Biological Conservation 302 (2025) 111009

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Shifts in habitat suitability for harbour porpoises leads to reduced importance of marine protected areas

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ARTICLE INFO

Keywords:
Marine spatial planning
Maximum entropy
Natura2000
Phocoena phocoena

ABSTRACT

Marine ecosystems across the globe are under pressure requiring evaluations of whether marine protected areas (MPAs) remain effective in safeguarding marine life and critical habitats. Our objectives were to 1) estimate shifts in seasonal habitat suitability over a 25-year period (1997–2022) for the harbour porpoise (*Phocoena phocoena*) across the North Sea–Baltic Sea transition zone, and 2) quantify any spatiotemporal changes in the overlap between suitable habitats and an existing network of 62 MPAs (an area covering 16,404 km^2) dedicated to harbour porpoise protection. Habitat suitability was estimated using the maximum entropy (MaxEnt) algorithm, based on satellite tag data of 111 individuals and a range of dynamic and static environmental conditions as predictor variables. Model output revealed a northward shift of medium and high suitable habitats during winter (Nov–Apr) over the study period. Changes in habitat suitability during summer (May–Oct) were also evident though without clear directional shifts. A maximum of 14.5 % of the MPAs ($n = 9$; area of 1096 km^2) were found to overlap with highly suitable habitat during the summers of 2005–2012, with a minimum of 6.4 % ($n = 4$ MPAs; area of 194 km^2) during the winters of 2013–2022. These results clearly indicate a decline in the spatiotemporal overlap between habitat suitability during winter and the location of MPAs dedicated to harbour porpoise protection in the North Sea–Baltic Sea transition zone. The model output may inform effective design of forthcoming MPAs under the EU Biodiversity Strategy for 2030.

1. Introduction

Marine ecosystems across the globe are under growing pressure from human activities (Halpern et al., 2015; Korpinen et al., 2021) and climate change (Barnett et al., 2005; Doney et al., 2012). These pressures can have detrimental impacts on animal populations, biodiversity, and ecosystem functioning (Estes et al., 2011; Rocha et al., 2015). An important goal of the establishment of marine protected areas (MPAs) is to mitigate the decline of biodiversity by protecting important habitats and representative samples of marine life, thereby maintaining the resilience of ecosystems (Grorud-Colvert et al., 2021). Top predators, including marine mammals, are considered sentinels of habitat and ecosystem stability as they respond to shifts in abundance and distribution of prey at lower levels of the food-web, as well as environmental changes over large spatial and temporal scales (Hazen et al., 2019). As such, quantifying spatiotemporal dynamics in habitat suitability of marine mammals contributes to our understanding on how ecosystems respond to environmental change. Moreover, habitat suitability maps are valuable products to guide decision making in marine spatial planning, for example by informing on the design and placement of new MPAs (Bailey and Thompson, 2009; Embling et al., 2010). However, given the rapid rate of change in marine conditions and associated shifts in the distributions of both prey and predator species observed in recent years (Pinsky et al., 2020), there is a growing need to evaluate the effectiveness of already existing MPA networks in safeguarding marine life and critical habitat under changing conditions (Welch et al., 2018).

For marine predators, habitat suitability is primarily determined by availability of prey (Bennington et al., 2020; Benoit-Bird et al., 2013). Prey abundance in marine environments, in turn, is influenced by fisheries, pollution, and oceanographic gradients, such as sea temperature, salinity, nutrient concentrations, and physical forcing mechanisms, like fronts and eddies (Nian et al., 2021; Perelman et al., 2023). Species' responses to such environmental variability are often approximated through species distribution models (SDMs), which are common tools

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https://doi.org/10.1016/j.biocon.2025.111009
Received 22 October 2024; Received in revised form 14 January 2025; Accepted 29 January 2025

within ecology and conservation for assessing habitat suitability (Elith and Leathwick, 2009; Guisan et al., 2013). Conceptually rooted in ecological niche theory (Guisan and Zimmermann, 2000), SDMs are statistical techniques aimed at identifying the environmental conditions that species use and rely on to meet their ecological requirements (Peterson et al., 2011). For harbour porpoises (*Phocoena phocoena*), a small marine predator ranging across the cold to temperate coastal waters of the Northern Hemisphere (Read, 1999), both static variables (e.g. bathymetry, seabed sediment) and dynamic variables (e.g. currents, sea temperature and salinity) have been shown to influence habitat suitability and distribution patterns (Carlén et al., 2018; Chavez-Rosales et al., 2019; Edrén et al., 2010; Gilles et al., 2016).

In this study, we estimated spatiotemporal changes in habitat suitability of harbour porpoises across the North Sea–Baltic Sea transition zone, an area impacted by multiple human stressors (Andersen et al., 2020) and climate change (Meier et al., 2022). We then quantified temporal changes in the amount and extent of suitable habitat within an existing network of 62 MPAs designated for harbour porpoise protection under the Habitats Directive (EU, 1992). To do so, we capitalized on a long-term (1997–2022) movement dataset of 111 harbour porpoises fitted with satellite telemetry tags to estimate habitat suitability using the maximum entropy machine learning algorithm (MaxEnt: Phillips et al., 2006). Outlines of MPAs were then superimposed on habitat suitability maps to quantify any shifts in the amount of suitable porpoise habitat under protection over time. Given the pressures and environmental changes occurring in the study area, we expected habitat suitability of porpoises to have shifted over time and space with a direct effect on the amount of overlap between the existing network of MPAs and highly suitable habitat of this species.

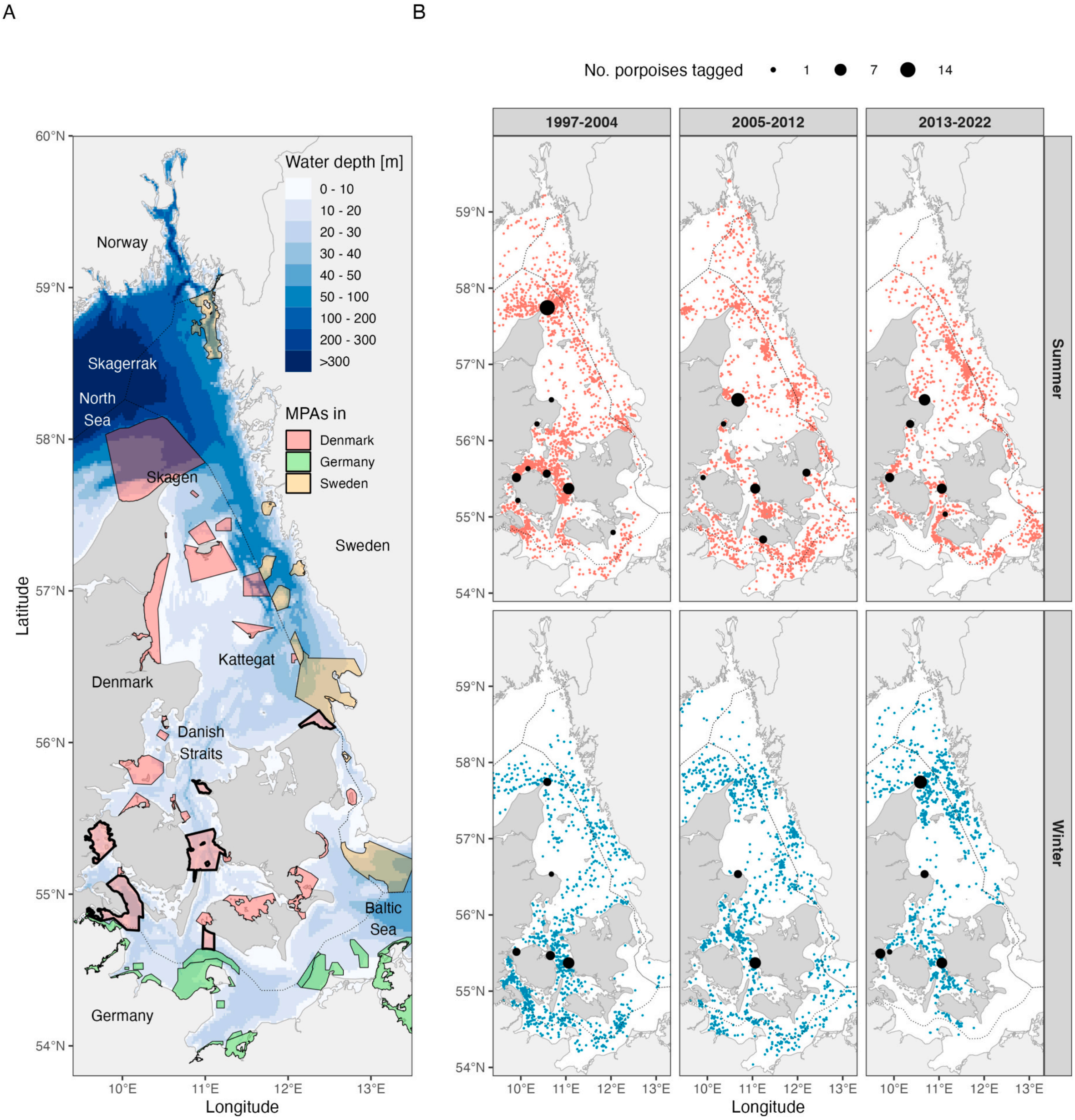

Fig. 1. Overview of the study area with panel A showing bathymetry and the outlines of 62 MPAs established in Danish (pink polygons), Swedish (blue polygons), and German (green polygons) waters designated to harbour porpoise protection. The six MPAs in Danish waters with thick black outline indicate MPAs that are monitored for changes in porpoise density under the NOVANA program using passive acoustic monitoring. Panel B shows Argos location data of 111 harbour porpoises used in this study with black circles indicating the location and number of individuals tagged per period and season. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Study area

The study area is considered a transition zone as it is located between, and influenced by, two marine systems (North Sea and Baltic Sea) with distinct hydrological properties (Andersen et al., 2020). Specifically, the study area (70,145 km^2) extends from the Skagerrak at the eastern part of the North Sea to the southwestern part of the Baltic Sea, including the Danish Straits and the Kattegat (9–13.5°E, 54–59.75°N: Fig. 1A). Most of the study area has shallow waters ($<$60 m) with a relatively flat seabed surface, but depths down to 700 m with steeper seabed slopes do occur in the Norwegian Trench of Skagerrak (Fig. 1A). Sediment types in the shallow areas are a mixture of sand, mud, and hard bottom complex, while mud and bedrock dominate the deeper areas of Skagerrak. Sea surface temperature and salinity vary across seasons but generally decline from north to south. This is due to a relatively warm and high saline Atlantic bottom current that flows from the North Sea into the Danish Straits, and a colder brackish surface current flowing out of the Baltic Sea. This causes an estuarine-like circulation with a permanent halocline located at around 15 m depth in the Kattegat and Danish Straits (Andersson and Rydberg, 1993).

Harbour porpoises reside in the study area year-round where they are divided into two populations, the so-called North Sea population (residing in the North Sea and Skagerrak) and the Belt Sea population (residing in Kattegat, the Belt Seas and the southwestern Baltic), a division that has probably evolved as a result of the changing environmental conditions and exploitation of different prey species (Sveegaard et al., 2015). Harbour seals (*Phoca vitulina*) and Baltic grey seals (*Halichoerus grypus*) also occur in the area (Dietz et al., 2013; Galatius et al., 2020) but the harbour porpoise is the most abundant marine mammal with an estimated stable population size of approximately 340,000 individuals across the entire North Sea management unit (Gilles et al., 2023) and a decreasing population of ca. 14,000 individuals in the Belt Sea management unit as estimated in 2022 (Owen et al., 2024).

In the EU, all relevant member states are legally obliged to protect the harbour porpoise by designating MPAs, referred to as Special Areas of Conservation (SAC) or Natura 2000 sites according to the EC Habitat Directive (92/43/EEC 1992). The study area is divided between Norway, Sweden, Denmark and Germany. As Norway is not an EU member state, no SACs or other MPAs are designated in Norwegian waters within the study area. A total of 62 SACs covering an area of 16,404 km^2 across the study area are designated in Sweden (11), Denmark (30) and Germany (21), to protect the harbour porpoises (Fig. 1A) Most of these MPAs also serve to protect other marine species (e.g. seals and seabirds) and important habitat types (e.g. reefs, mudflats, and sandbanks). Regulations in the region to protect harbour porpoises are primarily aimed at reducing bycatch in gillnet fisheries, which is considered a major threat to the resident populations (Owen et al., 2024). Specifically, regulations prohibit the use of bycatch related fishing gear during most of the year in all Swedish and German waters in the study area and the southeastern part of Danish waters (2022/303 EEC, 2021; 2022/952 EEC, 2022).

2.2. Location data

Location data from tracked harbour porpoises were collected over the period 1997–2022 as part of a long-term satellite telemetry monitoring program in Denmark (Stalder et al., 2020; Sveegaard et al., 2011; Teilmann et al., 2007). Individual harbour porpoises were fitted with Argos satellite tags after being incidentally trapped in pound nets, which are used in near-shore commercial fisheries in the Inner Danish waters. A detailed description of how individuals were captured, handled, and tagged is available elsewhere (Sveegaard et al., 2011; Teilmann et al., 2007; van Beest et al., 2018a,b). Argos tags were programmed to make a limited number of daily satellite uplinks and acquire a location at predefined times (time of day and duty cycles) to increase the battery lifetime. Duty cycles of the tags varied between 1 and 4 days. Preprocessing of location data included filtering out unlikely locations using the Argos-Filter v7.03 (Sveegaard et al., 2011) and the removal of locations on land and those collected within 24 h after tagging to reduce behavioural bias caused by capture and tagging (van Beest et al., 2018b). After the data cleaning process, 9345 locations collected by 111 harbour porpoises were included in this study with an average tracking duration of 118.5 days per individual (min = 8 days, max = 522 days).

Location data were categorized into periods of six months: May–Oct (summer) or Nov–Apr (winter). This division separates distinct phases in the annual reproductive cycle of harbour porpoises, with mating and calving peaking in the summer months, followed by energetically costly lactation in the winter months (Lockyer, 2007). Moreover, the seasonal division corresponds with shifts in distribution patterns of porpoise populations in adjacent waters (Carlén et al., 2018). Location data were further classified into three multi-year periods (1997–2004, 2005–2012 and 2013–2022) to assess shifts in habitat suitability over time (Fig. 1B). Delineation of these temporal scales was chosen to obtain approximately the same number of locations and number of porpoises in different seasons and multi-year periods (Fig. S1 in the Supporting Information).

2.3. Environmental data

We considered eight environmental variables (Table 1) that were expected to influence habitat suitability of harbour porpoises (Edrén et al., 2010; Gilles et al., 2016; Isojunno et al., 2012). These included static environmental variables: “bathymetry” (m), “seabed slope” (°) and “sediment type” (categorical variable including sand, mud, bedrock and hard bottom complex) (Fig. S2) and dynamic environmental variables: “current velocity” (m/s), “mixed layer thickness” (m), “sea surface salinity” (PSU), “sea surface height” (m), and “sea surface temperature” (°C). The five dynamic environmental variables were downloaded as raster layers from the Copernicus Marine Environmental Monitoring Service as daily estimates produced by the Baltic Sea Physical Reanalysis modelling product. This product provides daily maps of the physical conditions for the whole Baltic Sea area, including the transition zone to the North Sea. Layers of daily estimates were subsequently used to calculate period- and season-specific mean and standard deviation (SD) layers for each variable (Figs. S3–S8). The SD of each variable was

Table 1
Overview of the environmental variables, their units, the original resolution of the raster data, and the source of data download. For the five dynamic variables downloaded from Copernicus, layers of daily estimates were used to calculate period- and season-specific mean and standard deviation (SD) layers. Thus, a total of 13 variables were considered as potential predictors in the analyses.

Variable	Unit	Original resolution	Source[1,2,3]
Bathymetry	m	500 m	HELCOM
Seabed slope		500 m	Calculated from bathymetry data in R package “terra” (Hijmans et al., 2024)
Sediment type	4-class factor	150 m	EMODnet
Sea surface current velocity	m/s	1800 m	Copernicus
Mixed layer thickness	m	1800 m	Copernicus
Sea surface salinity	PSU	1800 m	Copernicus
Surface height	m	1800 m	Copernicus
Sea surface temperature	°C	1800 m	Copernicus

[1] HELCOM: https://metadata.helcom.fi/.
[2] EMODnet: https://emodnet.ec.europa.eu/en/seabed-habitats.
[3] Copernicus: doi:10.48670/moi-00012.

calculated to allow within-season variation in environmental conditions to influence harbour porpoise habitat suitability (Gilles et al., 2016). Thus, with three static variables and the mean and SD of five dynamic variables, a total of 13 candidate covariates were considered for the period- and season-specific habitat suitability models. Importantly, the tagged harbour porpoises spent most of their time in waters shallower than 200 m (Fig. 1 and Fig. S9). Therefore, we ran an additional set of habitat suitability analyses in which we excluded areas with waters deeper than 200 m and compared model fit to the set of models with the entire bathymetry range. Because layers from the different sources had variable spatial resolution (i.e. cell size; Table 1), bilinear resampling was used where needed to ensure that all raster layers had a spatial resolution of 1 km^2.

2.4. Habitat suitability analyses

Habitat suitability of harbour porpoises was estimated through the machine learning algorithm maximum entropy (MaxEnt: Phillips et al., 2006). MaxEnt belongs to a broad class of numerical SDMs that contrast environmental or climatic conditions at species occurrence sites with conditions across the landscape (Elith and Leathwick, 2009). The output of MaxEnt models can be interpreted as a spatially explicit probability of species presence (0 = absent, 1 = present) or habitat suitability (0 = unsuitable habitat, 1 = optimal habitat). MaxEnt is particularly suited for presence-only data with relatively small sample sizes, which is often the case in tagging studies (Elith et al., 2006). We constructed separate MaxEnt models for each season and period (six models in total) using the pruning and variable selection procedures outlined below.

Presence data in the MaxEnt models were harbour porpoise locations collected in the study area using Argos tags between 1997 and 2022 (Fig. 1). An important assumption of SDM studies is that sampling of location data is adequate and representative, which we could not determine here given the rather opportunistic nature of where in the study area and how many harbour porpoises were tagged over the sampling years and seasons. To address this issue, background points (10000) in each model were generated using spatial sampling bias files (Fig. S10) to increase the probability of sampling background locations in geographic areas where species occurrences were highest, which is expected to improve model predictions (Merow et al., 2013; Phillips et al., 2009). Spatial sampling bias files were constructed for each model separately by computing a Gaussian kernel density raster (Brown, 2014; Inman et al., 2021) of all harbour porpoise locations. Gaussian kernel density rasters were created using period-specific vectors of bandwidths (h) in both x and y directions, which were calculated using the normal reference technique (Kernohan et al., 2001).

Multicollinearity among the 13 candidate predictor variables was substantial with variance inflation factor > 20 and Spearman's rho >0.7 for various variable combinations. As we had no a priori knowledge of which of the correlated predictor variables were most influential in describing habitat suitability, we employed a completely data-driven variable selection approach through the 'SDMtune' package (Vignali et al., 2020) in the statistical software program R (R Development Core Team, 2024). This approach selects the variable that best fits the data (using Akaike Information Criterion value corrected for small sample sizes: AICc) among those that are highly correlated, here using a threshold of Spearman's rho ≥ 0.7. Starting from a trained model with all variables included, the function checks if the variable ranked as the most important (i.e. highest percent contribution) is correlated with any of the other variables. If this was the case, a leave-one-out Jackknife test was performed, starting with the full model, and among all correlated variables, the one variable that decreased model fit the most was discarded. A new model was then trained without this variable, which was again checked for highly correlated variables. The process was repeated until the pairwise correlations among all retained variables had Spearman's rho <0.7. Through this iterative procedure, five of the initial 13 predictor variables were subsequently dropped from further model development: the means of "sea surface salinity" and "sea surface temperature", the mean and SD of "sea surface height" and the SD of "current velocity".

To protect against overfitting and to reduce model complexity, MaxEnt uses regularization multiplier values (RMs) (Phillips et al., 2006). RMs give a penalty for each term included in the model and the strength of the penalty should be estimated for each unique dataset (Merow et al., 2013). Here, we tested different settings of RMs in the range 0.5–5.0 with increments of 0.5 for each feature class through the 'ENMeval' package in R (Kass et al., 2021; Muscarella et al., 2014). Moreover, we restricted all possible features to 'linear', 'quadratic' and 'linear & quadratic' functions to avoid overly complex response curves that would be difficult to explain ecologically. During this model structure pruning procedure, potential spatial autocorrelation in the location data was accounted for as much as possible by implementing the 'block' partitioning method. Here, occurrence locations were partitioned into four equal geographic blocks with models being trained using k-1 blocks and evaluated on the withheld bin. Background localities were restricted to blocks corresponding to the occurrence data. Such 'masked geographically structured' data partitioning approaches are expected to yield more realistic predictions than random and unmasked spatial partitioning (Radosavljevic and Anderson, 2014). The amount of overfitting for each candidate model was subsequently quantified by calculating the '10% training omission rate' (OR_{10}). Omission rates >10 % typically indicate model overfitting (Muscarella et al., 2014). From the candidate models, we selected the optimal model settings (i.e. RM and feature class) using two sequential criteria (Kass et al., 2021). First, we filtered candidate models with $OR_{10} < 10$ % and then selecting the model structure with the highest predictive performance as determined by the area under the receiver operating characteristic curve (AUC) value. Results of the model structure pruning procedure are provided in Table S1. Results of the model structure pruning procedure when considering a cut-off value for bathymetry at -200 m are provided in Table S2. Models with a cut-off value for bathymetry performed poorer in terms of AUC (predictive performance) and OR_{10} (overfitting) values. Therefore, we did not pursue these models further.

Once the optimal model settings were identified for each season and period, we reran the models 100 times with each iteration using a randomly drawn subset of the presence locations (80 %), using the remaining 20 % of presence locations for testing predictive performance (AUC) and to confirm lack of overfitting (OR_{10}). All model iterations had AUC > 0.75 and most had $OR_{10} < 0.1$ (Fig. S11), which are threshold values indicative of good predictive performance without model overfitting (Elith et al., 2006). Moreover, the AUC values for each model were higher than those from corresponding null models and the OR_{10} values were generally lower than those from corresponding null models (Fig. S11), indicating that the MaxEnt models predicted better than random and were not biased by overfitting (Bohl et al., 2019).

Finally, prediction rasters were created for each of the 100 MaxEnt model iterations by mapping the model-based probability of harbour porpoise habitat suitability across the study area. From these, we calculated season- and period-specific mean habitat suitability layers, as well as prediction uncertainty layers. The mean habitat suitability layers were calculated using the AUC values of each iteration as a weighting function. Prediction uncertainty was estimated by calculating the coefficient of variation (CV: range of 0–100 %) of the mean habitat suitability layers, with increased CV values indicating areas with increased uncertainty in the predicted mean habitat suitability layer for a specific season and period.

2.5. Spatiotemporal dynamics in habitat suitability

To assess changes in habitat suitability over time and space, we first defined and set thresholds for high, moderate, or low suitable habitat for harbour porpoises. Numerous thresholds exist to classify output of habitat suitability models (Liu et al., 2005). Here, we used two complementary SDM thresholds that, in a comparative study, have been identified to perform best under a presence-only study design (Liu et al., 2013), which is the case for this study. These thresholds were Kappa (the value of model output at which accuracy is highest) and MSSS (maximum sum of the sensitivity and specificity) and were extracted directly from the complementary log-log (cloglog) output of all 100 iterations of each MaxEnt model. The full range in habitat suitability threshold values for each model period are provided in Fig. S12. However, to facilitate comparison of spatial shifts in habitat suitability classes over time we only considered the mean Kappa and MSSS values calculated across all model periods. As a result, we categorized habitat suitability as follows: areas with predicted habitat suitability values above 0.751 (mean Kappa value) were considered highly suitable, predicted values between mean Kappa and 0.571 (mean MSSS value) were considered moderately suitable habitat, while areas with predicted values below mean MSSS values were considered habitat of low suitability.

Shifts in habitat suitability over time and across the entire study area were then quantified by calculating, for each model iteration and habitat suitability class, the centroid weighted mean latitude, the total area size (km^2), and the level of habitat connectivity (unitless) (Clark and Evans, 1954). For the latter, we relied on the nearest neighbour index (NNI) where NNI >1 indicate a clustered pattern (i.e. high connectivity) and NNI <1 indicate dispersion of habitat (i.e. low connectivity).

2.6. *Overlap between MPAs and harbour porpoise habitat suitability*

A shapefile with the outlines of all MPAs within the study area dedicated to porpoise protection was overlaid on the MaxEnt-based habitat suitability maps. We then calculated the weighted mean predicted habitat suitability values of all grid cells within each MPA. Combining these values with the habitat suitability thresholds (Kappa and MSSS), we were able to quantify how many MPAs were effectively positioned to protect highly suitable and moderately suitable porpoise habitat in each of the two seasons and the three model periods.

Finally, we averaged the six season- and period-specific habitat suitability maps into one raster layer (weighted by the models AUC value), to derive a long-term, season independent habitat suitability map for the entire study area. From this layer, we extracted all cells that were above the habitat suitability threshold of Kappa to identify areas with long-term highly suitable habitat in the study area. The same was done for cells above the threshold MSSS to identify areas with long-term moderate suitable porpoise habitat. We then compared the placement and total area size (km^2) of the current MPA network to those areas identified as moderate and highly suitable habitat identified with the long-term habitat suitability map.

3. Results

3.1. *Variable importance and response curves of habitat suitability*

Variable importance of the eight predictors differed between model periods and seasons (Fig. S13) with none of the predictor variables being consistently important in explaining habitat suitability over time (i.e. permutation or contribution of >20 %). Specifically, the percent contribution (i.e. amount of explained variance contributed to the model) of the parameter ‘standard deviation of surface temperature’ was >60 % in the summer model for the period 1997–2004, but the contribution declined to <10 % in the following model periods. Permutation importance (i.e. percent contribution to the model AUC value) of the parameter ‘standard deviation of surface salinity’ increased from 20 % in the winter 1997–2004 model to >50 % in the model period 2013–2022. Seabed slope was the only predictor with variable importance values <20 % across all six model periods (Fig. S13).

Response curves of the MaxEnt model outputs (Fig. S14) indicated that harbour porpoise habitat suitability decreased with increasing bottom depth (bathymetry) in both seasons and all model periods. Habitat suitability also decreased with increasing variation in sea surface temperature, but the effect was stronger in the winter models than in the summer models. In contrast, habitat suitability was positively correlated with ‘mean mixed layer thickness’ and ‘standard deviation of surface salinity’. The covariate ‘mean current velocity’ had no apparent relation (slope of response curve = 0) to habitat suitability during the early model period (1997–2004), but habitat suitability decreased with increasing current velocity during summer months in later years. The oppositive effect, i.e. habitat suitability increased with increasing current velocity, was detected during winter months in 2005–2012 and 2013–2022. Habitat suitability also varied depending on the seabed sediment type, with habitat suitability being generally lowest and most variable in areas with exposed bedrock and highest in areas with mud or sand, though this effect differed between model periods. Corroborating the results of the variable importance above, the covariate ‘seabed slope’ had no apparent relation to habitat suitability in most of the model iterations (Fig. S14).

3.2. *Spatiotemporal dynamics in habitat suitability*

Mapping of MaxEnt model outputs revealed contrasting seasonal shifts in habitat suitability (Figs. 2 & 3). Specifically, habitat suitability during summer was variable over time and space with an increase in MaxEnt model estimates in some sites by >0.6 on the cloglog scale between the periods 1997–2004 and 2005–-2012 (Fig. 2B), followed by a decrease in suitability of ca. 0.3 on the cloglog scale between the periods 2005–2012 and 2013–2022 (Fig. 2B). Despite these dynamic patterns in summer habitat suitability, no marked directional shifts were detected for high and medium suitability classes in terms of their latitudinal placement, spatial extents (i.e. area size in km^2) and connectivity (Fig. 3). In contrast, habitat suitability during winter consistently declined over time in the southern half of the study area (<56°N), with a reduction of nearly 0.5 on the cloglog scale in suitability in some sites (Fig. 2B). In parallel, winter habitat suitability in the northern half of the study area (>56°N) generally increased between model periods (Fig. 2B). This latitudinal shift in winter habitat suitability was detected for both highly suitable and medium suitable habitat classes (Fig. 3A). The spatial extents (i.e. area size in km^2) and connectivity index of the winter habitat suitability classes did not, however, show any consistent directional changes between model periods (Fig. 3).

Mapping the CV of MaxEnt model output revealed that the uncertainty in predicted habitat suitability was <5 % across most of the study area (Fig. S15). The highest uncertainty in model predictions (CV > 20 %) were consistently found in the deeper waters of the Norwegian Trench of Skagerrak and along coastlines in areas with bedrock on the seabed floor (Fig. S15).

3.3. *Overlap between MPAs and harbour porpoise habitat suitability*

The average habitat suitability value across all 62 MPAs (covering a total area of 16,404 km^2) peaked in the summers of 2005–2012 with an estimate of 0.62 on the cloglog scale and was lowest in the winters of 2013–2022 with an estimate of 0.40 on the cloglog scale (Fig. 4). During summers in the period 1997–2004, an area of 1096 km^2 (6.8 % of the total protected area) with a total of nine MPAs (14.5 % of the total number of MPAs) were found to be overlapping with highly suitable harbour porpoise habitat (Figs. S16–S17). For all other model periods the overlap between MPAs and highly suitable habitat was lower, with an area size of 194 km^2 (1.1 % of the total protected area) with a total of four MPAs (6.4 % of the total number of MPAs) during winters in the period 2005–2012 (Figs. S16–S17). Overall, the majority of existing MPAs were found to be in areas estimated to have low or medium habitat suitability for harbour porpoises (Figs. S16–S17). Comparing the relative amount (% of area size) of the three habitat suitability classes

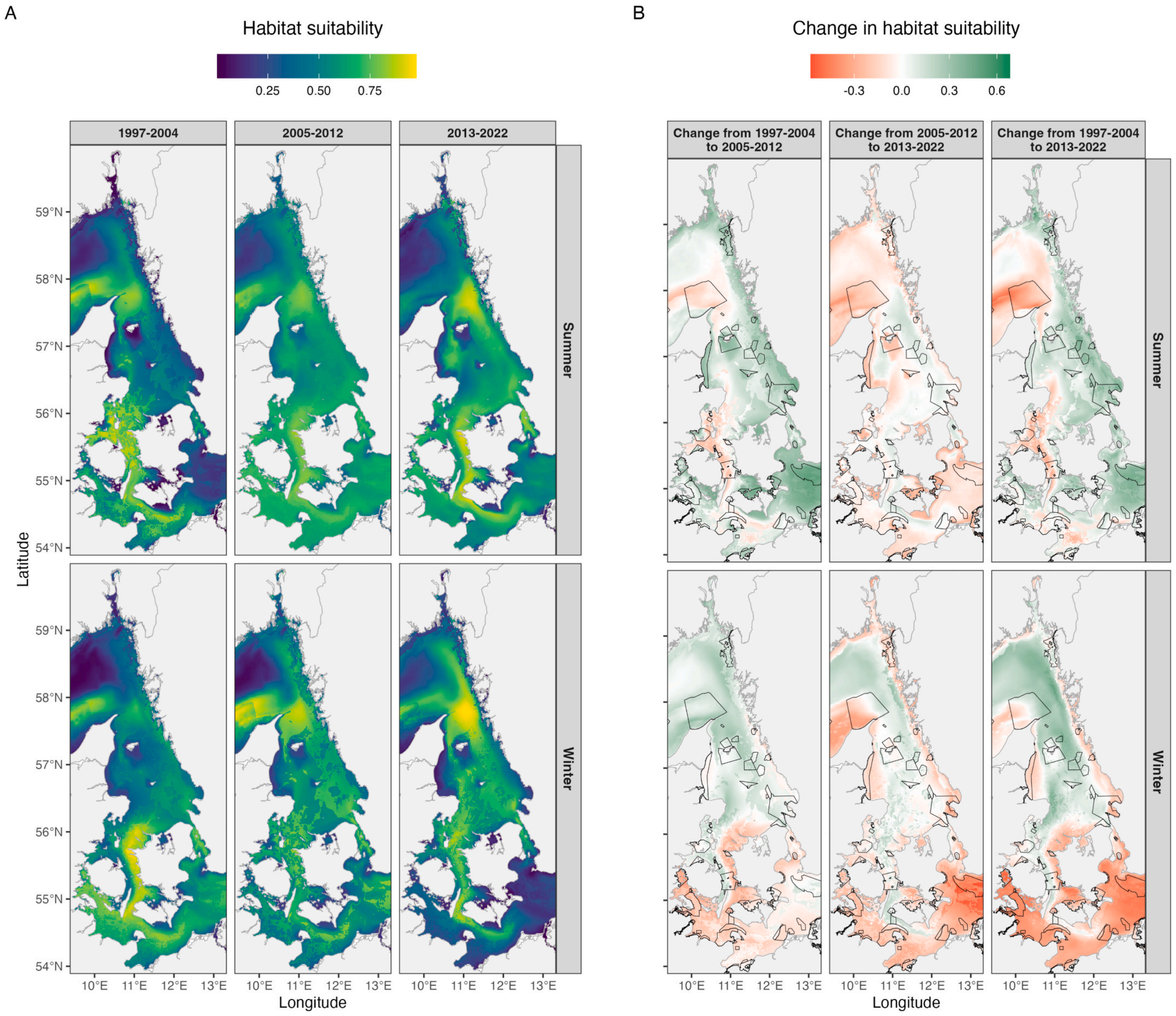

Fig. 2. Results of the MaxEnt analyses. Panel A shows maps of the predicted mean habitat suitability (cloglog) for harbour porpoises during summer (May–Oct) and winter (Nov–Apr) months in three model periods as derived from 100 MaxEnt model iterations using Argos-based location data collected in the North Sea–Baltic Sea transition zone. Habitat suitability ranges from 1 (optimal in yellow) to 0 (poor in dark blue). Panel B shows the change in habitat suitability over time and space as well as the outline of 62 MPAs (in black) dedicated to harbour porpoise protection in the area. Green refers to areas with increased habitat suitability over time, areas in white showed no change in habitat suitability between model periods, and red refers to areas with a decrease in habitat suitability over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

within the MPA network to the entire study area revealed that highly suitable winter habitat within the MPA network has declined over the different time periods at a faster rate than observed in the entire study area (Fig. S18). In parallel, the percentage of low suitable winter habitat has increased over time and at a faster rate than in the entire study area, but no such patterns were evident for summer habitat (Fig. S18).

Based on the long-term habitat suitability map (Fig. 5A), a total area of 5505 km^2 of highly suitable porpoise habitat was present in the study area, which increased to 21,946 km^2 when also including medium suitable habitat (Fig. 5B). Within the border of the MPAs, a total of 524 km^2 of highly suitable habitat and 5748 km^2 of high to medium suitable harbour porpoise habitat was present (covering a total area of 16,404 km^2). This suggests a 3 % to 35 % spatial overlap between the MPA network and areas predicted to be high and high to medium suitable habitat for harbour porpoises during the period 1997–2022, respectively.

4. Discussion

This study provides a unique insight into the spatiotemporal dynamics of habitat suitability for a small marine predator ranging across the North Sea–Baltic Sea transition zone. Most importantly, our models predicted a northward shift of suitable winter habitat and marked geographical oscillations in the suitability of summer habitat over the period 1997–2022. Despite these shifts, the extent (i.e. total area size) and connectivity of highly suitable habitat appeared relatively stable over the study period. Importantly, we also found that during the winter months the spatial overlap between highly suitable habitat and MPAs in the area has diminished over time and that the overall suitability of habitat within the borders of the MPA network dedicated to harbour porpoise protection has decreased.

During the 25 years covered by this study, the estimated population size of harbour porpoises in the Belt Sea has declined by about two

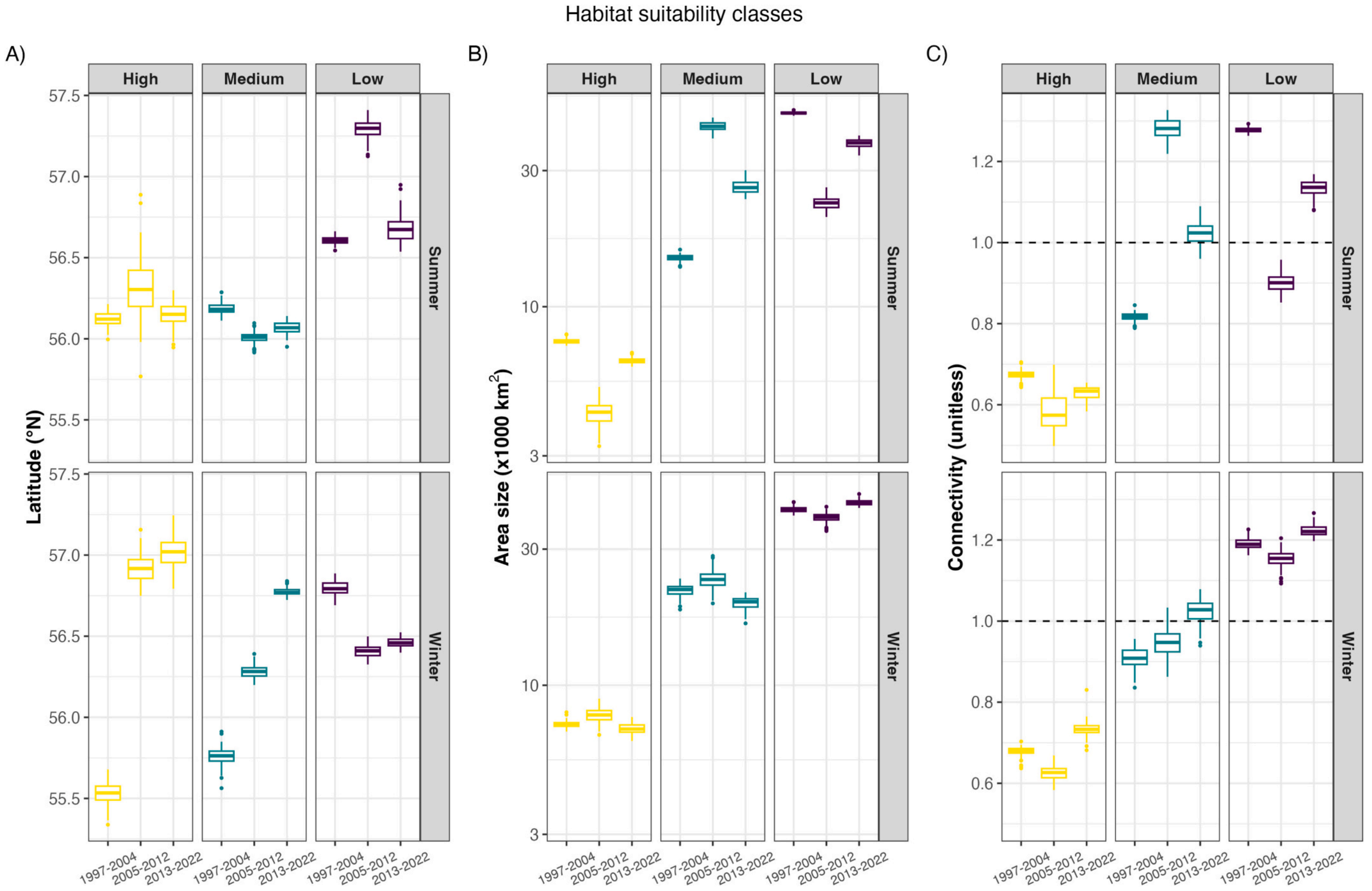

Fig. 3. Boxplots showing the output of 100 MaxEnt model iterations for each season and model period used to assess spatial and temporal changes in habitat suitability classes (high, medium, low as indicated by different colours) for harbour porpoises in the North Sea–Baltic Sea transition zone. Column A shows the variation in latitudinal positioning of habitat suitability classes over time, column B shows the variation in area size of habitat suitability classes over time, and column C shows changes in connectivity of habitat suitability classes over time. Connectivity values >1 indicate a clustered pattern (i.e., increasing connectivity), while values <1 indicate dispersion of habitat (i.e., decreasing connectivity).

thirds, likely due to unsustainable bycatch rates in gillnet fisheries (Owen et al., 2024), and a near collapse of important prey species' abundance and biomass, especially Atlantic cod (*Gadus morhua*) in the Kattegat and the Belt seas (ICES, 2022). These trends could be underlying causes of the geographic shifts in habitat suitability across the study area and the decline of porpoise habitat suitability during winter within MPAs detected here. Importantly, we were unable to include prey density or biomass as explanatory variables in our models. Despite dedicated efforts to generate species distribution models of marine fish species (Rufener et al., 2021), these data are not yet available in sufficiently fine resolution and across the large spatial and long temporal scales required for marine mammal species modelling. Instead, we relied on landscape-scale raster data of static and dynamic environmental forcing variables known to influence movement and habitat preference of harbour porpoises (Gilles et al., 2016; Stalder et al., 2020; van Beest et al., 2018a) but also of their prey (Lehtonen et al., 2016; Pécuchet et al., 2015). As such, we argue that the influence of prey species' abundance on harbour porpoise habitat suitability is to some extent incorporated in our models, yielding results that are informative and reliable. This is also supported by the fact that the predictive performance of our models was high with AUC > 0.75 (Elith et al., 2006) and the similarity in our model results during the period 1997–2004 compared to the first habitat suitability model based on tracking data of harbour porpoises by Edrén et al. (2010) despite differences in input data and model settings.

The model output presented here should be interpreted as long-term and landscape-scale dynamics in habitat suitability, and they do not necessarily correlate directly with activity or density of harbour porpoises at a local scale. For example, the Danish national monitoring program (NOVANA) uses passive acoustic monitoring in key harbour porpoise MPAs in the Belt Sea region to assess variations in their use (Hansen and Høgslund, 2023). These data (up until 2021) indicated that relative harbour porpoise density has increased in five out of six key MPAs (Fig. 1A), a trend that does not align with the model results of this study. In contrast, the decreasing trend in harbour porpoise abundance as estimated from aerial surveys in the MPA north of Skagen (Hansen and Høgslund, 2023) matches well with our model prediction of reduced habitat suitability in that area. Difficulties in correlating landscape-scale habitat suitability to local densities is a long-standing challenge in ecology (Brown, 1984; Edrén et al., 2010) and likely reflects that some habitat deemed suitable by our models may not (yet) be used extensively, while habitat currently experiencing high densities are predicted to be sub-optimal given the environmental conditions available in the entire region.

An important assumption of SDM studies is that sampling of location data is adequate and representative. Although the analysed harbour porpoise location dataset is the most extensive that currently exists for the North Sea-Baltic Sea region, our study may still suffer from a relatively low number of tagged harbour porpoises during some of the model periods (minimum $N = 22$; Fig. S1). To fulfil this assumption as well as possible, we incorporated spatial sampling bias files in the period-specific MaxEnt models, which is an established method to restrict background points to areas where species occurrences were found, leading to more realistic predictions (Phillips et al., 2009). We also

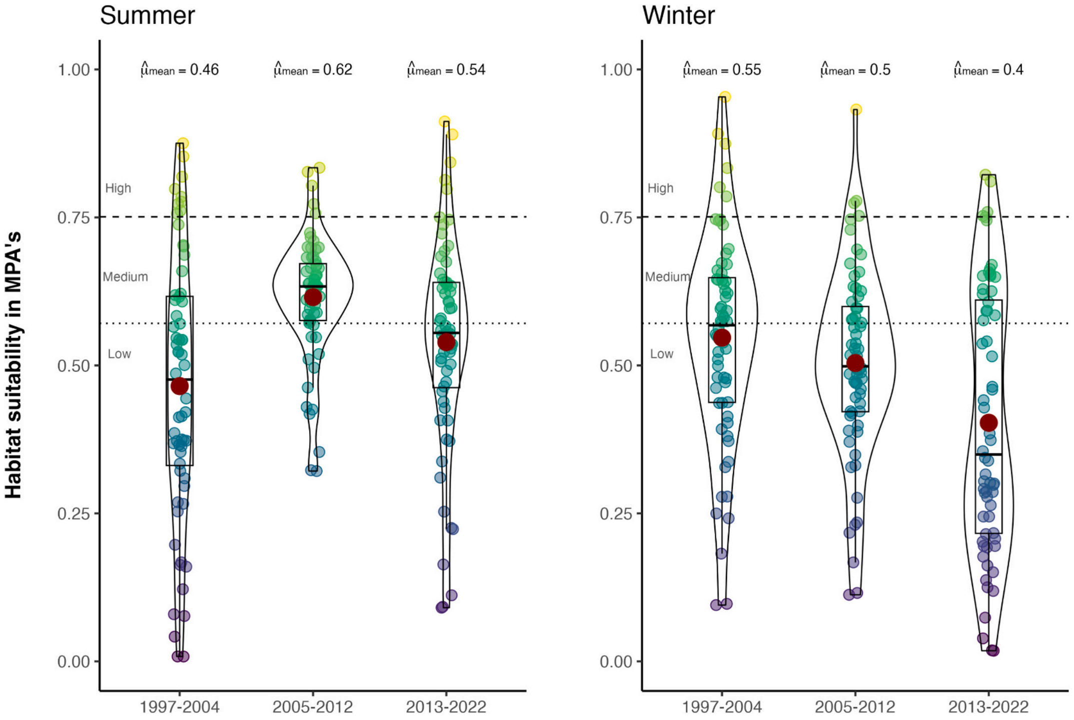

Fig. 4. Season and period-specific violin and boxplots showing the range in habitat suitability as predicted by the MaxEnt models (Fig. 2A) across 62 MPAs in the North Sea–Baltic Sea transition zone dedicated to harbour porpoise protection. The red dot indicates the mean habitat suitability value across all MPAs in that season and period, and is also provided on the top of each boxplot. The horizontal dashed and dotted lines indicate the MaxEnt model derived thresholds values for Kappa and MSSS respectively, which delineate high, medium, and low habitat suitable classes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tailored the entire analytical procedure to increase reliability of model predictions by e.g. limiting overparameterization through extensive MaxEnt model pruning (Kass et al., 2021). Finally, MaxEnt is known to perform well with low sample size compared to other SDM techniques (Wisz et al., 2008). It is also important to note that anthropogenic activities such as commercial fisheries, offshore windfarm construction, and shipping occur widely throughout the North Sea (Schupp et al., 2021) and Baltic Sea (Reusch et al., 2018) and may have marked effects on the habitat suitability of marine predators through competition for fish (Hansson et al., 2018) and disturbance through underwater noise (Jalkanen et al., 2018). However, these variables were not considered in our study because, as also stated above for prey distribution, data of these stressors are not available in sufficiently fine resolution and across the large spatial and long temporal scales required for ou purpose here. This does not imply, however, that these variables do not affect the ecology of harbour porpoises or other marine mammal species. In fact, we recommend that future studies try to estimate their impacts on habitat suitability through e.g. scenario-based simulation models (following: Gallagher et al., 2020; Nabe-Nielsen et al., 2018) to identify the main threats to marine mammal conservation and how these may be mitigated through future MPA placement and designation. Moreover, integration of data streams from multiple sources (e.g. telemetry, aerial and vessel-based surveys, and passive acoustic monitoring) into a unifying SDM framework may provide novel insight on the discrepancy between landscape-scale habitat suitability (this study) and temporal changes in local densities (Hansen and Høgslund, 2023).

Our study focussed on quantifying spatiotemporal dynamics in habitat suitability for harbour porpoises only. The Natura 2000 network typically considers multiple species in the planning- and decision-making process for MPA designation. Consequently, multi-species MPAs do not always cover the most critical habitat for a particular species. Most of the MPAs considered in this study were established to protect multiple marine species (harbour porpoises, harbour and grey seals and seabirds) and important habitat types (e.g. reefs, mudflats, and sandbanks). Nonetheless, the diminishing spatial overlap between highly suitable harbour porpoise habitat during winter and MPAs in the region is concerning, especially given the decline in abundance of the Belt Sea population (Owen et al., 2024). The ultimate causes for the observed reduction in spatial overlap remain unknown and deserve further research but our results do align with those found in other studies across the globe highlighting a mismatch between the geographic location of suitable habitat of marine mammal and the placement of MPAs (Rodríguez-Rodríguez and Martínez-Vega, 2022). In fact, several studies have questioned the capacity of the current Natura2000 network (to which the MPAs in this study belong) to effectively protect multiple marine species under current and future environmental conditions and call for an increase in MPA size and stricter enforcement of the exclusion of anthropogenic pressures or activities (Batista and Cabral, 2016; Fortuna et al., 2018). Indeed, species' protection is most likely to succeed when MPAs are in areas that encompass and connect a large extent of highly suitable habitat of a given species over long periods of time (Gormley et al., 1988). Based on this notion, there has been a push in establishing large marine protected areas (>30,000 km^2) to buffer against shifts in species' habitat suitability given contemporary and projected changes in environmental conditions (Davies et al., 2017). In areas where space is limited and/or competing socio-economic demands hinder the establishment of large MPAs, the implementation of mobile MPAs, whose boundaries shift across space and time following changes in the habitat suitability of target species, is considered a valuable conservation strategy to safeguard marine life in a changing environment (Maxwell et al., 2020). However, this may be challenging in European waters that are intensively used by fisheries, shipping, military operations, oil industry and wind farms, resulting in little space to move MPAs around without compromising protective measures. We propose that the development of long-term habitat suitability maps (Fig. 5) is another potentially valuable approach to guide

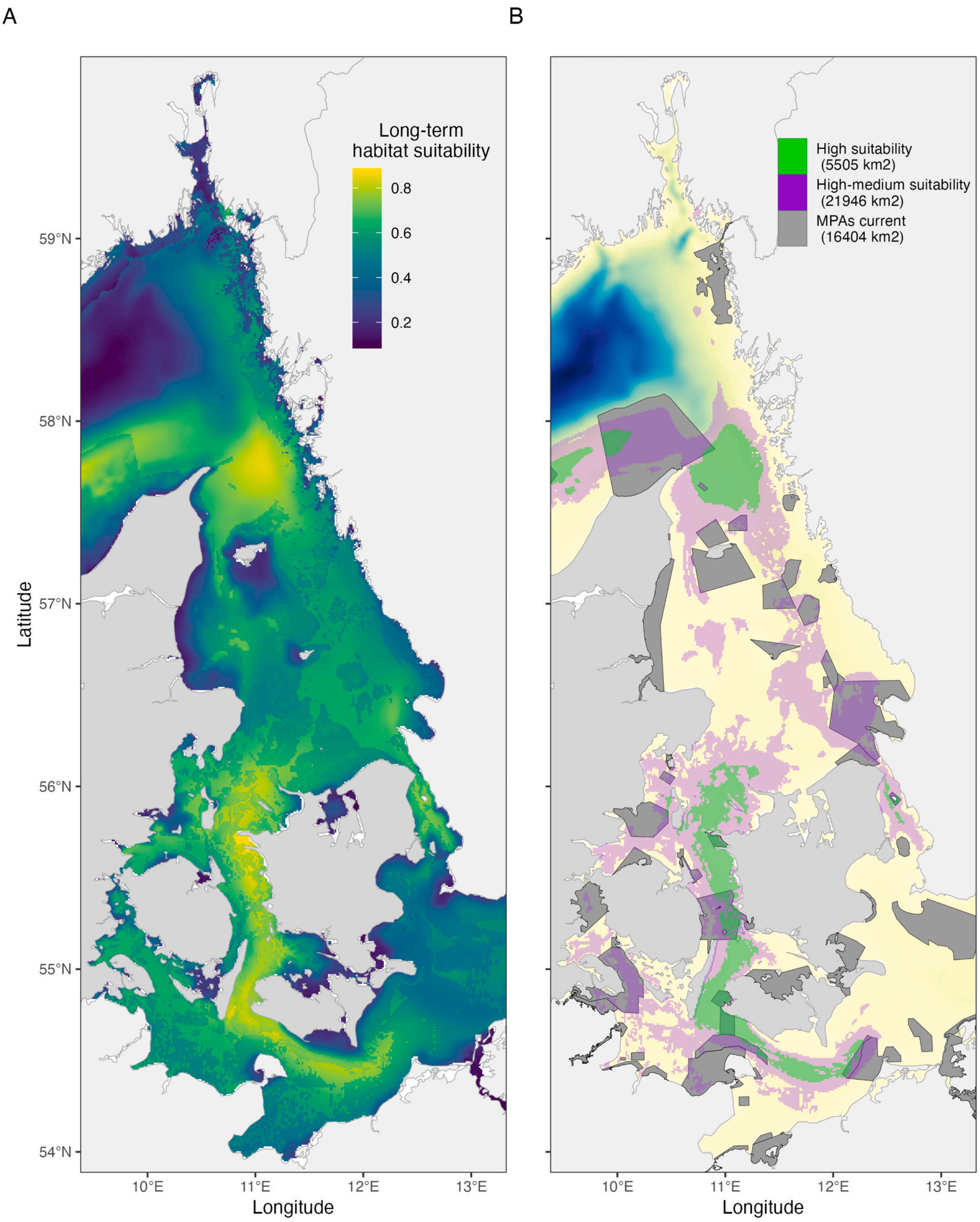

Fig. 5. Map of long-term habitat suitability for harbour porpoises (A) as predicted by season- and period-specific MaxEnt models (Fig. 2A) using Argos-based location data collected in the North Sea–Baltic Sea transition zone during 1997–2022. Panel B shows the outlines of areas with highly suitable habitat (green), areas with high and medium suitable habitat (purple), and the outlines of the 62 MPAs dedicated to harbour porpoise protection (dark grey polygons). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

MPA establishment and the evaluation of their effectiveness. Based on 25 years of data, we found a 5505 km^2 area of highly suitable harbour porpoise habitat, which is smaller and less fragmented than the 16,404 km^2 covered by the MPA network currently in place. It seems imperative that these long-term highly suitable habitat areas are considered in marine spatial planning and for the designation of potential forthcoming MPAs as part of the EU Biodiversity Strategy for 2030 (Hermoso et al., 2022).

CRediT authorship contribution statement

Floris M. van Beest: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Jacob Carstensen:** Writing – review & editing, Funding acquisition, Conceptualization. **Rune Dietz:** Writing – review & editing, Resources, Data curation. **Jacob Nabe-Nielsen:** Writing – review & editing, Resources, Investigation, Funding acquisition. **Signe Sveegaard:** Writing – review & editing, Resources, Investigation, Data curation. **Jonas Teilmann:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation.

Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could influence the work reported in this paper.

Acknowledgements

We wish to thank all the people from the Marine Mammal Research section at the Department of Ecoscience, Aarhus University, Denmark, involved in handling and tagging of the harbour porpoises, as well as all volunteers and fishermen. We also thank two anonymous reviewers for their constructive feedback on our manuscript, which greatly improved this article. We also wish to thank Julia Carlström (Swedish Museum of Natural History), Sven Koschinski and Mirko Hauswirth (German Federal Agency for Nature Conservation) for help with the national MPA regulations for harbour porpoises. Tracking data for the harbour porpoises were provided by Aarhus University under various projects in cooperation with the Danish Institute for Fisheries Research, the Fjord and Belt Centre, and University of Southern Denmark in the years 1997–2002. During 2003–2013, porpoises were tagged as part of cooperation between National Environmental Research Institute and Research and Technology Centre - University of Kiel and University of Veterinary Medicine, Hannover Germany. During 2014-2022 the tagging program was partly funded by DEPONS (Vattenfall, Forewind, ENECO Luchterduinen, Ørsted, and Scottish Power Renewables), and the Wildlife Contract (Danish Ministry of Environment). Additional funding for this study was provided by the Danish Environmental Protection Agency, Ministry of Environment, Denmark and by the GES4-SEAS and OBAMA-NEXT projects funded under the Horizon Europe program (grant agreements 101059877 and 101091642). Handling and tagging of porpoises were carried out under permission issued to Jonas Teilmann by the Danish Forest and Nature Agency/Danish Environmental Protection Agency, Ministry of Environment and Food of Denmark (SNS-342-00042, NST-3446-0016) and the Animal Welfare Division/Animal Experiments Inspectorate (Ministry of Justice and Ministry of Environment and Food of Denmark) (2010/561-1801, 2015-15-0201-00549, 2020-15-0201-00545, 2020-14262).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111009.

Data availability

Data used in this study are available at Zenodo (van Beest et al., 2024).

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