the random effects for individual and year were significant, revealing substantial individual variation ($p < 0.001$, edf =225.6) and strong interannual variation ($p <0.001$, edf = 10.12), with notable variation across the study period (Figure 10). In contrast to the trip duration model, body length had a significant and nonlinear effect on maximum distance ($p = 0.003$, edf = 1.99), with small individuals showing the lowest predicted displacement, increasing almost linearly with body sizes (Figure 8). Season was also a significant nonlinear predictor ($p < 0.001$, edf = 6.85), with peak displacement in December–March (Figure 9).

The tensor product interaction term between body length and season was marginally non-significant ($p = 0.070$, edf =32.72). The interaction between season and sex was significant, showing that females had significantly distinct seasonal smooth ($p = 0.031$), while the male-specific seasonal smooth was near-zero ($p = 0.015$, edf = 0.001). The full model explained 43.0% of deviance (R^2adj = 0.247; Table 2).

Table 2. *Summary of parametric and smooth terms from generalised additive models (GAMs) predicting maximum trip distance and trip duration. Models used a Gamma error distribution with log link. edf = estimated degrees of freedom; bold = significant at $p < 0.05$.*

	Maximum distance			**Trip duration**		
Term	**edf**	**F**	**p**	**edf**	**F**	**p**
Parametric terms						
Sex (male vs. female)		-	0.551		-	0.283
Random effects						
s(individual)	**225.6**	**13.35**	**<0.001**	**209.7**	**7.00**	**<0.001**
s(year)	**10.12**	**152.5**	**<0.001**	**9.66**	**52.46**	**0.002**
Main smooth terms						
s(body length)	**1.99**	**63.26**	**0.003**	0.001	0.00	0.329
s(season)	**6.84**	**9.57**	**<0.001**	**11.41**	**54.34**	**<0.001**
Sex-specific interaction						
s(body length) × female	<0.001	0.00	0.375	**0.99**	**9.51**	**0.049**
s(body length) × male	0.001	0.00	0.634	0.001	0.00	0.739
s(season) × female	**4.78**	**8.34**	**0.031**	**2.68**	**5.50**	**0.027**
s(season) × male	0.001	0.00	**0.015**	0.001	0.00	**0.008**
Age-specific interaction						
ti(body length, season)	32.72	3.75	0.070	**27.11**	**3.43**	**0.002**
R^2 (adj)			0.247			0.21
Deviance explained			43.0%			35.7%
n			8835			8835
fREML			9277.6			11066

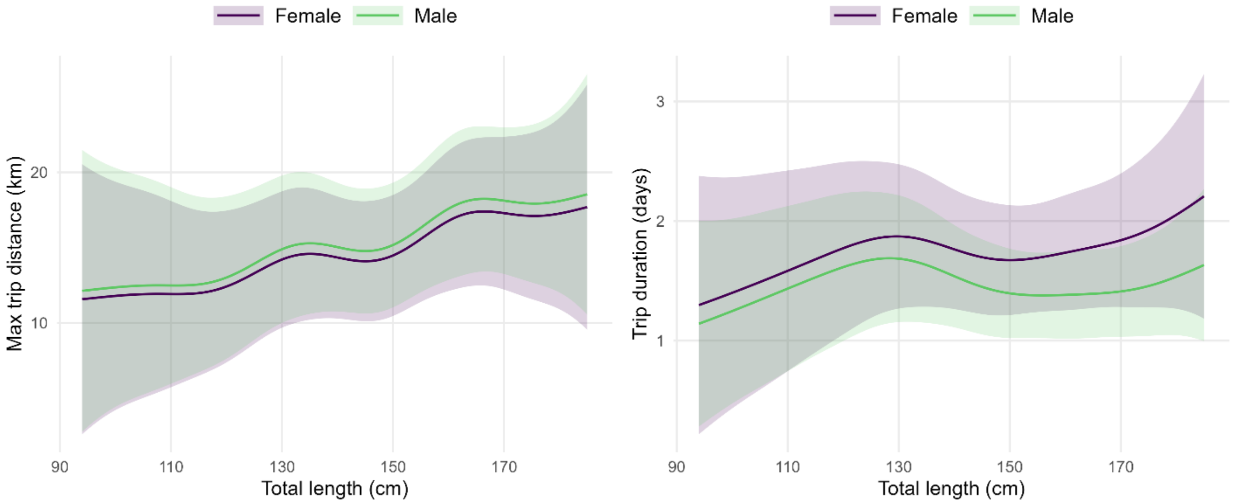

Figure 8. *Predicted maximum distance (in km, left panel) and trip duration (in days, right panel) as a function of total body length (cm) for female and male harbour seals. Lines represent population-level predictions at median season day and year, with shaded bands indicating 95% confidence intervals. The random effect of individual was excluded from predictions.*

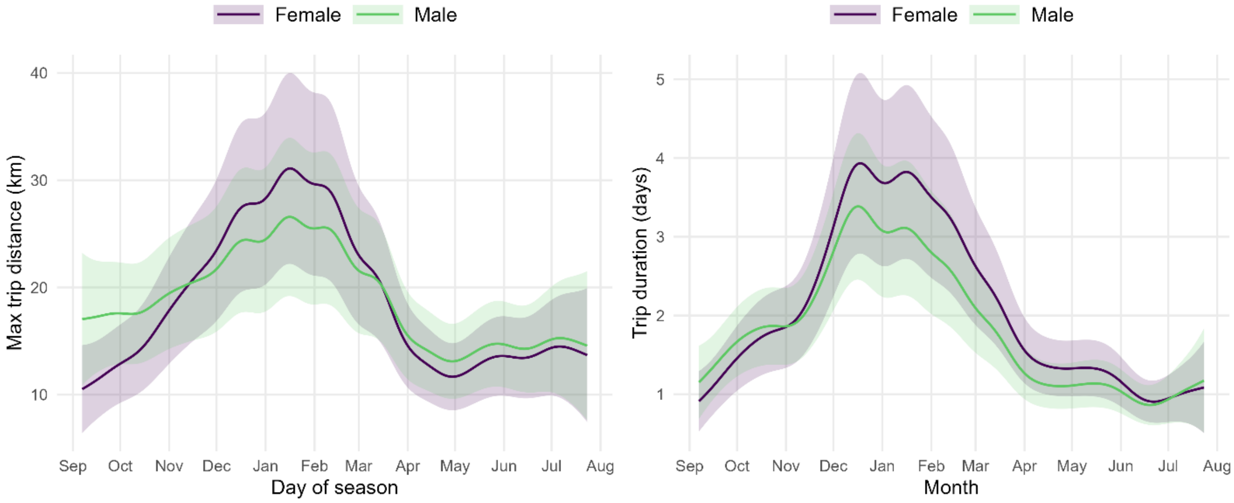

Figure 9. *Predicted maximum distance (in km, left panel) and trip duration (in days, right panel) across the months for female and male harbour seals. Lines represent population-level predictions at median body length and year, with shaded bands indicating 95% confidence intervals. Season starts 1 September.*

Figure 10. *The year random effect on predicted average maximum trip distance (in km, left panel) and trip duration (in days, right panel) averaged over sex, body length, and season. Shaded band indicates 95% confidence interval. The random effect of individual was excluded from predictions. The dashed horizontal line indicates the mean predicted distance or duration across all years. No data were available for 2021–2024.*

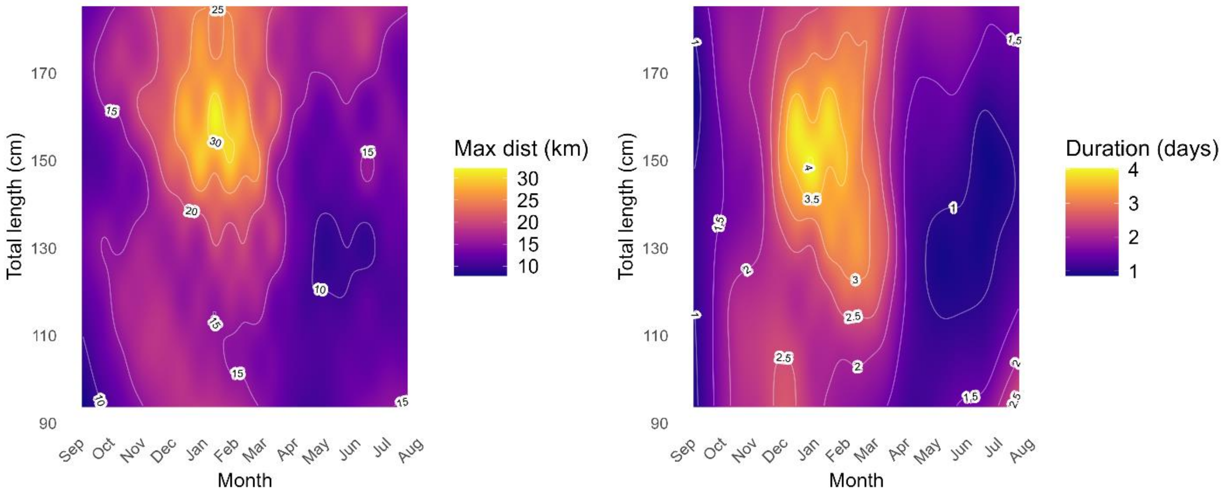

Figure 11. *Predicted average maximum trip distance (in km, left panel) and trip duration (in days, right panel) as a joint function of body length and season, derived from GAM predictions at median year. Contour lines and labels indicate predicted values. Season starts 1 September.*

4.5 Habitat selection model

The spatial distribution of tracked harbour seals reveals large individual variation (see also Figures 2–5). Many tracked seals use well-defined, individual-specific foraging regions to which they regularly return. This regional foraging site fidelity is also reflected in the estimated individual-specific latent fields, which quantifies the residual variation in spatial distribution not explained by the model (Figure 10). A key advantage of these individual-specific latent fields in the model is that they also account for spatial and temporal correlation in the observations.

Variation between individual harbour seals is also apparent from the individual-specific habitat preference estimates derived using factor-level smooths as shown in Figure 13. Nevertheless, population-level selection for specific environmental conditions is apparent. The most important explanatory environmental variable is distance from the haul-out, with seals (as foragers making trips from a central-place/haulout) spending more time closer to haul-out sites. On average, seal density also shows a relationship with depth, with lower densities in deeper (>30 m) regions of the coastal zone. Seals select areas with both high Topographic Position Index (TPI) values (peaks and ridges) and low TPI values (troughs and gullies). They also select areas with low Phi50 values, i.e. coarser sediment types. The Phi50 values represent the -log2 of the median grain size (Bockelmann et al., 2018), where low Phi50 values represent coarser sediment types (i.e. sand and gravely sand) and high Phi50 represent fine sediment (i.e. mud/silt). Finally, seals on average are more often observed at higher values of the “distance ratio”, defined as the ratio between the distance to the nearest haul-out and the distance to the trip haul-out site. The higher prevalence at values close to 1 indicates that seals are more likely to forage within the hinterland of their haul-out site or choose a haul-out site in the vicinity of their feeding grounds. In summary, seals are more likely to be found closer to their haul-out site, in sandy areas with low mud content, near both throughs and ridges and are more likely to forage within their own hinterland. Although harbour seals may occasionally venture into deeper areas, they are generally less observed in areas >30m deep.

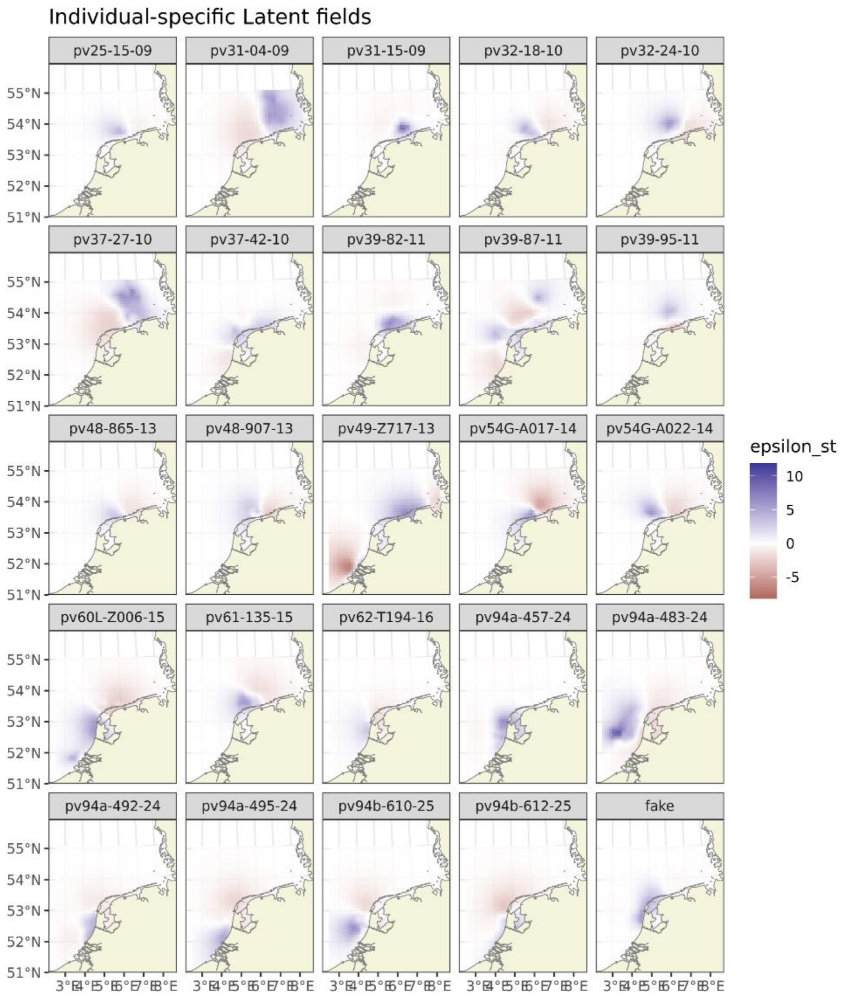

Figure 12. *Examples of individual-specific latent fields from the sdmTMB model, illustrating residual spatial variation in seal distributions that are not explained by the habitat covariates or the shared (global) spatial field. The term* ε_{st} *(epsilon_st) represents this unexplained individual-level variation. Blue areas indicate regions where an individual used the area more than expected based on the model, whereas red areas indicate lower-than-expected use. These patterns highlight differences in space use among individuals that are not captured by the measured environmental variables.*

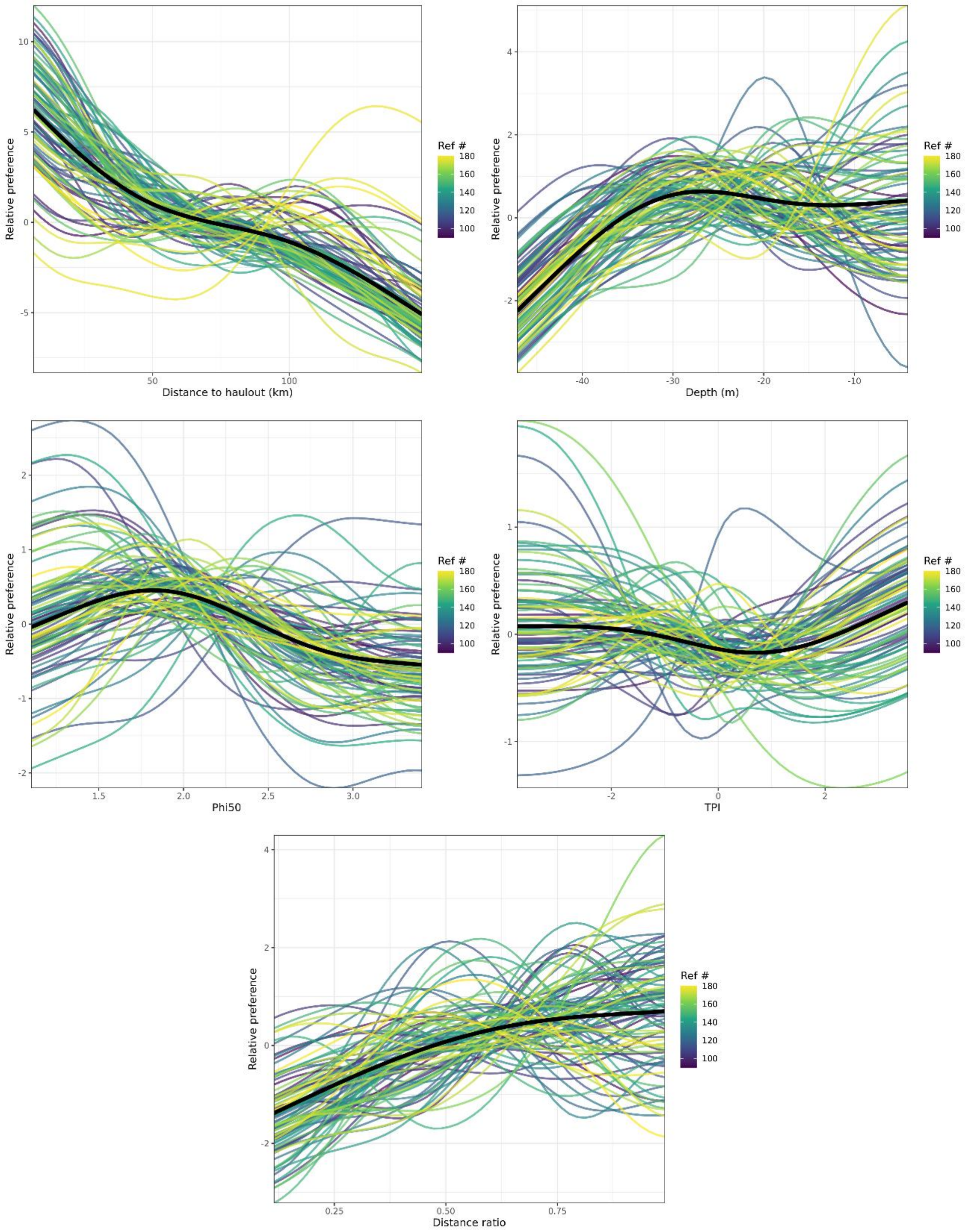

Figure 13. *Relative habitat preference of harbour seals as a function of environmental variables included in the model. Higher values indicate greater use of a habitat relative to its availability. The five environmental variables included in the model: distance to haul-out (top left); depth (top right); Phi50* $(-log_2(median\ grain\ size))$*, where smaller values indicate coarser sediment – centre left), topographic position index TPI (centre right), distance ratio (the distance between the nearest haul-out divided by the distance to the trip haulout – bottom centre). The blue–green–yellow-coloured lines indicate the individual-specific estimates (denoted by Ref #in the legend). The solid black line indicates the average population-level estimate. Harbour seals prefer areas that are closer to their haul-out sites, as illustrated by the negative relationship between habitat preference and distance to the haul-out site (black line in the top-left figure). They generally use deeper waters less relative to their availability, although there is little differentiation in occurrence across depths between 0 and 30 m (black line in the top-right figure). Harbour seals also prefer*

areas with high Phi50 values, indicating a preference for coarser sediment types such as sandy substrates (centre-left figure). In addition, they favour areas with both high and low Topographic Position Index (TPI) values — corresponding to peaks/ridges and troughs/gullies, respectively (centre-right figure). Finally, they prefer areas with a high ratio between the distance to the nearest haul-out site and the distance to the haul-out site from which they departed or to which they returned. This suggests that harbour seals are more likely to remain within their own hinterland and generally avoid foraging within the hinterlands of neighbouring haul-out sites (bottom figure).

The trip analysis revealed seasonal patterns in trip duration, with, on average, longer trips occurring during the winter months (~November–February, see Figure 9). We also attempted to capture this effect in the habitat selection model by including an interaction smooth between distance to the haul-out and day number (with 1 September defined as day 1). Figure 14 shows this interaction effect for each month. Consistent with the trip analysis, the relative preference for more distant areas (>60 km from the haul-out) was strongest during the winter months, with the highest offshore use observed between January and March.
An interaction between distance to the haul-out and animal size (used here as a proxy for age) was also explored in earlier model fits. Those models suggested that smaller individuals (representing 0-year-olds) reveal a flatter response curve beyond approximately 60 km from the haul-out site, indicating that they are more likely to occur further offshore compared to adults. However, because the current iPCOD used in the KEC assessment does not consider age-specific differences, this interaction term between distance to the haul-out and size was not included in the final model.

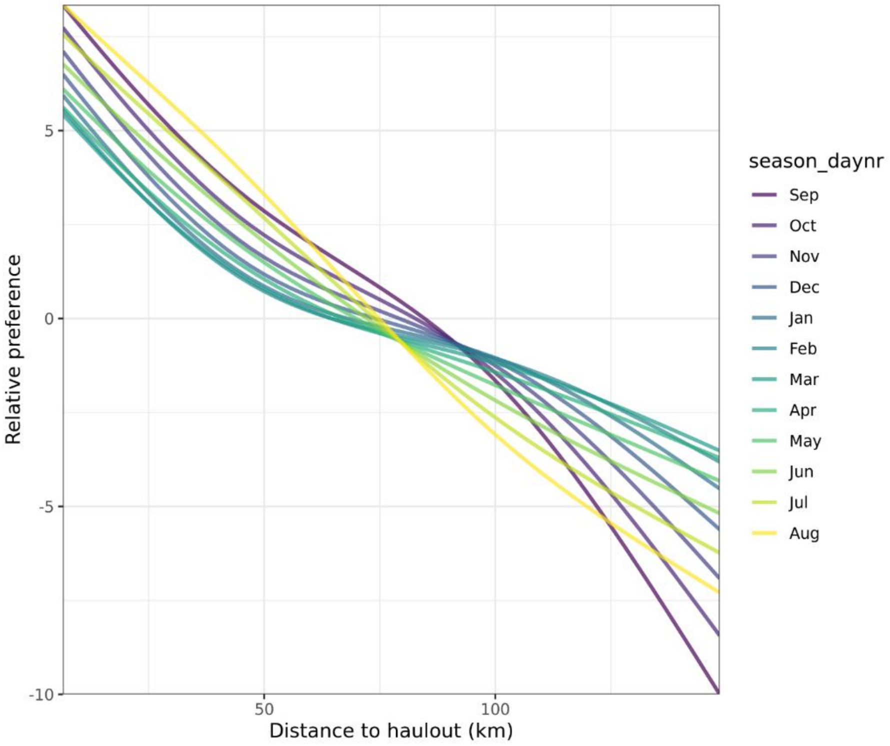

Figure 14. *Seasonal variation per month in relative preference for distance to the haul-out site. Note that very little tracking data are available for July and August; therefore, the estimated curves for these months should be interpreted with caution.*

In addition to the estimated smooth relationships between seal density and the environmental variables included in the model (Figures 13 and 14), and the individual-specific latent fields that capture site fidelity at an individual-level that is not explained by the environmental covariates (Figure 12), there is also evidence for unexplained population-level spatial distribution, as captured by the global latent field (Figure 15, right). In particular, along the central part off the west coast, observed seal density is higher than can be explained by the environmental covariates included in the model (Figure 15, left).

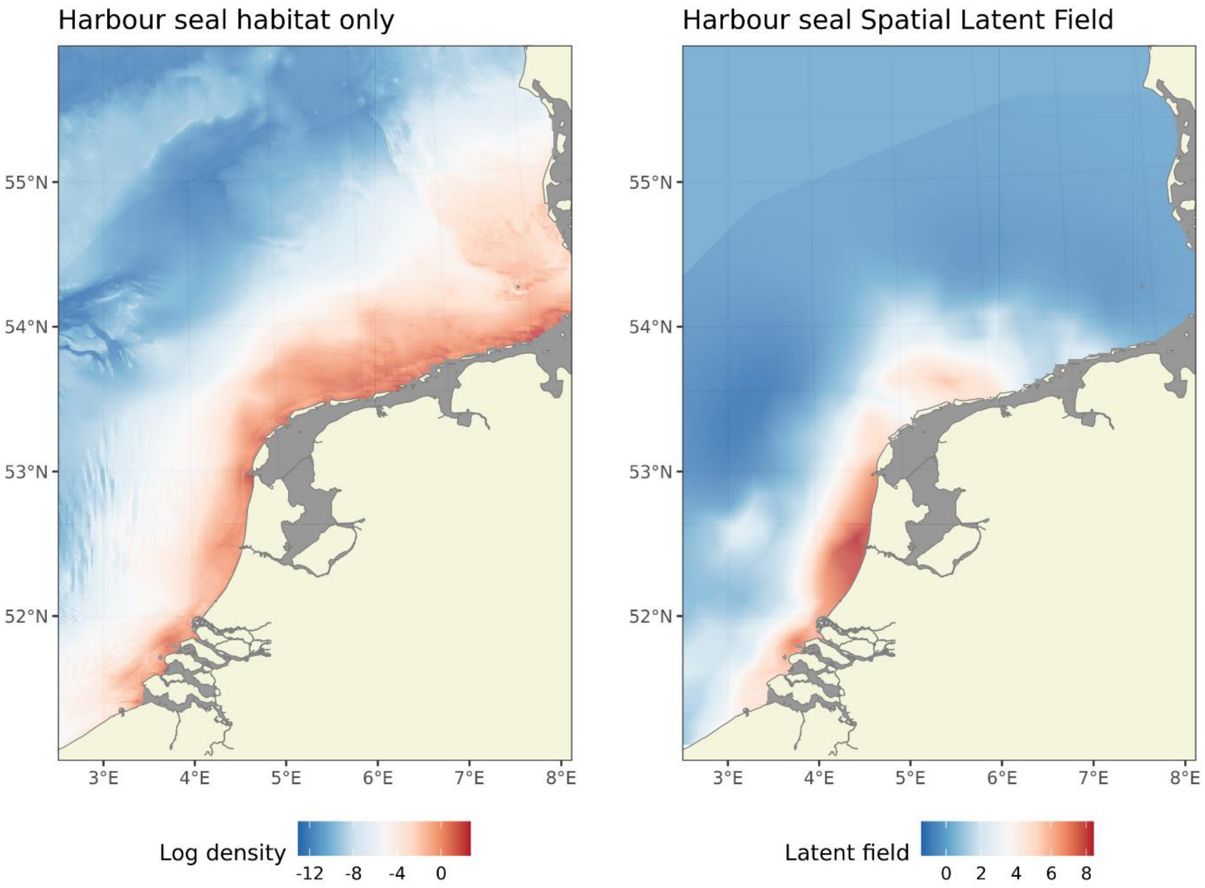

Figure 15. *Spatial distribution of harbour seals illustrated for seals making trips from haul-out sites located in the Delta area, the Dutch Wadden Sea and haul-out sites located in Lower Saxony. Left: The spatial distribution as predicted by the five environmental covariates: distance to the haul-out, depth, topographic position index, sediment grain size and the ratio between the distance to the nearest haulout and distance to trip haulout. This prediction excludes the effect of the global latent field shown on the right. Note the relatively low predicted density in the central part west of the coastal zone of Zuid-Holland and Noord-Holland. Right: Estimated global spatial latent field, capturing the remaining population-level variation in seal density not explained by the environmental covariates included in the model. This term may also provide insight into the influence of unmeasured or omitted environmental drivers not captured by the habitat model.*

4.6 Spatial prediction

The model consists of four components:

1. The average (population-level) relationships between the environmental variables and seal density, represented by the smooth functions (black bold lines in Figure 13).

(2) Individual-level variation around these average relationships, captured by the factor-level smooths (green/yellow lines in Figure 13).
(3) Global latent field capturing population-level spatial structure not explained by the environmental covariates included in the model (Figure 15).
(4) Individual-specific latent field quantifying site fidelity, reflected by spatial clustering of GPS tracking locations (Figure 12).

Individual latent fields were included in the model to account for individual-specific spatial correlation in the tracking data, arising from repeated observations of the same individuals combined with strong site fidelity. Because our objective was to estimate the population-level distribution of seals, the individual latent fields were excluded from the model predictions. To include the effects of the environmental variables on seal distribution, individual predictions were generated based on the estimated response curves shown in Fig. 13. The model was then used to estimate the spatial distribution of seals undertaking foraging trips from each haul-out cluster (see Figures 6 and 7). Figure 16 illustrates the predicted distribution of seals originating from two randomly selected haul-out clusters. According to the model, the spatial patterns are primarily driven by distance to the haul-out, with the highest seal densities occurring in close proximity to the haul-out site.

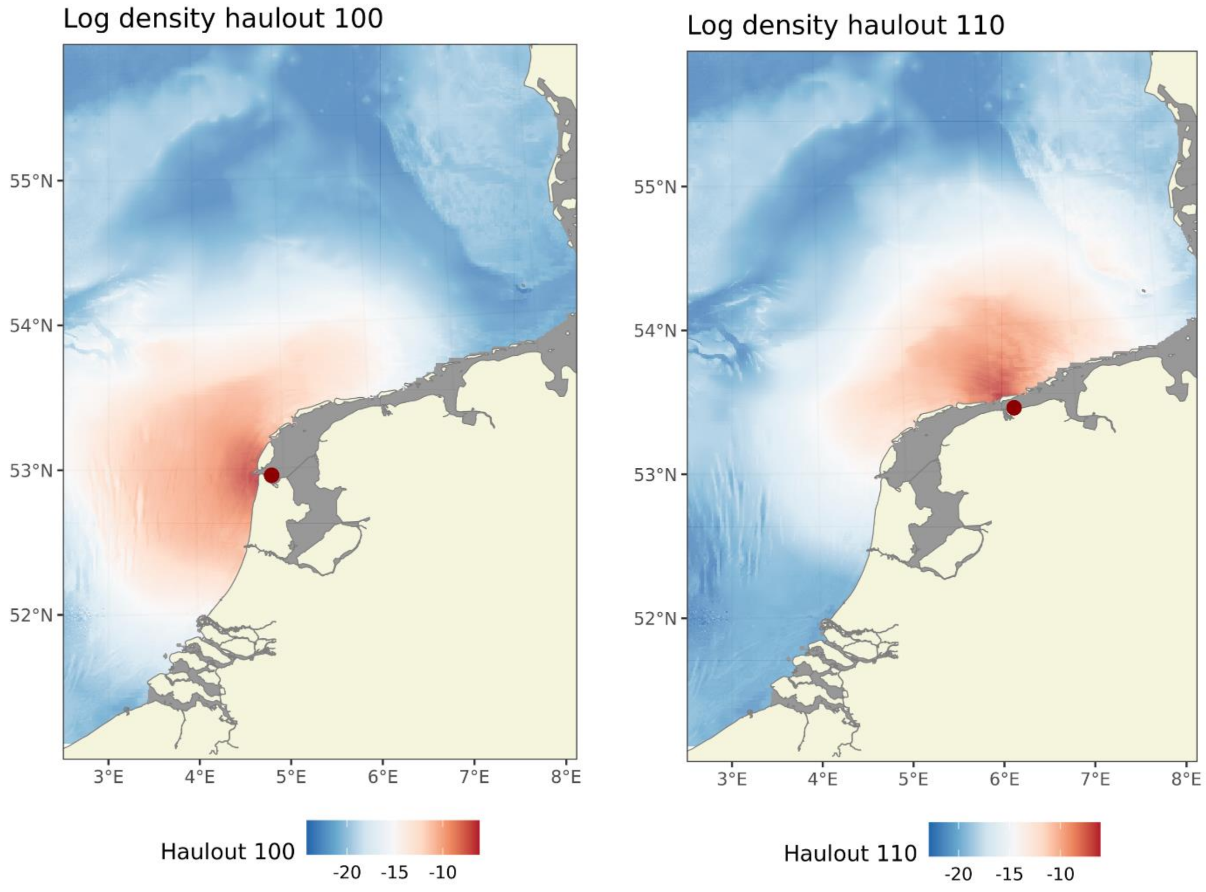

Figure 16. *Spatial distribution of seals associated with two randomly selected haul-out sites. Note that the model was fitted exclusively to tracking data collected in the North Sea after 2013 and excluded GPS fixes located in the Wadden Sea. This was done to maximize predictive accuracy and produce the most robust habitat model for the more westerly North Sea region, where the offshore wind farms whose effects will be assessed in KEC6.0 are located. Consequently, no predictions were generated for the inshore areas such as the Wadden Sea or Dutch delta regions.*

Haul-out-specific predictions of relative densities (integrating to 1 over space) were generated for each site and subsequently scaled to total absolute seal density per km^2 using the average moult counts observed in August at the respective haul-outs. The habitat model, which included an interaction between distance to the haul-out site and time of year, was used to generate predictions for two periods: September, when seals showed the lowest use of far offshore areas (see Fig. 14; hereafter referred to as "summer"), and February, when seals showed the highest use of far offshore areas ("winter"; Figure 17). The proportion of time spent within the Wadden Sea and within 3 km of haul-out sites were used to adjust (down-weight) the predicted seal densities in the Dutch North Sea. A random realization (simulated seals) based on these estimates is shown in Figure 18.

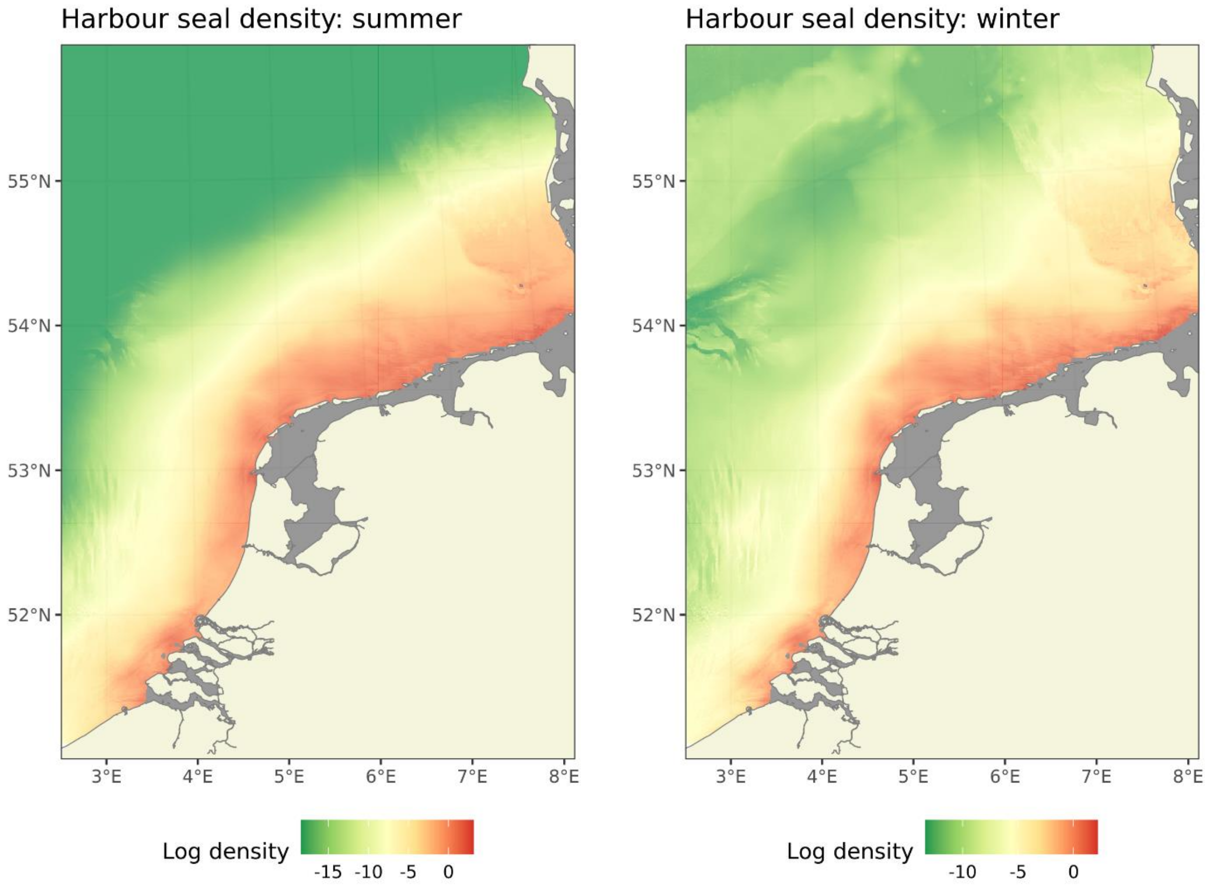

Figure 17. *Predicted absolute abundance of seals in September (**left**; "summer" distribution) and February (**right**; "winter" distribution), based on the number of seals hauled out along the Dutch coasts (Dutch Wadden Sea and Delta region) and Lower Saxony in Germany.*

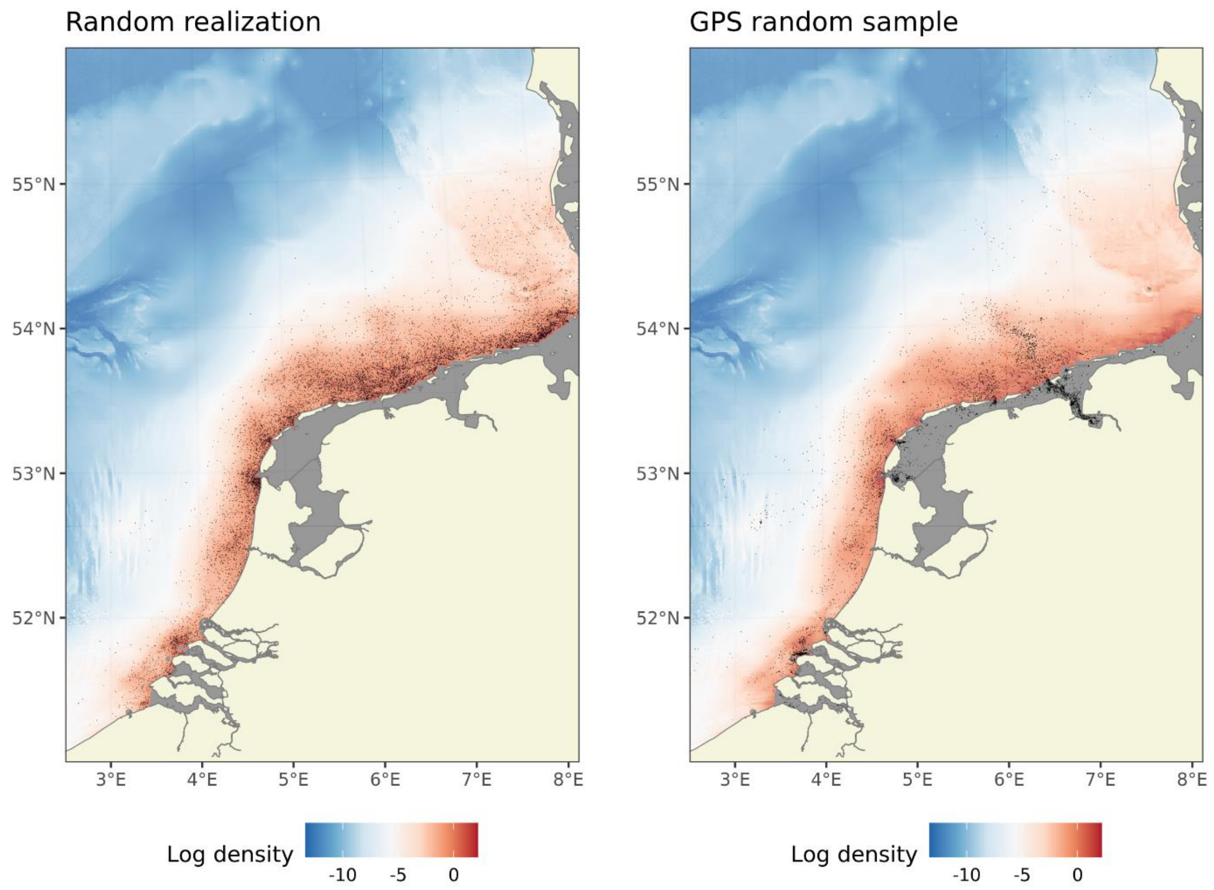

Figure 18. Left: *Example simulated distribution of seals in February based on the habitat model predictions as shown in figure 17. Each black point represents an individual seal. This figure shows only a single simulated realization of the spatial distribution. If one would repeat this simulation (random realization) this would produce a different set of points, although the overall spatial pattern is expected to remain similar.* ***Right:*** *Randomly selected GPS tracking locations with a sample size equal to the simulated population size shown in the left panel. Note that the GPS tracking effort is strongly biased toward certain regions (e.g. the Ems estuary), whereas the simulated seal locations shown on the left are corrected for differences in seal abundance among haul-out sites.*

5 Discussion

5.1 Trip duration and distance

In 2025, a total of 28 harbour seals were equipped with GPS trackers, including ten 0-year-old individuals (Brasseur and Aarts, 2026). A first impression was that young animals would undertake longer trips. However, this pattern was not clearly supported by the model-based analysis. However, this pattern should be interpreted cautiously given that tagging effort was skewed towards younger individuals in more recent years, potentially confounding both the body size and interannual trends in the analysis as shown in Figure 10. The analysis indicates that larger individuals, on average, made longer trips and travelled greater distances from the haul-out, with the relationship being broadly positive across the size range observed. For trip duration (Figure 8), a slight mid-size peak at length of ~130 cm was observed, though the overall trend remained positive. One possible explanation is that older individuals have higher energetic demands due to reproductive activity and greater structural body size resulting in higher overall energy requirements. Previous studies have suggested that partial depletion of prey near the haul-out sites is likely (Aarts et al., 2019; Harding et al., 2018), which could force those individuals with high energy demand to more offshore regions. Because few 0-year-old harbour seals were tracked in previous years, the observations of the young animals are biased towards the latest data (2025). It is therefore not possible to determine conclusively whether this distribution pattern is a recent phenomenon or whether yearlings exhibited a more offshore distribution in the past.

Trip duration showed a pronounced seasonal pattern, peaking in December–January and reaching a minimum in June–July. Season and body size were the primary drivers of both trip distance and trip duration, with females showing a distinct seasonal movement pattern in both metrics. Females travelled greater distances and undertook longer trips than males particularly in midwinter, though this difference was uncertain with broadly overlapping confidence intervals. Harbour seals from the Wadden Sea regularly undertake offshore trips to the North Sea that can cover several hundred kilometres and last for several days to weeks, with haul-out sites used more frequently during key life-cycle events (pupping, lactation, mating, and moulting) between May and September (Brasseur, 2017). The mid-winter peak in trip duration likely reflects increased foraging effort during an energetically demanding period, as individuals may have lost approximately 20–30% of their body weight during the breeding and moulting season and replenish their reserves. Moreover, potentially reduced prey availability (Aarts et al., 2019), particularly in late winter, may require animals to spend more time at sea to meet their daily energy requirements. The minimum in May–July may reflect satiation and behavioural changes associated with the pupping season. Pregnant females in particular, are known to increase haul-out time and reduce at-sea activity in the weeks prior to parturition. Also, the reduction in trip duration during this period could indicate a broader seasonal decrease in foraging effort, as animals approach the energetically less demanding post-winter period. The sex difference in seasonal movement patterns, with females showing longer trip durations and higher distances in midwinter, may reflect the energetic demands of gestation, as female harbour seals are pregnant through winter with foetal growth accelerating in the months preceding pupping. This contrasts with Scottish harbour seals, where trip duration and foraging range were shorter for females (Thompson et al., 1998), suggesting population-specific reproductive strategies may drive the divergence. The interaction between body length and sex was significant only for trip duration in females (Table 2) but non-significant for maximum distance and was near-zero for males across both metrics. Despite this female-specific effect, predicted values for both sexes followed broadly similar trends with overlapping confidence intervals. The overall weak pattern of size-sex interactions further supports the hypothesis that reproductive state, rather than body size, is the primary driver of seasonal differences between sexes.

The interaction between body length and season was marginally non-significant for maximum distance but significant for trip duration (Table 2). In both metrics, peak values were concentrated in medium to larger sized individuals (approximately 145–165 cm) during mid-winter (November–February) (Figure 11). Smaller individuals (sub-adults), show a much less pronounced seasonal pattern, possibly because they do not yet participate in reproductive activities.

The significant interannual random effect in both trip distance and trip duration (Figure 10) suggests the spatial extent of North Sea trips has changed over the study period. In recent times the seals do seem to travel further. This may reflect changes in environmental conditions, which could also be reflected in the observed decline in population size in recent years. However, these trip analysis results should be interpreted with caution, as tagging effort was unevenly distributed across space and time and age classes (e.g. high sampling effort in the Ems estuary during 2009–2012). Consequently, apparent year effects may be confounded with sample size and potentially, spatial effects. The strong individual random effect in both models highlights consistent among-individual differences in foraging behaviour that merit further investigation.

5.2 Habitat selection

The effects of the environmental covariates were broadly consistent with the previous habitat selection study carried out for KEC 4.0. Harbour seals rarely venture far from the coastal zone but tend to remain in relatively shallow waters (~20m) and seal density is on average higher in coarser sandy or gravely habitats. The effect of the topographic position index – indicating that harbour seals may use both elevated features (ridges/peaks) and lower-lying areas (gullies/troughs) – warrants further investigation, particularly with respect to potential seasonal or individual-specific differences.

New findings from the trip analysis were incorporated into the development of the habitat model. For example, the model described in Aarts et al. (2019) and used for KEC 4.0 was extended by including an interaction between distance to the haul-out site and time of year. The estimated seasonal patterns in spatial distribution were consistent with those identified in the trip analysis: seal density was higher in more offshore areas during the winter months.

In alternative model formulations fitted in this study, an interaction between distance to the haul-out and body size was also included as a covariate. This revealed a very weak effect of length, with smaller individuals spending slightly more time in offshore areas. In contrast, the trip analysis did not provide strong evidence that 0-year-old seals undertake longer trips on average. However, inspection of the distribution of trip durations suggests that the smallest individuals are more likely to undertake exceptionally long trips, which warrants further investigation.

One possible explanation for the weak effect of length is the relatively small number of 0-year-old seals included in the dataset (see Brasseur and Aarts, 2026), combined with substantial individual variation in movement patterns, particularly among these young animals. In addition, younger individuals may respond differently to environmental covariates such as water depth. Future model extensions, including alternative factor-level smooths and interactions between body size and environmental variables (e.g. depth or topographic position index), may help explain and account for part of the observed variation among length classes. However, because the iPCOD framework currently used in the KEC does not differentiate between age or size classes, such more complex model formulations were beyond the scope of this study.

5.3 Spatial distribution

The spatial distribution of seals is partly explained by the habitat covariates included in the model, with distance to haul-out sites emerging as the most important predictor. More importantly, however, predicted at-sea seal density is largely driven by the location and number of seals present at haul-out sites. A key limitation to predict at-sea seal density during the winter is the limited number of haul-out counts for harbour seals carried out during these winter months, when foraging activity is most intense. As s proxy for the winter distribution, we collated counts from March and April. However, both the habitat model and the trip analyses indicate that foraging trip distance and duration peak between November and February, well before the March–April count period. Consequently, these counts may not fully reflect the spatial distribution of seals during their primary foraging season. Furthermore, seals are known to redistribute among the Danish, German, and Dutch Wadden Sea regions throughout the season. For example, historic tracking data showed a westward movement after the pupping season and the moult (Brasseur, 2017). Because these observations suggest that seal distribution across haul-out sites in March and April is not necessarily representative of the winter season, and given the lack of comparable winter data from Lower Saxony, the low number of surveys (n = 4), and the high variability between surveys, we decided to use the moult counts for all regions and seasons.

In addition to the habitat model, the individual-level and global latent fields revealed areas of unexplained at-sea usage. The individual latent fields were not incorporated into the model predictions because our primary objective was to estimate the population-level distribution, including regions where only few seals were tracked. However, a potential consequence of excluding the individual latent fields is that some far offshore areas used by individual seals may not be fully captured in the predicted distribution. Although the predicted distribution closely resembled the observed tracking data (Figure 18), use of far offshore areas appeared to be slightly underpredicted, which may partly reflect the omission of the individual latent fields.

The global latent field also identified areas of unexplained at-sea usage, particularly along the central Dutch coast. The reasons why the habitat model does not fully capture seal density in this region remain unclear, although several underlying mechanisms may contribute to this pattern.

First, collinearity between distance to haul-out sites and depth may obscure the true drivers of distribution. In regions north of the Wadden Sea islands – where most tracking data have historically been collected – distance to haul-out sites may partially capture variation that is actually driven by depth, or other factors aligned with depth (including prey distribution and human activities like shipping). This confounding effect could propagate to other regions, including the western Dutch coastal zone.

Second, density-dependent processes such as local prey depletion may explain the mismatch between the habitat model and the tracking data. Areas that are relatively distant from major haul-out sites but still offer high-quality habitat may experience reduced foraging pressure, resulting in higher prey availability and, consequently, might make them more attractive for seals to forage.

Finally, behavioural adaptations may also play a role. Seals in this region may utilize alternative haul-out strategies, such as occasionally hauling-out along the coast at sites that are not regularly used by seals, or remain in the water, thereby reducing the energetic costs associated with long-distance travel to established haul-out sites. Such behaviour could lead to higher-than-expected usage in these areas despite their distance from primary haul-out locations.

5.4 Limitations of distribution maps

The primary purpose of the seal distribution maps presented in this study is to support the KEC in estimating the potential impacts of future offshore wind farm construction on seal populations. However, several limitations should be considered when interpreting and applying these maps.

First, it remains uncertain whether current distribution patterns are already influenced by human activities and whether they will remain representative of future conditions, as most planned wind farms have yet to be constructed. In addition, environmental change, shifts in prey availability, and behavioural adaptations by seals may alter spatial distribution over time, thereby affecting the reliability of current predictions.

Second, the absolute seal density estimates do not explicitly account for the timing of mortality. Although the harbour seal population has stabilized and even declined in recent years, pup production remains substantial, suggesting that a large proportion of pups do not survive. The timing of windfarm construction relative to these mortality events is therefore critical. If harbour seal 0-year-olds primarily die early in summer or autumn, then only a small number of the (remaining) 0-year-olds would be exposed to the construction of offshore wind farm during the following autumn or winter season. Conversely, if substantial mortality would occur later in winter or even early spring, construction activities during this winter period could affect the survival of a larger number of 0-year-olds. Consequently, uncertainty regarding the timing of mortality translates into uncertainty about the size and composition of the population exposed to disturbance.

Finally, the spatial distributions presented here reflect average, instantaneous densities, whereas many anthropogenic activities (such as the pile driving during the construction of offshore wind farm) occur over extended periods (ranging from hours to days). As a result, cumulative exposure may be underestimated when relying solely on static density maps. For example, the current distribution estimates exclude the proportion of time seals spend within the Wadden Sea and near haul-out sites. However, over longer time scales (e.g., daily movements), a substantial proportion of those individuals will move outside these excluded areas and into the North Sea, thereby increasing their likelihood of exposure to human activities considered within the KEC framework. One potential approach to address this limitation is the development of an individual-based movement model (IBM), informed by observed habitat preferences. Such an IBM would allow the simulation of movements of individual seals within the population, enabling estimates of where, how often, and for how long individuals are exposed to disturbance. It would also make it possible to distinguish between scenarios in which many individuals experience occasional exposure to human disturbance and those in which a smaller number of individuals are exposed repeatedly. The IBM could also be used to evaluate how reduced foraging opportunities, potentially combined with increased energetic costs of swimming, affect individual energy reserves and consequently influence starvation risk, survival, and reproductive output. In addition, such an approach could incorporate multiple natural and anthropogenic stressors, thereby providing more realistic estimates of cumulative exposure to anthropogenic disturbance.

5.5 Future extensions

This study contained two main components: a trip analysis and a habitat selection analysis used to generate spatial distribution maps. Although the trip analysis identified several variables that explain variation in trip duration and distance to the haul-out, the model explained only 36 and 43% of the variance, respectively, indicating that a large proportion of the observed variation remains unexplained. Future work could explore more complex model structures to explain the large variation in trip duration and distance. For example, while sex was included as a predictor, its effect is likely more complex than currently assumed. Males and females may exhibit age-specific (approximated by body length) and seasonal differences in trip characteristics, which would require higher-order interaction terms, and such relationships may vary between years, potentially driven by interannual variability in prey availability. In years of high food abundance, more experienced individuals may undertake shorter trips or return earlier, increasing their use of the Wadden Sea for resting after satiation. Incorporating proxies for prey availability (e.g. fish survey data), as well as the spatial location of tracked individuals, could improve future analyses.

An additional open question is whether harbour seal behaviour has changed since the decline in population counts observed from 2022 onwards, potentially in response to shifts in prey availability, intra- and interspecific competition, or broader environmental changes, including increasing human activity. Although the trip analysis suggests interannual variation that could be reflecting changes in the factors named above, this perceived change may be confounded by spatial differences in tagging effort. For instance, a large proportion of individuals (n = 142) were tagged in the Ems estuary in the eastern Dutch Wadden Sea, whereas more recent tagging has primarily occurred in the western Wadden Sea and Delta region. Moreover, there is a substantial temporal gap between earlier tagging efforts and the most recent deployments in 2025. Future studies would benefit from more consistent spatial and temporal tracking effort, alongside more flexible modelling approaches, to better detect potential trend-like changes.

Finally, this study focused on harbour seals, as no new tracking data were available for grey seals. For harbour seals, additional data were incorporated, and several methodological improvements were implemented, most notably the inclusion of individual-level and global latent fields. The global latent field in particular, captured elevated use (relative to habitat model predictions) along the west coast of the Dutch mainland, a pattern not explained by environmental covariates alone. This is a key region for existing and planned offshore wind farm development, and previous habitat models that excluded such latent structure likely underestimated seal use in this area. Applying a similar approach to grey seals may also have been valuable. In addition, the grey seal numbers using the Dutch waters have increased considerably, as a consequence, higher absolute number of animals could potentially be affected by future human activities.

6 Acknowledgements

We thank our national and international collaborators who kindly provided the aerial survey count data: Anders Galatius (DK), Armin Jeß (SH), Christian Abel (LS), Ole Stejskal (LS), Jens Brackmann (LS), Floor Arts (ZE) and Mark Hoekstein (ZE). The following crew assisted in seal tagging (alphabetic order): Bakker Arnold, Baptist Martin, Boersma Eelke, Booij Peggy, Bos Oscar, Bravo Rebolledo Elisa, Chris Veenstra, Cornelisse Suzanne, Cremer Jenny, Dankers, Norbert, de Jong Martin, de Vries Simon, de Wal Freek-Jan, Dijkstra Arjen, Dijkstra Eelke Sybren, Jol Johan, Kirkwood Roger, Klaas Kreuijer, Koelemij Erica, Laros Nico, Leeuwen van Piet Wim, Meerstra Bert, Meesters Erik, Meijboom Andre, Noort Bart, Perdon Jack, Pool Chris, van der Wal Nanneke, Reijnders Peter, Sonneveld Cor, Wouter Suykerbuyk, Tamara van Polanen Petel, Jan van Dijk, Ad van Gool, Maarten Hoppe, van Leeuwen Piet-Wim, Vrooman Jip, van Zweeden Carola, Verdaat Hans. The Dutch Ministry of Agriculture, Fisheries, Food Security and Nature (LVVN), Groningen Sea Port, Eneco, Gemini windpark, Borssele windpark, and RWS funded the seal GPS transmitters. LVVN funded the aerial surveys in the Wadden Sea, and we thank the pilots, particularly Aad Droge. Amber Jägers and Marieke Stuijt have been instrumental as project managers for this project. We thank Maarten Mouissie and particularly Eleni Melis for a very detailed and constructive review. We thank Martine Graafland and Marije Siemensma for their constructive comments. Finally, we would like to thank RWS (Wozep program) for funding this research.

Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system, certified since February 27, 2001, by DNV. ISO 9001 is an international standard for quality management, focused on the continuous improvement of processes and ensuring customer satisfaction.

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Justification

Report C048/26
Project Number: 4315100272

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

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Annex 1 Methods

In this Annex, we describe the methods used to carry out the analyses. Disclaimer: Parts of the methodology from previous study (Aarts et al., 2025) have been copied and modified for inclusion here. All analysis was carried out in R (R Core Team, 2026)

A1.1 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. 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 harbour seals tagged in the Ems estuary, between 2009 and 2011. GPS tagging generally took place in March (n = 123) and September (n = 104), and most GPS location data were collected during the first months following tagging. In 2025, an additional 28 harbour seals (six in March and 22 in October/November) were tracked. These data include a relatively high proportion of 0-year-olds (10 individuals). Further details are provided in Brasseur & Aarts (2026).

The seals were caught on the haul-out sites 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, 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). Dive records included maximum dive depth, dive duration, and surface interval duration. The most recent transmitters, deployed in 2025 and on seals released from captivity in 2020 and 2022, were also equipped with a tri-axial accelerometer, enabling the detecting of prey capture attempts and dive pitch. Locations, dive, haul-out, summary and accelerometry 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.

A1.2 Aerial and boat-based haul-out counts.

In the international Wadden Sea bordering the Netherlands, Germany (Lower Saxony and Schleswig-Holstein) and Denmark, multiple annual aerial surveys were conducted to count harbour and grey seals, (Brasseur et al., 2015, 2018; Reijnders et al., 1997). For both species, five aerial surveys were carried out each year, three during pupping periods (Jun. – Jul. for harbour seals; Nov. – Jan. for grey seals) and two during moulting period (Aug. for harbour seals; Mar. – Apr. for grey seals). In the Dutch Delta area aerial surveys were conducted monthly, except for September and October. The Grevelingen area was monitored by boat (Hoekstein et al., 2024).

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. Since 2000, all observed seals were photographed, from which animals were counted at the species level, with pups distinguished from adults where possible.

For spatial predictions of seals at sea, we used average harbour seal counts collected between 2000-2025, during the harbour seal moult season in August. Harbour seals are typically more widely distributed across numerous haul out sites, while grey seals tend to concentrate on fewer, higher-elevation sites, mostly in the western part of the Wadden Sea. Therefore, the focal grey seal moult surveys may not include all harbour seal haul-out sites. For the March/April survey, only the surveys covering at least 90% of the known harbour seal haul outs were selected and presented in figure 7 (but not used for spatial prediction).

A1.3 Telemetry data pre-processing and trip definition

First, we only selected tracking data within the deployment data. For example, during the deployment period seal tags may fall off on land – particularly during the moult period – and may continue to transmit. Those tracking data need to be removed. To achieve this, we identified the first and last valid dive for each individual, defined as a dive exceeding 5 m but shallower than 100 m. The upper threshold (100m) excluded occasional erroneous extreme dive records, likely associated with tag testing. Only GPS and haul-out data occurring between these first and last valid dives were retained. Additionally, the first three days of tracking data were removed to account for potential post-tagging behavioural disturbances.

We then refined haul-out location estimates, which are originally calculated based on interpolation of the GPS locations. For each haul-out event, the location was recalculated as the mean position of all GPS fixes recorded during that event. In cases where no GPS fixes were obtained during a haul-out event, we implemented a two-step procedure. First, we defined "true" haul-out locations as events lasting at least three hours and containing at least one GPS fix. Next, for haul-out events lacking GPS data, the nearest GPS fix (either preceding or following the event) was linked to the nearest true haul-out location, and the coordinates of that true location were assigned to the event. This approach minimized the loss of haul-out events in subsequent filtering steps.

To remove erroneous haul-out events caused by seals resting at the water surface, we applied a spatial filter using on the EMODnet bathymetry. All grid cells with an elevation higher than −3 m (encompassing intertidal areas) were classified as potential land. 'Haul-out events' located more than 1 km from any such land cell were considered at-sea resting events during which seals keep their heads above water for prolonged periods and were excluded.

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 GPS location at sea was linked to the corresponding start and end haul-out in the following manner. The GPS and wet-dry sensor on the tag recorded 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. For all GPS locations it was then possible to estimate the start and end time and location of a trip. As seals rarely return to exactly the same resting location, most trips were transitory, with differing start and end haul-out sites. Therefore, GPS locations occurring before the temporal midpoint of a trip were assigned to the start haul-out, and those after the midpoint to the end haul-out.

Finally, to reduce data volume and improve temporal regularity, we subsampled the tracking data. Although GPS fixes could occur every 10–20 minutes, intervals could extend to several hours when stayed at the surface only briefly. For each individual, a regular sequence of two-hour time points was generated across the deployment period, and only the GPS fixes closest in time to these points were retained. This approach reduced data volume while preserving the overall temporal structure of movements, preferentially retaining less frequent observations and removing clusters of closely spaced GPS fixes.

A1.4 Explanatory environmental variables used for habitat modelling

Harbour seals are central-place foragers, feeding predominantly near the bottom on benthic prey species. Studies have shown that harbour 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 (percentage mud) were used (see sections 10.4.1 – 10.4.5 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.

A1.4.1 Distance to haul-out

Foraging sites closer to haul-out sites are more easily accessible to the seals. Even if they select areas further offshore to forage, they always must cross the intermediate areas between the haul-out and foraging sites. 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 every 1km) further 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 (method = "average") and cutree (both R package = stats), 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.

A1.4.2 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 the distance to the seal's trip haul-out for each cell in space 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.

A1.4.3 Sediment

To describe sediment type in this study, we used the Phi50 values representing the -log2 of the median grain size (Bockelmann et al., 2018), where low Phi50 values represent coarser sediment types (i.e. sand and gravely sand) and high Phi50 represent fine sediment (i.e. mud/silt) (Figure A1). 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).

A1.4.4 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 (Figure A1). 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.

A1.4.5 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.

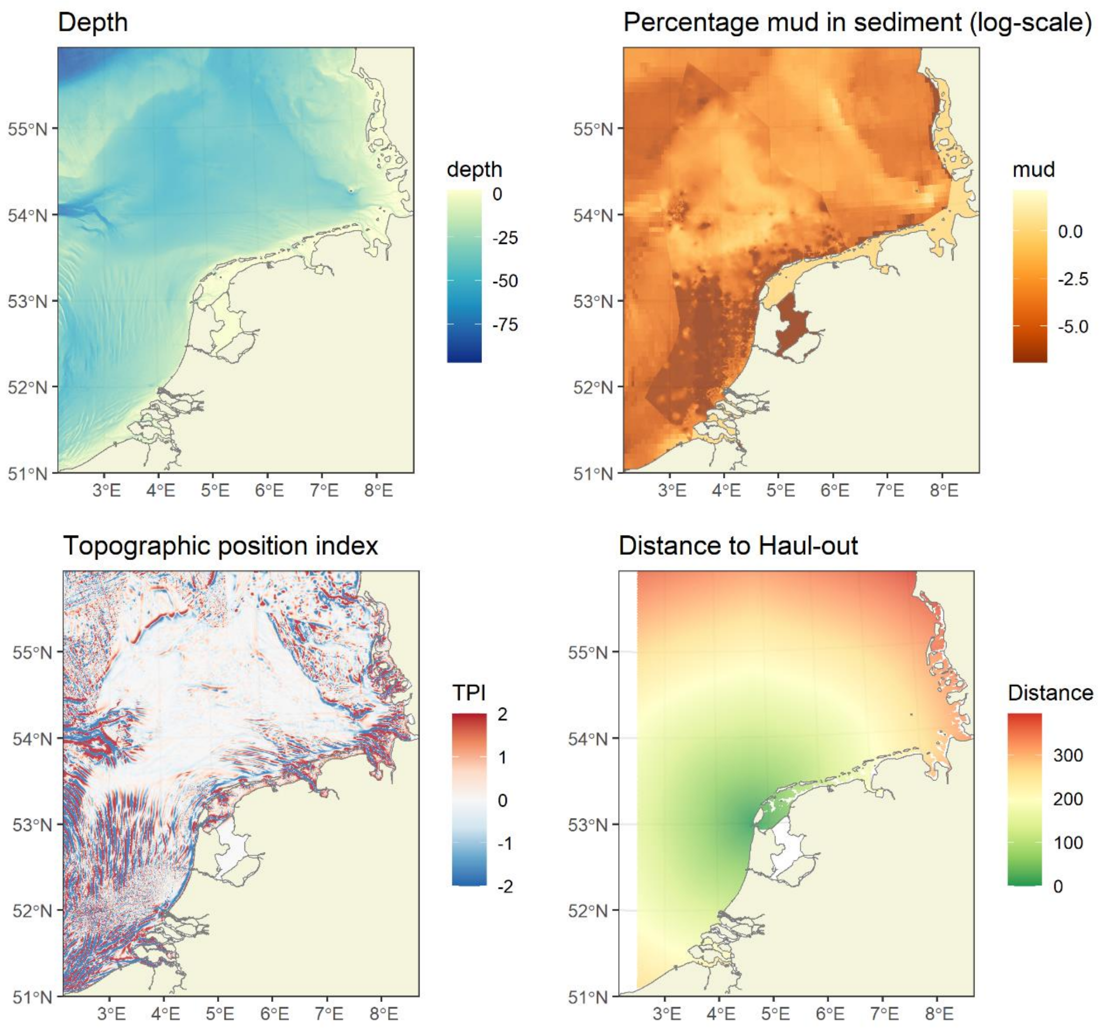

Figure A1. *Maps of the explanatory variable depth (m), percentage mud in the sediment, topographic position index, and distance to one haul-out location (km) (here Razende Bol, the sand bank between Den Helder and Texel as an example).*

A1.5 Trip analysis

Preliminary observations suggest that, compared to previous years, some of the seals tagged in 2025 exhibit distinct movement patterns. Some individuals appear to undertake longer trips, extending far into the North Sea, whereas others make intensive use of the Wadden Sea, remaining at sea for prolonged periods without hauling out. Additionally, two individuals have been observed using the North Sea mainland coast as haul-out sites. This analysis aims to determine whether the foraging trips of recently tagged seals differ significantly from those observed in earlier tagging efforts. To this end, statistical models will be developed to assess variation in trip duration and distance as a function of year, season, sex, and age. This preliminary step is essential, as it informs the structure of the subsequent habitat model, particularly with respect to the inclusion of seasonal and interannual effects.

Harbour seal trip duration and maximum trip distance were modelled as a function of individual, day of year, body length, and year using a Generalised Additive Mixed Modelling (GAMM) framework, implemented in the R package mgcv (S. Wood, 2017).

In preliminary analyses, we considered both Gamma and Tweedie error distributions for each response variable. The Tweedie distribution was initially favoured as it accommodates non-negative continuous data, however the estimated Tweedie power parameter consistently approached 2 across model iterations, indicating that a Gamma distribution with a log link was the more appropriate and parsimonious choice for both response variables.

The full model structure was determined a priori based on biological knowledge rather than purely data-driven selection, following recommendations for ecologically motivated inference (Burnham & Anderson, 2002; Zuur et al., 2009). Candidate terms were retained if they had clear mechanistic justification and showed no signs of overfitting. Models were fitted using the bam() function in the R package mgcv (S. N. Wood et al., 2017) with fREML for smoothing parameter selection and computational efficiency. Given the computational demands of the dataset but even more so model complexity (i.e. including various tensor interactions), models were not compared via AIC under ML estimation. Instead, model adequacy was assessed through residual diagnostics, inspection of effective degrees of freedom for each smooth term, and concurvity checks. An additional shrinkage penalty was applied to all smooth terms (select = TRUE), allowing terms with negligible explanatory power to be penalised effectively to zero, providing automatic term selection within the model fitting procedure. Basis dimensions (k) were selected to be sufficiently large to avoid constraining the smooths, verified using the k-index diagnostic in the function gam.check (S. Wood, 2017).

The structure of the explanatory variables in the model was specified as follows: Individual was included as a random effect (bs = "re") to account for repeated measurements on the same individual. Day of year was included as a continuous smooth term (bs = "tp") to capture seasonal variation in foraging behaviour. A tensor product interaction term between body length and day of year was included to test whether the effect of body size on trip duration varied across seasons. Body length was retained as an independent smooth term. Year was included as a random effect in the full model to account for interannual variation in sampling effort and individual composition between cohort groups.

The full model included sex-specific smooths for body length and season, allowing the shape of these relationships to differ between sexes while retaining a shared tensor product interaction. All smooths used thin plate regression splines unless otherwise specified.

A1.6 Habitat Association Analysis

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, 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 SHA model $w(X)$.

To approximate the integral of the IPP likelihood, increasing the number of availability points per GPS location improves the precision of the estimate. However, a large number of points also increases computational cost. Therefore, the number and placement of availability points should balance computational efficiency with accurate approximation of the IPP likelihood. This can be achieved by allocating availability points more densely in areas that are heavily used by harbour seals, while still ensuring sufficient coverage in less frequently used regions. Including points in these low-use areas is important to represent rare habitats and to avoid excessively large quadrature weights. To address this, we use a mixture sampling design. One set of availability points are sampled based on the following the sampling probability $\rho(s)$:

$$\rho(s) = \lambda(s)^{1/2}$$

Here, λ is a kernel density estimate (bandwidth σ = 10km) of the telemetry locations for each individual. In total we selected for each individual seal $200 + 10N_i^{1/2}$ availability points from the kernel density, where N is the number of GPS locations for that seal. Because λ can be extremely large in high-use regions, potentially leading to an excessive number of availability points, we apply a stratified sampling approach based on a 200 × 200 m grid, selecting only the centre point of each grid cell once. To represent availability elsewhere, a 10 x 10 km grid was constructed, and one availability point was generated within each grid cell. The quadrature weights q_n are defined as the areas of the corresponding Voronoi, which are estimated as the total area of grid cells closest to each availability point.

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). The product of the observation specific weight factors (i.e. quadrature weights q and time-interval weights r) was included as model weights for the availability points and the time-interval weights were included as model weights for the used/telemetry points.

A1.7 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.

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

The simplest form of the linear predictor is to assume that it is a linear function of the environmental variables x1 – xJ. 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.

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

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

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

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 50 km 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 using the function sdmTMB of the sdmTMB package (Anderson et al., 2024). 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 percentage 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").

A1.8 Habitat-based prediction of distribution at sea

The habitat model fitted to tracking data was used to predict the expected distribution of an individual seal undertaking a foraging trip from a haul-out site. To estimate the distribution of the entire at-sea population, these individual-level predictions were scaled using counts of seals observed at haul-out sites. These haul-out sites in intertidal areas are not always clearly defined. Depending on tidal conditions and weather (e.g. wind direction and speed), seals may use different edges of sandbanks for hauling out. In addition, aerial surveys record the position of the survey aircraft rather than the exact locations of individual seals. To group observed seals into haul-out clusters, and to reduce computational time, hierarchical clustering was applied to the pairwise distances between all observations (photographs for the Dutch Wadden Sea data and aggregated counts for other regions). Similar to the clustering of haul-out sites applied on the seal tracking data, clustering was performed using the hclust function (method = "average") followed by cutree, applying a cut-off distance of 10 km. Subsequently, the species-habitat association (SHA) model, including distance to the haul-out cluster as a covariate, was used to predict space use for each haul-out cluster across the study area. These haul-out-specific usage estimates were then scaled by the corresponding haul-out counts.

To estimate absolute abundance, two additional adjustments were applied. First, not all seals are hauled out during aerial surveys, meaning that counts represent only a fraction of the total population. To account for this, the average moult counts were divided by a haul-out probability of 0.68 (as estimated by (Ries et al., 1998), ensuring that predicted distributions represented the total population size.

Second, the SHA model was developed for offshore North Sea conditions and was fitted using tracking data that excluded the Wadden Sea and areas within 3 km of haul-out sites. To account for this in the predictions, we calculated, for each month, the proportion of time seals spent in the North Sea outside the excluded areas and used this to adjust the predicted distributions accordingly.

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