Inter-Research Science Publisher
Marine Ecology Progress Series
Volume 792:meps15206
Published August 20, 2026
https://doi.org/10.3354/meps15206



# Habitat suitability and distribution of harbour and grey seals in the Baltic Sea region

**Anders Galatius[1,✉], Jonas Teilmann[1], Markus P. Ahola[2,3], Anja M. Carlsson[2], Rune Dietz[1], Carla Freitas[4], Inari Helle[5], Ivar Jüssi[6], Mart Jüssi[6,7], Mervi Kunnasranta[8,9], Morten Tange Olsen[1,10], Jacob Carstensen[1], Floris M. van Beest[1,✉]**

[1]Marine Mammal Research, Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
[2]Department of Population Analysis and Monitoring, Swedish Museum of Natural History, 10405 Stockholm, Sweden
[3]Marine Environment Research Group, Turku University of Applied Sciences, 20520 Turku, Finland
[4]Institute of Marine Research, Flødevigen Research Station, 4817 His, Norway
[5]Natural Resources Institute Finland, 00790 Helsinki, Finland
[6]Pro Mare, Vintriku, 75121 Kose, Estonia
[7]Institute of Ecology and Earth Sciences, University of Tartu, 50409 Tartu, Estonia
[8]University of Eastern Finland, Department of Environmental and Biological Sciences, 80100 Joensuu, Finland
[9]Natural Resources Institute Finland, 80100 Joensuu, Finland
[10]Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, 1353 Copenhagen K, Denmark

ABSTRACT: The Baltic Sea region is impacted by pollution, noise, offshore construction, shipping, fisheries, eutrophication and climate change. Seals are important top predators here, but little is known about their at-sea distribution. Using satellite telemetry data from 90 harbour seals *Phoca vitulina* and 65 grey seals *Halichoerus grypus* together with haulout counts, we modelled habitat suitability and relative population densities across the region. We used generalized additive mixed models (GAMMs), incorporating a range of static and dynamic environmental variables. Habitat suitability of both species was positively related to proximity to haulouts, explaining 25–30% of the total deviance. Other important variables, explaining 2.5–6% of the deviance in habitat suitability, were increased wave exposure and colder sea surface temperature for harbour seals and wave exposure and higher sea bottom oxygen saturation for grey seals. Harbour seals showed a preference for more coastal habitats than grey seals. The analyses revealed an imbalance between habitat suitability and actual distribution, particularly for grey seals, where some areas with high suitability had low seal densities. This likely reflects the dramatic population fluctuations of seals in the area over recent centuries related to hunting and pollution. Overlap of suitable habitats between the species in the southern and western Baltic indicates interspecific competition that will likely increase as grey seals recolonise their previous range. Our study constitutes the first comprehensive analysis of seal distribution in the Baltic area and is a valuable tool for managers and ecologists assessing pressures and ecosystem interactions in an area where anthropogenic activities are increasing.

KEY WORDS: Central place forager · Density maps · Interspecific competition · Pinniped · Species distribution model · SDM · Satellite tracking · *Phoca vitulina* · *Halichoerus grypus*

## 1. INTRODUCTION

Coastal marine habitats around the world are affected by pollution (Sonne et al. 2020), offshore construction and shipping (Duarte et al. 2021), fisheries (Jackson et al. 2001), eutrophication (Maúre et al. 2021) and climate change (Meier et al. 2022). Marine apex predators are often used as indicators for ecosystem health as they are affected by changes at lower trophic levels and shape ecosystems by top-down regulation (Moore 2008, Hazen et al. 2019). Their distribution provides valuable information regarding interactions with other ecosystem components in time and space.

✉Corresponding authors: agj@ecos.au.dk, flbe@ecos.au.dk



Publisher: Inter-Research · www.int-res.com

Four marine mammals inhabit the Baltic Sea ecosystem: harbour porpoise *Phocoena phocoena*, ringed seal *Pusa hispida*, harbour seal *Phoca vitulina* and grey seal *Halichoerus grypus*. The semi-enclosed nature of the Baltic Sea means that pollutants and other anthropogenic impacts accumulate, leading to drastic environmental effects (Reusch et al. 2018). In the past century, all 4 species have undergone substantial declines in abundance due to overhunting, reproductive deficiencies caused by pollutants, bycatch in fishery, overfishing and eutrophication leading to food web disruption (Heide-Jørgensen & Härkönen 1988, Harding & Härkönen 1999, Kokko et al. 1999, HELCOM 2009, Olsen et al. 2018, Dietz et al. 2026).

At-sea distribution of marine predators is heavily impacted by prey distribution (Benoit-Bird et al. 2013, Bennington et al. 2020). Both grey and harbour seals are piscivores and opportunistic foragers, adapting their diet to locally and temporarily available species (Wilson & Hammond 2016, Scharff-Olsen et al. 2019, Kappa et al. 2026). Distributions of fish are governed by a range of geophysical and biological factors, such as depth, fronts, currents, stratification and salinity, as well as human impacts from fisheries, offshore construction, dredging, sand extraction and pollution (Nian et al. 2021, Perelman et al. 2023, Gordó-Vilaseca et al. 2024, Rosciszewski-Dodgson & Cirella 2024). Species' responses to environmental variability are often approximated through species distribution models (SDMs), used in ecology and conservation for assessing habitat suitability (Elith & Leathwick 2009, Guisan et al. 2013). Conceptually rooted in ecological niche theory (Guisan & Zimmermann 2000), SDMs are statistical techniques aimed at identifying the environmental conditions that species use and rely on for their ecological requirements, which are extrapolated to the surface area of interest (Peterson et al. 2011).

Harbour and grey seals are important predators in temperate and subarctic coastal and shelf waters of the North Atlantic (Hall & Russell 2018, Teilmann & Galatius 2018). In the Baltic Sea region, harbour seals range from the Skagerrak in the northwest, through the Kattegat and the Danish Straits to the southwestern Baltic, with genetically distinct populations in the Skagerrak, Kattegat, southwestern Baltic and around Kalmarsund in the central Baltic Sea (see Fig. 1 for place names) (Goodman 1998, Olsen et al. 2014). Grey seals range throughout the Baltic area; although in the southern Baltic Sea, Danish Straits and Kattegat, densities are low, as they have only recently started recolonising after local extinctions in the early 20$^{th}$ century (Galatius et al. 2020, 2024b). All grey seal colonies in the Baltic Sea are connected by gene flow but are genetically distinct from grey seals in the North Sea (McCarthy et al. 2025).

Grey and harbour seals may compete for space and resources. In areas where prey composition has been analysed, there are considerable dietary overlaps (Wilson & Hammond 2016, Scharff-Olsen et al. 2019). In addition, investigations have shown substantial overlap in habitat use (Thompson et al. 1996, Jones et al. 2013), also close to shore (McConnell et al. 1999, Dietz et al. 2003, Cordes et al. 2011). In Orkney, Shetland and the Firth of Tay in Scotland, recovery of grey seal populations has coincided with abundance declines of harbour seals, although no direct link has been established (SCOS 2014). Similar dynamics have occurred in the western North Atlantic (Hammill et al. 2010).

Information on seal distribution in the larger Baltic Sea region is available from monitoring programmes, where seals are counted at their haulouts during the moulting season and in some areas also during the pupping season (Galatius et al. 2014). This information is limited to haulout distribution and only pertains to these specific periods of the annual cycle. There have been local investigations of seal distribution based on satellite telemetry (e.g. Sjöberg & Ball 2000, Dietz et al. 2013, Oksanen et al. 2014, van Beest et al. 2022), but knowledge regarding pan-Baltic at-sea distributions is lacking. This also prevents comparisons with grey and harbour seal at-sea distributions in the neighboring North Sea region (Carter et al. 2022, 2026).

Both harbour and grey seals are listed under Annexes II and V of the European Union's Habitats Directive, meaning that special areas of conservation must be designated and that exploitation and pressures must be compatible with favourable conservation status. Identifying important habitat for seals is thus important, and increasingly so, as anthropogenic pressures are increasing.

In the current study, we aimed to produce habitat suitability and relative at-sea density maps for grey and harbour seals in the Baltic Sea area using telemetry and census data from the last 2 decades. Seal distribution is of profound interest in studies of ecosystem processes throughout the area, and in the management of populations in relation to anthropogenic pressures. Additionally, grey seals are currently expanding their range and recolonising the southern and western parts of the area, where harbour seals currently dominate. Hence, we aimed to use the resulting models to evaluate the emerging competition between the 2 species in these areas of increasing overlap.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area comprises the Baltic Sea and its adjacent Kattegat and Skagerrak seas (Fig. 1). The Baltic Sea is a semi-enclosed sea in northwestern Europe and the World's largest brackish water basin, stretching 1200 km from 54 to 66° N, covering temperate and subarctic climate zones. It is connected to the North Atlantic through the narrow and shallow Danish Straits, Kattegat and Skagerrak. There is substantial variation in salinity from 0.1–0.4% in the Bay of Bothnia through the central Baltic to 2.0–2.5% in the Kattegat (Leppäranta & Myrberg 2009) and 3.4% in the Skagerrak (Kristiansen & Aas 2015). The Baltic Sea region is generally shallow, with a mean depth of 54 m and maximum depth of 459 m (Meier et al. 2022). Sea surface temperature varies markedly by area and season (Bradtke et al. 2010). These differences in temperature and salinity mean that biodiversity varies greatly, with higher biodiversity in more saline areas (Kniebusch et al. 2019).

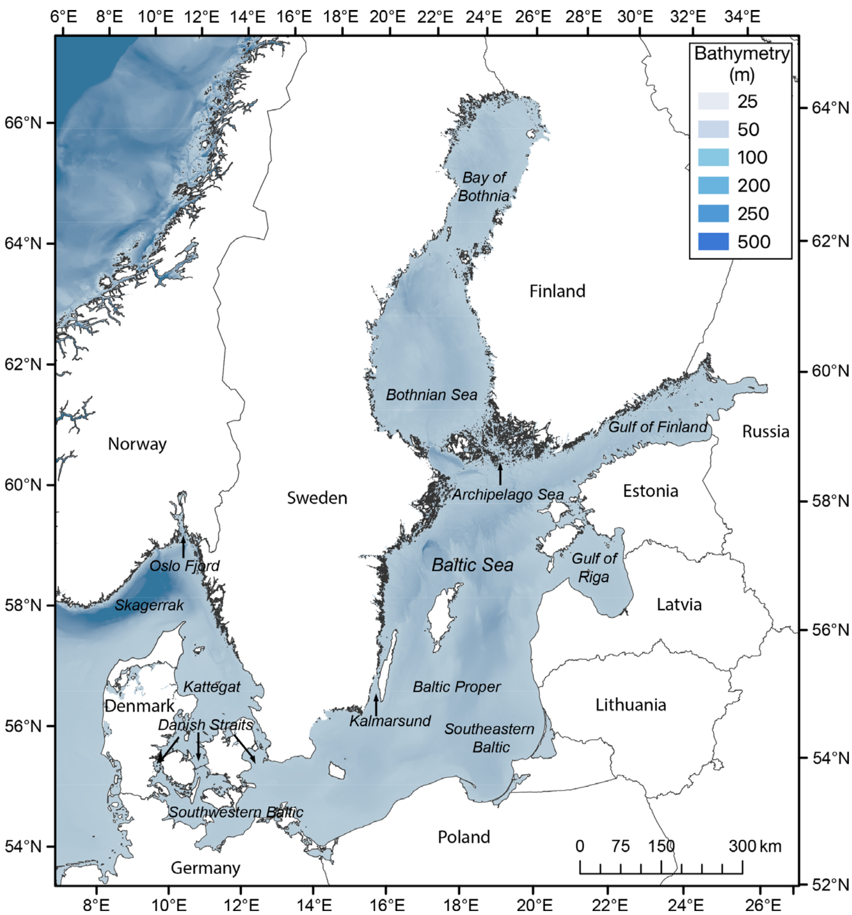

Fig. 1. Baltic Sea region with bathymetry and place names used in the text

### 2.2. Tracking data

We compiled all available telemetry data from harbour seals spanning the area from the Skagerrak to the western Baltic Sea. No data were available from the isolated population in Kalmarsund, and hence, the inner Baltic area was not covered for harbour seals. Grey seal data spanned the entire Baltic Sea region, except the Kattegat (Fig. 1). A total of 99 harbour seals (59 males, 38 females, 2 unknown sex) and 70 grey seals (45 males, 17 females, 8 unknown sex) were captured and tagged with GPS or Argos satellite tags at 22 haulout sites across Denmark and Sweden (both species), Norway (harbour seals) and Estonia (grey seals). In Finland, only male grey seals were captured in fish traps. All seals were tagged between 2000 and 2024 (Tables S1.1 & S1.2 in Section S1 in the Supplement at www.int-res.com/articles/suppl/meps15206_supp.pdf). A description of capture and handling methods used in each country is provided in Section S1. Tracking data collected with GPS tags were cleaned by removing the few outlier locations (n = 12 and 22 for harbour and grey seal data, respectively) that were identified based on unrealistic movements between relocations. Unrealistic movements were defined as relocation events where a seal moved faster than 2.5 m $s^{-1}$ between 2 GPS locations and thereafter returned with the same speed to the first location (van Beest et al. 2019). Argos satellite tags provide less precise position data than GPS tags and these were consequently filtered using the Argos- Filter v7.03 following Dietz et al. (2013). Further processing of tracking data included removal of locations on land and locations collected within 24 h after tagging to reduce behavioural bias caused by capture and tagging (van Beest et al. 2018). Following Carter et al. (2022), we removed locations collected during the breeding and moulting seasons (grey seals: February–June, harbour seals: June–August), as behaviour during these seasons is not representative of the key foraging season. After this procedure, we only retained individuals with at least 10 d of tracking data to give all seals meaningful representation, thus removing 6 harbour and 5 grey seals. We also removed tracking data from 3 harbour seals captured in Norway, as they spent most of their time in the western Skagerrak (Riaz et al. 2026), outside the boundaries of the area for which environmental data were available (see Section 2.4.2 below). In the end, we retained data from 90 harbour seals and 65 grey seals (Fig. S1.1, Tables S1.1 & S1.2).

Given the temporal differences in position interval between GPS and Argos tags, as well as tag programming between countries, the data were interpolated and standardised to a constant 4 h time step interval using a continuous-time state space model implemented in the R package 'aniMotum' (Jonsen et al. 2023). This procedure is particularly useful when combining GPS and Argos tracking data, as it incorporates differences in accuracy level of positional estimates during the standardisation process. When the time difference between 2 subsequent GPS or Argos locations was >24 h, the track was split into separate movement bursts prior to standardisation. The final data sets comprised 37 832 at-sea locations for harbour seals (Fig. 2A), and 43 544 at-sea locations for grey seals (Fig. 2B).

### 2.3. Haulout counts

Counts of seals (from Denmark, Norway, Sweden, Germany, Poland, Estonia and Finland; Russian data were not available) on known haulouts were collected by aerial, boat and drone surveys. Although no grey seals were tagged in Germany and Poland, annual censuses were done during the moulting periods in late May to early June for grey seals (Hiby et al. 2007, Galatius et al. 2024a) and August for harbour seals (Härkönen et al. 1999, Galatius et al. 2021). Descriptions of the count methods used are provided in Section S6. For each seal species and haulout, count data were averaged across all survey years for further analyses (Fig. 3).

### 2.4. Species distribution modelling

SDMs are a broad class of numerical models that aim to predict distribution, density or habitat suitabil-

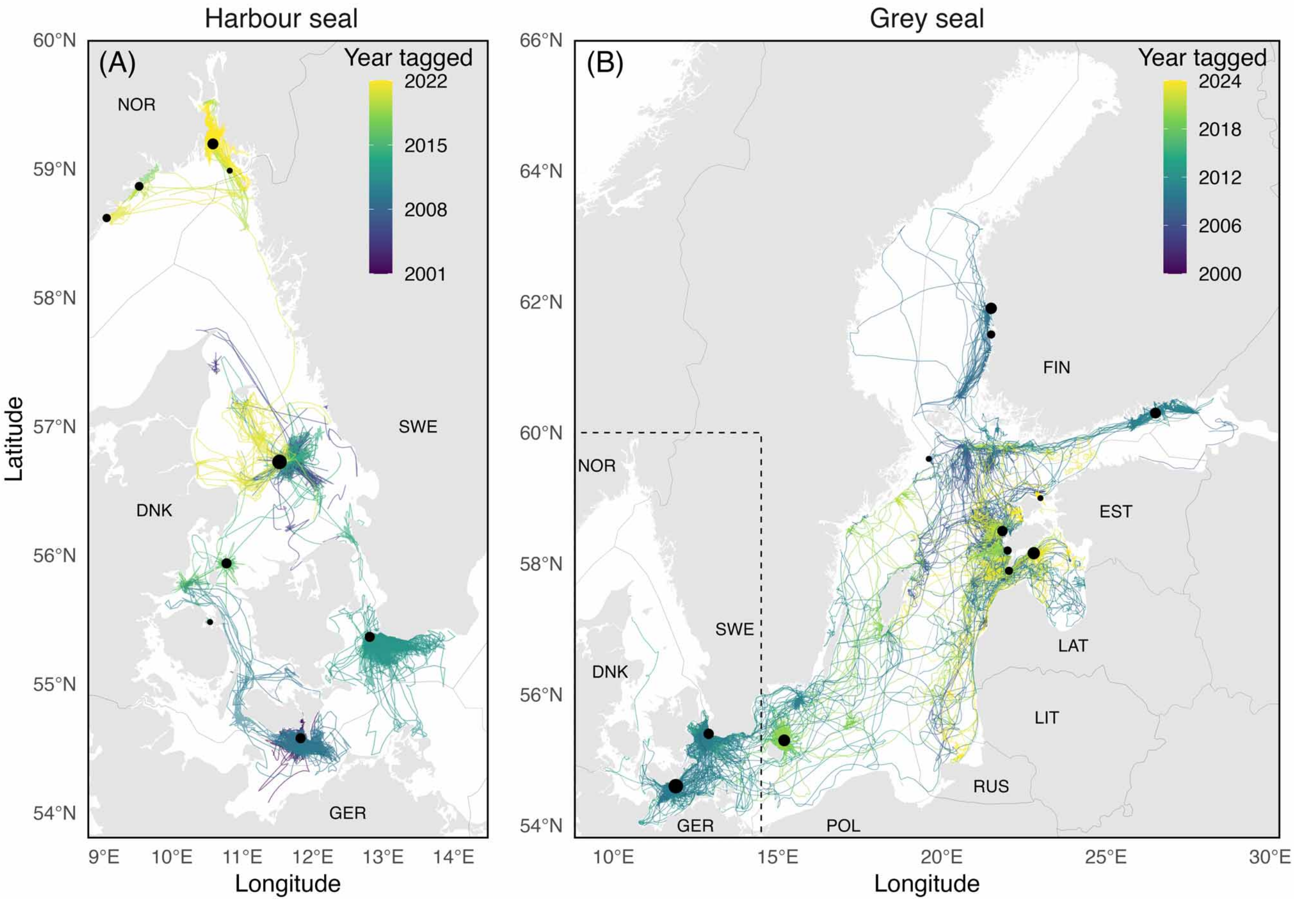


Fig. 2. (A) Tracking data of 90 harbour seals and (B) 65 grey seals colour coded by year of tagging (release). Black circles highlight locations where individual seals were tagged (size of the circle is proportional to the number of seals tagged). The dashed lines in (B) indicate the spatial extent of the area used by harbour seals in panel (A). Country names are given in full in Fig. 1

ity of a species across space and time using environmental data (Elith & Leathwick 2009). We followed the analytical approach of Carter et al. (2022) to predict habitat suitability for both seal species separately and weighting the predicted outputs by haulout counts to compute relative at-sea density maps across the study areas.

### 2.4.1. Use—availability study design

SDMs typically contrast environmental conditions at presence or used locations to those encountered at available locations, also known as a 'use—availability' study design (Johnson 1980, Warton & Aarts 2013). Under this study design, preference for a particular habitat type or environmental condition is inferred where its use is disproportionate to its availability (Aarts et al. 2008, Beyer et al. 2010). In our case, the standardised at-sea seal locations were the used locations. Available locations were randomly drawn from a circular buffer around each used location with the radius set to the maximum distance from a known haulout by any seal in the cleaned tracking data set (grey seals: 711 km, harbour seals: 314 km), ensuring that all available locations were potentially accessible to the seals (Matthiopoulos et al. 2020). We generated several availability data sets that varied in the ratio of the number of used:available locations (1:1, 1:5, 1:10, 1:15, 1:20, 1:25 and 1:30) to assess at which ratio model estimates stabilised and thus adequately captured the variation in environmental conditions present within the study areas, which is a critical aspect for robust SDM inference (Northrup et al. 2013). The results suggested that model estimates stabilised at a use:availability ratio of 1:10 for harbour seals and 1:20 for grey seals (see Section S2 for more details). These ratios were subsequently used in further analyses.

### 2.4.2. Environmental data

Twelve environmental variables were considered as candidate predictor variables in the species-specific

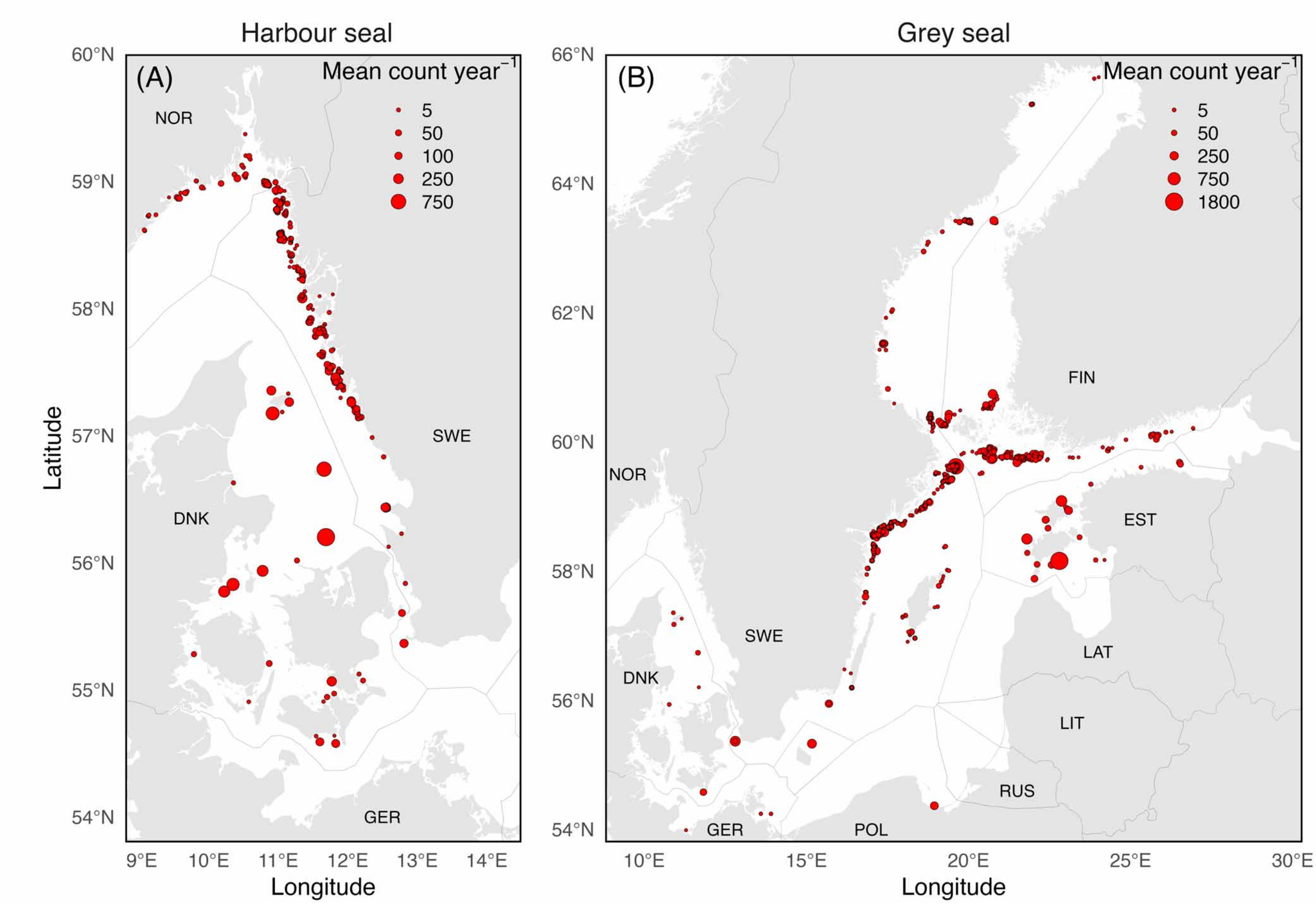


Fig. 3. Surveyed haulout locations (in red) and mean annual counts of (A) harbour seals (N = 462 haulouts) and (B) grey seals (N = 841 haulouts) during the period 2000—2024. Circle size is proportional to the number of seals counted

SDMs (Table 1; Figs. S3.1 & S3.2 in Section S3). These variables were selected because of known influence on habitat suitability and movement behaviour of seals or their prey in the Baltic Sea and transition zone to the North Sea (Sjöberg & Ball 2000, Bergström et al. 2013, Dietz et al. 2013, Oksanen et al. 2014, van Beest et al. 2019, 2022). Static environmental variables included: 'bathymetry' (m), 'seabed rugosity' (m) and 'sediment type' (categorical variable including sand, mud, coarse and mixed sediments). Dynamic environmental variables included: 'wave exposure' ($m^2$ $s^{-1}$), 'current velocity' (m $s^{-1}$), 'mixed layer thickness' (m), 'sea surface salinity' (PSU), 'sea surface height' (m), 'sea surface temperature' (°C), 'sea bottom oxygen' (mmol $m^{-3}$), 'sea ice cover' (%) and 'distance to known haulout site' (km).

Multicollinearity among the 12 candidate predictor variables was substantial, with variance inflation factors >20 and Spearman's rho >0.7 for various variable combinations across the spatial extent of both study areas. To reduce bias and uncertainty due to multicollinearity, we used a stepwise procedure to remove 1 of 2 correlated predictor variables and repeated this until all variables had variance inflation factors <5 and Spearman's rho <0.5. To decide which of 2 correlated variables was to be retained, we compared Bayesian information criteria (BIC) values of univariate SDMs and retained the variable producing the lowest BIC. We relied on BIC instead of other criteria, e.g. Akaike's information criterion (AIC), as BIC imposes a stronger penalty on model complexity and is considered more reliable for identifying the most informative predictor (Aho et al. 2014). Based on this procedure, bathymetry, mixed layer thickness, and ice cover were removed as candidate predictor variables from both the harbour and grey seal SDMs. Sea bottom oxygen and surface salinity were removed as candidate predictor variables for the harbour seal SDM. For the grey seal SDM, we removed sea surface height and sea surface temperature. Ultimately, 7 predictor variables remained in each species-specific SDM (Figs. S3.1 & S3.2 in Section S3).

For each used and available point in the seal data sets, we georeferenced the *x,y* coordinates with the environmental raster layers and extracted the values of the 7 environmental conditions retained as species-specific SDM predictor variables using the R package 'terra' (Hijmans et al. 2024). For the dynamic variables from Copernicus (daily products), we georeferenced the location data and the environmental raster layers by matching them based on both spatial coordinates and the corresponding date of the year.

Table 1. Overview of the 12 candidate environmental variables, the spatial resolution of the raster data and the source of the data. Dynamic variables from Copernicus had a temporal resolution of 1 d. The column 'Included in model' indicates whether the variable was included in the final model after accounting for multicollinearity (see Section 2.3.2 for details), where No: not included in the harbour seal and grey seal models; Yes: included in both harbour seal and grey seal models; Harbour: included in harbour seal model only; and Grey: included in grey seal model only

| Variable | Unit | Spatial resolution | Source[a,b,c] | Included in model |
|---|---|---|---|---|
| Bathymetry | m | 500 m | HELCOM | No |
| Seabed rugosity | m | 500 m | Calculated from bathymetry data using the R package 'terra' Hijmans et al. (2024) | Yes |
| Sediment type | 4-class factor | 150 m | EMODnet | Yes |
| Wave exposure | m | 250 m | EMODnet | Yes |
| Current velocity | m $s^{-1}$ | 1800 m | Copernicus | Yes |
| Mixed layer thickness | m | 1800 m | Copernicus | No |
| Sea surface salinity | PSU | 1800 m | Copernicus | Grey |
| Surface height | m | 1800 m | Copernicus | Harbour |
| Surface temperature | °C | 1800 m | Copernicus | Harbour |
| Sea-bottom oxygen | mmol $m^{-3}$ | 1800 m | Copernicus | Grey |
| Sea ice cover | % | 1800 m | Copernicus | No |
| Distance from haulout site | km | 500 m | Calculated from haulout location data using the R package 'terra' Hijmans et al. (2024) | Yes |

[a]HELCOM: https://metadata.helcom.fi/
[b]EMODnet: https://emodnet.ec.europa.eu/en/
[c]Copernicus: https://data.marine.copernicus.eu/product/BALTICSEA_MULTIYEAR_PHY_003_011/

### 2.4.3. Statistical analyses

All analyses were conducted using R version 4.5.1 (R Core Team 2025). Species-specific SDMs were fitted using generalized additive mixed models (GAMMs) through the 'bam' function in the R package 'mgcv' (Wood 2020). Each SDM was fitted using the equation:

$$g(P) = \beta_0 + \beta_i + f_1(x_{1k}) + f_2(x_{2k}) + \ldots + f_p(x_{pk}) + Y_i + C_k + \epsilon_t \quad (1)$$

Here, $P$ is the expected outcome of the binomial response variable, with used locations coded as 1 and available locations coded as 0 and the error family specified with the logit link function: $g(p) = \ln\left(\frac{p}{1-p}\right)$. The term $\beta_0$ is the global intercept and $\beta_i$ is the fixed effect for the categorical variable sediment type ($i$ = 1...4). The terms $f_1(x_{1k}) + f_2(x_{2k}) + \ldots + f_p(x_{pk})$ are the continuous covariates fitted as cubic regression splines with shrinkage, meaning that uninformative terms could be penalised to zero, effectively making them linear (Wood 2020). The optimal number of knots ($k$) of the spline function was determined for each covariate separately by trialling different values ($3 \leq k \leq 8$) and selecting the value for $k$ that minimised the BIC value of the model (Figs. S4.1 & S4.2 in Section S4). The terms $Y_i + C_k$ are the random effects for the observation 'year' and 'country of tagging', which were fitted using the 're' basis spline. This was done to indirectly account for the unbalanced data (i.e. differences in tracking duration across individual seals) and to ensure that data-rich years and countries did not have disproportionate influence on overall trends. Finally, $\epsilon_t$ has a first-order autoregressive (AR1) correlation structure implemented through the R package 'itsadug' (van Rij et al. 2022). The AR1 structure was incorporated to reduce serial autocorrelation in model residuals [$\epsilon_t$] by treating each movement burst (see Section 2.2 above) as a separate time series, i.e. no autocorrelation between movement bursts. Following Carter et al. (2022), we included a weighting function in each SDM, where used points had a value of 1 and available points had a value of 0.1 (1/10) in the harbour seal data set, while available points had a value of 0.05 (1/20) in the grey seal data set. Doing so ensured that each set of available points contributed the same weight to the model as the corresponding point that was used.

Once the final structure of the species-specific SDMs was determined, we evaluated model fit by extracting the amount of deviance explained for the full model as well as for models from which each covariate was dropped one by one. We evaluated predictive performance using the $k$-fold cross-validation procedure as proposed by Wiens et al. (2008) and adapted by Carter et al. (2022) for GAMMs based on use:availability ratios greater than 1:1. Briefly, individual seals were randomly assigned to 1 of 3 folds. The GAMM was then fitted to 2 folds, and predictions were made for the remaining fold (Wiens et al. 2008). Predictive performance of the GAMM was then evaluated by the coefficient of the Spearman rank correlation between binned predicted probabilities and the area-adjusted frequency of presences (Wiens et al. 2008).

### 2.4.4. Habitat suitability maps

The output of the species-specific GAMMs included partial response curves for each environmental variable on the log-odds scale. Habitat suitability raster maps (spatial resolution of 1 × 1 km) were subsequently generated for each species separately by predicting (on a probability scale) the combined effects of all environmental conditions across the study areas. For the dynamic environmental variables used in the spatial prediction of habitat suitability (Table 1), we averaged the values across the year 2022. For the variable 'distance to haulout site', we calculated a raster layer considering all known haulout locations in the study areas, as opposed to the seal- and haulout site-specific calculations used in the GAMM analyses.

To incorporate uncertainty into the habitat suitability predictions, we used a Bayesian posterior simulation approach (Marra & Wood 2012, Wood 2020, Carter et al. 2022). Specifically, 100 simulations of the model coefficient vector were drawn from a multivariate normal distribution, with the mean equal to the estimated coefficients and the covariance equal to the unconditional variance—covariance matrix from the fitted GAMMs. For each simulation, we computed the linear predictor by multiplying the model matrix with the simulated coefficients, then applied the inverse logit transformation to obtain predictions on the response scale (Manly et al. 2002). For each raster cell, we then calculated the mean predicted probability and associated 95% credible intervals (i.e. the $2.5^{th}$ and $97.5^{th}$ percentiles across simulations).

To minimise risk of extrapolating model predictions into areas with novel conditions (i.e. environmental values for which the model has no training and testing data, thus making predictions unreliable), a multivariate environmental similarity surfaces (MESS) analysis was performed. Following Elith et al. (2010), we used seal presence locations with associated environmental values as input points and then estimated (dis)similarities with the combination of environmental conditions across the entire study area. The MESS analysis was performed for each seal species separately. Predictions of habitat suitability derived by the GAMMs were subsequently restricted (i.e. masked) to areas where environmental conditions were within the range used by the seals (i.e. MESS similarity value of >0; Fig. S5.1 in Section S5). Results of the MESS analyses identified deeper waters in the Skagerrak off the coast of Norway and colder waters in the northern parts of the Gulf of Bothnia to be dissimilar (i.e. MESS similarity value of <0) from the conditions used by the seals.

### 2.5. Relative population density maps

Spatial predictions of relative at-sea population density were generated per haulout site and species using the corresponding habitat suitability model. Specifically, for each haulout site, raw habitat suitability predictions (on the logit scale) were back-transformed using the inverse logit as in the habitat suitability prediction explained above. Each haulout-specific prediction surface was then weighted by the mean number of seals counted on each haulout during all surveys. The weighted, haulout-specific prediction surfaces were then summed into a cumulative surface layer for the whole study area. The cumulative surface was then normalized by dividing each raster cell value by the total sum of all predicted values and scaled to a percentage, such that the surface sums to 100% (Carter et al. 2022). The unit of the resulting map represents the percentage of the at-sea population estimated to be present in a cell at any one time (% at-sea $km^{-2}$). Cell-wise lower and upper 95% credible intervals of the relative density maps were calculated for each haulout using the same Bayesian posterior simulation approach as described above for the habitat suitability maps.

### 2.6. Species co-occurrence

To assess inter-specific differences in habitat suitability and relative population density, we calculated Schoener's *D* niche overlap index (Schoener 1968) and Warren's *I* niche similarity index (Warren et al. 2008). To do so, we cropped the grey seal prediction surfaces for habitat suitability and relative population density to the same spatial extent as used for the harbour seal analyses (i.e. focus on the southwestern region where both species co-occur). We then calculated the *D* and *I* metrics for the mean and associated lower and upper 95% credible interval raster layers, where 0 indicates no overlap or similarity between species and 1 indicates complete overlap or similarity in habitat suitability and relative population density.

## 3. RESULTS

### 3.1. Habitat suitability

The environmental covariates in the species-specific GAMMs explained a total of 54.1 and 64.2% of the deviance in habitat suitability for harbour seals and grey seals, respectively (Table S7.1 in Section S7). The predictive performance of the GAMMs, estimated using *k*-fold cross validation, was considered adequate with a mean (SD) $r_s$ of 0.897 (0.06) and 0.723 (0.182) for harbour seal and grey seal models, respectively.

Predicted mean habitat suitability maps for both species are provided in Fig. 4 (see Figs. S7.1 & S7.2 in Section S7 for the predicted lower and upper 95% credible interval layers). For both seal species, distance to haulout was the primary driver of habitat suitability, explaining 24.6 and 29.2% of the total deviance explained for harbour and grey seals, respectively, with predicted habitat suitability declining with increasing distance from haulouts (Fig. S7.3 and Table S7.1 in Section S7). For harbour seals, sea surface temperature was the second most important predictor of habitat suitability, explaining 3.5% of deviation with a preference for mean annual water temperature of <9.75°C, followed by wave exposure explaining 2.5% of the deviance (Fig. S7.3). The remaining variables included in the harbour seal GAMM explained <3% of the total deviation (Table S7.1). For grey seals, sea bottom oxygen was the second most important predictor of habitat suitability, explaining 5.9% of deviation with a preference for areas with oxygen levels >300 mmol $m^{-3}$, while increased wave exposure explained 4.7% of the deviance (Fig. S7.3). The remaining variables included in the grey seal GAMM explained <5% of the total deviation (Table S7.1).

### 3.2. Relative population density

The mean relative density maps for both seal species are provided in Fig. 5 (see Figs. S7.4 & S7.5 in Section S7 for the predicted lower and upper 95% credible interval layers for harbour seals and grey seals, respectively). The relative density of harbour seals was high-

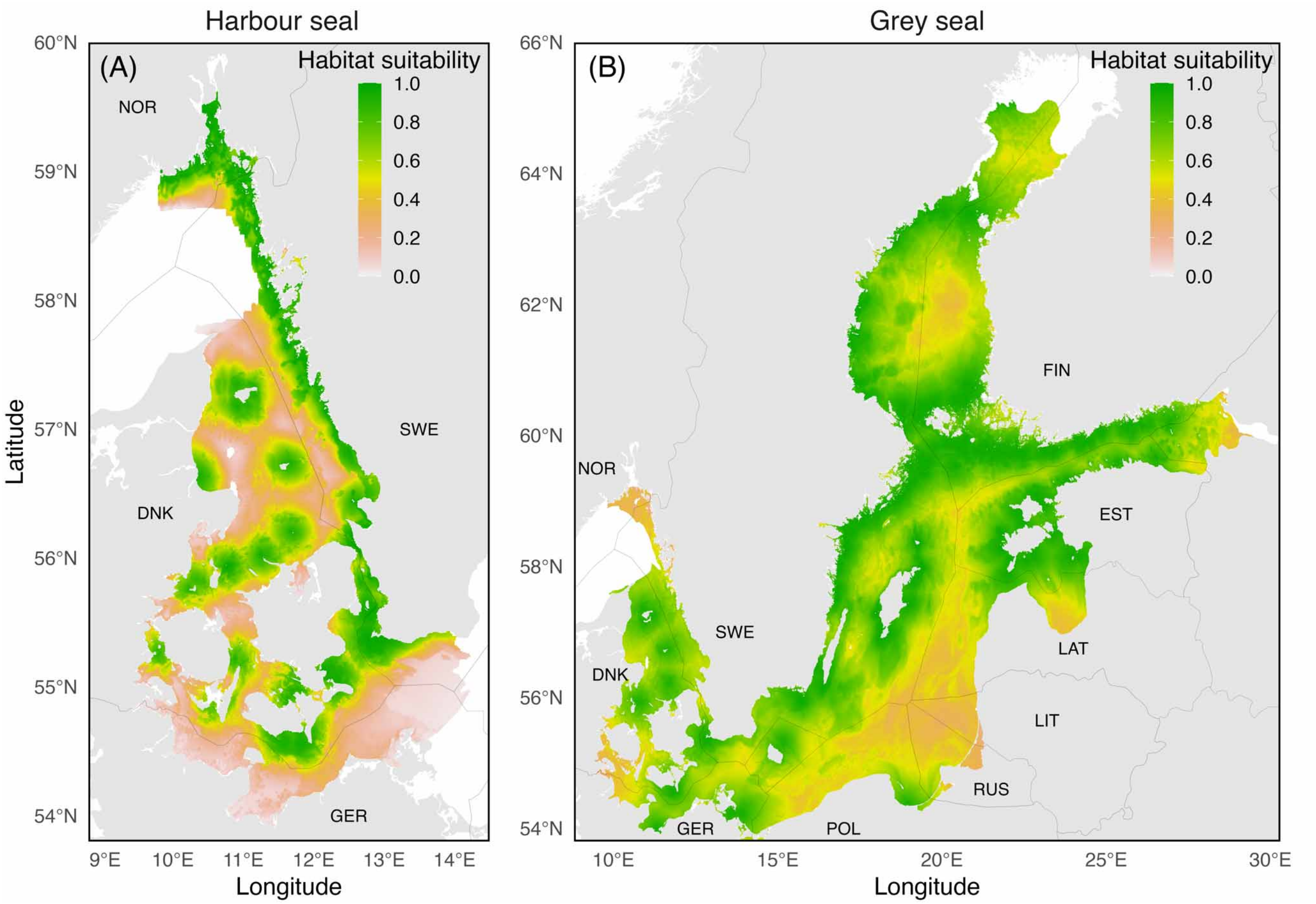


Fig. 4. Results of the generalized additive mixed model (GAMM) analyses showing the predicted mean habitat suitability maps for (A) harbour seals and (B) grey seals. Sea areas in white were not included in the model predictions due to environmental dissimilarity (see Section 2.4.4 for details). See Figs. S7.1 & S7.2 in Section S7 for the predicted lower and upper 95% credible intervals associated with the predicted mean habitat suitability layers for harbour and grey seals, respectively

est along the west coast of Sweden and the outer Oslo fjord (Fig. 5A). The map also revealed hotspots of harbour seal densities around the islands Hesselø, Anholt and Læsø in the Kattegat, and, moreover, that the harbour seal density declined rapidly south of the Danish Straits, towards German waters and the Baltic Sea. The relative density of grey seals was highest within the Archipelago Sea, offshore from the Swedish and Finnish coasts (Fig. 5B). Grey seal densities remained high farther north into the Bothnian Sea and south towards the Gulf of Riga, while the density declined farther east into the Gulf of Finland. The grey seal density also steadily declined towards the Baltic Proper, the southwestern Baltic and into the Kattegat (Fig. 5B).

### 3.3. Species co-occurrence

Focusing on the predicted habitat suitability and relative at-sea population density maps of grey and harbour seals in the southwestern Baltic Sea region (Fig. S7.6 in Section S7), we found that the mean proportion of overlap (Schoener's $D$) exceeded 0.5 for both maps, while the mean proportion similarity (Warren's $I$) exceeded 0.75 for both maps (Fig. 6). Importantly, $D$ and $I$ values were consistently higher when computed from the predicted habitat suitability maps compared to those derived from the relative at-sea density maps (Fig. 6), implying that the densities of both species are not at equilibrium with their suitable habitat.

## 4. DISCUSSION

### 4.1. Habitat suitability

We present the first comprehensive species distribution models for grey seals and harbour seals in the Baltic Sea region. As central place foragers often

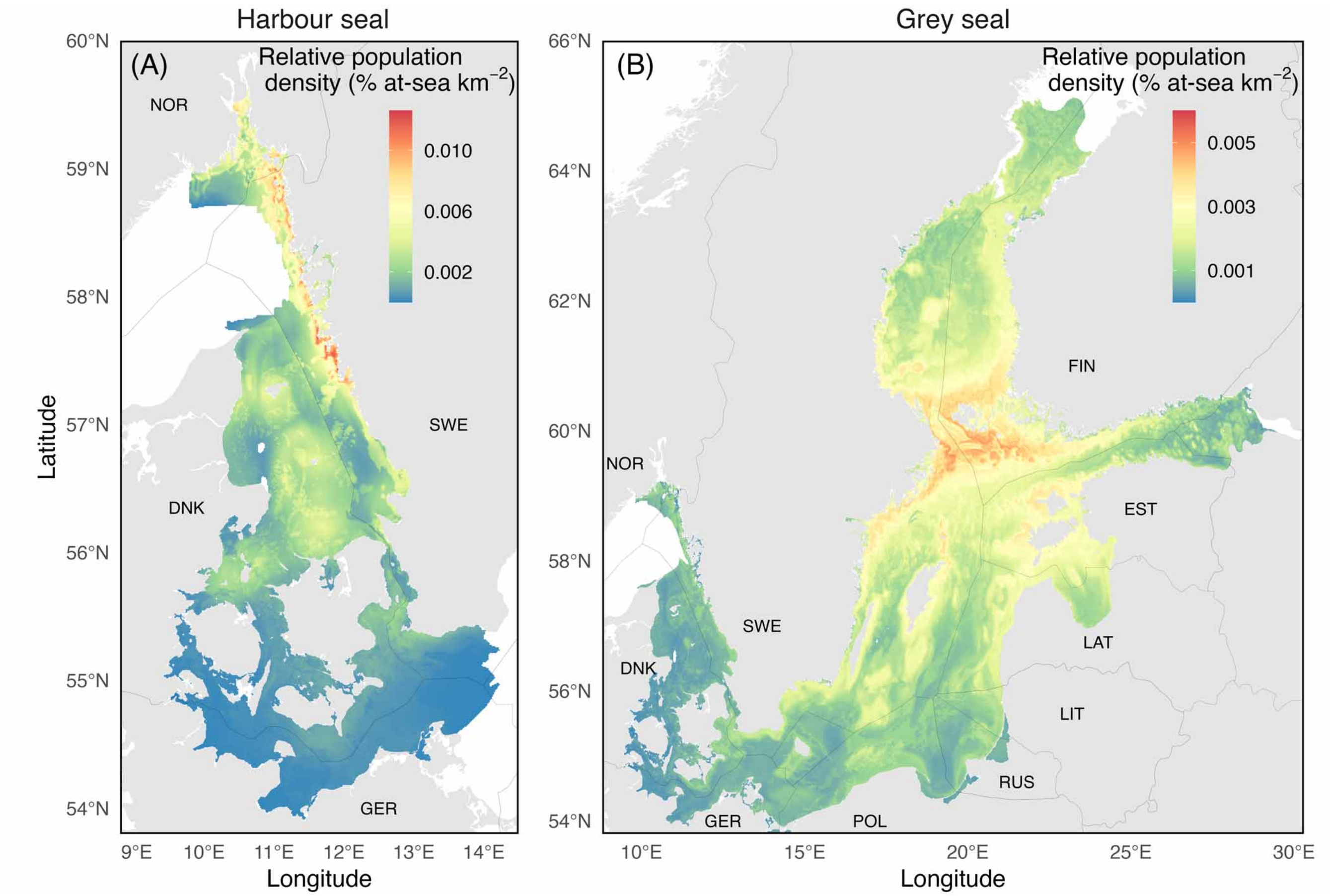


Fig. 5. Mean relative population density maps (% at-sea km$^{-2}$) of (A) harbour seals and (B) grey seals. Sea areas in white were not included in the calculations due to environmental dissimilarity (see Section 2.4.4 for details). See Figs. S7.4 & S7.5 in Section S7 for the lower and upper 95% credible intervals associated with the predicted mean relative population density layers for harbour and grey seals, respectively

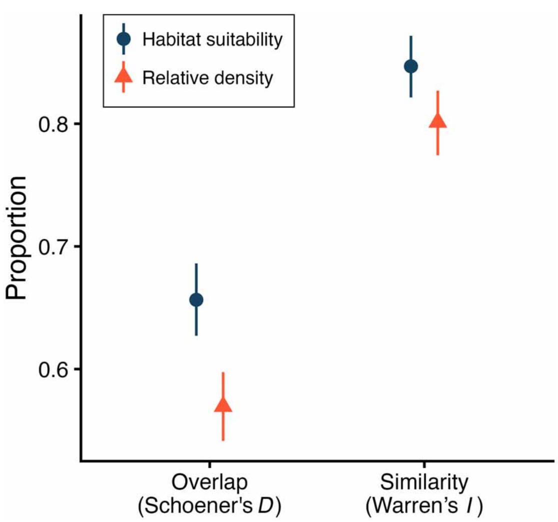


Fig. 6. Mean (95% confidence intervals) proportion of overlap (Schoener's *D*) and similarity (Warren's *I*) in habitat suitability and relative population density between harbour and grey seals in the southwestern Baltic Sea region

return to the same or few specific haulouts, seal distribution can be expected to be determined by the availability of haulouts on one hand and distribution of food resources on the other hand (Vance et al. 2021). In line with this, both species showed strong habitat preferences related to distance to haulouts, with harbour seals being more constricted to areas close to haulouts than grey seals, in agreement with previous studies (e.g. Dietz et al. 2013, Carter et al. 2022, Carter et al. 2026). For harbour seals, suitability was low along the German coast, possibly because many haulouts have been destroyed by excavation of sand, gravel and rocks (von Nordheim et al. 2011). Suitable at-sea habitats for grey seals were distributed throughout the modelled part of the Baltic Sea area, with the least suitable areas being farther from the coastline. An exception was the southeastern Baltic, bordered by the coasts of Latvia, Lithuania, the Russian exclave Kaliningrad and much of the Polish coast, where habitat, also along the coastline, was predicted to have relatively low suitability. One factor behind this may be the availability of only 1 haulout locality in the area, at the Vistula River in Poland (Fig. 2B). No grey seals were tagged in this area, but individuals tagged elsewhere used the area (Fig. 2).

Around the UK, where there is much more variation in sea depth than in our study area, harbour seal habitat preference was inversely related to depth (Carter et al. 2022). We did not find this relationship in our area, which is uniformly shallow, except for deeper waters in the northern Skagerrak, which seem to be rarely used by harbour seals (Figs. 1 & 2A). Harbour seal habitat suitability was also associated with colder surface water temperatures and increased wave exposure. Low surface water temperatures may be associated with upwelling, which may again be associated with prey availability (Lehmann & Myrberg 2008). Wave exposure was also important for grey seal distribution and may be a proxy for prey density, being a predictor of distribution for several Baltic fish species (Bergström et al. 2013). Since the early 20$^{th}$ century, the Baltic Sea has experienced increasing oxygen depletion related to excess eutrophication (Conley et al. 2009, Gustafsson et al. 2012, Carstensen et al. 2014, Meier et al. 2019). As fish will likely avoid areas with low oxygen concentrations (Randall 1970, Stramma et al. 2012, Miethe et al. 2014), it is unsurprising that grey seal habitat suitability is positively related to increased oxygen concentration. Harbour seals may show a similar pattern, but the most severely affected areas in the Baltic are outside of our modelled range for harbour seals, potentially precluding us from detecting a relationship. Also, most of the oxygen-depleted areas in the Baltic are in deeper parts, farther from shore, thus likely having greater impact on grey seals.

### 4.2. Historical context

The harbour and grey seal populations in the Baltic area have experienced drastic abundance fluctuations since the 19$^{th}$ century due to culling, hunting, pollution and virus epidemics (Harding & Härkönen 1999, Härkönen et al. 2006, Härkönen & Isakson 2010, Dietz et al. 2021, Carroll et al. 2024, 2025). As a result, both grey and harbour seals are still recolonising parts of their former range (Galatius et al. 2020, 2024a,b). This has implications for our models. In some of the areas of recolonisation, such as the South Funen Archipelago and Little Belt for harbour seals and the Kattegat for grey seals, no seals were tagged, and model results in these areas are largely extrapolations of data from areas with seal positions. In these areas, the density models are based on current survey data, which will lead to underestimates relative to seal densities at carrying capacity. Both grey and harbour seals are known to show considerable site fidelity to breeding and haulout sites as well as foraging areas (Pomeroy et al. 2000, Härkönen & Harding 2001, Karlsson et al. 2005, Dietz et al. 2013, Nowak et al. 2025), which will likely result in inertia of expansion to new areas. Comparison of the estimates of actual density with the habitat suitability reveals that for both species, the densities do not thoroughly align, as areas with high predicted suitability do not necessarily have high density. For grey seals, densities are greatest in the Stockholm Archipelago and the Finnish Archipelago Sea, with lower densities towards the southwestern Baltic, even though the habitat suitability in the latter region is predicted to be equally high. There have already been signs of density dependence in Finland in terms of links between available prey quality and nutritional condition and reproductive rate of grey seals (Kauhala et al. 2017, 2019), so the imbalance between habitat suitability and actual distribution likely reflects inertia in expansion of grey seal distribution.

### 4.3. Species overlap and competition

Following the local extinction of grey seals in the Kattegat and the southern Baltic (Olsen et al. 2018, Galatius et al. 2020), there has been little overlap of the 2 species in the Baltic Sea region. On one hand, this means that the habitat preferences of the species may change during interspecific competition; on the other hand, our models allow some insight into the level of competition. Results of the co-occurrence analyses revealed considerable overlap and similarity in habitat suitability between the 2 species in the southwestern Baltic Sea and the Kattegat. In the southwestern Baltic, there was also similarity regarding density; however, the similarity was clearly higher for habitat suitability. This suggests that despite shared habitat preferences, high-density areas largely remain spatially segregated. Grey seal presence in these areas is increasing (Galatius et al. 2020, 2024b), so suitability and density trend towards higher alignment. This may cause enhanced competition in areas where the habitat is predicted to be suitable for both species, although high predicted suitability may also mean that resources can support co-existence. Around the British Isles, similar models have found high predicted densities for grey seals in areas where harbour seals have suffered rapid, dramatic declines in relation to grey seal recovery (Carter et al. 2022).

Although our data were collected over 24 yr, temporal and spatial gaps prevent us from analysing temporal patterns in the predicted habitat suitability and densities. Harbour seal abundance shows different trends between areas in the Baltic region. In the southwestern Baltic Sea, the harbour seal population is growing, despite increasing numbers of grey seals (Galatius et al. 2021, HELCOM 2023, Carroll et al. 2025). Here, harbour seals were driven to the brink of extinction in the 1970s (Søndergaard et al. 1976, Härkönen & Isakson 2010), which may explain why this population is still below the carrying capacity of the environment and growing despite increased presence of grey seals. In the Kattegat and Skagerrak, where there are still few grey seals (Galatius et al. 2024b), harbour seal abundance has been declining over the last decade, probably because of competition with fisheries and habitat degradation (Carroll et al. 2025).

The potential for future interspecific competition indicated by our models is supported by observations of declining harbour seal abundance following grey seal recovery in other areas (Thompson et al. 2019), overlaps in diet (Wilson & Hammond 2016, Scharff-Olsen et al. 2019) and sources indicating that grey seals were previously more abundant than harbour seals in the southwestern Baltic and Kattegat (Søndergaard et al. 1976, Olsen et al. 2018). Besides competing for resources, it has also been documented that grey seals may kill harbour seals in the Baltic region (Westphal et al. 2023).

### 4.4. Caveats

Along with suitable haulout sites, prey density is known to be important in determining seal habitat suitability (Thompson et al. 1996, McConnell et al. 1999, Vance et al. 2021). Our models do not directly include prey density, but rather proxies. The models presented here are built on more than 20 yr of telemetry data from this dynamic environment. There have been drastic changes in the Baltic Sea ecosystem during this period, including climate change, oxygen depletion and fisheries activities which affect the abundance, distribution and composition of fishes, as well as activities causing disturbance of seals, such as commercial and leisure activities and seal hunting (Carstensen et al. 2014, Hansson et al. 2018, Meier et al. 2022, Cerwenka et al. 2023, Svedäng 2023, Moll et al. 2024, van Meurs et al. 2024, Lundström et al. 2025). With data of higher temporal resolution, future models could investigate the effects of changes in anthropogenic pressures on habitat suitability and densities.

Comprehensive coverage of an area at the scale of the Baltic Sea is challenging, and although the seals moved throughout most of the Baltic Sea, tagging sites were unequally distributed, with western Estonian waters and the southwestern Swedish and Danish Baltic more comprehensively covered than other areas for grey seals (Fig. 2B). For harbour seals, no data were available from seals tagged along the Swedish coasts of the Skagerrak and Kattegat, although more than 40% of the seals in the area are counted here during the moulting season (ICES 2024). Due to low densities, grey seals were not tagged in the Kattegat. The indication from the analyses is that the effects of this unequal distribution on the validity of the models are minor; the predictive performance (*k*-fold) of the models was high, indicating that the models worked well throughout the heterogeneous habitat of the study area. Age and sex were not considered in the models, as separate models for different segments of the populations would reduce the amount of data and their spatial coverage, causing loss of predictive power. There are known differences in movement behaviour between sexes and age-classes of seals, with juveniles typically having larger ranges (Lowry et al. 2001, Dietz et al. 2013). For harbour seals, there was a higher proportion of adults tagged in Norway than in Sweden and Denmark, and for grey seals, all seals tagged in Finland were males, while only a couple of the seals tagged in Denmark were adults (Table S1.2). The effects of such differences are partially mitigated by excluding data from the breeding and moulting seasons but could be a focus for future efforts on seal habitat suitability in the region.

The haulout counts used to calculate relative densities at sea represent seal distributions during the annual moulting seasons. This is the only season during which seals are counted throughout the study area and distribution is known to be different during the breeding season (Galatius et al. 2020, 2024a). Further differences are likely to be present outside the breeding and moulting seasons, particularly for grey seals, which move over wider areas than harbour seals and potentially use different areas in different seasons (Russell et al. 2013).

### 4.5. Conclusions

We present the most comprehensive analysis of at-sea habitat suitability and density of 2 apex predators in the Baltic Sea region. As such, the outputs may serve as valuable tools for managers and ecologists assessing threats, pressures and interactions of these species with the ecosystem at large. Our analyses provide evidence that current distributions of both species are not at equilibrium with the available suitable habitat. This reflects the dramatic history of seals in the region over the past centuries, with hunting, culling, pollution, haulout destruction and virus epidemics causing massive fluctuations in abundances and ranges, from which the populations are still recovering. Our study also indicates a substantial overlap in habitat suitability between the 2 species in the southwestern Baltic and Kattegat. In these areas, harbour seals are currently more abundant than grey seals. Harbour seals are already in decline in the Kattegat and Skagerrak, although grey seals only occur in low numbers. As the habitat suitability and distribution of both species is likely to change with interspecific competition, predation and environmental changes, we encourage continued tagging efforts and monitoring of haulouts to understand how the changing environment affects habitat use by the 2 largest marine predators in the Baltic Sea region.

*Data availability.* The data sets generated in this study are available at https://github.com/OBAMANEXT/SDM_seals_IP21.

*Acknowledgements.* We thank Debbie J. F. Russell and Matt I. D. Carter for sharing their code to implement the *k*-fold cross-validation of GAMMs. We thank K. T. Nilssen, M. Biuw, E. Moland, M. Poltermann and M. Kristiansen for their contribution to the Norwegian data collection and curation. We thank a long list of assistants and volunteers helping out in the field during seal tagging and surveys over the years. Funding for this study was provided by the GES4SEAS and OBAMA-NEXT projects funded under the Horizon Europe programme (grant agreements 101059877 and 101091642). C.F. was supported by the Horizon Europe project MARHAB (grant agreement 101135307). We are grateful to the funding sources and colleagues contributing to the multitude of tagging studies providing data for this study (see cited studies for details). Haulout surveys were funded by the Danish Environmental Protection Agency, the Estonian Environment Agency, the Finnish Ministry of Agriculture and Forestry, the Norwegian Ministry of Trade, Industry and Fisheries and the Swedish Agency for Marine and Water Management.

## LITERATURE CITED


Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160

Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. Ecology 95: 631–636

Bennington S, Rayment W, Dawson S (2020) Putting prey into the picture: improvements to species distribution models for bottlenose dolphins in Doubtful Sound, New Zealand. Mar Ecol Prog Ser 653:191–204

Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B and others (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLOS ONE 8:e53348

Bergström U, Sundblad G, Downie AL, Snickars M, Boström C, Lindegarth M (2013) Evaluating eutrophication management scenarios in the Baltic Sea using species distribution modelling. J Appl Ecol 50:680–690

Beyer HL, Haydon DT, Morales JM, Frair JL, Hebblewhite M, Mitchell M, Matthiopoulos J (2010) The interpretation of habitat preference metrics under use-availability designs. Philos Trans R Soc B 365:2245–2254

Bradtke K, Herman A, Urbanski JA (2010) Spatial and interannual variations of seasonal sea surface temperature patterns in the Baltic Sea. Oceanologia 52:345–362

Carroll D, Ahola MP, Carlsson AM, Sköld M, Harding KC (2024) 120-years of ecological monitoring data shows that the risk of overhunting is increased by environmental degradation for an isolated marine mammal population: the Baltic grey seal. J Anim Ecol 93:525–539

Carroll D, Ahola MP, Carlsson AM, Galatius A, Nilssen KT, Härkönen T, Harding KC (2025) Declining harbour seal abundance in a previously recovering meta-population. PLOS ONE 20:e0326933

Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during the last century. Proc Natl Acad Sci USA 111:5628–5633

Carter MID, Boehme L, Cronin MA, Duck CD and others (2022) Sympatric seals, satellite tracking and protected areas: habitat-based distribution estimates for conservation and management. Front Mar Sci 9:875869

Carter MID, Aarts G, van Beest FM, Bivins M and others (2026) At-sea distribution of seals on the Northwest European Shelf: towards transboundary conservation and management. J Appl Ecol 63:e70236

Cerwenka AF, Brandner J, Dashinov D, Geist J (2023) Small but mighty: the round goby (*Neogobius melanostomus*) as a model species of biological invasions. Diversity (Basel) 15:528

Conley DJ, Björck S, Bonsdorff E, Carstensen J and others (2009) Hypoxia-related processes in the Baltic Sea. Environ Sci Technol 43:3412–3420

Cordes LS, Duck CD, Mackey BL, Hall AJ, Thompson PM (2011) Long-term patterns in harbour seal site-use and the consequences for managing protected areas. Anim Conserv 14:430–438

Dietz R, Teilmann J, Henriksen OD, Laidre K (2003) Movements of seals from Rødsand seal sanctuary monitored by satellite telemetry. Relative importance of the Nysted Offshore Wind Farm area to the seals. Tech Rep, Book 429. National Environmental Research Institute, Roskilde

Dietz R, Teilmann J, Andersen SM, Rigét F, Olsen MT (2013) Movements and site fidelity of harbour seals (*Phoca vitulina*) in Kattegat, Denmark, with implications for the epidemiology of the phocine distemper virus. ICES J Mar Sci 70:186–195

Dietz R, Sonne C, Jenssen BM, Das K and others (2021) The Baltic Sea: an ecosystem with multiple stressors. Environ Int 147:106324

Dietz R, Berenguer López G, Bossi R, Eulaers I and others (2026) Decreases in contaminant loads and risk of adverse effects in harbour porpoises (*Phocoena phocoena*) from Inner Danish waters over three decades. Chemosphere 398:144850

Duarte CM, Chapuis L, Collin SP, Costa DP and others (2021) The soundscape of the Anthropocene ocean. Science 371:eaba4658

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Galatius A, Ahola M, Härkönen T, Jüssi I, Jüssi M, Karlsson O, Verevkin M (2014) Guidelines for seal abundance monitoring in the HELCOM area 2014. https://helcom.fi/wp-content/uploads/2019/08/Guidelines-for-Seal-Abundance-Monitoring-HELCOM-2014.pdf

Galatius A, Teilmann J, Dähne M, Ahola M and others (2020) Grey seal *Halichoerus grypus* recolonisation of the southern Baltic Sea, Danish Straits and Kattegat. Wildl Biol 2020:wlb.00711

Galatius A, Engbo SG, Teilmann J, van Beest FM (2021) Using environmental variation to optimize aerial surveys of harbour seals. ICES J Mar Sci 78:1500–1507

Galatius A, Dietz R, Olsen MT, Teilmann J (2024a) Recolonisation of former habitat by harbour seals in southern Denmark despite intense anthropogenic activity. J Mar Biol Assoc UK 104:e85

Galatius A, Olsen MT, Allentoft-Larsen M, Balle JD, Kyhn LA, Sveegaard S, Teilmann J (2024b) Evidence of distribution overlap between Atlantic and Baltic grey seals. J Mar Biol Assoc UK 103:e30

Goodman SJ (1998) Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina*) revealed using microsatellite DNA polymorphisms. Mol Biol Evol 15:104–118

Gordó-Vilaseca C, Costello MJ, Coll M, Jüterbock A, Reiss H, Stephenson F (2024) Future trends of marine fish biomass distributions from the North Sea to the Barents Sea. Nat Commun 15:5637

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I and others (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435

Gustafsson BG, Schenk F, Blenckner T, Eilola K and others (2012) Reconstructing the development of Baltic Sea eutrophication 1850–2006. Ambio 41:534–548

Hall AJ, Russell DJF (2018) Gray seal *Halichoerus grypus*. In: Würsig B, Thewissen JGM, Kovacs K (eds) Encyclopedia of marine mammals. Academic Press, San Diego, CA, p 420–422

Hammill MO, Bowen WD, Sjare B (2010) Status of harbour seals (*Phoca vitulina*) in Atlantic Canada. NAMMCO Sci Publ 8:175–190

Hansson S, Bergström U, Bonsdorff E, Härkönen T and others (2018) Competition for the fish — fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. ICES J Mar Sci 75:999–1008

Harding KC, Härkönen TJ (1999) Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Pusa hispida*) populations during the 20th century. Ambio 28: 619–627

Härkönen T, Harding KC (2001) Spatial structure of harbour seal populations and the implications thereof. Can J Zool 79:2115–2127

Härkönen T, Isakson E (2010) Status of harbour seals (*Phoca vitulina*) in the Baltic proper. NAMMCO Sci Publ 8: 71–76

Härkönen T, Hårding KC, Lunneryd SG (1999) Age- and sex-specific behaviour in harbour seals (*Phoca vitulina*) leads to biased estimates of vital population parameters. J Appl Ecol 36:825–841

Härkönen T, Dietz R, Reijnders P, Teilmann J and others (2006) A review of the 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Dis Aquat Org 68:115–130

Hazen EL, Abrahms B, Brodie S, Carroll G and others (2019) Marine top predators as climate and ecosystem sentinels. Front Ecol Environ 17:565–574

Heide-Jørgensen MP, Härkönen TJ (1988) Rebuilding seal stocks in the Kattegat-Skagerrak. Mar Mamm Sci 4: 231–246

HELCOM (2009) Eutrophication in the Baltic Sea. An integrated thematic assessment of the effects of nutrient enrichment in the Baltic Sea region. Baltic Sea Environment Proceedings, Book 115B. HELCOM, Helsinki

HELCOM (2023) Population trends and abundance of seals. HELCOM core indicator report. https://indicators.helcom.fi/wp-content/uploads/2023/04/Population-trends-and-abundance-of-seals-Harbour-seals_Final_April_2023-1.pdf

Hiby L, Lundberg T, Karlsson O, Watkins J, Jüssi M, Jüssi I, Helander B (2007) Estimates of the size of the Baltic grey seal population based on photo-identification data. NAMMCO Sci Publ 6:163–175

Hijmans RJ, Bivand R, Cordano E, Dyba K, Pebesma E, Sumner MD (2024) terra: spatial data analysis. R package version 1.7-78. https://cran.r-project.org/web/packages/terra/index.html

ICES (2024) Working group on marine mammal ecology. ICES Sci Rep Book 6:82

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Jones E, McConnell BJ, Sparling C, Matthiopoulos J (2013) Grey and harbour seal usage maps. Marine Mammal Scientific Support Research Programme, Marine Scotland

Jonsen ID, Grecian WJ, Phillips L, Carroll G and others (2023) aniMotum, an R package for animal movement data: rapid quality control, behavioural estimation and simulation. Methods Ecol Evol 14:806–816

Kappa F, Härkönen T, Freitas C, Carroll D, Harding KC (2026) Shifting harbor seal (*Phoca vitulina*) diet may reflect ecosystem changes in Skagerrak. Mar Mamm Sci 42:e70069

Karlsson O, Hiby L, Lundberg T, Jüssi M, Jüssi I, Helander B (2005) Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. Ambio 34:628–634

Kauhala K, Bäcklin BM, Raitaniemi J, Harding KC (2017) The effect of prey quality and ice conditions on the nutritional status of Baltic gray seals of different age groups. Mammal Res 62:351–362

Kauhala K, Korpinen S, Lehtiniemi M, Raitaniemi J (2019) Reproductive rate of a top predator, the grey seal, as an indicator of the changes in the Baltic food web. Ecol Indic 102:693–703

Kniebusch M, Meiert HEM, Radtke H (2019) Changing salinity gradients in the Baltic Sea as a consequence of altered freshwater budgets. Geophys Res Lett 46:9739–9747

Kokko H, Helle E, Lindström J, Ranta E, Sipilä T, Courchamp F (1999) Backcasting population sizes of ringed and grey seals in the Baltic and Lake Saimaa during the 20th century. Ann Zool Fenn 36:65–73
Kristiansen T, Aas E (2015) Water type quantification in the Skagerrak, the Kattegat and off the Jutland west coast. Oceanologia 57:177–195
Lehmann A, Myrberg K (2008) Upwelling in the Baltic Sea — a review. J Mar Syst 74:S3–S12
Leppäranta M, Myrberg K (2009) Physical oceanography of the Baltic Sea. Springer-Verlag, Berlin
Lowry LF, Frost KJ, Ver Hoef JM, DeLong RA (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mamm Sci 17: 835–861
Lundström K, Carlsson AM, Karlsson M, Mion M, Eriksson P, Ahola MP (2025) The reintroduction of grey seal hunting in Sweden — a review of hunting and seal population data (2001–2024). NAMMCO Sci Publ 14: 3.8086
Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical analysis and design for field studies. Kluwer Academic Publishers, Dordrecht
Marra G, Wood SN (2012) Coverage properties of confidence intervals for generalized additive model components. Scand J Stat Theory Appl 39:53–74
Matthiopoulos J, Fieberg J, Aarts G, Barraquand F, Kendall BE (2020) Within reach? Habitat availability as a function of individual mobility and spatial structuring. Am Nat 195:1009–1026
Maúre ER, Terauchi G, Ishizaka J, Clinton N, DeWitt M (2021) Globally consistent assessment of coastal eutrophication. Nat Commun 12:6142
McCarthy ML, Cammen KM, Granquist SM, Dietz R and others (2025) Range-wide genomic analysis reveals regional and meta-population dynamics of decline and recovery in the grey seal. Mol Ecol 34:e17824
McConnell BJ, Fedak MA, Lovell P, Hammond PS (1999) Movements and foraging areas of grey seals in the North Sea. J Appl Ecol 36:573–590
Meier HEM, Eilola K, Almroth-Rosell E, Schimanke S and others (2019) Disentangling the impact of nutrient load and climate changes on Baltic Sea hypoxia and eutrophication since 1850. Clim Dyn 53:1145–1166
Meier HEM, Kniebusch M, Dieterich C, Gröger M and others (2022) Climate change in the Baltic Sea region: a summary. Earth Syst Dyn 13:457–593
Miethe T, Gröhsler T, Böttcher U, von Dorrien C (2014) The effects of periodic marine inflow into the Baltic Sea on the migration patterns of Western Baltic spring-spawning herring. ICES J Mar Sci 71:519–527
Moll D, Asmus H, Blöcker A, Böttcher U and others (2024) A climate vulnerability assessment of the fish community in the Western Baltic Sea. Sci Rep 14:16184
Moore SE (2008) Marine mammals as ecosystem sentinels. J Mammal 89:534–540
Nian R, Yuan Q, He H, Geng X, Su CW, He B, Lendasse A (2021) The identification and prediction in abundance variation of Atlantic cod *via* long short-term memory with periodicity, time-frequency co-movement, and lead-lag effect across sea surface temperature, sea surface salinity, catches, and prey biomass from 1919 to 2016. Front Mar Sci 8:665716
Northrup JM, Hooten MB, Anderson CR, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463
Nowak BVR, Bowen WD, Lidgard DC, Den Heyer CE (2025) Habitat fidelity of adult grey seals over multiple years in a changing marine ecosystem. Mov Ecol 13:82
Oksanen SM, Ahola MP, Lehtonen E, Kunnasranta M (2014) Using movement data of Baltic grey seals to examine foraging-site fidelity: implications for seal–fishery conflict mitigation. Mar Ecol Prog Ser 507:297–308
Olsen MT, Andersen LW, Dietz R, Teilmann J, Härkönen T, Siegismund HR (2014) Integrating genetic data and population viability analyses for the identification of harbour seal (*Phoca vitulina*) populations and management units. Mol Ecol 23:815–831
Olsen MT, Galatius A, Härkönen T (2018) The history and effects of seal–fishery conflicts in Denmark. Marine Ecology Progress Series 595:233–243
Perelman JN, Ladroit Y, Escobar-Flores P, Firing E, Drazen JC (2023) Eddies and fronts influence pelagic communities across the eastern Pacific ocean. Prog Oceanogr 211:102967
Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton, NJ
Pomeroy PP, Twiss SD, Redman P (2000) Philopatry, site fidelity and local kin associations within grey seal breeding colonies. Ethology 106:899–919
R Core Team (2025) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Randall DJ (1970) Gas exchange in fish. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol 4: The nervous system, circulation, and respiration. Academic Press, San Diego, CA, p 253–292
Reusch TBH, Dierking J, Andersson HC, Bonsdorff E and others (2018) The Baltic Sea as a time machine for the future coastal ocean. Sci Adv 4:eaar8195
Riaz J, Nilssen KT, Biuw M, Moland E, Poltermann M, Kristiansen M, Freitas C (2026) Haul-out site use and connectivity of harbour seals between management units in southern Scandinavia. Ecol Evol 16:e72718
Rosciszewski-Dodgson MJ, Cirella GT (2024) Environmental drivers affecting the status of top commercial fish stocks in the Baltic Sea: review. Front Mar Sci 11:1399707
Russell DJF, McConnell B, Thompson D, Duck C, Morris C, Harwood J, Matthiopoulos J (2013) Uncovering the links between foraging and breeding regions in a highly mobile mammal. J Appl Ecol 50:499–509
Scharff-Olsen CH, Galatius A, Teilmann J, Dietz R and others (2019) Diet of seals in the Baltic Sea region: a synthesis of published and new data from 1968 to 2013. ICES J Mar Sci 76:284–297
Schoener TW (1968) Anolis lizards of Bimini — resource partitioning in a complex fauna. Ecology 49:704–726
SCOS (2014) Scientific advice on matters related to the management of seal populations: 2014. University of St Andrews. https://www.smru.st-andrews.ac.uk/files/2016/08/SCOS-2014.pdf
Sjöberg M, Ball JP (2000) Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? Can J Zool 78: 1661–1667
Søndergaard NO, Joensen AH, Hansen EB (1976) Sælernes

forekomst og sæljagten i Danmark. Dan Vildtunders 26: 1–80
Sonne C, Siebert U, Gonnsen K, Desforges JP and others (2020) Health effects from contaminant exposure in Baltic Sea birds and marine mammals: a review. Environ Int 139:105725
Stramma L, Prince ED, Schmidtko S, Luo JG and others (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat Clim Change 2:33–37
Svedäng H (2023) The development of fish stocks and fisheries in the Baltic Sea since the last glaciation. Oxford Research Encyclopedia of Climate Science. Oxford University Press, Oxford
Teilmann J, Galatius A (2018) Harbor seal *Phoca vitulina*. In: Würsig B, Thewissen JGM, Kovacs K (eds) Encyclopedia of marine mammals, 3rd edn. Elsevier, San Diego, CA, p 451–455
Thompson D, Duck CD, Morris CD, Russell DJF (2019) The status of harbour seals (*Phoca vitulina*) in the UK. Aquat Conserv 29:40–60
Thompson PM, McConnell BJ, Tollit DJ, Mackay A, Hunter C, Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. J Appl Ecol 33:1572–1584
van Beest FM, Teilmann J, Hermannsen L, Galatius A and others (2018) Fine-scale movement responses of free-ranging harbour porpoises to capture, tagging and short-term noise pulses from a single airgun. R Soc Open Sci 5: 170110
van Beest FM, Mews S, Elkenkamp S, Schuhmann P and others (2019) Classifying grey seal behaviour in relation to environmental variability and commercial fishing activity — a multivariate hidden Markov model. Sci Rep 9:5642
van Beest FM, Dietz R, Galatius A, Kyhn LA, Sveegaard S, Teilmann J (2022) Forecasting shifts in habitat suitability of three marine predators suggests a rapid decline in inter-specific overlap under future climate change. Ecol Evol 12:e9083
van Meurs E, Moland E, Bjørge A, Freitas C (2024) Haulout patterns of harbour seal colonies in the Norwegian Skagerrak, as monitored through time-lapse camera surveys. Diversity (Basel) 16:38
van Rij J, Wieling M, Baayen RH, van Rijn D (2022) itsadug: interpreting time series and autocorrelated data using GAMMs. R package version 2.5. https://cran.r-project.org/package=itsadug (accessed 28 March 2025)
Vance HM, Hooker SK, Mikkelsen L, van Neer A, Teilmann J, Siebert U, Johnson M (2021) Drivers and constraints on offshore foraging in harbour seals. Sci Rep 11:6514
von Nordheim H, Maschner K, Liebschner A (2011) Die Rückkehr der Kegelrobben an die deutsche Ostseeküste. Meer Mus 23:237–250
Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883
Warton D, Aarts G (2013) Advancing our thinking in presence-only and used-available analysis. J Anim Ecol 82: 1125–1134
Westphal L, Klemens L, Reif F, van Neer A, Dähne M (2023) First evidence of grey seal predation on marine mammals in the German Baltic Sea. J Sea Res 192:102350
Wiens TS, Dale BC, Boyce MS, Kershaw GP (2008) Three way *k*-fold cross-validation of resource selection functions. Ecol Model 212:244–255
Wilson L, Hammond P (2016) Comparing the diet of harbour and grey seals in Scotland and eastern England. Sea Mammal Research Unit Report to Scottish Government. Scottish Marine and Freshwater Science Vol 7, No. 19. Marine Scotland Science, Scottish Government. https://doi.org/10.7489/1798-1
Wood S (2020) mgcv: mixed GAM computation vehicle with automatic smoothness estimation. Version 1.9-1. https://rdrr.io/cran/mgcv/ (accessed 3 October 2024)

*Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA*
*Reviewed by: A. Lowther and 1 anonymous referee*
*Submitted: January 10, 2026; Accepted: May 6, 2026*
*Proofs received from author(s): August 10, 2026*