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Seals at sea: modelling seal distribution in the German bight based on aerial survey data

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Abstract The Wadden Sea is an important habitat for harbour seals and grey seals. They regularly haul-out on sandbanks and islands along the coast. Comparably little is known about the time seals spend at sea and how they use the remainder of the North Sea. Yet, human activity in offshore waters is increasing and information on seal distribution in the North Sea is crucial for conservation and management. Aerial line transect surveys were conducted in the German bight from 2002 to 2007 to investigate the distribution and abundance of marine mammals. Distance sampling methodology was combined with density surface modelling for a spatially explicit analysis of seal distribution in the German North Sea. Depth and distance to coast were found to be relevant predictor variables for seal density. Density surface modelling allowed for a depiction of seal distribution in the study area as well as an abundance estimate. This is the first study to use aerial survey data to develop a density surface model (DSM) for a spatially explicit distribution estimate of seals at sea.

Introduction

Two seal species reside in German waters, the harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) (Reijnders et al. 2005). Both are listed in the European Habitats Directive (EEC 1992) as an important species and are protected by the Seal Management Plan and the Monitoring and Assessment Program of the Trilateral Wadden Sea Cooperation (CWSS 1992). Their numbers have been monitored for decades (Reijnders 1976, 1992; Reijnders et al. 1997, 2005; TSEG 2008a). Harbour seal abundance in the Wadden Sea is currently estimated at 17,605 animals (TSEG 2008b). Grey seals are far less common in the Wadden Sea and amount to approximately 2,139 animals (TSEG 2006). Population estimates of both harbour and grey seals are based on regular counts of hauled-out seals on the islands and sandbanks of the Wadden Sea in the moulting season during low tide (Reijnders et al. 1997; TSEG 2008a). The importance of these haul-out sites to both the species is well recognised, as they use them for resting, moulting, pupping and lactation (Thompson and Harwood 1990; Brasseur et al. 1996; Leopold et al. 1997; Thompson et al. 1997; Adelung et al. 2006). However, at no point in the annual cycle all seals are ashore at the same time (TSEG 2003, 2006). Only a fraction of the population is hauled-out at any time and many animals remain in the water also during low tide (Leopold et al. 1997). Harbour seals and grey seals spend on an average 70–80% of their time in water (estimate by S. Tougaard and P. Reijnders in 1992, cited in Leopold et al. 1997; Austin et al. 2006; Adelung et al. 2006; Liebsch 2006), mainly to forage. Despite the large share of time at sea, comparably little is known about how and where seals spend this time (Liebsch et al. 2006). Telemetry data from Germany showed that harbour seals go on foraging trips of 3–16 days (Adelung et al. 2006). During foraging trips they are known to leave the Wadden Sea and frequently visit North Sea waters (in the following referred to as “offshore”) (Ries 1993; Adelung et al. 2006; Liebsch et al. 2006). Tougaard et al.

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(2008) found that harbour seals spend considerable time in the central North Sea. There are indications that foraging takes place almost exclusively in offshore waters (Liebsch 2006; Tougaard et al. 2006). Leopold et al. (1997) evaluated line transect data from a winter shipboard survey in Dutch, German and Danish North Sea waters between the Wadden Sea and the 20 m depth curve. They found that 20% of that year's summer population estimate of harbour seals was prevalent in these waters, indicating a high importance of North Sea offshore waters for Wadden Sea harbour seals in winter. The general distribution of seals at sea, however, is poorly understood.

Increasing pressures from human development in offshore waters necessitate the identification of habitat important to the species (Madsen et al. 2006) and information on the distribution of seals offshore is ever more needed for management and protection. Seal conservation at present is focussed on protecting major haul-out sites during breeding and moulting seasons (CWSS 1992). If seals rely on offshore waters, e.g. as feeding habitat, conservation strategies should be adjusted to include these areas.

So far, only telemetry data give insight on the whereabouts of seals at sea. Such telemetry data can be used to make population level estimates on distribution (Matthiopoulos et al. 2004; Aarts et al. 2008), but this information is closely related to individual behaviour (Judson 1994; Bolnick et al. 2003). Recent studies have indicated that individuals of a population often show remarkable variation or specialization in foraging behaviour (Bolnick et al. 2003; Estes et al. 2003). Consequently, a large number of (expensive) transmitters are needed to make accurate estimates on seal distribution at sea.

At the same time, seals are often recorded as non-target species during dedicated cetacean surveys following distance sampling methodology. These surveys provide a rich source of opportunistically collected line-transect data. Until now, these data were mostly not evaluated in terms of density and abundance estimates, as traditional distance sampling requires minimum sighting numbers during single surveys. A newly integrated modelling tool of the program Distance 6.0 (Thomas et al. 2006), however, allows for the modelling of spatial variation in animal density from standard line-transect data (Hedley and Buckland 2004) using generalised additive models (GAM; Hastie and Tibshirani 1990). As a model-based approach, density surface modelling does not require a formal sampling scheme, but employs model-based inference for density and abundance estimation. This way the method opens options for analyses of data collected opportunistically during line transect surveys aimed at other species.

To assess the distribution of seals in German waters, we evaluated seal sighting data from aerial cetacean surveys by means of the program Distance 6.0 (Thomas et al. 2006). By relating animal density to spatial variables, density surface modelling allowed for the estimation and visualization of the spatial distribution of seals at sea, as well as an abundance estimate. This is the first study to use aerial sighting data from the North Sea to model seal distribution.

Materials and methods

Data collection

From 2002 to 2007, aerial line-transect surveys for the assessment of harbour porpoise distribution were conducted in German waters. During these surveys all marine mammal sightings were recorded. The study area comprised the 12 nm zone and the exclusive economic zone (EEZ) of Germany with a total surface area of 41,043 km^2. Within that area, transect lines of varying lengths and distance to each other were surveyed over 6 years. The direction of tracks was either north–south or east–west to follow gradients of depth. Though effort varied between areas, the whole study area was covered multiple times during the study period. Flights were conducted independent of tides and represent a random sample of all tidal stages. All surveys were conducted following standard line transect methodology for aerial surveys (Hiby and Hammond 1989; Buckland et al. 2001). The survey platform used was a high-wing twin engine aircraft (Partenavia 68) flying at an altitude of 600 ft (182 m) and at a speed of 90–100 kn (167–186 km/h). The aircraft was equipped with two bubble windows, allowing unobstructed observation of the water surface on both sides, from the abeam line forward to the track line.

Data collection was based on the VOR software (described in Hammond et al. 1995). Every 4 s the aircraft position was recorded automatically onto a laptop computer connected to a GPS. Additionally, the position was stored whenever a sighting occurred. Sea state (according to the Beaufort scale), glare, turbidity (judged visually: 0—clear water with several meters of visibility to 3—very turbid water with no visibility under the surface) and fraction cloud cover (parts of eight) were judged and entered at the beginning of each transect and whenever environmental conditions changed. Sighting data were acquired by two observers located one at each bubble window of the aircraft. Any seal sighted in water was recorded. Hauled-out animals on land were not recorded. Data were immediately entered into the computer by a third observer team member, located in the co-pilot's position and only responsible for data entry. Sighting data included group size, behaviour and clinometer angle from the aircraft to the sighting abeam, in order to calculate the perpendicular distance of the sighting to the transect line.

As it was impossible to distinguish between harbour and grey seals from 600 ft altitude, all seal sightings were categorised as “seals” and evaluated together.

Data analysis

Modelling the detection function

At first a detection function $g(x)$ for seals in the study area was estimated from the perpendicular distances (x) of the detected animals to the transect line according to Buckland et al. (2001) by means of the Distance 6.0 software (Thomas et al. 2006). $g(x)$ describes the probability of detecting an object at any given distance from the transect line. The data were left truncated at 25 m, as the histogram of the distances (x) revealed too few detections up to 25 m of the transect line, probably as a result of inadequate view onto the area directly under the plane. The data were right truncated at 300 m to exclude outlier sightings. To reduce heterogeneity, the effects of several covariates on the detectability of seals in the study area were considered by incorporating them into the detection function modelling process (Marques and Buckland 2003). As data from 6 years were accumulated and all seasons, first of all detection functions were compared between years and months. They proved to be similar for all years and seasons and data were then pooled. Two key functions were explored for modelling the detection function, the one-parameter half-normal function $g(x) = \exp\left({x^2}/{2\sigma^2}\right)$ and the two-parameter hazard-rate function $g(x) = 1 - \left[-\left({x}/{\sigma}\right)^{-b}\right]$, where σ is a scale parameter and b a shape parameter. Each function was tested with varying numbers and types of covariates. It was assumed that covariate z affects detectability via the scale term σ, according to the relationship $\sigma = \exp(\beta_0 + \beta_1 z)$, as described in Marques and Buckland (2003). Covariates considered potentially relevant for the detection probability were observer, sea state, turbidity, cloud cover and behaviour. They were tested singly and in additive combination. The best model was chosen based on lowest Akaike information criterion (AIC) (Akaike 1973; Burnham and Anderson 2002). The AIC differences, $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$ were computed over all candidate models. Goodness-of-fit was assessed with Q–Q plots and the Cramér-von Mises test as described by Burnham et al. (2004). Only the best rated model was further used for density surface modelling.

Modelling the density surface

For the modelling process the survey effort was divided into 1-min-effort-segments, resulting in 17,734 segments of length $L_i = \sim 3$ km, i = 1, …, 17,734. The number of seals detected in each segment was denoted by n_i. The probability of detecting the observed animal j in segment i was denoted by $\hat{p}ij$ and was acquired from the estimated detection function. The total number of individuals within segment i was estimated using the Horvitz–Thompson-like estimator $\hat{n}_i = \sum_{j=1}^{n_i} {1}/{\hat{p}_{ij}}$ (Hedley et al. 2004). Four spatial covariates were considered as predictor variables for a density surface model (DSM): latitude (*lat*), longitude (*lon*), depth (*depth*) and distance to coast (*coastdis*). Latitude and longitude, however, were only tested for comparison, as they were not considered ecologically meaningful in our study. For each segment, the values of all four covariates were calculated in ArcView 3.2 (ESRI). The expected abundance of seals in each segment was related to the spatial covariates using GAMs (Hastie and Tibshirani 1990), according to the formulation $f\left({E[\hat{n}_i]}/{2wl}\right) = \alpha + \sum_m s_m(z_{mi})$, where f is the link function, α is the intercept, $s_m(\cdot)$ is the one-dimensional smooth function for spatial covariate m, z_{mi} is the value of spatial covariate m for segment i and $a_i = 2wL_i$ is the area of the segment. The logarithmic link (which ensures positive values of the mean response) and a quasipoisson error distribution were used. With a logarithmic link, the above equation becomes $f(E[\hat{n}_i]) = \alpha + \sum_m s_m(z_{mi}) + f(a)$. For generalised additive modelling the package mgcv (Wood 2006) was used in R v.2.3.1 (R Development Core Team 2006) as integrated in Distance 6.0. The best model was determined in a stepwise selection procedure to decide what predictor variables to include. Variables were selected based on their estimated degrees of freedom as well as assessment of the confidence band of their smooth. The overall fit of all models tested was judged by comparing the generalised cross validation scores. A model with lowest generalised cross validation (GCV) score fits the data best (Wood 2006). Final model selection among the set of DSMs was conducted based on their GCV score. Models with equal GCV scores were rated according to the percent of deviance they explained.

Abundance estimation

By means of ArcView 3.2 a prediction grid was produced for the study area, consisting of $r_n = 540$ cells, each 100 km^2 in size and each holding information on mean distance to coast and mean depth, as well as latitude and longitude of the centre of each cell. The minimum abundance of seals in the study area was estimated as the sum of $\text{E}[\hat{n}_r]$ at each cell r of the prediction grid, i.e. $\hat{N} = \sum_r \text{E}[\hat{n}_r]$ where $\text{E}[\hat{n}_r]$ are the predictions according to the selected spatial DSM (where in the offset term the area of the segment $a_i = 2wL_i$ was replaced by the surface of the prediction cell = 100 km^2). The above abundance estimation was conducted using the DSM analysis engine of the Distance 6.0 software (Thomas et al. 2006). Based on the predictions $E[\hat{n}_r]$ an interpolated distribution map of seals in the study area was produced using ArcView 3.2.

The variance of the abundance estimate had to be calculated from two separate components, one arising from the detection function model and the other from the DSM. It was assumed that these components were independent and thus the delta method (Seber 1982) was used to estimate the total variance according to the relationship $\left[\text{cv}(\hat{N})\right]^2 = [\text{cv}(\hat{p})]^2 + \left[\text{cv}(\hat{N}_{\text{DSM}})\right]^2$, where $\text{cv}(\hat{p})$ is the coefficient of variation of the estimator of detection probability and $\text{cv}(\hat{N}_{\text{DSM}})$ is the coefficient of variation related to the DSM. The first component was obtained analytically according to Buckland et al. (2001). For the second component, a parametric bootstrap was conducted (Efron and Tibshirani 1993), with sample size $B = 999$. For the bootstrap a moving block method was applied, with moving blocks of three segments as a sampling unit.

To correct for diving seals we derived a correction factor from knowledge on diving behaviour. Harbour and grey seals show species specific behaviour concerning the length of dive bouts (Thompson et al. 1994, 1996). Since by numbers harbour seals dominate grey seals in the Wadden Sea (TSEG 2006, 2008b) the estimates for correction were based on information about harbour seal behaviour. Harbour seals from the German Wadden Sea have been found to conduct dives of averagely 4.5 min with 0.5 min surface intervals (Adelung personal communication; Liebsch 2006). These findings suggest harbour seals to be visible to an observer for a minimum of 10% of their time at sea. Telemetry studies from Germany showed that apart from normal diving behaviour, harbour seals at sea exhibit sleeping behaviour. During foraging trips harbour seals rest and sleep, sometimes vertically, sometimes horizontally positioned, by drifting at the surface or by slowly sinking and ascending to and from the ground (Liebsch et al. 2006). Including these resting phases, Liebsch et al. (2006) calculated that harbour seals spend 79% of their time at sea submerged. Based on these assumptions the abundance estimate of seals at sea was corrected for $N = \left(\hat{N}/t_{\text{sea},s}\right)$, with $t_{\text{sea},s}$ being the proportion of time seals at sea spend close to the surface ($t_{\text{sea},s} = 0.21$).

Results

Data collection

From May 2002 to June 2007 52,588 km of track lines were covered on effort. The allocation of effort according to years and months is given in Table 1 and covered track lines and sightings are shown in Fig. 1. Over all 329 sightings with 367 seals were recorded. Median group[1] size was 1.14 animals with a maximum group size of 10. All sightings of more than one animal occurred close to land (<10 km). Larger group sizes (>3 animals) were only observed in direct proximity to haul-out sites. Recorded behaviours of seals were classified as "headup"[2] (105), swimming (81), slow swimming (17), milling (30), resting (58), diving down (4) and unknown (72). Median group sizes of animals swimming, slow swimming, showing "headup" or diving down were <1.2, while 2.2 for animals milling and 1.4 for animals resting.

Table 1 Survey effort allocation by year and by month accumulated over survey years

Year	Effort (km)	Month	Effort (km)2
2002	8,447.54	Jan	314.25
2003	9,588.93	Feb	1,509.00
2004	7,981.00	Mar	1,343.43
2005	15,251.37	Apr	4,223.31
2006	8,827.13	May	11,504.78
2007	2,693.73	Jun	9,419.44
		Jul	6,545.99
		Aug	4,281.00
		Sep	4,611.60
		Oct	5,232.52
		Nov	3,805.08
		Dec	0.00

Data analysis

Modelling the detection function

As rated by lowest AIC, the best model of the detection function among all models tested was model g_4, the hazard-rate function with *cloud* as the scale parameter (Table 2; Fig. 2). Of all tested covariates *cloud* improved the fit of the detection function best. A combination with the second best rated, singly used covariates, i.e. seastate and turbidity, produced no further improvement. Besides the lowest AIC value, model g_4 provided a good absolute fit as assessed by the Q–Q plot and the Cramér-von Mises test ($P = 0.02$). Detectability was constant and common for all sightings after integrating out distance and scaling by *cloud*. The corresponding probability of detection (±SE) was $\hat{p} = 0.518 \pm 0.037$ (cv = 0.0711). Hence, this model was

[1] In this context, group is defined as a number of animals engaged in similar behaviour, not to be confused with a "social group" as found with e.g. cetaceans.

[2] Animal positioned vertically in the water column with its head out of the water.

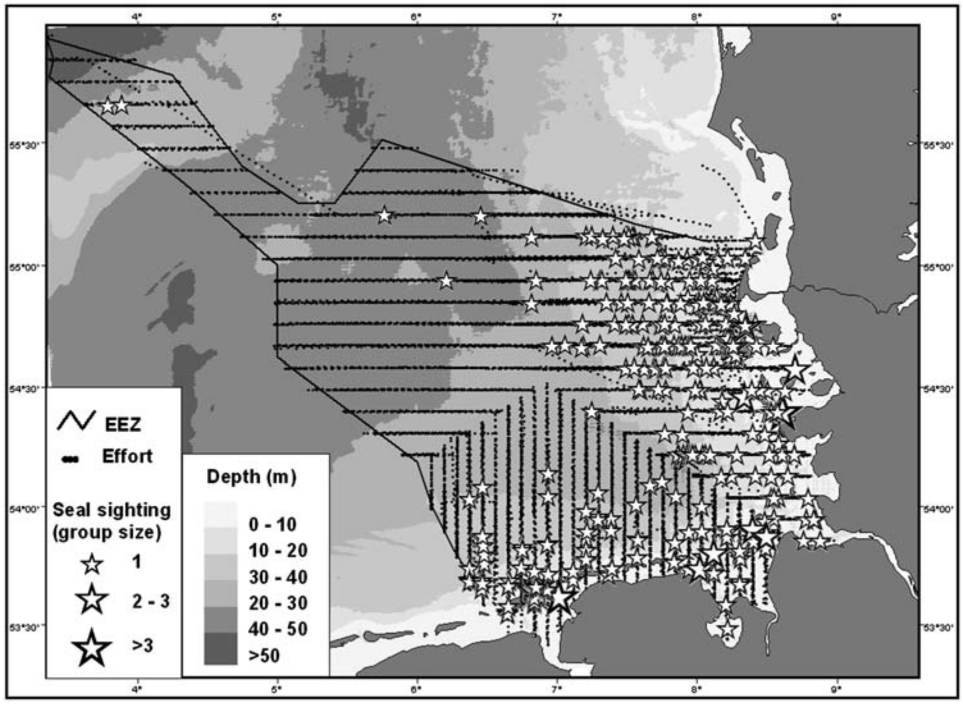


Fig. 1 Survey area and sightings. The *outlined area* represents the German EEZ and 12 nm zone. The *dotted lines* are the covered survey track lines as recorded by GPS. Most lines have been covered multiple times during 6 years of survey. Each *star symbol* indicates a sighting of one or more seals

chosen as the detection function which the density surface modelling was based on.

Modelling the density surface

The best DSM, as indicated by lowest GCV score and highest explained deviance, was model h_6, which incorporated a two-dimensional smooth of *depth* and *coastdis* (Table 3). The expression of the model was $\log(E[\hat{n}_i]) = \alpha + s_1(\text{coastdis, depth}) + \log(a)$, where $a = 2wL$, and the

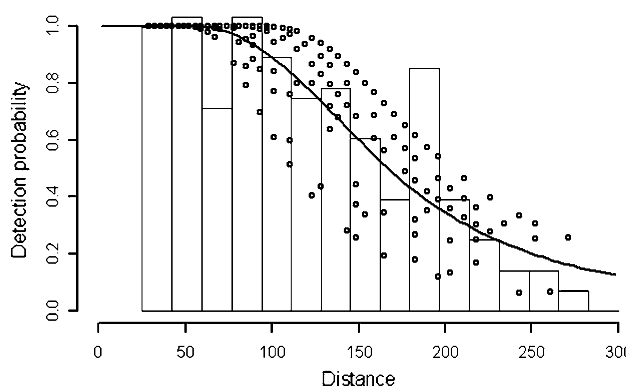


Fig. 2 Histogram of the sighting data. Sightings are binned according to their distance from the transect line and scaled. Truncation has been performed at 25 and 300 m from the transect line. The *solid line* represents the detection function with the best fit (hazard rate model with cloud cover as a scaling parameter)

Table 2 AIC ratings of all tested models of the detection function

Model	Scaling parameter	AIC	ΔAIC
g_1 Half normal	–	2,755.38	4.88
g_2 Hazard rate	–	2,759.04	8.54
g_3 Half normal	Cloud cover	2,751.08	0.58
g_4 Hazard rate	Cloud cover	2,750.5	0
g_5 Half normal	Seastate	2,757.09	6.59
g_6 Hazard rate	Seastate	2,760.87	10.37
g_7 Half normal	Turbidity	2,757.08	6.58
g_8 Hazard rate	Turbidity	2,757.08	6.58
g_9 Half normal	Behaviour	2,756.93	6.43
g_{10} Hazard rate	Behaviour	2,760.16	9.66
g_{11} Half normal	Observer	2,758	6.00
g_{12} Hazard rate	Observer	2,760.88	10.38
g_{13} Half-normal	Cloud cover + behaviour	2,760.96	10.46
g_{14} Hazard-rate	Cloud cover + turbidity	2,752.44	1.94

Model g_4 was rated best model by lowest AIC and was used in the further modelling process

Table 3 Evaluation of all density surface models tested

Model	Predictors	GCV score	Dev. Expl. (%)
h_1	s(lat)	0.175	6.85
h_2	s(lon)	0.176	6.53
h_3	s(coastdis)	0.166	12.1
h_4	s(depth)	0.161	14.4
h_5	s(depth) + s(coastdis)	0.160	15.2
h_6	s(depth, coastdis)	0.159	15.3

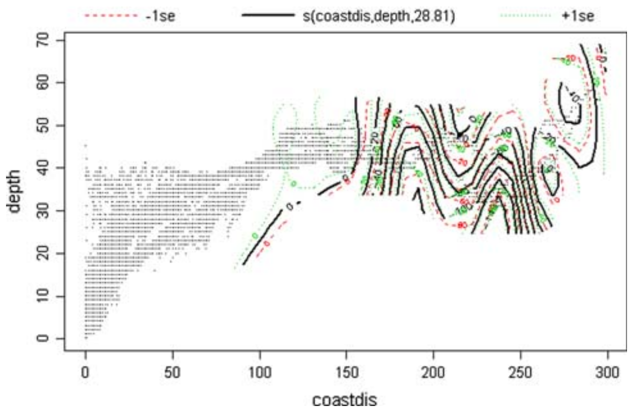


Fig. 3 Two-dimensional smooth term of depth and distance to coast, selected as the best DSM for seal abundance in the study area based on 10 × 10 km cells. The 95% confidence intervals are given with *dotted lines*. Explained deviance is 16%

smooth function s_i is given in Fig. 3. The distribution map of seals according to model h_6 applied to the prediction grid is given in Fig. 4. High densities were predicted in coastal areas, gradually decreasing up to 100 km offshore, followed by a strip of no predicted seals. 250–275 km offshore, in the area of the Dogger Bank, another area of higher density compared to surrounding areas was predicted.

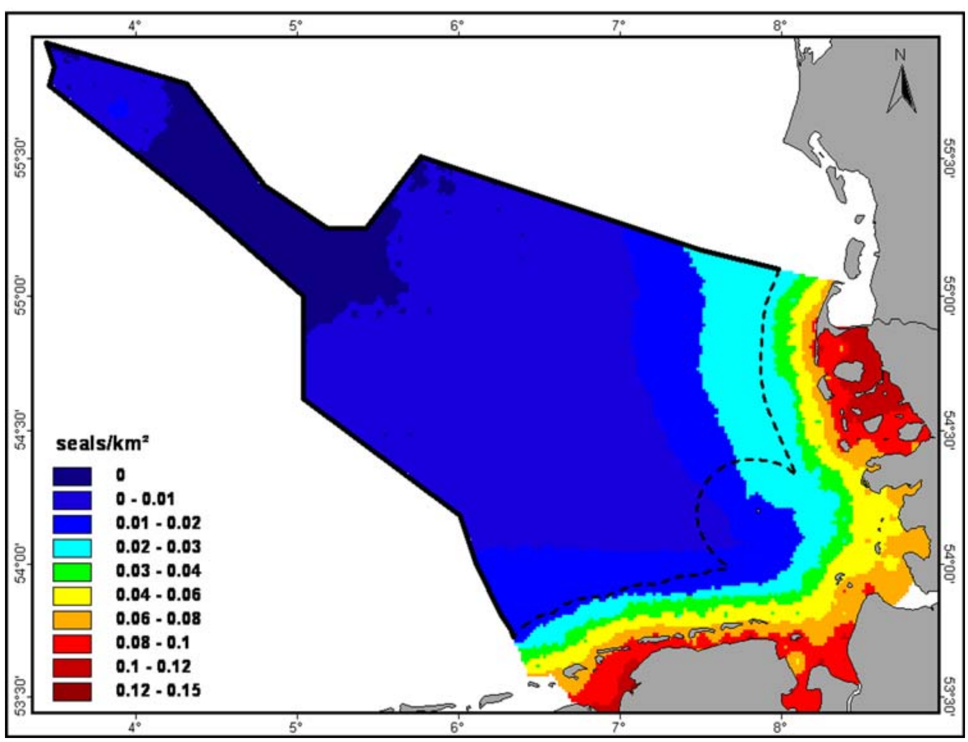
Abundance estimation

The abundance of seals in the study area (not corrected for the proportion of time diving) was predicted at $\hat{N} = 1,017$ [cv($\hat{N}$) = 0.0714] animals. The variation component due to uncertainty in the estimation of the detection function was cv $(\hat{p}) = 0.0711$, while the component due to density surface modelling was $\mathrm{cv}(\hat{N}_{\mathrm{DSM}}) = 0.006$. Corrected for diving seals the abundance estimate was calculated at 4,843 individuals in the study area.

Discussion

In this first assessment, the general distribution of seals at sea and the identification of areas of high seal density were of primary interest, as baseline data are urgently needed for management and protection. Aerial surveys offered unique area coverage and sampling size for this purpose, allowing for an offshore distribution assessment of seals in German waters, otherwise not possible. Though species identification may not always be essential for conservation purposes, from a biological point of view it is a limitation to the model, that harbour and grey seals could not be distinguished in this study. Both species are likely to exhibit a specific distribution and density pattern at sea which could not be differentiated in this study. In the future an attempt should be made to further evaluate the distribution at species level, e.g. by directly comparing aerial survey data and telemetry data. However, harbour seals are likely to represent the major part of all sightings during this study, as they are not only far more common along the German coast, but also in German waters. Between 2002–2006

Fig. 4 Predicted seal distribution in the German North Sea. The *outlined area* indicates the German EEZ bordering the 12 nm zone along the coast. Seal density (animals/km²) is predicted according to model h₆. Visualization was performed in ArcView 3.2. Explained deviance is 16%



aerial bird surveys conducted in the German bight at a lower flight altitude (250 ft; method described in Garthe et al. 2004) were able to distinguish seals sighted at sea at species level: Out of 513 identified seals only 8 were grey seals and all others harbour seals (Garthe personal communication). Accordingly, the predicted distribution is likely to represent harbour seal distribution. Therefore, in the following discussion results are mainly evaluated with respect to harbour seals.

Detection function and detectability

When estimating density or abundance one has to account for differences in the probability of detection (Pollock et al. 2002). We used a model adjustment scaled by covariates to make detectability constant over space and time. Among the covariates affecting detectability, cloud cover had the highest explanatory power. Barlow et al. (1988) found that by decreasing penetration of sunlight into the sea, higher cloud cover lowered detectability of porpoises during aerial surveys. Moreover, certain light conditions related to specific cloud coverage might have influenced the detectability of one ore more types of behaviour of seals, so e.g. the behaviour described as "head up", where seals are positioned vertically in the water column. Most likely cloud cover affected visibility in general by changing watercolours and contrasts as well as glare and the reflection of clouds on the water.

Density surface model

Sixteen percent of deviance were explained by the model integrating distance to coast and depth as explanatory variables. The inferred relationships of animal density to these spatial covariates may function as a starting point for further ecological investigations. Depth and distance to coast can be seen as proxies for other covariates such as salinity, turbidity and prey distribution. In the German North Sea depth and distance to coast for example are known to have a major impact on fish assemblage (Ehrich et al. 2006). Including other oceanographic features like sediment type, slope and primary production could probably advance the model and more variables especially concerning prey availability might improve its predictive power.

The predicted distribution of seals shows high densities in a continuous band along the coast. In the North of the study area the strip extends to 100 km, in the South of the study area to 40–50 km offshore. These predictions are supported by the results of telemetry studies from German and Danish waters, showing seals to preferably utilise the North Sea waters up to the 20 m depth contour (Adelung et al. 2006; Liebsch 2006) and to spend most time during foraging trips in waters between the coast and 100 km offshore (Tougaard et al. 2006). The predicted stretch of higher densities is therefore likely to represent the outline of a continuous foraging habitat, as suggested by Tougaard et al. (2003). The area of highest density, predicted south east of the island of Sylt, has been shown to be visited by seals from haul out sites north as well as south of the island (Reijnders et al. 2005) and it is located in close proximity to a major haul out site ("Lorenzenplate", see Adelung et al. 2006). Hence, high densities in the area seem plausible.

Higher density compared to surrounding waters was predicted for the area of the Dogger Bank (>200 km offshore). It can be argued, that sightings at the Dogger Bank were grey seals only, as they are known to travel very long distances during foraging trips (Thompson et al. 1996; Austin et al. 2006). Sighted animals could belong to the larger grey seal populations of the British coast, which is as far from the Dogger Bank as the German coastline. This assumption may be supported by the strip for which no seals are predicted, separating the Dogger Bank from the rest of the German North Sea. Yet, recent telemetry data have shown that harbour seals from the Wadden Sea do go as far as the Dogger Bank on their foraging trips: harbour seals tagged in the Danish Wadden Sea by Tougaard et al. (2003) were tracked to 200–300 km offshore. Although the Dogger Bank is far offshore, as a submerged sandbank it features shallow water depths of up to 13 m, which might be considered attractive foraging areas. Thompson and Miller (1990) found that harbour seals from the Moray Firth returned regularly to feeding areas associated with habitats such as rocky reefs and shallow offshore sandbanks. Likewise, grey seals off the Canadian coast showed a preference for feeding over offshore banks (Austin et al. 2006). Our findings suggest that apart from the coastal region, maybe the area of the Dogger Bank is important to harbour and/or grey seals, most likely as a foraging ground. Still, one has to bear in mind that the prediction in this area is based on only few data points and further research in the area is needed.

Generally, concerning distribution and density of seals at sea, one has to take into account that during the annual cycle the distribution of seals at sea is likely to vary. Haul-out behaviour and the duration of foraging trips are known to be subject to seasonal changes (Thompson et al. 1994, 1998; Van Parijs et al. 1997; Liebsch et al. 2006). Data numbers were too small for seasonal separation and accordingly the model represents a mean distribution. Taking the seasonal distribution of survey effort into account, the presented distribution is likely to be biased towards spring and summer densities of seals. As harbour seals are known to spend more time away from their haul-outs in winter (Tougaard et al. 2003), winter distribution might show even higher off-shore dispersal. With a continuation of data collection, seasonal investigations might become possible and represent a promising next step.

Abundance estimation

The abundance correction for the time seals spend submerged was based on the best estimates available from harbour seals of the German Wadden Sea. The applied estimate of seals spending 79% of their time submerged ranges closely to estimates obtained from seals in other areas. Fedak et al. (1988) found harbour seals to be diving 75–80% of their time in water. Krafft et al. (2002) estimated harbour seals to be diving 66% (±3%) of their time in water, during transit 73.5%. According to Bekkby and Bjørge (2000) harbour seals spend 86% of their time at sea submerged. The corrected abundance of 4,843 animals is a minimum estimate and represents a first approximation of an average number of seals at sea in German North Sea waters. As described for the distribution, the number of seals at sea is likely to change according to the seasonal cycle seals exhibit. Moreover, the seal epizootic in 2002 led to a die-off of estimated 47% of the population of harbour seals (Härkönen et al. 2006; Siebert et al. 2007). Between 2002 and 2007 harbour seal numbers from the official seal counts on haul-out sites during the moulting season ranged from 10,800 to 20,975 (mean abundance 15,314) (Wadden Sea Secretariat 2008). The number of seals at sea must thus be expected to have varied accordingly and the predicted abundance represents a mean of all years surveyed. Along the German coast the mean abundance was 8,967 harbour seals and less than 300 grey seals (Wadden Sea Secretariat 2008). Assuming that harbour seals from the German coast on an average spend 75% of their time at sea (Adelung et al. 2006; Liebsch 2006), the number of predicted seals at sea is small in comparison to the number of "German" seals. Yet, as Germany holds a comparably small offshore area with respect to the length of its coastline, a proportion of seals from the German coast must be expected to forage in Dutch and Danish waters. Accordingly, the number of seals in the German North Sea cannot be assumed to be the number of "German" seals at sea. The abundance estimate rather represents an approximation to the average number of seals spending time in the German North Sea.

Conclusion

Our results show that density surface modelling offers a chance to assess seal distribution and abundance from aerial survey data, despite low sighting numbers and data collected during a survey designed for another species. By modelling the density as a smooth gradient it allows for a detailed picture of seal distribution at sea. Moreover, it allows for an approximation of abundance. As an alternative or complementary method to telemetry data it provides a means to obtain base line data on seal distribution in offshore waters. With respect to other species or areas, the reanalysis of other data sets with low sighting numbers, but good coverage, should be encouraged. Analysing data on non-target species of other surveys with this method could provide baseline information on species that little is known about or that are difficult to assess due to offshore distribution or low numbers (e.g. basking sharks, turtles, etc.).

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References

Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160. doi:10.1111/j.2007.0906-7590.05236.x

Adelung D, Kierspel MAM, Liebsch N, Müller G, Wilson RP (2006) Distribution of harbour seals in the German bight in relation to offshore wind power plants. In: Köller J, Köppel J, Peters W (eds) Offshore wind energy. Research on environmental impacts. Springer, Heidelberg, pp 65–75

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csa'aki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Austin D, Bowen WD, McMillan JI, Iverson SJ (2006) Linking movement, diving and habitat to foraging success in a large marine predator. Ecology 87:3095–3108. doi:10.1890/0012-9658(2006)87[3095:LMDAHT]2.0.CO;2

Barlow J, Oliver CW, Jackson TD, Taylor BL (1988) Harbour porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Arial surveys. Fish Bull 86:433–444

Bekkby T, Bjørge A (2000) Diving behaviour of harbour seal *Phoca vitulina* pups from nursing to independent feeding. J Sea Res 44:267–275. doi:10.1016/S1385-1101(00)00048-4

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Husley CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28. doi:10.1086/343878

Brasseur S, Creuwels J, v/d Werf B, Reijnders P (1996) Deprivation indicates necessity for haul-out in harbour seals. Mar Mamm Sci 12:624–627. doi:10.1111/j.1748-7692.1996.tb00077.x

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, London

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin

Burnham KP, Buckland ST, Laake JL, Borchers DL, Marques TA, Bishop JRB, Thomas L (2004) Further topics in distance sampling. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, New York, pp 307–392

CWSS (1992). Sixth trilateral Governmental Wadden Sea Conference 1991. Ministerial declaration—seal conservation and management plan. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, p 55

EEC (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, New-York

Ehrich S, Kloppmann MHF, Sell AF, Boettcher U (2006) Distribution and assemblages of fish in German waters. In: Koeller J, Koeppel J, Peters W (eds) Offshore wind energy. Springer, Berlin, pp 149–180

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72:144–155. doi:10.1046/j.1365-2656.2003.00690.x

Fedak MA, Pullen MR, Kanwisher J (1988) Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. Can J Zool 66:53–60

Garthe S, Dierschke V, Weichler T, Schwemmer P (2004) Rastvogelvorkommen und Offshore-Windkraftnutzung: Analyse des Konfliktpotenzials für die deutsche Nord- und Ostsee. In: Kellermann A, et al (eds) Marine Warmblüter in Nord- und Ostsee: Grundlagen zur Bewertung von Windkraftanlagen im Offshore-Bereich. Endbericht

Hammond PS, Benke H, Berggren P, Borchers DL, Buckland ST, Collet A, Heide-Jørgensen MP, Heimlich-Boran S, Hiby AR, Leopold MF, Øien N (1995) Distribution and abundance of harbour porpoises and other small cetaceans in the North Sea and adjacent waters. European Community LIFE programme, Life, LIFE 92-2/IL/027, p 242

Härkönen TJ, Dietz R, Reijnders P, Teilmann J, Harding K, Hall A, Brasseur S, Siebert U, Goodman SJ, Jepson PD, Rasmussen TD, Thompson P (2006) A review of the 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Dis Aquat Org 68:115–130. doi:10.3354/dao068115

Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman & Hall, London

Hedley SL, Buckland ST (2004) Spatial models for line transect sampling. J Agric Biol Environ Stat 9:181–199. doi:10.1198/1085711043578

Hedley SL, Buckland ST, Borchers DL (2004) Spatial distance sampling models. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, New York, pp 48–70

Hiby AR, Hammond PS (1989) Survey techniques for estimating the abundance of cetaceans. Rep Int Whal Comm Spec Issue 11:47–80

Krafft BA, Lydersen C, Gjertz I, Kovacs KM (2002) Diving behaviour of sub-adult harbour seals (*Poca vitulina*) at Prins Karls Forland Svalbard. Polar Biol 25:230–234. doi:10.1007/s00300-001-0330-2

Judson OP (1994) The rise of the individual-based model in ecology. Trends Ecol Evol 9:9–14

Leopold MF, v/d Werft B, Ries EH, Reijnders PJH (1997) The importance of the North Sea for winter dispersal of harbour seals *Phoca vitulina* from the wadden sea. Biol Conserv 81:97–102. doi:10.1016/S0006-3207(96)00092-4

Liebsch NS (2006) Hankering back to ancestral pasts: constraints on two pinnipeds, *Phoca vitulina* & *Leptonychotes weddellii* foraging from a central place. Ph.D. Thesis, University of Kiel, p 161

Liebsch N, Wilson RP, Adelung D (2006) Utilisation of time and space by harbour seals (*Phoca vitulina vitulina*) determined by new remote-sensing methods. In: von Nordheim H, Boedeker D, Krause JC (eds) Progress in marine conservation in Europe: NATURA 2000 sites in German offshore waters. Springer, Berlin, pp 178–188

Madsen PT, Wahlberg M, Tougaard J, Lucke K, Tyack P (2006) Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. Mar Ecol Prog Ser 309:279–295. doi:10.3354/meps309279

Marques FFC, Buckland ST (2003) Incorporating covariates into standard line transect analyses. Biometrics 59:924–935. doi:10.1111/j.0006-341X.2003.00107.x

Matthiopoulos J, McConnell B, Duck C, Fedak M (2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. J Appl Ecol 41:476–491. doi:10.1111/j.0021-8901.2004.00911.x

Pollock KH, Nickels JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13:105–119. doi:10.1002/env514

Reijnders PJH (1976) The harbour seal *Phoca vitulina* population in the Dutch Wadden Sea: size and composition. Neth J Sea Res 10:223–235. doi:10.1016/0077-7579(76)90016-8

Reijnders PJH (1992) Retrospective population analysis and related future management perspectives for the harbour seal *Phoca vitulina* population in the Wadden Sea. Netherlands Institute for Sea Research. Spec Publ Ser 20:193–197

Reijnders PJH, Ries EH, Tougaard S, Norgaard N, Heidemann G, Schwarz J, Vareschi E, Traut IM (1997) Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. J Sea Res 38:161–168. doi:10.1016/S1385-1101(97)00031-2

Reijnders PJH, Abt KF, Brasseur SMJM, Camphuysen KCJ, Reineking B, Scheidat M, Siebert U, Stede M, Tougaard J, Tougaard S (2005) Marine mammals. In: Essink K, Dettmann C, Farke H, Laursen K, Lürßen G, Marencic H, Wiersinga W (Trilateral Monitoring and Assessment Group) (eds) Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No.19. Common Wadden Sea Secretariat, Wilhelmshaven, pp 305–318

Ries EH (1993) Monitoring the activity patterns of free-ranging harbor seals (*Phoca vitulina*) by means of VHF telemetry. Wadden Sea Newsl 3:11–14

Seber GAF (1982) The estimation of animal abundance and related parameters. Griffin, London

Siebert U, Wohlsein P, Lehnert K, Baumgärtner W (2007) Pathological findings in harbour seals (*Phoca vitulina*): 1996–2005. J Comp Pathol 137:47–58. doi:10.1016/j.jcpa.2007.04.018

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org

Thomas L, Laake JL, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Hedley SL, Pollard JH, Bishop JRB, Marques TA (2006) Distance 6.0. beta. Research unit for wildlife population assessment, University of St. Andrews, http://www.ruwpa.st-and.ac.uk/distance/

Thompson PM, Harwood J (1990) Methods for estimating the population size of common seals, *Phoca vitulina*. J Appl Ecol 27:924–938. doi:10.2307/2404387

Thompson PM, Miller D (1990) Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina* L.) in the Moray Firth, Scotland. J Appl Ecol 27:492–501. doi: 10.2307/2404296

Thompson PM, Miller D, Cooper R, Hammond PS (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. J Appl Ecol 63:24–30

Thompson PM, McConnell BJ, Tollit DJ, Mackay A, Hunter C, Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth. N.E. Scotland. J Appl Ecol 33:1572–1584. doi:10.2307/2404795

Thompson PM, Tollit DJ, Wood DG, Corpe HM, Hammond PS, Mackay A (1997) Estimating harbour seal abundance and status in an estuarine habitat in N.E. Scotland. J Appl Ecol 34:43–52. doi:10.2307/2404846

Thompson PM, Mackay A, Tollit DJ, Enderby S, Hammond PS (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. Can J Zool 76:1044–1053. doi: 10.1139/cjz-76-6-1044

Tougaard J, Ebbesen I, Tougaard S, Jensen T, Teilmann J (2003) Satellite tracking of harbour seals on Horns Reef. Use of the wind farm area and the North Sea. Report to Techwise A/S

Tougaard J, Tougaard S, Jensen RC, Jensen T, Adelung D, Liebsch N, Müller G (2006) Harbour seals on horns reef before, during and after construction of horns rev offshore wind farm. Final report to Vattenfall A/S. Biological Papers from the fisheries and maritime museum No. 5. Esbjerg, Denmark

Tougaard J, Teilmann J, Tougaard S (2008) Harbour seal spatial distribution estimated from argos satellite telemetry—overcoming positioning errors. Endanger Species Res 4:113–122. doi: 10.3354/esr00068

TSEG (Trilateral Seal Expert Group) (2003). Sense and sensibility in evaluating aerial counts of harbour seals in the Wadden Sea. Wadden Sea Newsletter, Wilhelmshaven, http://www.waddensea-secretariat.org/news/publications/Wsnl/Wsnl03-1/articles/4-seal-counts.pdf

TSEG (Trilateral Seal Expert Group) (2006) Aerial surveys of harbour seals in the Wadden Sea in 2006: puzzling results and counting grey seals in the Wadden Sea in 2006. Wadden Sea Newsletter, Wilhelmshaven, http://www.waddensea-secretariat.org/news/news/Seals/Annual-reports/Annual-counts-2006.pdf

TSEG (Trilateral Seal Expert Group) (2008a). Annual Reports. Wadden Sea Newsletter, Wilhelmshaven, http://www.waddensea-secretariat.org/news/news/Seals/Annual-reports/seals2007.html

TSEG (Trilateral Seal Expert Group) (TSEG) (2008b) Aerial surveys of harbour seals in the Wadden Sea in 2007: population age-composition returning to a stable age-structure? Wadden Sea Newsletter, Wilhelmshaven, http://www.waddensea-secretariat.org/news/news/Seals/Annual-reports/Annual-counts-2007-seals.pdf

Van Parijs SM, Thompson PM, Tollit DJ, Mackay A (1997) Changes in the distribution and activity of male harbour seals during the mating season. Anim Behav (in press)

Wadden Sea Secretariat (2008) http://www.waddensea-secretariat.org/. Accessed October 2008

Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Florida