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RESEARCH ARTICLE

High-resolution sea duck distribution modeling: Relating aerial and ship survey data to food resources, anthropogenic pressures, and topographic variables

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ABSTRACT

Anthropogenic developments in marine coastal zones potentially overlap with areas of conservation interest, including important areas for birds. Ideally, spatial patterns of species abundance should be considered at ecologically relevant spatial resolutions (high resolutions) to inform spatial planning and environmental assessments. Most planning so far, however, has relied on coarse-resolution distribution maps from atlas projects or models often based on limited datasets (few surveys), and relationships with environmental variables have rarely been taken into account, leaving many studies and recommendations vulnerable to criticism. We therefore combined the strengths of a detailed database of spatially explicit aerial and ship surveys with high-resolution environmental predictors and species distribution models to predict detailed density patterns for 3 sea duck species, as part of an environmental impact assessment (EIA) in the southern Baltic Sea. We also compared the results from 2 different survey platforms to assess potential differences. We related survey data for Common Eiders (*Somateria mollissima*), Long-tailed Ducks (*Clangula hyemalis*), and Common Scoters (*Melanitta nigra*) to topographic variables, food resources, and anthropogenic pressures using 2-step generalized additive models accounting for zero inflation, nonnormality, and nonlinearity. We accurately predicted distribution patterns (the area under the receiver operating characteristic curve [AUC]: 0.79–0.84) and abundances (Spearman's correlation: 0.36–0.62) at a resolution of 750 m. However, abundance predictions based on aerial survey data differed in magnitude in comparison with predictions from ship survey data, particularly for the frequently diving Long-tailed Duck. We suggest that the main source of the differing abundance estimates was differences in the input data collected using different survey platforms, rather than the modeling approach. A correction factor for birds missed during surveys due to diving activity would therefore increase the accuracy of abundance estimates. Our results show that it is possible to fit ecologically interpretable relationships between species and environmental variables, allowing for the creation of high-resolution predictions useful for management and conservation.

Keywords: aerial surveys, Common Eider, Common Scoter, GAM, habitat modeling, Long-tailed Duck, ship surveys, species distribution modeling

Modélisation à haute résolution de la répartition des oiseaux de mer: relier les données des relevés aériens et par navire aux ressources alimentaires, aux pressions anthropiques et aux variables topographiques

RÉSUMÉ

L'expansion rapide des développements anthropiques dans les zones côtières marines chevauche potentiellement des zones d'intérêt pour la conservation, notamment des zones importantes pour les oiseaux. Idéalement, les patrons spatiaux d'abondance des espèces devraient être considérés à des résolutions spatiales écologiquement pertinentes (haute résolution) afin d'étayer la planification spatiale et les évaluations environnementales. Cependant, la plupart des planifications reposent jusqu'à maintenant sur des cartes de répartition à résolution grossière provenant de projets d'atlas ou de modèles souvent basés sur des ensembles de données limités (peu de relevés) et non reliés à des caractéristiques environnementales, laissant plusieurs études et recommandations vulnérables à la critique. Nous avons donc combiné les forces d'une base de données détaillée de relevés aériens et par navire spatialement explicites avec des variables prédictives environnementales à haute résolution et des modèles de répartition des espèces, afin de prédire des patrons de densité détaillés de trois espèces d'oiseaux de mer, et ce, dans le cadre d'une étude d'impact sur l'environnement (ÉIE) au sud de la mer Baltique. Nous avons ensuite comparé les résultats provenant de deux plateformes d'inventaires différentes afin d'évaluer les différences potentielles. Nous avons relié les données d'inventaires de *Somateria mollissima*, *Melanitta nigra* et *Clangula hyemalis* à des variables topographiques, des ressources alimentaires et des pressions anthropiques à l'aide de modèles additifs généralisés en deux étapes tenant compte d'une inflation nulle, d'une non-normalité et d'une non-linéarité. Nous avons prédit avec exactitude les patrons de répartition (AUC: 0,79–0,84) et les abondances (corrélation de Spearman: 0,36–0,62) à une résolution de 750 m. Cependant, les prédictions d'abondance basées sur les données d'inventaires aériens différaient en importance comparativement aux données des relevés par navire, particulièrement pour *Clangula hyemalis* qui plonge fréquemment. Nous suggérons que la principale source de différence dans les estimations d'abondance correspondait aux différences dans les données d'entrée recueillies par diverses plateformes d'inventaire, plutôt que l'approche de modélisation. Un facteur de correction pour les oiseaux manqués au cours des relevés en raison d'une activité de plongée devrait donc augmenter la précision des estimations d'abondance. Nos résultats montrent que nous pouvons établir des relations écologiquement interprétables entre les espèces et des variables environnementales, ce qui permet d'établir des prédictions à haute résolution utiles en gestion et en conservation.

Mots-clés: relevés aériens, *Somateria mollissima*, *Melanitta nigra*, MAG, modélisation de l'habitat, *Clangula hyemalis*, relevés par navire, modélisation de la répartition des espèces

INTRODUCTION

Anthropogenic pressures on marine coastal and offshore areas are continually increasing. The pressures arise from a wide range of activities, including construction and operation of oil and gas platforms, bridges, and offshore wind farms, as well as dredging, sand extraction, aquaculture, fishing, and shipping, and have led to an urgent need for environmental assessments and marine spatial planning (Douvere 2008). In order to efficiently incorporate ecosystem components into planning processes, regardless of purpose (e.g., mapping of cumulative anthropogenic pressures, impact assessments, baseline investigations, or designation of conservation areas), accurate information is needed about the spatial and temporal distributions of species, and knowledge is required of the factors driving distribution and abundance in an area (Pittman and Brown 2011). Species distribution models (SDMs) are one approach for predicting and explaining the distribution of species. There are various methods available for creating SDMs, but the general principle is the same: to statistically relate observations of species to environmental characteristics (e.g., Elith and Leathwick 2009, Franklin 2009). SDMs are frequently used in terrestrial settings, and also more and more in the marine realm (Robinson et al. 2011), including for seabirds (e.g., Clark et al. 2003, Yen et al. 2004, Louzao et al. 2009, Nur et al. 2011, Oppel et al. 2012, McGowan et al. 2013, Bradbury et al. 2014, Winiarski et al. 2014). Studies modeling presence–absence or presence only based on survey or telemetry data predict the probability of presence or habitat suitability (e.g., Louzao et al. 2009). However, information on abundance in addition to occurrence is often required when dealing with seabirds, for example, when defining marine protected areas (Camphuysen et al. 2012, Oppel et al. 2012). Thus far, however, there have been rather few studies that have succeeded in predicting accurate abundance estimates at a high resolution based on environmental relationships (but see McGowan et al. 2013, Winiarski et al. 2014, Johnston et al. 2015, Skov et al. 2016).

Offshore seabird surveys are logistically challenging and expensive, and the survey coverage in time and space is therefore usually restricted. Survey results, by themselves, are therefore only snapshots of species' distributions in both time and space. Being able to accurately describe distribution and abundance using environmental variables in a model framework is therefore highly useful as it enables predictions over larger areas, interpolations between transect lines, or extrapolations to areas with similar environmental gradients, both in time and space. However, it can be challenging to model the spatial distribution and particularly the abundance of highly mobile seabirds or other marine animals. Animals may not always occupy apparently suitable areas, while less suitable areas, in contrast, might be occupied at the time of a survey. It is therefore important to include relevant ecological variables, e.g., food resources and anthropogenic pressures, as either direct or indirect variables capable of describing the distribution of a species, and not to rely only on geographic predictors (coordinates). Purely geographic models (based on coordinates only) can only describe and predict the particular survey (the snapshot). However, if meaningful, significant, and general ecological relationships are included in a model, it can potentially be used for "transferable" predictions in both time and space (Randin et al. 2006, Heinänen et al. 2012). If a model is not general enough (overfitted) or is extrapolated beyond the range of the environmental gradients included in the model, it tends to have low transferability, however (e.g., Torres et al. 2015). Properties of the response variable (observations of the species) also need to be considered, because biases in the response variable due to detection probability or other aspects related to the survey method need to be accounted for, as the model is data driven and fitted purely to the data that is fed into the model. Certain properties that are common to at-sea survey data further complicate distribution modeling and need to be considered: the relationships between predictor variables and the response variable are often nonlinear, the response variable is commonly not normally distributed, and the data are also often zero-inflated (Martin et al. 2005, Zipkin et al. 2014).

Despite the challenges, a model framework capable of dealing with the issues is a framework that can make the most of the survey data and therefore will greatly enhance the applicability of, for example, environmental impact assessments (EIA), strategic environmental assessments (SEA), and spatial planning.

In this paper, we present a case study of 3 sea duck species, the Common Eider (*Somateria mollissima*), Long-tailed Duck (*Clangula hyemalis*), and Common Scoter (*Melanitta nigra*), wherein we take into consideration all of the above-mentioned data challenges. The study was conducted as part of an environmental impact assessment for the construction and operation of a planned fixed link between Denmark and Germany in the southwestern Baltic Sea (FEBI 2013a, 2013b). The populations of the 3 study species are all declining, and the Long-tailed Duck in particular has shown signs of a rapid decline (Nilsson 2008, Skov et al. 2011). It is therefore important to define the significant factors shaping their distributions and to estimate population sizes and distribution patterns as accurately as possible. To do this we related observed bird densities, from both aerial and ship surveys (separately), to ecologically relevant environmental variables (food resources, topographic variables, and anthropogenic pressures) at a high resolution using a 2-step generalized additive modeling (GAM) approach. Our main aims were, first, to develop species distribution models capable of accurately predicting and describing seasonal densities and distribution patterns and, second, to compare the models and predictions based on the input data collected using the 2 different survey platforms.

METHODS

Study Area

Our study area, the Fehmarn Belt, is located in the southwestern Baltic Sea between Denmark and Germany (Figure 1). The area is of international importance for wintering waterbirds and parts of it have been designated as Special Protection Areas for birds (SPAs) within the European Network of Protected Areas, Natura 2000 (http://natura2000.eea.europa.eu). The area covered by aerial surveys was 4,875 km^2. The area surveyed by ships was smaller (2,350 km^2), as shallow areas (<7 m water depth) could not be surveyed by ships, and also due to time constraints as ship surveys are more time-consuming than aerial surveys (Figure 1).

Surveys

Aerial surveys. Aerial surveys were conducted every month (when weather conditions allowed) between November 2008 and November 2010, using a standard line transect survey method with 4 perpendicular distance bands: A = 0–44 m, B = 45–166 m, C = 167–441 m, and D = 442–1,500 m (Diederichs et al. 2002, Camphuysen et al. 2004). The aerial surveys, consisting of 36 parallel transects with a distance of 3 km between each (total transect length of ~1,600 km), were conducted by 2 planes in 1 day or 1 plane in 2 days (Figure 1). The flight track was continuously logged at intervals of 3 s (survey effort), and the exact time and location within a distance band for each sighting were recorded using dictaphones by 2 principal observers and 1 control observer. Flight speed was 100 knots and flight height was 76 m. The surveys were conducted only in good weather conditions: Beaufort sea state <3 and visibility >5 km (see detailed survey description in FEBI 2013a).

Ship surveys. As with the aerial surveys, ship surveys were conducted every month when weather conditions allowed. Two survey designs were used for the ship surveys. In coastal waters, a "zig-zag" transect line design was used (7–18 m depth), and in offshore areas, parallel transect lines with 3 km spacing were used (Figure 1). The ship's track was continuously logged and sightings (observations of swimming birds) were assigned to distance bands (A = 0–49 m, B = 50–99 m, C = 100–199 m, D = 200–300 m, and out-of-transect E = >300 m) and noted at intervals of 1 min. Snapshot counts of flying birds 300 m in front of the ship were also done every 1 min. The sailing speed was 10 knots. The duration of 1 ship survey was usually 3–4 days. Surveys were only conducted during good to moderate conditions, defined as Beaufort sea state <4 and visibility >3 km (see detailed survey description in FEBI 2013a). For estimating corrected densities, we used the count of birds during every 1-min survey segment as a data unit, hereafter referred to as an "observation."

Environmental Predictors

Previous studies have shown that available and accessible food resources are the most important drivers behind the distribution patterns of wintering sea ducks (Kaiser et al. 2006, Žydelis et al. 2006, Kirk et al. 2008). It has also been shown that sea ducks are sensitive to anthropogenic disturbances, such as shipping (Bellebaum et al. 2006, Kaiser et al. 2006, Schwemmer et al. 2011) and the presence of wind farms (Petersen and Fox 2007). We therefore included the following environmental predictors as being potentially important for describing the distribution patterns of the 3 focal sea ducks: water depth, bottom slope, proportion of hard substrate, distance to land, distance to wind farm (truncated at 4 km as we assumed no impact farther away; Petersen and Fox 2007; all other values were set to 4,001 m), shipping intensity (AIS), and modeled blue mussel (*Mytilus edulis*) biomass (Table 1; see Supplemental Material Appendix A for an extended description). Before extraction, the raster layers (except for the mussel model) were resampled to the same resolution (750 m × 750 m) and extent. The original

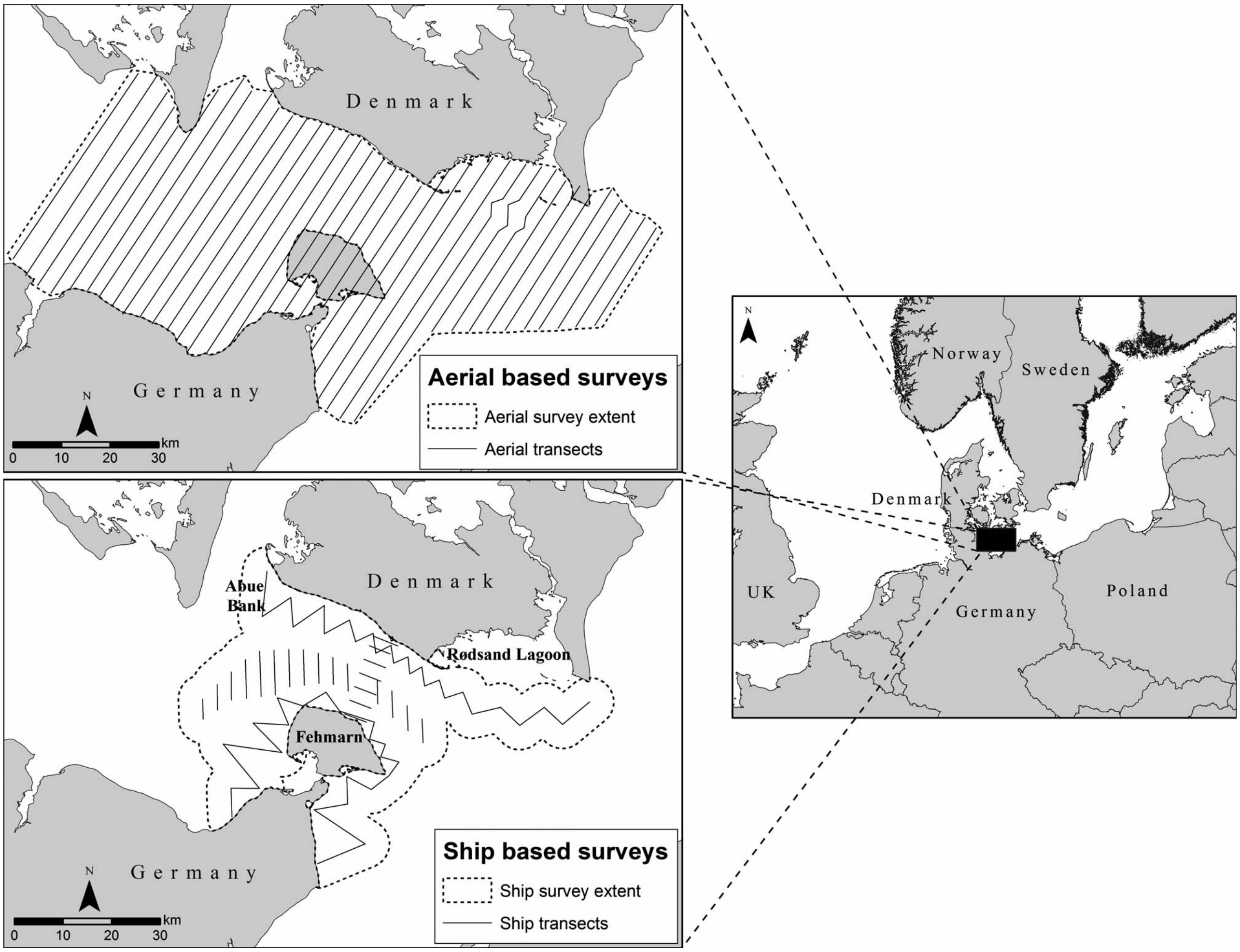

FIGURE 1. Study area in the Fehmarn Belt (located in the southwestern Baltic Sea between Denmark and Germany), showing the 2 different survey extents, aerial and ship surveys, used to predict density patterns of 3 sea duck species in relation to topographic variables, food resources, and anthropogenic pressures.

TABLE 1. Predictor variables assessed for inclusion in generalized additive models (GAMs) used to predict density patterns of 3 sea duck species in relation to topographic variables, food resources, and anthropogenic pressures in the Fehmarn Belt, southwestern Baltic Sea, 2008–2010.

Predictor	Source	Process
Water depth (m)	DHI [a]	Indirect predictor of food resource
Blue mussel biomass (AFDW)	Modeled using DHI ECO Lab modeling software [b]	Direct predictor of food resource
Bottom slope (degree)	Calculated based on water depth in ArcGIS 9.3 [c]	Indirect predictor of food resource
Proportion hard substrate	DHI [a]	Indirect predictor of food resource
Distance to land (m)	Calculated in ArcGIS 9.3 [c] using Euclidian distance tool	Disturbance and location of food resource
Distance to wind farm (m)	Calculated in ArcGIS 9.3 [c] using Euclidian distance tool	Disturbance
No. of ships (per grid cell)	Monthly AIS (shipping intensity) data [d]	Disturbance
x–*y* interaction term	UTM zone 32N coordinates	Geographic descriptor

[a] http://www.dhigroup.com/
[b] https://www.mikepoweredbydhi.com/products/eco-lab
[c] ESRI, Redlands, California, USA.
[d] Data from Danish Maritime Authorities (http://www.dma.dk/ais/Sider/default.aspx) and analyzed and provided by Ramboll (www.ramboll.com).

TABLE 2. Species-specific seasons used for grouping survey data of 3 sea duck species in the Fehmarn Belt (located in the southwestern Baltic Sea between Denmark and Germany), in order to predict density patterns in relation to topographic variables, food resources, and anthropogenic pressures.

	Common Eider		Long-tailed Duck		Common Scoter	
	Aerial	Ship	Aerial	Ship	Aerial	Ship
Winter 1	Dec 2008–Feb 2009	Nov 2008–Feb 2009	Dec 2008–Mar 2009	Nov 2008–Apr 2009	Dec 2008–Mar 2009	Nov 2008–Apr 2009
Spring 1	Mar 2009	Mar 2009				
Autumn 1	Oct 2009	Oct 2009				
Winter 2	Nov 2009–Feb 2010	Nov 2009–Feb 2010	Nov 2009–Apr 2010	Nov 2009–Mar 2010	Nov 2009–Apr 2010	Nov 2009–Mar 2010
Spring 2	Mar 2010–Apr 2010	Mar 2010–Apr 2010				

flexible mesh (changing cell size) of the mussel model ranged between ~800 and 1,500 m, with all the other predictors (rasters) having a finer resolution prior to the resampling.

Processing of Survey Data

The bird observations (see above) were corrected for detection errors (distance biases) by using estimated correction factors based on modeled detection functions. A set of different key functions were fitted (uniform, half-normal, and hazard-rate), and cosine and simple polynomial adjustment terms were added to the models, in Distance 6.0 (Buckland et al. 2001, Thomas et al. 2010; Supplemental Material Appendix A). Additional covariates were not included in the models, and the best-fitting function was chosen on the basis of the smallest Akaike's Information Criterion (AIC) value (Burnham and Anderson 2002; Supplemental Material Table S1). For aerial surveys, different detection functions were fitted for swimming and flying birds, and for ship surveys, detection functions were only fitted for swimming birds within transects. For ship surveys, flying birds counted using the snapshot technique (300 m ahead of the ship in intervals of 1 min; Tasker et al. 1984) were added to the distance-corrected data assuming 100% detection. The global estimated detection functions (based on the entire dataset) were used to estimate species-specific and survey platform–specific effective strip widths (ESW), which represented the width within which the expected number of detected seabirds would be the same as the numbers actually detected within the full width of the transect (Buckland et al. 2001). We then corrected the abundance of swimming birds observed during a 1-min survey segment by dividing this observed abundance by the mean probability of detection (ESW/transect width), thus calculating abundance within each 1-min survey segment corrected for observation bias. The distance-corrected observations were finally converted to densities (birds km^{-2}) based on transect width and segment length, and were combined with the survey effort data (0 observations).

In the next step, the environmental data were extracted to the distance-corrected survey data. The modeled dynamic mussel biomass (Supplemental Material Appendix A) was integrated with the survey data based on time and position; the semidynamic AIS data (monthly means) were extracted on a monthly basis; and the static environmental variables were integrated with the survey data by position only. During the study period, we defined 5 seasons for the Common Eider: 2 winter seasons, and 3 transition seasons (2 spring seasons and 1 autumn season) when bird numbers could be expected to vary due to migration (Table 2). We could not distinguish clear transition periods for the Common Scoter and Long-tailed

TABLE 3. Seasonal sample sizes (*n*), with percentages of occurrence (prevalence) in parentheses, used for density distribution modeling of 3 sea duck species (Common Eider, Long-tailed Duck, and Common Scoter), aggregated (within grid cells of 750 × 750 m) within aerial and ship surveys in the Fehmarn Belt (located in the southwestern Baltic Sea between Denmark and Germany). See Table 2 for definitions of the different survey seasons.

		Winter 1	Spring 1	Autumn	Winter 2	Spring 2
Aerial	Common Eider	3,052 (42%)	2,684 (24%)	2,067 (16%)	2,827 (37%)	2,965 (30%)
Ship	Common Eider	826 (73%)	616 (53%)	548 (45%)	676 (74%)	603 (55%)
Aerial	Long-tailed Duck	3,096 (16%)			3,350 (12%)	
Ship	Long-tailed Duck	852 (37%)			680 (45%)	
Aerial	Common Scoter	3,096 (16%)			3,350 (14%)	
Ship	Common Scoter	852 (35%)			680 (43%)	

Duck, and we therefore defined only 2 winter seasons for these 2 species (Table 2).

The data on bird density and associated environmental parameters were aggregated by averaging bird densities in 1-min segments within 750 × 750 m grid cells, grouped by season (assuming density to be equal within the whole grid cell). The distance corrections were based on a greater transect width (3 km or 1.5 km on each sides). However, the influence of this spatial mismatch (between 750 m grid cell width and 3 km transect width) was minor, as supported by the fact that most birds were recorded close to the airplane, and the fact that the correlation between, for example, Common Eider densities recorded in distance band A and densities estimated using distance analysis was almost perfect ($r = 0.95$). Finally, the average species density in a surveyed grid cell was used as the response variable and the extracted mean environmental and geographic variables were included as predictor variables in the distribution model (see below). Sample sizes for the datasets used in the modeling are shown in Table 3.

Statistical Analysis

Modeling approach. We used generalized additive models (GAMs) as they are capable of fitting different family distributions and nonlinear responses (Hastie and Tibshirani 1990). To be able to deal with zero inflation we fitted a "2-step" GAM, also called a "delta" or a "hurdle" model (Stefánsson 1996, Heinänen et al. 2008). The first step of the modeling process was to fit a presence–absence model (binomial distribution, with a logit link), and the second step was to fit a positive model, wherein all records with 0 observations of birds were excluded (Potts and Elith 2006). The positive (density) part of the model was fitted with a gamma distribution and a log link (Stefánson 1996). The final density predictions (birds km^{-2}) were derived by multiplying the probability of presence (derived from the binomial model) with the expected density (derived from the gamma model). The associated model standard errors were calculated by using the formula for the variance of the product of 2 random variables (Goodman 1960, Webley et al. 2011).

We fitted a model (with the 2 model parts) for each species and survey platform and included season as a factor variable. All predictor variables were included in an initial "full" model (the same variable selection method was used for both model parts). Uninfluential variables were removed from the model in a stepwise manner, starting with the least significant. A variable was excluded if the predictor error criterion GCV/UBRE score (Generalized Cross Validation/Un-Biased Risk Estimator; see Wood 2006) fell when the variable was dropped (Wood and Augustin 2002). Variables displaying ecologically meaningless responses (based on expert judgment) were also removed (Austin 2002, Wintle et al. 2005). The GAM models were fitted using thin plate regression splines (the default spline in the mgcv package; Wood 2006), and the degree of smoothing was based on generalized cross validation (Wood 2006). To reduce potential overfitting of the GAMs, smooth functions for each environmental variable were limited to 5 ($k = 5$), or 3 if needed, based on a visual assessment of spline shapes (e.g., Redfern et al. 2008, Gowan and Ortega-Ortiz 2014). The default maximum degree of smoothing was not reduced for the interaction term, x and y coordinates, to allow for more complex geographical patterns. The models were fitted in R 2.9.0 (R Development Core Team 2004) using package mgcv (Wood 2006).

We checked collinearity between predictor variables before model fitting, as strong correlations between variables could result in inaccurate model parameterization and decreased predictive accuracy (Dormann et al. 2013). We found a strong negative Pearson's pairwise correlation between water depth and mussel biomass (ranging between –0.72 and –0.79 in the different species-specific model datasets) because blue mussel biomass increases with decreasing water depth; all other variables had a correlation coefficient <0.6. We included both water depth and mussel biomass as variables in the models (because sea ducks do not feed exclusively on blue mussels), but inspected the behavior of the predictors closely; inclusion of both predictors improved the predictive ability of the models. We accepted the high correlation between these 2 variables as the models were

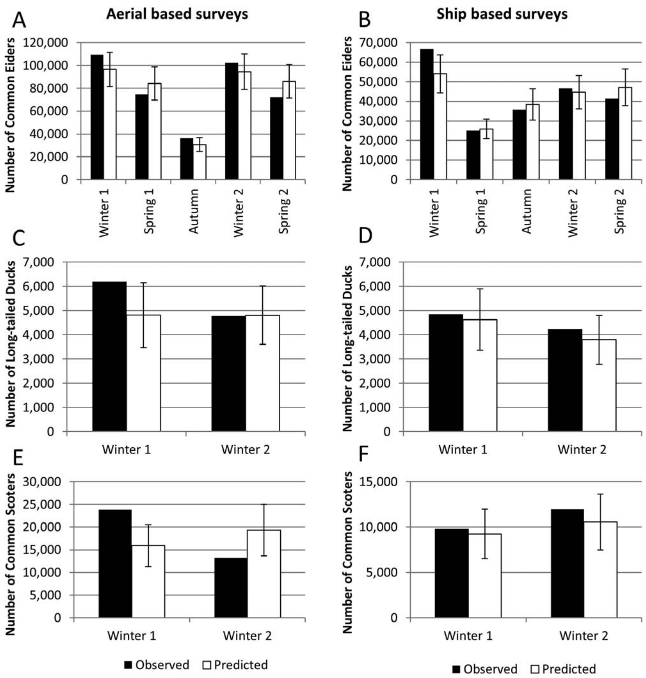

FIGURE 2. Observed and predicted abundances (counts) from aerial and ship surveys of 3 sea ducks conducted in winter and transitional (autumn and spring) seasons in the southwestern Baltic Sea, 2008–2010: (**A**, **B**) Common Eider, (**C**, **D**) Long-tailed Duck, and (**E**, **F**) Common Scoter. Model standard errors for the predicted abundances are shown as error bars.

used for predicting distributions within the same area, with the same correlation structure, and were not used for extrapolation (Dormann et al. 2013).

Assessment of fit and predictive accuracy. We assessed the fit of the GAMs based on the deviance explained and by inspecting residual plots. Model residuals were also checked for spatial autocorrelation by using a correlogram displaying Moran's *I* values over 10 lags, with 1 lag being the defined nearest neighborhood of 1,500 m (R package spdep; Bivand 2009). The predictive accuracy of each model was assessed by fitting the model using 70% of the data (randomly selected) and making predictions using, and comparing predictions against, the remaining 30% of semi-independent data points (Araújo et al. 2005). The presence–absence parts of the models were assessed using the threshold independent measure, the area under the receiver operating characteristic curve (AUC; Pearce and Ferrier 2000). An AUC value of 0.9 indicates that a model is able to discriminate between occupied cells and unoccupied cells 90% of the time, and an AUC value of 0.5 is thus no better than random (Fielding and Bell 1997). The combined predictions from both model parts, fitted using 70% of the data, were further evaluated using Spearman's rank correlation, which revealed whether the predictions were of the right order of magnitude (Potts and Elith 2006). We also evaluated the full models (all data used) with Spearman's rank correlation using "truly" independent data, the observations from the other survey platform (i.e. the aerial survey predictions were evaluated using ship survey observations and vice versa). In addition, we assessed predicted abundances (counts) against observed counts, and, lastly, we mapped predicted density (birds km^{-2}) against observed density in order to inspect the reliability of the spatial patterns.

Predictions

The final models (fitted using all data from each survey platform) were used to predict the densities and distributions of the 3 sea duck species in the complete survey-specific study area. The survey extents were different for aerial surveys and ship surveys (Figure 1). We therefore also predicted densities based on aerial surveys at the smaller ship survey extent to be able to compare the results of the 2 different survey methods. The comparisons, in terms of total numbers, were based on abundances (converted back from the predicted densities). As we used season as a factor variable in the models, we were able to predict season-specific densities. In the prediction models for each season, we calculated average values for the dynamic variables of mussel biomass and ship numbers (AIS). The other predictor variables were static and did thus not change between seasons.

RESULTS

Species-specific Models and Predictions

Common Eider models. The highest average abundance of Common Eiders was observed during the 2 winter seasons; their numbers were lower during the transition seasons when migration was ongoing (Figure 2). According to the binomial model based on the aerial survey data, Common Eiders occurred in shallow areas with high blue mussel biomass and a high proportion of hard substrate. The probability of presence decreased with increasing distance to land (after ~5 km) and increasing numbers of ships. The probability of presence was highest during the 2 winter seasons Supplemental Material Table S4, Supplemental Material Figure S1). In the positive model part, a somewhat sloping bottom was important, in addition to mussel biomass and water depth. Significantly higher concentrations were observed during the first spring season in comparison with other seasons (Supplemental Material Figure S1).

When fitting models to the data collected during ship surveys, the important predictors and their shapes were similar to those in the aerial survey models (Supplemental Material Figure S1). The interaction term between x and y coordinates was influential in models fitted to both the aerial and the ship survey data, indicating that a large degree of variance in the data could not be accounted for by the environmental predictors alone (Supplemental Material Table S4). The models accounted for most of the spatial autocorrelation of the datasets. Significant ($P <$ 0.01) spatial autocorrelation remained in 2 lags of both aerial survey model parts and in 3 lags of the positive model part of the ship survey model. The Moran's I values were, however, very low ($<$0.07), indicating a weak and therefore not influential correlation (Supplemental Material Figures S4, S5).

Common Eider predictions. The fitted models were used to predict bird densities across the entire survey area. Distribution maps for the winter season, when Common Eiders were most abundant, showed that the highest densities occurred west of Fehmarn Island and southeast of the coast of Lolland; patterns were similar for both survey platforms, airplanes and ships (Figure 3). Maps for the other surveyed seasons can be found in Supplemental Material Figures S10–S12. The highest total abundance based on aerial survey data was predicted to occur in the second winter, and the lowest total abundance was predicted to occur in the autumn season (Figure 4). The ship survey predictions were generally higher than the aerial survey predictions when compared within the same (small) survey extent; however, only the autumn season predictions were outside the range of the model standard errors (Figure 4).

Long-tailed Duck models. The highest average abundances of Long-tailed Ducks in both the aerial and the ship surveys were observed during the first winter (Figure 2). The influential variables included in the fitted presence–absence part of the aerial survey model indicated that the birds preferred shallow, offshore areas with low shipping activity (Supplemental Material Figure S2). The positive part of the model further indicated that the probability of higher densities of Long-tailed Ducks was highest in shallow, sloping areas with increasing distance from land and low proportions of hard substrate.

The results of the ship survey models indicated that the probability of Long-tailed Duck presence increased in areas with increasing mussel biomass, in water depths of ~10 m, and with low proportions of hard substrate. In contrast, the probability of highest densities increased with increasing distance to land in shallow waters with intermediate proportions of hard substrate (Supplemental Material Figure S2). The interaction term between coordinates was influential in all models, indicating that a large degree of the variance in the data could not be accounted for by the environmental predictors alone (Supplemental Material Table S4). The models were able to account for all of the spatial autocorrelation in the model data (Supplemental Material Figures S6, S7).

Long-tailed Duck predictions. The predicted distributions indicated that the highest densities of Long-tailed Ducks were located southeast and southwest of Fehmarn Island, and the predicted densities were much higher based on ship surveys (Figure 3, Supplemental Material Figure S13). Abundance estimates from aerial survey models were considerably smaller than those from ship survey models when predicted for the same area. Annual differences in abundance were quite small (Figure 4).

Common Scoter models. The average abundance of Common Scoters observed during aerial surveys was clearly higher in the first winter than in the second winter. In the ship surveys, more birds were observed during the second winter than the first (Figure 2). The influential variables included in the fitted presence–absence part of the aerial survey model indicated that the birds preferred shallow, gently sloping offshore areas with low shipping activity (Supplemental Material Figure S3). The positive density part of the model further indicated that the probability of higher densities of Common Scoters was highest in water depths of ~5–6 m with an intermediate proportion of hard substrate in areas with low shipping intensity and an increasing distance to wind farms. The results of the ship survey models were similar to those of the aerial survey models (Supplemental Material Figure S3). The interaction term between coordinates was influential in all models, indicating that a large degree of variance in the data could not be accounted for by the environmental predictors (Supplemental Material Table S4). Both presence–absence model parts were able to account for all spatial autocorrelation in both the aerial survey and the ship survey data. Significant ($P < 0.01$) spatial autocorrelation remained only in the first lags in the residuals of both positive model parts (based on both aerial survey and ship survey data), but Moran's I was low ($<$0.10; Supplemental Material Figures S8, S9).

Common Scoter predictions. The predicted distributions indicated that the highest densities of Common Scoters occurred southeast and southwest of Fehmarn Island (Figure 3, Supplemental Material Figure S14). The predicted total abundance from both the aerial survey and ship survey models was lower during the first winter than the second winter (Figure 4). In the smaller survey area, the abundance predicted by the aerial survey models was lower than that predicted by the ship survey models; however, the ranges of the model standard errors overlapped (Figure 4).

Model Evaluation

The variance explained (deviance explained) was in the same order for all species and model parts, with the Common Scoter having the highest deviance explained and Common Eider the lowest (Table 4). The deviances explained in the presence–absence parts of the aerial

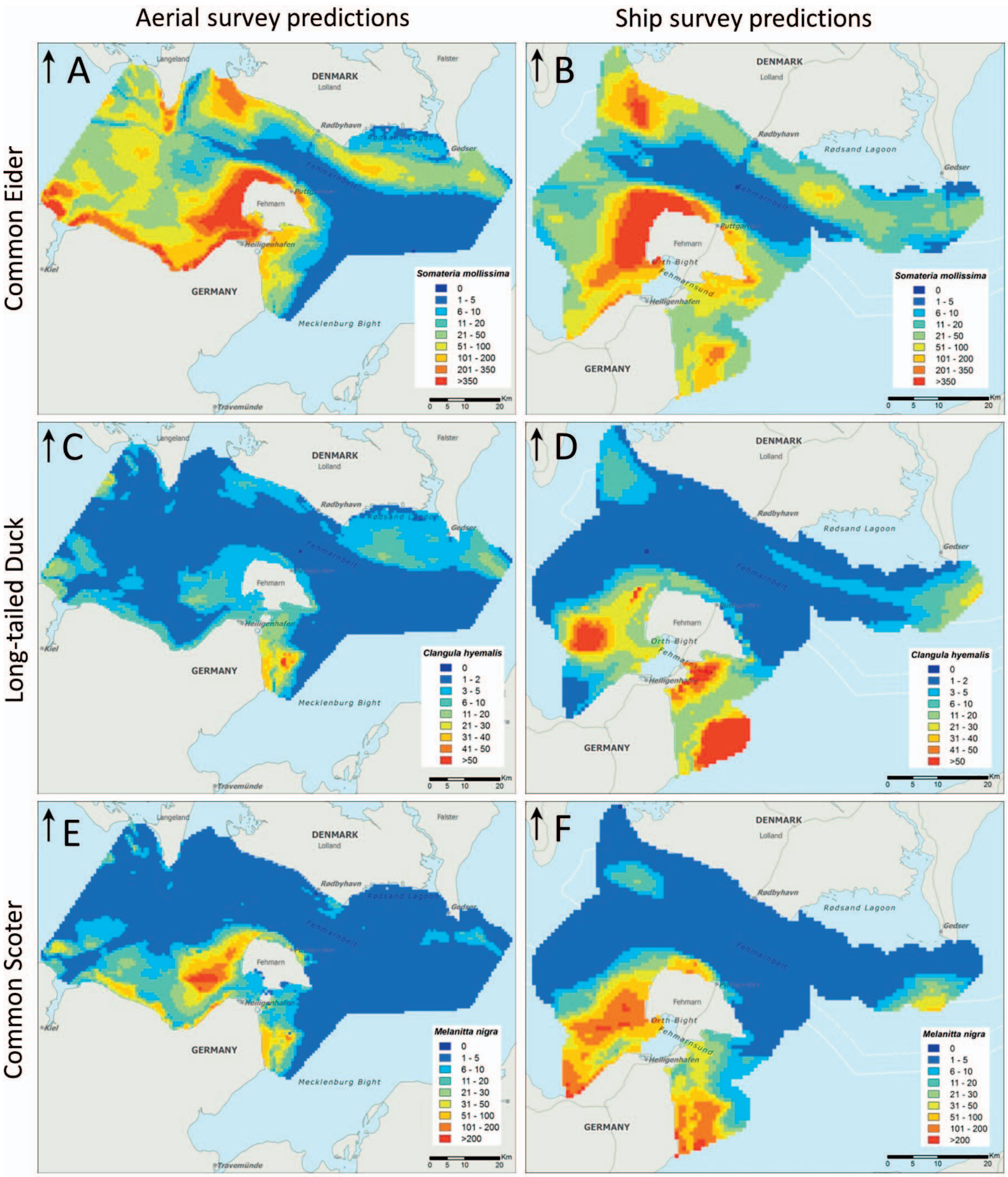

FIGURE 3. Mapped densities (birds km^{-2}) in 750 × 750 m grid cells based on model predictions using both aerial survey and ship survey data for (**A**, **B**) Common Eider (winter 2), (**C**, **D**) Long-tailed Duck (winter 1), and (**E**, **F**) Common Scoter (winter 1) in the southwestern Baltic Sea, 2008–2010. Note that the ship survey extent was smaller (2,350 km^2) than the aerial survey extent (4,875 km^2).

survey models were all close to 20% and in the ship survey models close to 30%. The positive parts of the models generally had higher deviances explained, with those in the aerial survey models close to 25% and those in the ship survey models close to 45% (Table 4). When evaluating the models using the 30% withheld data, the AUC values of the presence–absence model parts were all close to 0.80, varying between 0.79 (aerial survey Common Eider and

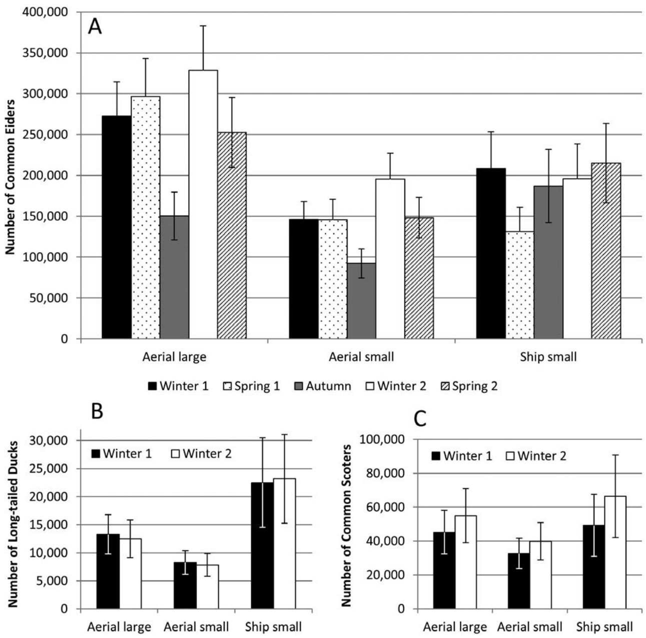

FIGURE 4. Predicted total abundance (counts) during different seasons for (**A**) Common Eider, (**B**) Long-tailed Duck, and (**C**) Common Scoter at 2 different survey extents (aerial vs. ship surveys; Figure 1) in the Fehmarn Belt area of the southern Baltic Sea, 2008–2010. Predictions from the aerial survey models (with a larger extent) are also shown at the smaller ship survey extent to facilitate comparisons with the ship models. Standard errors for the predictions are shown as error bars.

Long-tailed Duck models) and 0.84 (ship survey Long-tailed Duck model). The combined predictions were further assessed using Spearman's rank correlation. The correlation coefficients for the aerial survey models varied between 0.355 (Long-tailed Duck) and 0.424 (Common Eider) and for the ship survey models between 0.554 (Common Eider) and 0.618 (Common Scoter; Table 4). As these evaluation statistics are not spatial, we also mapped the observed distributions of the 3 species against their predicted distributions, and the predicted patterns of distribution were highly similar to the observed patterns (Supplemental Material Figures S15–S19). The models were also capable of predicting a similar seasonal order of density as the observed order, within the same modeling dataset (Figure 2).

When evaluating the modeled predictions against observations from the other survey platform (i.e. when evaluating aerial survey predictions using ship survey observations and vice versa), the Spearman's rank correlation coefficients were generally high (Table 5), and predicted abundances were generally comparable to observations from the other survey platform for the Common Eider and Common Scoter, although the ship survey data yielded higher observed estimates (Figure 5). However, for the Long-tailed Duck, the predicted abundances based on ship surveys were much higher than aerial survey predictions (Figure 5).

TABLE 4. Model evaluation results for generalized additive models (GAMs) used to predict density patterns of 3 sea duck species in relation to topographic variables, food resources, and anthropogenic pressures in the Fehmarn Belt, southwestern Baltic Sea, 2008–2010. The deviance explained (dev. exp.) indicates how much of the variance in the data was explained by both model parts, presence–absence (P–A; binomial distribution) and positive part (POS, wherein all records with 0 observations of birds were excluded). The area under the receiver operating characteristic curve (AUC) was used for evaluating the predictive performance of the binomial parts of the models, and Spearman's rank correlation coefficient (rho) was used for assessing the final combined density predictions.

	Dev. exp.	AUC	rho
Common Eider			
Aerial P–A	19.9	0.788	0.424
Aerial POS	24.7		
Ship P–A	26.2	0.801	0.554
Ship POS	45.5		
Long tailed Duck			
Aerial P–A	18.3	0.787	0.355
Aerial POS	25.1		
Ship P–A	31.9	0.841	0.589
Ship POS	45.2		
Common Scoter			
Aerial P–A	23.9	0.835	0.385
Aerial POS	33.3		
Ship P–A	35.3	0.818	0.618
Ship POS	48.6		

DISCUSSION

Predictive Accuracy of the Models

The first aim of this study was to create models capable of accurately predicting the seasonal density and distribution of 3 sea duck species in the Fehmarn Belt area of the southwestern Baltic Sea. We achieved this aim, as we were able to predict accurate density patterns of our study species at a high resolution (Table 4). The AUC values of all presence–absence models were close to 0.80, indicating good ability of the models to distinguish between presence and absence (Swets 1988). This is particularly good considering that our study species are highly mobile and in some instances occurred in less-suitable feeding areas, for example, if birds were surveyed while resting during migration. The correlation coefficients of the combined predicted densities were also high, ranging from 0.355 to 0.618, indicating that the order of magnitude of the predictions was comparable to that of the observations, which is in contrast to the findings of Oppel et al. (2012), who found only weak agreement between predicted and observed densities in an independent dataset. However, waterbirds that rely on sessile benthic prey have a more

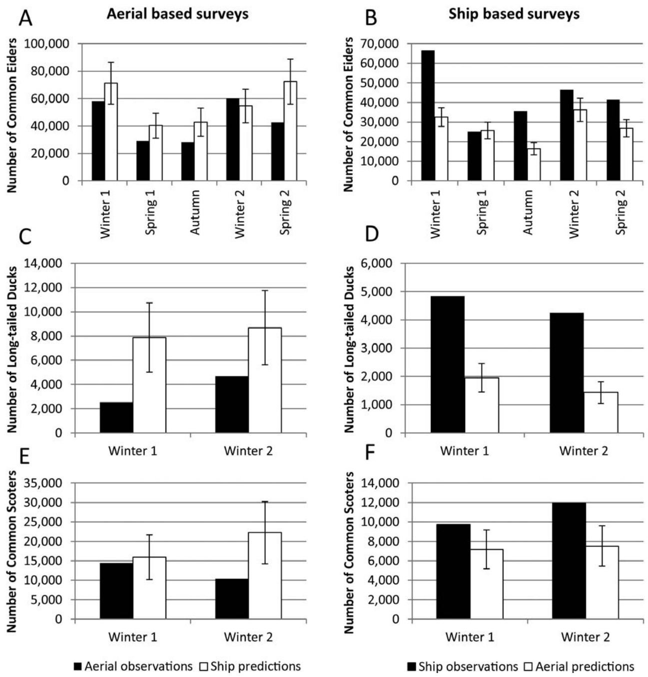

FIGURE 5. Crosswise evaluation of observed abundance (counts from the survey data at a resolution of 750 × 750 m) compared with abundance predicted by the other survey method, for (**A**, **B**) Common Eider, (**C**, **D**) Long-tailed Duck, and (**E**, **F**) Common Scoter in the southern Baltic Sea, 2008–2010. The 2 survey methods that were compared were aerial and ship surveys. Note that the number of samples in the ship surveys was smaller than that in the aerial surveys.

consistent spatial distribution than pelagic-feeding birds that rely on mobile prey in a highly dynamic environment. This might explain the differences in the predictive accuracy of our models in comparison with those of Oppel et al. (2012). Sea ducks are nevertheless also mobile and all suitable areas are not occupied at all times (at the time of a survey, for example). Our model was also not able to explain peak densities (large concentrations), which are due to factors other than the environmental and geographic predictors included in the model (for example, conspecific attraction). This consequently complicates validation of the model predictions. The resulting density surface is therefore "smoothed" (peak densities are underestimated and absences are overestimated), and the correlation should not be expected to be perfect, but rather to give an indication of the order of agreement between predicted and observed densities. The close agreements in observed and estimated total abundances for the different seasons in the model datasets (Figure 2), and the highly similar spatial distribution patterns of the model predictions compared with the survey observations (Supplemental Material Figures S15–S19), provide further support for the predictions based on these models being reliable.

As an indication of prediction uncertainty, we show only the combined standard errors related to the distribution model parts (i.e. the standard errors of the GAMs). The errors related to the distance corrections are reported separately (Supplemental Material Table S3) and were not combined with the standard errors of the final predictions. We did not include these as there were also other errors related to the raw survey data (all types of possible observer mistakes, e.g., species identification and placement in distance bands), and it was not possible to quantify all these errors in a reasonable way. Further, the variability and accuracy of the predictor variables (predicted covariates) were also not taken into account as they were not quantified and were not possible to quantify in all cases, but certainly also introduced uncertainty (Foster et al. 2012). However, as the survey coverage was dense and the models were only used for interpolation (not extrapolation), the uncertainty or error associated with the predictors could have influenced the modeled responses (the statistical relationships), but only to a lesser degree the predictions (because the same uncertainty or error of the predictors in the model dataset would have been found in the predictions covering the whole study area). Few studies so far have been able to include a complete propagation of uncertainty (but see Beale and

TABLE 5. Cross-evaluation of aerial survey model predictions correlated (Spearman's rank correlation) against ship survey observations and vice versa for abundance of 3 sea duck species in the Fehmarn Belt, southwestern Baltic Sea, 2008–2010. See Table 2 for definitions of the different survey seasons.

	Winter 1	Spring 1	Autumn	Winter 2	Spring 2
Common Eider					
Aerial predictions	0.601	0.515	0.402	0.632	0.529
Ship predictions	0.498	0.322	0.356	0.476	0.287
Long-tailed Duck					
Aerial predictions	0.533			0.584	
Ship predictions	0.342			0.237	
Common Scoter					
Aerial predictions	0.513			0.647	
Ship predictions	0.455			0.350	

Lennon 2012) and further development is required in this field of research.

Model Interpretations

Our predictions are based on the modeled relationships between the species and the environmental predictors, and it is therefore important that the reliability of these ecological relationships are carefully interpreted. The variables shown to be important in our models coincide well with the current knowledge that we have of the drivers of sea duck wintering distributions (e.g., Bräger et al. 1995, Kaiser et al. 2006, Sonntag 2009).

The most important factor defining the distribution of benthivorous sea ducks in winter is usually considered to be food resources at accessible water depths (Bräger et al. 1995, Guillemette and Himmelman 1996, Kaiser et al. 2006), which was also shown by our models (Supplemental Material Figures S1–S3). The distribution of food resources was directly included in the models as blue mussel biomass, and indirectly as water depth and the proportion of hard substrate. The staple food for Common Eiders in our study area is blue mussels (FEBI 2013a), and for Common Scoters infaunal bivalves have also been shown to be important (Meiner and Bräger 1990). Long-tailed Ducks, on the other hand, are generalists and utilize various food resources (Stempniewicz 1995, Žydelis and Ruškytė 2005, FEBI 2013a). This was also apparent from our models, in which blue mussel biomass was a significant predictor in all model parts for the Common Eider, was important for the Long-tailed Duck only in the presence–absence part of the ship survey model, and was not a significant predictor at all for the Common Scoter. In contrast, water depth was a significant predictor in all models, defining suitable feeding depths for all 3 benthivorous duck species (Supplemental Material Figures S1–S3). In the different model parts for the Long-tailed Duck, the proportion of hard substrate indicated that the species used various food resources from both soft and hard bottom types (Supplemental Material Figure S2).

Sea ducks have further been shown to be sensitive to anthropogenic pressures (Kaiser et al. 2006), e.g., shipping (Schwemmer et al. 2011), which was also confirmed by our models (Supplemental Material Figures S1–S3). The number of ships was a significant factor and therefore included in 3 of 4 model parts for both the Common Eider and Common Scoter, and in 1 model part for the Long-tailed Duck. However, shipping lanes are usually correlated with deeper water and therefore not the preferred habitat of sea ducks. Nevertheless, the shipping variable was able to capture and account for some of the displacement effect documented by Schwemmer et al. (2011). Sea ducks have also been shown to avoid wind farms (Desholm and Kahlert 2005, Petersen et al. 2014). In our models, the variable "distance to wind farm" was only included in 1 model part for the Common Scoter (Supplemental Material Figure S3). However, potential avoidance of wind farms might have been explained by other factors in our models, e.g., the x–y coordinates, particularly as wind farm areas are not of high importance for sea ducks in our study region. The predictor "distance to land" can be considered as representative of another anthropogenic pressure (disturbance from land-based developments), as well as a descriptor of the location of suitable food resources. All species seemed to prefer areas a few kilometers off the coast, with Common Eiders preferring the shortest distance and Long-tailed Ducks the farthest from the shoreline (Supplemental Material Figure S1–S3). This is in accordance with the findings of Sonntag (2009).

Finally, the interaction term between the geographic coordinates was important in all model parts and was included to account for some of the unexplained variance that was not accounted for by the environmental variables alone. The unexplained variance could be due to, for example, site fidelity, conspecific attraction, density dependence, and other unknown factors that we were not able to define. However, although the inclusion of the geographic coordinates improved our models, it also limits their application, as they cannot be used for extrapolation beyond the studied area. Therefore, if a model is to be used for extrapolation, geographic coordinates should not be included. Our models were aiming at describing the distribution and abundance of our study species as accurately as possible within our study area, and therefore coordinates were included. Consequently, in addition to accurate abundance predictions and distribution maps, our modeling approach also provided ecologically interpretable results, which may be used for characterizing the important factors driving the distributions of the study species. The relationships between the static environmental variables (those other than mussel biomass and shipping intensity) and the geographic variables were assumed to be similar during all seasons because the 3 sea ducks rely on sessile food resources. Therefore, the distribution patterns reflected the mean relationships with the static variables during all seasons, although the level of density may have varied among seasons.

Comparison of Results from Each Survey Method

The second of our 2 main aims was to compare the predictions based on the 2 different survey platforms (aerial and ship surveys). The Spearman's rank correlation coefficients ranged from 0.237 to 0.647 when the methods were compared against each other, indicating that the predictions were of a similar order of magnitude (Table 5). The spatial distribution patterns were also comparable (Figure 3), based on similar relationships with the environmental variables (Supplemental Material Figures

S1–S3), bearing in mind that different parts of the environmental gradients were sampled by the 2 survey platforms (the ship survey area being much smaller than the aerial survey area).

However, when assessing the observed and predicted abundances from the models based on the 2 different survey platforms, observations and predictions from the ship surveys were much higher than those from the aerial surveys for the Long-tailed Duck, while the differences between survey methods for the Common Scoter were smaller, and no clear differences could be distinguished for the Common Eider (Figures 4, 5). We suggest that this is at least partly due to the foraging ecology of Long-tailed Ducks (Nilsson 1970, Goudie and Ankney 1986, Systad et al. 2000). Many Long-tailed Ducks may remain undetected during aerial surveys because they spend a substantial proportion of their time feeding underwater, up to twice as long as the other 2 studied sea duck species (FEBI 2013a). Telemetry studies conducted in the same study area showed that Long-tailed Ducks spent up to 60% of the daytime underwater and thus would not be visible from the air during that time, while the percentage for Common Eiders was much lower (FEBI 2013a). During ship surveys, diving birds are less of a problem, because the ship moves much more slowly and surfacing birds usually flush when the ship approaches.

An advantage of using aerial surveys, although the abundance of some ducks, particularly the Long-tailed Duck, may be underestimated, is that larger areas can be covered and thereby larger parts of environmental gradients. As a consequence, ecological relationships are better described by aerial surveys in comparison with ship surveys. On the other hand, ship surveys can potentially provide more accurate abundance estimates as there is more time for an observer to detect and record numbers of birds, although at the cost of reduced survey extent.

We are confident that the same modeling approach that we employed could be used with data collected by other survey methods as well, for example, digital aerial surveys, in which the numbers and locations of birds are estimated from aerial photos or videos without the need for distance corrections (Buckland et al. 2012). Digital survey methods also contribute to more accurate spatial positioning of sightings and the possibility of checking and recounting birds if needed. However, these new, improved survey methods do not account for the missed birds feeding underwater either. A correction factor for diving birds would therefore improve the accuracy of abundance estimates.

Conclusions

The models that we have described here, based on both aerial and ship survey data linked to food resources, topographic variables, and anthropogenic pressures, were capable of predicting the distribution patterns and describing the relationships between the environmental predictors and the responses of our 3 study species. The models were also capable of predicting abundances of a similar order of magnitude when assessed against observations. We can therefore conclude that the approach used in this study is suitable for different types of data, and thus is a good and efficient way for analyzing and mapping survey data to be used for management and spatial planning. Our results were also successfully used in an environmental impact assessment (EIA), as the complete density surface allowed us to extract predicted densities from the affected area and thus to quantify the impact of the proposed development, which would not have been possible without the models (FEBI 2013b). Our case study contributes an example of species distribution models that can be highly useful in regional and local assessments (and already have been; FEBI 2013b), as they can provide a complete density surface based on ecological relationships at a high resolution, a detailed map that can be used for assessing impacts on species at the desired scale.

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LITERATURE CITED

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard (2005). Validation of species–climate impact models under climate change. Global Change Biology 11:1504–1513.

Austin, M. P. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. Ecological Modelling 157:101–118.

Beale, C. M., and J. J. Lennon (2012). Incorporating uncertainty in predictive species distribution modelling. Philosophical Transactions of the Royal Society B 367:247–258.

Bellebaum, J., A. Diederichs, J. Kube, A. Schulz, and G. Nehls (2006). Flucht- und Meidedistanzen überwinternder Seetaucher und Meeresenten gegenüber Schiffen auf See.

Ornithologischer Rundbrief für Mecklenburg-Vorpommern 45:86–90.

Bivand, R. (2009). Spatial dependencies: Weighting schemes, statistics and models. R package version 0.4-34. https://cran.r-project.org/web/packages/spdep/index.html

Bradbury, G., M. Trinder, B. Furness, A. N. Banks, R. W. G. Caldow, and D. Hume (2014). Mapping seabird sensitivity to offshore wind farms. PLOS One 9:e106366. doi:10.1371/journal.pone.0106366

Bräger, S., J. Meiner, and M. Thiel (1995). Temporal and spatial abundance of wintering Common Eider *Somateria mollissima*, Long-tailed Duck *Clangula hyemalis*, and Common Scoter *Melanitta nigra* in shallow water areas of the southwestern Baltic Sea. Ornis Fennica 72:19–28.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas (2001). Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Buckland, S. T., M. L. Burt, E. A. Rextad, M. Mellor, A. E. Williams, and R. Woodward (2012). Aerial surveys of seabirds: The advent of digital methods. Journal of Applied Ecology 49: 960–967.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, USA.

Camphuysen, K. C. J., A. D. Fox, M. F. Leopold, and I. K. Petersen (2004). Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K.: A comparison of ship and aerial sampling methods for marine birds, and their applicability to offshore wind farm assessments. Report COWRIE–BAM-02-2002, Royal Netherlands Institute for Sea Research, Texel, The Netherlands.

Camphuysen, K. C. J., J. Shamoun-Barnes, W. Bouten, and S. Garthe (2012). Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. Biological Conservation 156:22–29.

Clark, E. D., L. B. Spear, M. L. McCracken, F. F. C. Marques, D. L. Borchers, S. T. Buckland, and D. G. Ainley (2003). Validating the use of generalized additive models and at sea surveys to estimate size and temporal trends of seabird populations. Journal of Applied Ecology 40:278–292.

Desholm, M., and J. Kahlert (2005). Avian collision risk at an offshore wind farm. Biology Letters 1:296–298.

Diederichs, A., G. Nehls, and I. K. Petersen (2002). Flugzeugzählungen zur groflächigen Erfassung von Seevögeln und marinen Säugern als Grundlage für Umweltverträglichkeitsstudien im Offshorebereich. Seevögel 23:38–46.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Douvere, F. (2008). The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32:762–771.

Elith, J., and J. R. Leathwick (2009). Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40: 677–697.

FEBI (2013a). Fehmarnbelt Fixed Link EIA: Bird Investigations in Fehmarnbelt—Baseline. Volume II. Waterbirds in Fehmarnbelt. Report No. E3TR0011 commissioned by Femern A/S, Copenhagen, Denmark. http://vvmdocumentation.femern.com/

FEBI (2013b). Fehmarnbelt Fixed Link EIA. Fauna and Flora: Birds. Birds of the Fehmarnbelt Area: Impact Assessment. Report No. E3TR0015 commissioned by Femern A/S, Copenhagen, Denmark. http://vvmdocumentation.femern.com/

Fielding, A. H., and J. F. Bell (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Foster, S. D., H. Shimadzu, and R. Darnell (2012). Uncertainty in spatially predicted covariates: Is it ignorable? Applied Statistics 66:637–652.

Franklin, J. (2009). Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge, UK.

Goodman, L. A. (1960). On the exact variance of products. Journal of the American Statistical Association 55:708–713.

Goudie, R. I., and C. D. Ankney (1986). Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

Gowan, T. A., and J. G. Ortega-Ortiz (2014). Wintering habitat model for the North Atlantic right whale (*Eubalaena glacialis*) in the southeastern United States. PLOS One 9:e95126. doi: 10.1371/journal.pone.0095126

Guillemette, M., and J. H. Himmelman (1996). Distribution of wintering Common Eiders over mussel beds: Does the ideal free distribution apply? Oikos 76:435–442.

Hastie, T. J., and R. J. Tibshirani (1990). Generalized Additive Models. Chapman and Hall/CRC Press, London, UK.

Heinänen, S., J. Erola, and M. von Numers (2012). High resolution species distribution models of two nesting water bird species: A study of transferability and predictive performance. Landscape Ecology 27:545–555.

Heinänen, S., M. Rönkä, and M. von Numers (2008). Modelling the occurrence and abundance of a colonial species, the Arctic Tern *Sterna paradisaea* in the archipelago of SW Finland. Ecography 31:601–611.

Johnston, A., C. B. Thaxter, G. E. Austin, A. S. C. P. Cook, E. M. Humphreys, D. A. Still, A. Mackay, R Irvine, A. Webb, and N. H. K. Burton (2015). Modelling the abundance and distribution of marine birds accounting for uncertain species identification. Journal of Applied Ecology 52:150–160.

Kaiser, M. J., M. Galanidi, D. A. Showler, A. J. Elliott, R. W. G. Caldow, E. I. S. Rees, R. A. Stillman, and W. J. Sutherland (2006). Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. Ibis 148:110–128.

Kirk, M., D. Esler, S. Iverson, and W. S. Boyd (2008). Movement of wintering Surf Scoters: Predator responses to different prey landscapes. Oecologia 155:859–867.

Louzao, M., J. Bécares, B. Rodríguez, K. D. Hyrenbach, A. Ruiz, and J. M. Arcos (2009). Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Marine Ecology Progress Series 391:183–197.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham (2005). Zero tolerance ecology: Improving ecological interference by modelling the source of zero observations. Ecology Letters 11:1235–1246.

McGowan, J., E. Hines, M. Elliott, J. Howar, A. Dransfield, N. Nur, and J. Jahncke (2013). Using seabird habitat modelling to inform marine spatial planning in central California's national marine sanctuaries. PLOS One 8:e71406. doi:10.1371/journal.pone.0071406

Meiner, J., and S. Bräger (1990). The feeding ecology of wintering Eiders *Somateria mollissima* and Common Scoters *Melanitta nigra* on the Baltic Sea coast of Schleswig-Holstein, FRG. Wader Study Group Bulletin 58:10–12.

Nilsson, L. (1970). Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.

Nilsson, L. (2008). Changes in numbers and distribution of wintering waterfowl in Sweden during forty years, 1967–2006. Ornis Svecica 18:135–226.

Nur, N., J. Jahncke, M. P. Herzog, J. Howar, K. D. Hyrenbach, J. E. Zamon, D. G. Ainley, J. A. Wiens, K. Morgan, L. T. Balance, and D. Stralberg (2011). Where the wild things are: Predicting hotspots of seabird aggregations in the California Current System. Ecological Applications 21:2241–2257.

Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A. F. O'Connell, P. I. Miller, and M. Louzao (2012). Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biological Conservation 156:94–104.

Pearce, J., and S. Ferrier (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Petersen, I. K., and A. D. Fox (2007). Changes in bird habitat utilisation around the Horns Rev 1 offshore wind farm, with particular emphasis on Common Scoter. National Environmental Research Institute, University of Aarhus, Denmark.

Petersen, I. K., R. D. Nielsen, and M. L. Mackenzie (2014). Post-construction evaluation of bird abundances and distributions in the Horns Rev 2 offshore wind farm area, 2011 and 2012. DCE – Danish Centre for Environment and Energy, Aarhus University, Denmark.

Pittman, S. J., and K. A. Brown (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. PLOS One 6:e20583. doi:10.1371/journal.pone.0020583

Potts, J. M., and J. Elith (2006). Comparing species abundance models. Ecological Modelling 199:153–163.

Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmerman, M. Zappa, and A. Guisan (2006). Are niche-based models transferable in space? Journal of Biogeography 33:1689–1703.

R Development Core Team (2004). A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Redfern, J. V., J. Barlow, L. T. Ballance, T. Gerrodette, and E. A. Becker (2008). Absence of scale dependence in dolphin–habitat models for eastern tropical Pacific Ocean. Marine Ecology Progress Series 363:1–14.

Robinson, L. M., J. Elith, A. J. Hobday, R. G. Pearson, B. E. Kendall, H. P. Possingham, and A. J. Richardson (2011). Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. Global Ecology and Biogeography 20:789–802.

Schwemmer, P., B. Mendel, N. Sonntag, V. Dierschke, and S. Garthe (2011). Effects of ship traffic on seabirds in offshore waters: Implications for marine conservation and spatial planning. Ecological Applications 21:1851–1860.

Skov, H., S. Heinänen, C. B. Thaxter, A. E. Williams, S. Lohier, and A. N. Banks (2016). Real-time species distribution models for conservation and management of natural resources in marine environments. Marine Ecology Progress Series 542: 221–234.

Skov, H., S. Heinänen, R. Žydelis, J. Bellebaum, S. Bzoma, M. Dagys, J. Durinck, S. Garthe, G. Grishanov, M. Hario, J. J. Kieckbusch, et al. (2011). Waterbird populations and pressures in the Baltic Sea. TemaNord 2011:550, Nordic Council of Ministers, Copenhagen, Denmark.

Sonntag, N. (2009). Investigating a seabird hotspot: Factors influencing the distribution of birds in the southern Baltic Sea. Ph.D. dissertation, Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität, Kiel, Germany.

Stefánsson, G. (1996). Analysis of groundfish survey abundance data: Combining the GLM and delta approaches. ICES Journal of Marine Science 53:577–588.

Stempniewicz, L. (1995). Feeding ecology of the Long-tailed Duck *Clangula hyemalis* wintering in the Gulf of Gdansk (southern Baltic Sea). Ornis Svecica 5:133–142.

Swets, K. (1988). Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Systad, G. H., J. O. Bustnes, and K. E. Erikstad (2000). Behavioral responses to decreasing day length in wintering sea ducks. The Auk 117:33–40.

Tasker, M. L., P. H. Jones, D. J. Dixon, and B. F. Blake (1984). Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. The Auk 101:567–577.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Torres, L. G., P. J. H. Sutton, D. R. Thompson, K. Delord, H. Weimerskirch, P. M. Sagar, E. Sommer, B. J. Dilley, P. G. Ryan, and R. A. Phillips (2015). Poor transferability of species distribution models for a pelagic predator, the Grey Petrel, indicates contrasting habitat preferences across ocean basins. PLOS One 10:e0120014. doi:10.1371/journal.pone.0120014

Webley, J. A. C., D. G. Mayer, and S. M. Taylor (2011). Investigating confidence intervals generated by zero-inflated count models: Implications for fisheries management. Fisheries Research 110:177–182.

Winiarski, K. J., M. L. Burt, E. Rexstad, D. L. Miller, C. L. Trocki, P. W. C. Paton, and S. R. McWilliams (2014). Integrating aerial and ship surveys of marine birds into a combined density surface model: A case study of wintering Common Loons. The Condor: Ornithological Applications 116:149–161.

Wintle, B. A., J. Elith, and J. M. Potts (2005). Fauna habitat modelling and mapping: A review and case study in the

Lower Hunter Central Coast region of NSW. Austral Ecology 30:719–738.
Wood, S. N. (2006). Generalized Additive Models: An Introduction with R. Chapman and Hall, London, UK.
Wood, S. N., and N. H. Augustin (2002). GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157:157–177.
Yen, P. P. W., F. Huettmann, and F. Cooke (2004). A large-scale model for the at-sea distribution and abundance of Marbled Murrelets (*Branchyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada. Ecological Modelling 171:395–413.
Zipkin, E. F., J. B. Leirness, B. P. Kinlan, A. F. O'Connell, and E. D. Silverman (2014). Fitting statistical distributions to sea duck count data: Implication for survey design and abundance estimates. Statistical Methodology 17:67–81.
Žydelis, R., and D. Ruškytė (2005). Winter foraging of Long-tailed Duck (*Clangula hyemalis*) exploiting different benthic communities in the Baltic Sea. The Wilson Bulletin 117:133–141.
Žydelis, R., D. Esler, W.S. Boyd, D. L. Lacroix, and M. Kirk (2006). Habitat use by wintering Surf and White-winged scoters: Effects of environmental attributes and shellfish aquaculture. The Journal of Wildlife Management 70:1754–1762.