Influence of environmental variability on harbour porpoise movement

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ABSTRACT: The harbour porpoise *Phocoena phocoena* is a small marine predator with a high conservation status in Europe and the USA. To protect the species effectively, it is crucial to understand its movement patterns and how the distribution of intensively used foraging areas can be predicted from environmental conditions. Here, we investigated the influence of both static and dynamic environmental conditions on large-scale harbour porpoise movements in the North Sea. We used long-term movement data from 57 individuals tracked during 1999–2017 in a state-space model to estimate the underlying behavioural states, i.e. whether animals used area-restricted or directed movements. Subsequently, we assessed whether the probability of using area-restricted movements was related to environmental conditions using a generalized linear mixed model. Harbour porpoises were more likely to use area-restricted movements in areas with low salinity levels, relatively high chlorophyll *a* concentrations and low current velocity, and in areas with steep bottom slopes, suggesting that such areas are important foraging grounds for porpoises. Our study identifies environmental parameters of relevance for predicting harbour porpoise foraging hot spots over space and time in a dynamic system. The study illustrates how movement patterns and data on environmental conditions can be combined, which is valuable to the conservation of marine mammals.

KEY WORDS: Switching state-space model · Harbour porpoise · Argos satellite tracking · Area-restricted search · Movement behaviour · *Phocoena phocoena* · Cetacean conservation · North Sea

1. INTRODUCTION

Movement ecology research provides valuable knowledge to inform conservation management (Allen & Singh 2016) and can help to better understand the mechanisms influencing population dynamics (Morales et al. 2010). Animals may switch between distinct movement modes, allowing them to swiftly pass through unfavourable areas or to spend more time on important foraging grounds (Fryxell et al. 2008, Owen-Smith et al. 2010, Gurarie et al. 2016). On foraging grounds, animals typically use convo-luted, area-restricted (AR) movements, and recent advances in animal tracking technology have enabled us to use movement data to pinpoint areas of particular importance for many species (Cagnacci et al. 2010, Allen & Singh 2016, Hindell et al. 2020). However, to extrapolate such findings beyond the areas where animal tracks are available and to understand the proximate cause of variations in animal movements, it is necessary to determine how movement modes are related to environmental conditions (Johnston et al. 2005, Bestley et al. 2013, Trudelle et al. 2016).

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Environmental conditions may induce changes in animal behaviour directly by influencing the animals' physiology or indirectly by affecting the distribution of their prey (Block et al. 2011, Hays et al. 2016). The importance of environmental variables on animal movement and the distribution of their prey typically varies among species and ecosystems. For example, chlorophyll *a* (chl *a*) concentration, water depth, salinity and temperature have often been used as proxies for resource availability in marine systems (Steingrund & Gaard 2005, Elith & Leathwick 2009, Scales et al. 2014, IJsseldijk et al. 2015). In coastal systems, tidal current strength is the most important driver of ecosystem dynamics due to its association with high primary productivity (Sharples et al. 2007, Embling et al. 2012), and in estuaries with strong tides, prey densities appear to be related to salinity (IJsseldijk et al. 2015). Both current strength and the location of highly productive upwelling zones are in turn influenced by seabed slope (Genin 2004, Embling et al. 2012, Amorim et al. 2017). Although these environmental variables are not independent, their relative importance can yield information about the underlying drivers of changes in animal movement behaviour.

Recent advances in biotelemetry and analytical frameworks such as state-space modelling (Morales et al. 2004, Jonsen et al. 2005) offer a way to characterize spatial and temporal patterns in animal movement data. State-space models (SSMs) are time-series models that can be used to infer an individual's behaviour (unobserved state) along its movement track (observed data), thereby offering the possibility to objectively estimate behaviour from satellite tracking data (Jonsen et al. 2013). The underlying assumption of this approach is that differences in behaviour are reflected by changes in the animal's movement path (Morales et al. 2004, Jonsen et al. 2005). For example, an animal that moves in a fast and directed manner is expected to move to another part of its range or between distinct foraging areas, while relatively slow movements with frequent changes in direction likely indicate that the animal is searching for food using AR movements (Turchin 1991). An advantage of SSMs is that error distributions from the observed data can be included and that the most probable movement track can be estimated at regular time intervals (Jonsen et al. 2005, 2013). This makes SSMs suitable for error-prone and irregular data such as those originating from Argos satellite transmitters (Vincent et al. 2002), which have often been used to track movements of marine species. Indeed, SSMs have been used to address a variety of ecological questions, e.g. identification of important breeding grounds of humpback whales *Megaptera novaeangliae* (Trudelle et al. 2016, Dulau et al. 2017), description of intermittent foraging by migrating blue whales *Balaenoptera musculus* and fin whales *B. physalus* (Silva et al. 2013) and identification of offshore foraging grounds for killer whales *Orcinus orca* (Reisinger et al. 2015).

The harbour porpoise *Phocoena phocoena* occurs in cold waters of the Northern Hemisphere and is the most abundant cetacean species in the North Sea (Hammond et al. 2013). Nonetheless, there are concerns that the species is negatively affected by bycatch (Bjørge et al. 2013), pollutants (Siebert et al. 1999) and underwater noise from pile-driving during the construction of offshore wind-farms (Tougaard et al. 2009), seismic surveys (Pirotta et al. 2014, Sarnocińska et al. 2020) and shipping (Dyndo et al. 2015, Wisniewska et al. 2016). Accordingly, harbour porpoises are protected in the European Union (EU) through the EU Habitats Directive (EU 1992) and in the USA through the Marine Mammal Protection Act of 1972. It is therefore a priority to identify areas of particular importance for harbour porpoises, which can be done based on their movement patterns.

Movement data of harbour porpoises have been collected from the east coast of the northern USA (Read & Westgate 1997, Johnston et al. 2005), Greenland (Nielsen et al. 2018) and Denmark (e.g. Teilmann et al. 2007, Sveegaard et al. 2011). In both the western Atlantic and the North Sea/Baltic Sea regions, porpoises are almost exclusively found on the continental shelf with water depth less than 200 m and little seasonal variation, while in Greenland, porpoises move towards deep, offshore habitats during winter and dive to >400 m. Thus far, only 1 other study has explored the effect of dynamic and static environmental conditions on movement patterns of harbour porpoises (van Beest et al. 2018a). This study used high-resolution GPS data, but was based on a relatively small sample size and movement data collected over small spatial and short temporal scales (i.e. several days).

Here, we used a long-term (1999–2017) movement dataset consisting of harbour porpoise Argos locations collected in Skagerrak and the North Sea to identify behavioural states using SSMs, and to assess how the probability that animals used AR movements was related to different environmental variables. We expected animals to be more likely to use AR movements in shallow coastal areas with strong tidal currents and steep seabed slopes, as such areas are often associated with productive upwelling zones.

Further, we expected the likelihood to be high in areas where inflow of fresh water caused productive frontal zones to occur and in productive areas with high chl *a* concentration. This is one of the first studies to assess how movements of a small marine predator are related to environmental conditions in the North Sea, and it provides important insight into the characteristics of areas of high conservation value for porpoises and other species with similar biology.

2. MATERIALS AND METHODS

2.1. Study area

The study area covered a major part of the North Sea from 53 to 62° N and from 3.0° W to 11.8° E. For estimation of behavioural states, we also included movement data from the northern part of the Kattegat (Fig. 1). However, since we suspected the influence of environmental conditions on behavioural states to be different in the Kattegat than in the North Sea due to the prevalence of frontal systems associated with inflow of brackish Baltic Sea water into the Kattegat, we excluded the Kattegat from the study area (see Section 2.3). Most of the North Sea is shallow, with water depths <100 m, and steeper seabed slopes are predominately found along the Norwegian trench where water depths reach >600 m (Fig. 1).

2.2. Tagging of harbour porpoises

The data used in this study are part of an ongoing, long-term tagging project on harbour porpoises in Danish waters (Teilmann et al. 2007). Most individuals were tagged after being incidentally caught in pound nets in the Skagerrak and Kattegat (Fig. 1), but 6 individuals were caught actively in the Danish Wadden Sea. All porpoises were fitted with an Argos satellite tag (from Wildlife Computers, Sirtrack or Telonics), which was attached to the dorsal fin with silicone-coated Delrin pins and iron nuts after drilling a hole through the fin using a 6 mm cork borer. The dissolvable iron nuts allowed the transmitter to detach from the individual after approximately 1 yr. See Teilmann et al. (2007) and van Beest et al. (2018a,b) for further details about capture and tagging procedures, and Table S1 in the Supplement at www.int-res.com/articles/suppl/m648p207_supp.pdf for details about individual animals.

The Argos tags were programmed to make a limited number of satellite uplinks at pre-defined times (duty cycles) to increase battery life. Duty cycles varied between 1 and 4 d. Animal tracks were only included in this study if: (1) the duty cycle was ≤3 d and (2) the individuals stayed ≥30 consecutive days in the study area. In this study, 48% of the tags used exclusively 1 or 2 d cycles, whereas the rest used a mixture of 1, 2 and 3 d cycles. To avoid splitting tracks, we
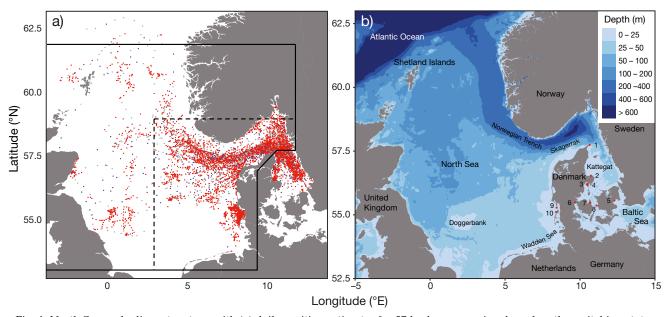

Fig. 1. North Sea and adjacent waters, with (a) daily position estimates for 57 harbour porpoises based on the switching state-space model (red dots: area-restricted movements; blue: directed; grey: uncertain). The solid line shows the delimitation of the study area and the dashed line shows the area where predictions on the use of area-restricted movement were made (see also Fig. 4). (b) Bathymetry and tagging sites (red dots); 1: Skagen, 2: Fjellerup Strand, 3: Knebel, 4: Begtrup Vig, 5: Køge Bugt, 6: Fænø, 7: Kerteminde, 8: Korsør, 9: Mandø, 10: Rømø

allowed for movements outside the study area. These departures from the study area usually lasted 1–4 d. However, these positions were not considered for further analyses due to lack of environmental data. The track of 1 individual was split into 2 sub-tracks because of an extended stay (>30 d) in the Baltic Sea. Finally, we removed locations from the first 24 h of each track to reduce behavioural bias caused by capture and tagging (following van Beest et al. 2018b).

2.3. Position and behavioural state estimation

To regularize the movement tracks and to infer the underlying movement mode at each position, we implemented a switching SSM (Morales et al. 2004, Jonsen et al. 2005, 2013). We fitted a Bayesian SSM using the JAGS software (Plummer & Denwood 2018) through the package 'bsam' (Jonsen et al. 2013) within R 3.6.1 (R Development Core Team 2018). The switching SSM is designed to discriminate between 2 movement modes: AR movements (with low autocorrelation in turning angles and distance travelled) and directed movements (strong autocorrelation). The package was developed specifically for Argos data, and Argos location error structure is incorporated into the model (Jonsen et al. 2005). Model parameters were estimated using Markov chain Monte Carlo methods. We used a hierarchical SSM allowing for joint movement parameter estimation across all individuals, potentially providing improved variable estimation (Brooks & Gelman 1998, Jonsen 2016). To run the model, all locations with the lowest quality class Z were removed (271 positions, 1.0% of the full dataset; see www.argos-system.org for definition of quality classes). The time interval for position and behavioural state estimation was set to 24 h. Two parallel

Markov chains were run, with 90 000 samples per chain. We used diagnostic plots to verify that (1) the Markov chains had converged (i.e. posterior samples were stationary and the chains were well mixed), (2) within-chain sample autocorrelation was low and (3) the Brooks-Gelman-Rubin potential scale reduction factors were <1.1 (following Jonsen et al. 2013). The first 50 000 samples of each chain were discarded as burn-in, allowing the chains to converge. From the remaining 40 000 samples, every 20th sample was retained to reduce autocorrelation with preceding samples. Daily position and behavioural state estimates were obtained from the remaining 4000 samples. The behavioural state for each location is given as an average estimate from the 4000 samples retained and ranges between 1 and 2. Positions with behavioural state estimates between 1 and 1.25 were classified as AR, those with estimates between 1.75 and 2 were classified as directed, and the remaining positions were considered uncertain (following Jonsen et al. 2007). The SSM was able to distinguish between the 2 behavioural states with clear differences in mean turning angles and distances travelled per day (Fig. 2). Animals remained in areas where their movements were classified as AR for extended periods of time (Fig. S1).

2.4. Quantifying the effect of environmental conditions on behavioural state

We used the dataset obtained from the SSM to assess how AR movement behaviour was related to static and dynamic environmental conditions. The static variables water depth and sea bottom slope corresponding to each position estimate were obtained from a digital terrain model with a resolution
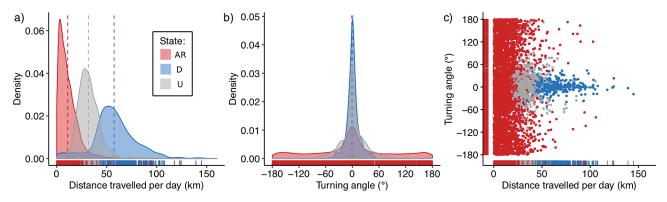

Fig. 2. Variation in (a) distance travelled per day, (b) turning angles and (c) relationship between distance travelled and turning angles for harbour porpoises using area-restricted movements (AR), directed movements (D) or where movement mode could not be assessed with certainty (U) using a switching state-space model. Mean values are indicated with dashed lines

of approximately 300 m (GEBCO 30 arc-second global grid, Weatherall et al. 2015). The dynamic environmental data included daily estimates on salinity, temperature, current velocity and chl *a* concentration and were obtained from the Copernicus Marine Environmental Monitoring Service (http://marine.copernicus.eu/; sea surface values used throughout; Table 1). Data were derived from forecast (1 July 2014 – 31 April 2017) and from reanalysis (1 January 1984 – 30 June 2014) of the Forecasting Ocean Assimilation Model Atlantic Margin model (von Schuckmann et al. 2016). We expected porpoises to use AR movements in areas that were relatively productive compared to other areas at a given point in time, i.e. with a relatively high chl *a* concentration. Since overall chl *a* concentration fluctuates throughout the year, we calculated the relative chl *a* concentration (henceforth called 'chlorophyll anomaly') as the deviation from the mean concentration for a given day. This mean concentration was calculated from a loess curve fitted to the daily chl *a* values (Fig. S2).

Before assessing the effect of environmental conditions on behavioural state, we omitted position estimates that were either (1) outside the study area and on land; (2) associated with aberrant environmental data (1 position with salinity <20 PSU); (3) assigned to uncertain behavioural state; or (4) associated with large error estimates. The position estimates from the SSM were in some cases associated with estimation errors that exceeded the resolution of the environmental variables. These position estimates were mostly assigned to the uncertain behavioural state. To reduce the risk of including positions that had been incorrectly matching with environmental variables, we therefore omitted positions whose 95% error ellipses had an area ≥196 km^2 (equal to 2 × 2 cells in the environmental variable grid).

We used a generalized linear mixed model with binomial error structure to assess if the probability of porpoises being in the AR state was related to water depth, salinity, temperature, current velocity, chlorophyll anomaly and sea bed slope (continuous variables). Depth, slope, current velocity and chlorophyll anomaly were log$_{10}$ transformed to avoid excess influence of outliers (Fig. S3). In the case of chlorophyll anomaly, we added 10 before log-transforming, and in the case of slope, we added 0.01 before log-transforming to avoid transforming negative values. All predictor variables were centred and scaled. We included 'individual' nested within either 'sex', 'year' or 'tagging location' as random grouping variables in 3 different models to assess if the probability of using AR movements varied in space, time or among sexes. Models with differences in Akaike's information criterion (ΔAIC$_c$) values <2 relative to the best model were considered strongly supported by the data, following Burnham & Anderson (2002).

Subsequently, we used the best of these models (i.e. the model with the lowest AIC) to assess how the probability of using AR movements was related to different predictor variables. We did this by fitting models with all possible combinations of the predictor variables and used Akaike weights to determine relative variable importance to build an average model for prediction (cf. Johnson & Omland 2004). This was done using the 'MuMIn' package in R (Bartoń 2019). Further, we tried fitting a model with the same random variables, but using behavioural state estimates as continuous dependent variables instead of as binary variables, but this model explained only little of the variation in data (conditional R^2 = 0.049, i.e. the variation explained by random and fixed effects jointly, cf. Nakagawa & Schielzeth 2013), so this was not pursued further.

Several of the predictor variables were correlated (Fig. S4), which leads to collinearity and introduces a risk of misinterpreting the results (Johnston et al. 2018). To assess whether the relative importance of the predictor variables was influenced by collinearity, we conducted the statistical analyses again after

Table 1. Ranges and sources of variables used to explain variation in movement mode. Variables were obtained from the Copernicus Marine Environmental Monitoring Service (CMEMS), General Bathymetric Chart of the Oceans (GEBCO)

Variable	Unit	Spatial resolution (km)	Temporal resolution	Range	Source
Water depth	m	0.3	Static	1–689	GEBCO
Sea bottom slope	°	0.3	Static	0–15	GEBCO
Sea surface temperature	°C	7	Daily	−1 to 22.7	CMEMS
Sea surface salinity	PSU	7	Daily	9.2–35.7	CMEMS
Sea surface current velocity	m s^{-1}	7	Daily	0–1.04	CMEMS
Sea surface chl *a* concentration	mg C m^{-3}	7	Daily	0.002–28.95	CMEMS
Chlorophyll anomaly	mg C m^{-3}	7	Daily	−3.1 to 26.4	CMEMS

transforming the predictor variables using principal components analysis (PCA). In this analysis, we used the same random grouping variable as in the best of the models above. The PCA transformation results in uncorrelated linear combinations of predictor variables (principal component axes) and is therefore often used for avoiding collinearity (e.g. Jolliffe 2002, Johnston et al. 2018). All mixed models were fitted using the 'glmer' function and maximum likelihood estimation in the 'lme4' package in R (Bates et al. 2015).

3. RESULTS

We used a total of 26 649 Argos locations from 58 tracks (from 57 individuals) to run the SSM, which excluded 271 locations of the lowest Argos quality class Z (1.0 % of the full dataset). The SSM was able to discriminate between 2 distinct movements modes for North Sea harbour porpoises: AR movements with variable turning angles and low autocorrelation between consecutive daily moves, and directed movements with turning angles close to 0 and high autocorrelation (Fig. 2). Movement state was categorized as uncertain for some of the daily position estimates, which is to be expected for animals that use a range of movement modes that do not fit into the 2 rather coarse behavioural modes quantified here. Gamma, which indicates the directional persistence, was 0.994 ± 0.0048 and 0.00156 ± 0.0016 (mean ± SD) for directed and AR movements, respectively. A total of 7762 positions and their underlaying behavioural state (80.9 % AR, 6.0 % directed [D] and 13.1 % uncertain [U]) were estimated by the SSM. Mean number of position estimates per individual was 124 (SD: 73.4, min: 48, max: 340; see details in Table S1) and mean number of position estimates per year was 597 (SD: 379, min: 65, max: 1192; see details in Table 2). Porpoise individuals used AR movements 50.5– 99.5 % of the time (Table S1; mean: 80.9 %), but all individuals tagged in the Wadden Sea on the Danish west coast (Mandø and Rømø sites) used AR movements >96 % of the time, which was more than any of the animals tagged in the Skagerrak or Kattegat. The Wadden Sea animals remained close to the tagging site during the whole tracking period, whereas some

of the other animals ventured across the North Sea to the British coast and Shetland, while occasionally shifting to AR movements (Figs. S1 & S6). Porpoises tended to avoid the deepest part of the study area, along the Norwegian coast (Fig. 1).

Before analysing how behavioural state was related to environmental variation, we removed data from outside the study area and retained only 5753 position estimates from 54 tracks (79.9 % AR, 6.0 % D and 14.0 % U; Fig. 1). Of these, we excluded 3294 positions with uncertain behavioural state, large error estimates and outliers and retained 2460 position estimates (94.2 % AR, 5.8 % D), corresponding to 42.8 % of the position estimates within the study area, or 31.7 % of all position estimates from the SSM.

The probability that animals used AR movements was best explained by a model with variation among individuals nested within sex, but almost equally well explained by a model which did not consider variation among sexes ($\Delta AIC_c = 0.54$). The models that included either tagging year ($\Delta AIC_c = 2.53$) or tagging location ($\Delta AIC_c = 1.70$) were also strongly supported by the data, but the analyses of the importance of environmental variability were based on the model that included variation among individuals nested within sex.

The probability of using AR movements was related to salinity, chlorophyll anomaly (variable importance ≥0.95; Table 3), current velocity and slope (importance ≥0.84), whereas temperature and water depth were less important as predictors. We had expected the likelihood of AR movements to be high in

Table 2. Number of tagged harbour porpoises and total number of positions per year. Position est. indicates the mean number of position estimates per year, estimated by the state-space model (SSM), and %AR indicates the proportion of the daily position estimates from the SSM that were characterized as area-restricted movements
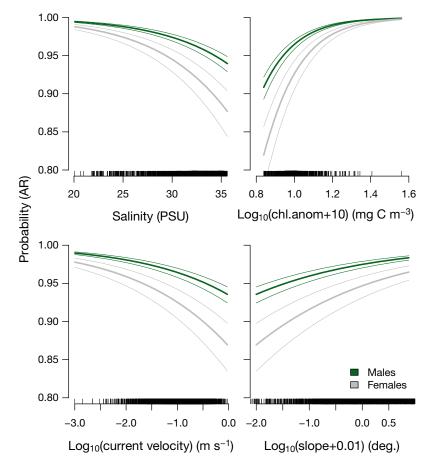
Year	No. of animals	No. of Argos positions	Position est.	Days per track (mean ± SD)	%AR
1999	1	313	65	65	73.8
2000	4	994	648	162.0 ± 94.9	85.5
2001	8	3915	1192	149.0 ± 102.3	76.1
2002	2	149	156	78.0 ± 5.7	74.8
2003	5	808	589	117.8 ± 62	71.9
2006	2	1477	326	163.0 ± 31.1	85.7
2008	2	490	160	80.0 ± 4.2	73.7
2009	5	1583	473	94.6 ± 33.8	79.2
2010	2	1013	368	184.0 ± 101.8	81.6
2011	5	4148	785	157.0 ± 137.3	76.4
2014	11	4702	1038	94.4 ± 38.7	86.0
2015	6	3856	1107	184.5 ± 58.9	76.1
2016	5	3201	855	171.0 ± 53.9	98.5
Total	58	26649	7762		

Table 3. Relative fit of the models that best explained the probability of using area-restricted (AR) movements (models with $\Delta AIC_c < 4$ are shown), relative importance of variables in the averaged model and model-averaged coefficients. Individual ID was nested within sex in all models (random grouping variable). Marginal R^2_m values indicate the variation explained by fixed effects alone, and conditional R^2_c values indicate the variation explained by the whole model. Dashes indicate that parameters are not included in the model. w: Akaike weight

Salinity	Temperature	Log(depth)	Log(chl.anomaly)	Log(current)	Log(slope)	R^2_m	R^2_c	df	logLik	ΔAIC_c	w
−0.42	−0.27	–	0.31	−0.29	0.24	0.11	0.28	8	−505.35	0.00	0.39
−0.43	−0.27	0.02	0.31	−0.29	0.24	0.11	0.29	9	−505.35	2.00	0.14
−0.38	–	–	0.30	−0.30	0.23	0.09	0.24	7	−507.53	2.34	0.12
−0.49	−0.25	–	0.30	−0.24	–	0.10	0.27	7	−508.30	3.88	0.06
−0.38	−0.29	–	0.29	–	0.20	0.09	0.29	7	−508.35	3.98	0.05

Variable importance

Salinity	Temperature	Log(depth)	Log(chl.anomaly)	Log(current)	Log(slope)
0.99	0.76	0.28	0.95	0.87	0.84

Model-averaged coefficients

	Estimate	SE	Adjusted SE	z	p
(Intercept)	2.99	0.33	0.33	8.93	<0.0001
Log(chl.anomaly)	0.29	0.13	0.13	2.24	0.03
Log(current)	−0.25	0.15	0.15	1.69	0.09
Log(slope)	0.20	0.12	0.12	1.60	0.11
Salinity	−0.42	0.14	0.14	3.00	0.00
Temperature	−0.20	0.16	0.16	1.27	0.20
Log(depth)	0.00	0.08	0.08	0.04	0.97

shallow areas with steep slopes, but this was only weakly supported by data. Porpoises used AR movements more often in areas with relatively high chlorophyll concentrations and in areas that were influenced by inflow of fresh water, as we had anticipated (Fig. 3). Predictions based on the averaged model indicate that animals are particularly likely to use AR movements along the coasts of Denmark, Germany and the Netherlands and in the Skagerrak area (Fig. 4), although the estimates are associated with high

Fig. 3. Probability that harbour porpoises use area-restricted (AR) movements as a function of the most important predictor variables. Thick lines show the mean predicted values based on averaged models, thin lines indicate 95% confidence intervals based on variation among animals (i.e. considering random effects only). The narrow range of the predicted values indicates that predictions are weakly influenced by the few positions where animals use directed movements. Predictions were made for 1 variable at a time, keeping other variables at their mean values. Tick marks along the x-axes show the distribution of data
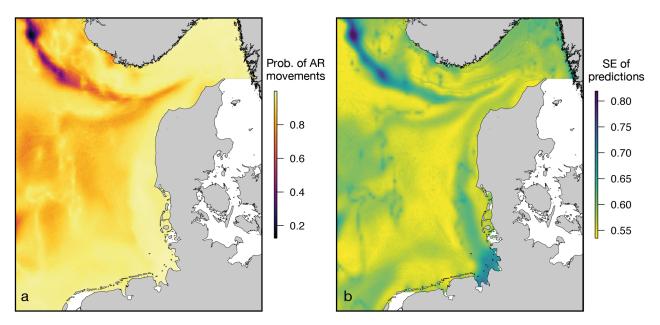
Fig. 4. (a) Probability of harbour porpoises using area-restricted (AR) movements in different areas, on average for all individuals. Predictions are only calculated for the part of the North Sea with available environmental data and high numbers of position estimates. (b) Standard error (SE) of predictions. Predictions were based on dynamic environmental data for 1 randomly selected day (1 April 2015) from the Copernicus Marine Environmental Monitoring Service (CMEMS) and water depth and sea bottom slope data from the General Bathymetric Chart of the Oceans (GEBCO)

uncertainty, particularly in the German Bight area. These areas are characterized by a high chlorophyll anomaly and high current velocity (Fig. S5). The full model explained 28.5% of the variation in probability of using AR movements (conditional R^2, model including environmental variables and random variation among individuals and sexes), and the environmental variables alone explained 11.1%.

The random variation among individuals (reflected in the confidence bands in Fig. 3) is related to differences in condition, sex, state and stochastic variations among animals. Overall, male porpoises had a slightly higher probability of using AR movements than females (95 vs. 87% of all daily positions; $\chi^2 = 94.9$, p < 0.001, chi-squared test), which is also evident from Fig. 3, but the proportion of time spent using AR was unrelated to animal length ($F_{1,53} = 0.12$, p = 0.73).

After transforming the predictor variables using a PCA to ensure that analyses were based on uncorrelated variables, the probability of using AR movements was best explained by the second principal component, which was strongly correlated with salinity and chlorophyll anomaly (variable importance = 1.0; Table S2 and plot of variable loadings, Fig. S7). It was also well explained by the fifth principal component, which was most strongly correlated with current velocity and slope (importance = 0.89).

The third-most important principal component was strongly correlated with temperature and weakly with other variables (importance = 0.64). The results are in line with those based on untransformed variables, suggesting that the results of the first analysis were not confounded by collinearity issues.

4. DISCUSSION

We used a unique long-term movement dataset of harbour porpoises in the North Sea to estimate switches in movement modes using a Bayesian SSM. The model enabled us to distinguish between directed movements and AR movements, the latter of which are typically associated with foraging activities (Fryxell et al. 2008, Owen-Smith et al. 2010, Gurarie et al. 2016). The number of positions that could be assigned to either mode was high (86.9%), although it was even higher in some comparable studies (e.g. Jonsen et al. 2007, Reisinger et al. 2015). By relating behavioural states to environmental parameters, we showed that AR movements were associated with a range of static and dynamic oceanographic conditions, which can be used to identify spatially and temporally dynamic areas of particular importance for porpoises.

Chl *a* anomaly was one of the variables that best explained variations in animal movements. Porpoises

were more likely to use AR movements in areas with relatively high chl *a* concentrations. Such areas are often found in frontal regions and upwelling zones (Polovina et al. 2001), oceanographic features that tend to aggregate primary consumers, which makes them important foraging grounds for marine predators (Embling et al. 2012, Gilles et al. 2016).

Harbour porpoises were less likely to use AR movements in areas with strong currents, which was not what we had expected. Tidal current strength is usually the main driver of ecosystem dynamics in coastal systems due to its association with high primary productivity (Sharples et al. 2007, Embling et al. 2012), and porpoises have been reported to aggregate and feed in locations with high tidal current velocities (Johnston et al. 2005, Pierpoint 2008, IJsseldijk et al. 2015). A possible reason for this discrepancy could be that average daily surface current strength, which is the variable we used in our model, does not reflect the fine-scale variations in current strength found in tidal areas. In such areas, currents alternate several times per day, but this generally does not result in a net daily movement of water, and mean current strength is therefore 0. To better understand the importance of current strength, it would be valuable to use high-resolution tidal models for regions where these are available.

The porpoises' tendency to use AR movements more often in less saline areas is also in accordance with our expectations. This trend is driven by their increased likelihood of using AR movements in the south-eastern part of the North Sea, which is influenced by inflow of freshwater from the Elbe River, and in the northern Kattegat, which is influenced by inflow of water from rivers along the Baltic Sea (Fig. S5). The northern Kattegat is characterized by pelagic fronts and high benthic biomass (Josefson & Conley 1997), which is likely to cause fish to aggregate. Such areas where saltwater and freshwater interact may generally be more productive, causing animals to forage more often. These findings are the opposite of those previously reported for porpoise fine-scale movements, based on GPS locations spanning a few days (van Beest et al. 2018a). The reason may be that the study by van Beest et al. 2018a) only included porpoises in the eastern North Sea and, consequently, included few high-salinity positions from the central North Sea. Also, the Argos dataset used in the present study allowed us to track movements over longer periods. The directed long-distance movements across the highly saline central part of the North Sea that we observed for some animals would not have time to develop in short-term

tracking datasets. Salinity was negatively correlated with bottom slope (Fig. S4), so the influence of salinity could also be partly mediated by high prey densities in productive coastal areas with relatively steep bottom slopes. The effects of salinity and chlorophyll anomaly on porpoise movements persisted after transforming the variables using a PCA to avoid collinearity, as revealed by their high contribution to the most important predictor variable in this analysis (Table S2).

Our study also demonstrates a great deal of variability in porpoise movements, with some animals staying in the same region using AR movements for many months (e.g. all animals tagged in 2016; Fig. S6) whereas others roamed over large distances and shifted between AR and directed movements (e.g. individual 2003-026642; Fig. S1). This variability could, to some extent, be attributed to regional differences in the animals' probability of using AR movements (the model including individual nested within tagging site was strongly supported by the data).

Previous studies have shown that harbour porpoise movements also vary greatly among habitats. At one extreme, porpoises in inner Danish waters sometimes stay year round in particular areas with strong currents where food is presumably abundant (Sveegaard et al. 2011). In contrast, porpoises tagged in Greenland show seasonal variability, with movements towards the shore in early summer and towards the central Atlantic in the fall (Nielsen et al. 2018). There is little evidence that porpoises in our study change movement behaviour in response to changing temperatures, i.e. among seasons, and the directed movements occasionally observed for some animals should probably be considered exploratory moves into less known areas, a behaviour that has been observed in a wide range of species (Mueller & Fagan 2008). This tendency to use directed, exploratory movements is higher for females than for males, possibly because they need to find additional foraging grounds due to their larger body size and during periods with increased energetic requirements during pregnancy and lactation. Females might therefore be disproportionally exposed to disturbance from human activities (e.g. shipping) when moving between foraging grounds. Negative effects of higher exposure to disturbances might be amplified when a female is accompanied by a calf. The variability among individuals seen in this study supports the picture of the porpoise as a species that is able to adapt its behaviour depending on local environmental conditions (Nabe-Nielsen et al. 2013).

We found that porpoise movements were related to several environmental factors and variations among individuals, but the environmental variables only explained 11.1% of the variation in data. The full model including random variation among individuals explained 28.5% of the variation. One obvious caveat with the environmental variables we used is that their spatial and temporal resolution may be too coarse to be suitable as proxies for porpoise prey distribution and availability. Resource availability is often high in the vicinity of ephemeral fronts and eddies (Biuw et al. 2007, Godø et al. 2012), tidal currents (Scott et al. 2010) or island and headland wakes (Johnston et al. 2005). Such features are weakly reflected in coarse-scale environmental variables like the ones used here, and future studies should aim at including fine-scale data on gradients in salinity and temperature that are likely to capture the presence of fronts and eddies. Further, even if high-resolution environmental data had been available, it would presumably not have been possible to detect the fine-scale variations in animal movements related to such fine-scale environmental features using daily Argos positions.

Another caveat in our analyses is that we did not explicitly incorporate or account for behavioural state estimation uncertainty. Although methods that try to account for such uncertainty exist (Andrews-Goff et al. 2018), this was not done here, as we preferred to delete all positions with high estimation error to minimize the risk that positions were incorrectly matched with environmental data. Another possible reason why the models only explained a small proportion of the variation in data is that animal foraging is predominately related to variations in prey availability that are not associated with environmental conditions. Prey may, for example, be aggregated at certain times of the year, and such small-scale prey patch characteristics can play a larger role in how predators perceive prey availability than the large-scale prey availability (Benoit-Bird et al. 2013). Prey movements may also be one of the explanations for the seasonal variations in porpoise behaviour previously observed in the Skagerrak (Sveegaard et al. 2011). Such variations in prey availability could result in temporal variation in the animals' probability of using AR movements that is not explicitly accounted for in our study due to a relatively small number of position estimates from the winter and early spring. Finally, our ability to predict porpoise foraging behaviour based on environmental conditions may be limited by variations among the individuals related to differences in their sex, reproductive state and memory of previously visited foraging patches,

and such differences among individuals were evident from the different behaviours of animals tracked in the same areas over the same period of time.

Despite the variation in how individuals move and the lack of fine-scale environmental data, our study illustrates several great advantages of using movement data to identify areas of particular importance for marine species. First, the use of movement data makes it possible to provide a measure of the long-term use of different habitats, which is not available from the aerial surveys often used for counting marine species and modelling their distribution (e.g. Hammond et al. 2013, Gilles et al. 2016). Second, movement data allow for more objective procedures to identify foraging hot spots of importance for long-term population survival. Since the North Sea is a very dynamic system, it can be challenging to pinpoint well-defined areas of particular importance to harbour porpoises. Knowledge on how environmental variables influence the availability of food in such a dynamic system therefore helps to predict where foraging hot spots are located when they cannot be predicted from density data of the species alone. Our study is a first step towards identifying important variables that can potentially be used for this case. Such information is becoming increasingly important in individual-based models where population effects of disturbances emerge from local competition for food (Nabe-Nielsen et al. 2014, 2018).

5. CONCLUSIONS

In this study, we have demonstrated how animal movement modes can be linked directly to environmental variables to assess the proximate cause of variations in animal movements. The study was based on a unique long-term data set including Argos movement data for 57 harbour porpoises from the North Sea region. Differences in large-scale movement behaviour were predominately related to variations in salinity, chl *a* concentration, current velocity and slope, suggesting that the most important foraging grounds were located in relatively productive areas with low current velocities. Several of these variables have previously been identified as important for fine-scale movements in porpoises and for the spatial distribution of other marine species. To further improve the predictive power of these models, fine-scale environmental data and telemetry data with a finer temporal resolution should be used, which will make the models more precise and useful for management and conservation of marine species.

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