Animal Conservation

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Movement Responses of Seals During Pile Driving for Offshore Wind Farm Construction

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ABSTRACT

Transitioning to renewable energy is essential to mitigate climate change and improve energy security; however, it is critical to understand potential impacts on wildlife. There is evidence of spatial redistribution in marine mammals during the high intensity sounds of pile driving construction activity, but the behavioural reactions of individuals is currently unknown, limiting the ability to predict energetic consequences, and robustly quantify or mitigate population-level impacts. Here, we address this knowledge gap using GPS tracking data (24 individuals) at the main centre of abundance for harbour seals (*Phoca vitulina*) in England; a Special Area of Conservation (SAC). We used Mahalanobis distance to identify instances of unusual movements, and quantified the association with estimates of received sound levels from piling. In total, there were 216 encounters between seals and elevated sound levels associated with piling, with 15 unusual movement instances detected. These consisted of either (1) high speeds, (2) cessation of horizontal movement or (3) suddenly initiating movement. The estimated mean population-level response threshold was 186 (95% CI: 169–199) dB re 1 $\mu Pa^2 \cdot s$. This study provides vital information which will facilitate environmentally sustainable development by (1) providing a dose–response relationship for environmental impact assessments to estimate the probability of responses, (2) enabling characterisation of responses for simulation-based assessments and evaluation of mitigation strategies, and (3) facilitating more robust links between piling sound levels, individual behavioural reactions, energetic consequences, and ultimately population-level impacts. Understanding how responses may vary across geographic contexts (e.g., sites with less constricted haulouts) and for populations with less prior anthropogenic exposure are critical areas of future research. More broadly, our study improves understanding of marine mammal responses to underwater sound, and our approach applying Mahalanobis distance to pinniped tracking data demonstrates a general framework which can be used to identify unusual movements across different disturbance sources and taxa.

1 | Introduction

The offshore renewable energy sector is expanding rapidly to meet ambitious global climate change and energy security targets (Baruch-Mordo et al. 2019; Gökgöz and Güvercin 2018). In the last 30 years, 34 GW of offshore wind capacity (~4000 turbines) have been constructed in European waters; a further ~90 GW is predicted by 2030 (WindEurope 2023). Developments are also increasing globally, including in the United States and Australia where there are large emerging markets (Larkin et al. 2024; McCoy et al. 2024). Understanding the potential effects of this activity on wildlife, and being able to robustly predict

impacts at the individual and population level, are critical steps in informing (i) environmentally sustainable proposals, (ii) levels and types of potential mitigation, and (iii) any additional environmental compensation required.

For animals that spend substantial time underwater, such as marine mammals, a key environmental concern are the high sound levels often produced during construction. Pile driving, a common method used in turbine installation, has been reported to produce (unmitigated) source levels of up to 250 dB re 1 μPa at 1 m (peak–peak) (Bailey et al. 2010), and typically consists of repeated hammering (~every 1–2 s) into the seafloor for several hours per turbine (Graham et al. 2019). With multiple developments now being constructed concurrently, piling sounds are increasingly prevalent within the underwater environment. In cetaceans, several studies have highlighted the effects of piling on habitat exclusion, disturbance and hearing damage for harbour porpoise (*Phocoena phocoena*; e.g., Brandt et al. 2011; Graham et al. 2019; Schaffeld et al. 2020). The effects on pinnipeds are less well-understood, with current evidence of potential hearing damage (Hastie et al. 2015) and changes to broadscale distribution (Russell et al. 2016; Whyte et al. 2020).

The at-sea distribution of seals, and the requirement to regularly return to haul-out sites, can lead to high spatial and temporal overlap between seals and areas of human activity (Carter et al. 2022; Jones et al. 2017; Sharples et al. 2012; van Neer et al. 2023). In general, studies of the at-sea behaviour of seals during exposure to anthropogenic sounds have produced mixed conclusions; however, many studies have relied on visual observations alone, making it difficult to follow how individuals responded. Visual observations at oil and gas construction sites (including pile-driving activity) reported no evidence of changes in grey seal (*Halichoerus grypus*) occurrence (Culloch et al. 2016), and limited observable reactions in ringed seals (*Phoca hispida*; Blackwell et al. 2004). Visual surveys of seals (ringed, bearded [*Erignathus barbatus*] and spotted [*Phoca largha*]) found similar sightings counts during different levels of seismic activity; however, seals were observed to be further away from the site during 'full-array' (8–11 airguns) seismic activity compared to no activity (mean distance of 234 vs. 144 m) (Harris et al. 2001). Whilst these visual observations can detect trends, they do not allow the magnitude of effects on individuals or individual-level variation to be quantified. In particular, there have been no studies examining individual responses to piling in any wild marine mammal species, and piling may elicit different reactions than other anthropogenic sounds. Changes in seal behaviour could contribute to reduced individual health via, for example, increased energetic expenditure, disrupted foraging, or changes in distribution to less favourable foraging sites. There is potential for these individual effects to scale up to population-level effects, such as reduced breeding success due to lower individual health or lower foraging success, impacting the status of the overall population (King et al. 2015).

The use of animal-attached tags (biologging; Wilmers et al. 2015) enables individuals to be tracked offshore and over long time periods. However, there have been a limited number of studies in which pinniped tracking data and pile driving activities have overlapped. For piling sounds, tracking data from harbour seals have been used to estimate seal density during offshore wind farm construction (Russell et al. 2016; Whyte et al. 2020). It was estimated that seal density significantly reduced during piling up to distances of 25 km, or above single-strike sound exposure levels (SELss) of 145 dB re 1 $\mu Pa^2 \cdot s$ (Whyte et al. 2020). The spatial modelling approach used in these studies necessarily pooled across all piling events and used a single estimated (mean) soundscape, in order to make a binary comparison between baseline versus piling. This provided no information on individual behaviour, limiting the ability to equate sound levels to particular behavioural responses and apply these results to other populations. To generate robust estimates of population-level effects, there is a need to understand how individuals may respond and change their movement behaviour during piling, and quantify variation in responses between and within individuals.

When considering how individual animals may behave during sound exposure, there are several possible scenarios. An individual may: (i) exhibit movement characteristics that are unusual or extreme compared to their normal behaviour(s); (ii) exhibit behaviour(s) from their normal behavioural repertoire (e.g., foraging trips, dives), but alter the usual pattern, frequency, or duration; (iii) exhibit no observable behavioural reaction. In this study, we chose to investigate scenario (i). Unusual responses may have the most immediate implications for an individual's ability to self-regulate (managing food, energy, oxygen stores), and potential negative consequences if reactions were to accumulate over time (e.g., Bejder et al. 2006; Holser et al. 2023). For example, unusual changes in an individual's movement speed or direction can indicate responses to sound exposure, and may contribute to altered energetic intake (foraging) or expenditure (movement costs).

Behavioural response studies investigating the effects of sound on cetaceans have illustrated how tracking individuals can provide insights into these unusual behaviours (e.g., Miller et al. 2015). The challenges of analysing these data include accounting for baseline variability, modelling repeated observations on individuals, and maximising the use of the multivariate movement metrics recorded (Harris et al. 2016). One potential approach is to reduce measurements of movement behaviour (e.g., heading variance, fluke interval) to a single number, using a multivariate statistic such as Mahalanobis distance (DeRuiter et al. 2013). Randomisation tests can then be used to compare this number (representing difference in movement behaviour) between times of known sound exposure and baseline, to identify times when individuals exhibited statistically unusual behaviour. While these methods have been used in examining cetacean responses to sonar (DeRuiter et al. 2013; Miller et al. 2014), they have largely been used on high-resolution and short-term data (e.g., accelerometers, hours–days), and have not yet been applied to other sound types or to seals (where typically GPS tags are deployed, weeks–months; e.g., Carter et al. 2022).

Here, we employ techniques including Mahalanobis distance to address key knowledge gaps in understanding pinniped responses to pile driving. We use the same data as the above-introduced studies that demonstrated short-term distributional impacts of piling on harbour seals. This allows us to understand the behavioural and individual mechanisms underlying those responses. The study site, The Wash and North Norfolk Coast Special Area of Conservation (SAC), is the main centre of harbour seal abundance in England. It holds the vast majority of the UK holdings of the European metapopulation of harbour seals (Carroll et al. 2020).

Although abundance was stable during this study, the population (and larger metapopulation) is now in decline (Galatius et al. 2023; SCOS 2024), therefore there is particular concern associated with planned wind farm developments in the area. Specifically, there is a need for dose–response relationships which quantify the relationship between piling sound level and seal behaviour. Here, we used data from 24 GPS-tagged seals to: (1) objectively identify potential behavioural responses to piling through randomisation tests; (2) quantify the relationship between received pile driving sound level and the probability of response; and (3) use the estimated dose–response relationship to predict the total number of seals likely to respond across the study area, providing further context to the obtained results. As well as providing information to underpin marine spatial planning and strategic assessments, robust estimates of the proportion of individuals responding to pile driving are required for environmental impact assessments.

2 | Materials and Methods

2.1 | Seal Telemetry

To record the movements of seals around pile driving activity, tags were deployed on 24 harbour seals in The Wash & North Norfolk Coast SAC, Southeast England (Figure 1). Seals were fitted with SMRU Instrumentation GPS telemetry tags (GPS/GSM tags; SMRU Instrumentation, University of St Andrews, Fife, UK), and all seal handling and procedures were carried out under Home Office Licence 60/4009. All seals (11 males, 13 females; 21 adults, 3 juveniles) were tagged in January 2012 and recorded information for 12–114 days per individual within the study period (Table S3). See Hastie et al. (2015) and Russell et al. (2016) for details of data collection and study site. Excluding haulouts, the median time interval between GPS locations was 10 min (~86% of locations < 20 min) and median tag duration was 99 days (SD = 26).

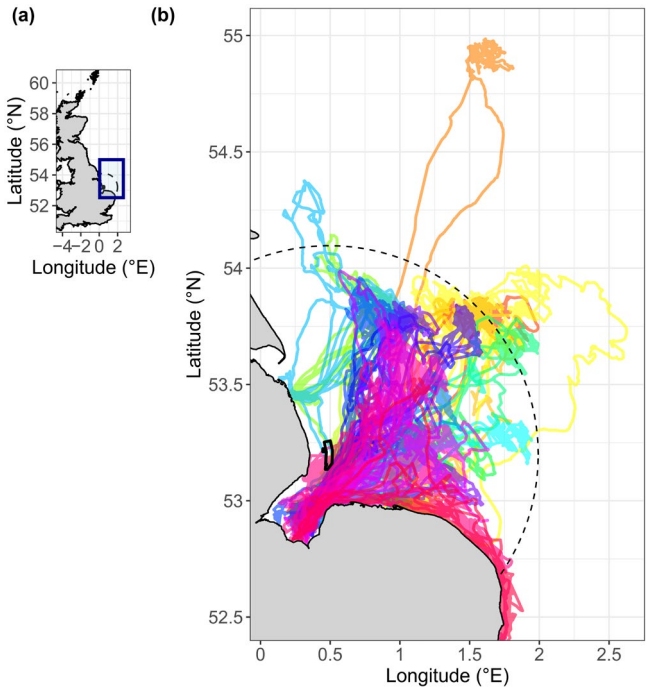

FIGURE 1 | (a) Study area location on the east coast of England, UK. (b) Movement tracks collected around The Wash & North Norfolk Coast SAC (UK) in 2012 from 24 GPS/GSM-tagged harbour seals (lines coloured by individual). Also shown are the outline of Lincs offshore wind farm (solid black line), and a line representing 100 km from the centre of the wind farm (dashed black line).

2.2 | Pile Driving

Operational data on pile driving at Lincs wind farm were provided by Centrica plc. Throughout the period of seal tag deployment, 27 (of a total of 75) monopiles were installed by pile driving. Between 28th January and 11th May 2012, a total of 77,968 piling strikes occurred, with a mean strike energy of 1202 kJ (SD = 613).

Pile driving at Lincs occurred intermittently across the study period, with a maximum gap of 19.5 days. To compare time intervals of piling and non-piling, individual records of piling strikes were divided into bouts, where bouts were > 1 h apart. There were 64 piling bouts, with a mean duration of 1.0 h (min = 0.2, max = 3.2), and an average of 1218 strikes each (min = 132, max = 3772).

2.3 | Acoustic Modelling

To estimate the sound levels resulting from piling, the Aquarius pile driving model (for model description and validation see de Jong et al. (2019)) was used to model source characteristics and acoustic propagation loss. The Aquarius model uses information on the hammer and pile properties to determine a source excitation spectrum, which is integrated into a range dependent propagation model to predict acoustic propagation loss across the study area, incorporating information on seabed characteristics and water depth. Depth-specific model predictions were output as estimated single strike sound exposure levels ($SEL_{ss,ref}$, dB re 1 $\mu Pa^2 \cdot s$) at a reference piling strike energy of 1000 kJ. These were calculated across a series of spatial grids (~279 m resolution, 2.5 m depth bins) for each of the 27 piling locations (Figure 2). For parameters used see Whyte et al. (2020).

2.4 | Acoustic Exposure

The received SEL_{ss} by seals was estimated by linearly interpolating the seal tracks to estimate locations at the time of each piling strike, and matching this to the corresponding estimate of received sound in the acoustic model. The median $SEL_{ss,ref}$ across all depth layers was identified, and energetic (broadband) scaling of the SEL_{ss} spectrum was used to obtain final estimates of the received SEL_{ss} at each seal location (accounting for piling blow energy; see Supporting Information). Values below the estimated median ambient sound level of 118 dB re 1 $\mu Pa^2 \cdot s$ (Nedwell et al. 2011) were assigned to 118 dB re 1 $\mu Pa^2 \cdot s$.

2.5 | Quantifying Movement

Following data cleaning (see Supporting Information), seal locations were used to calculate several informative movement metrics, quantifying movement behaviour

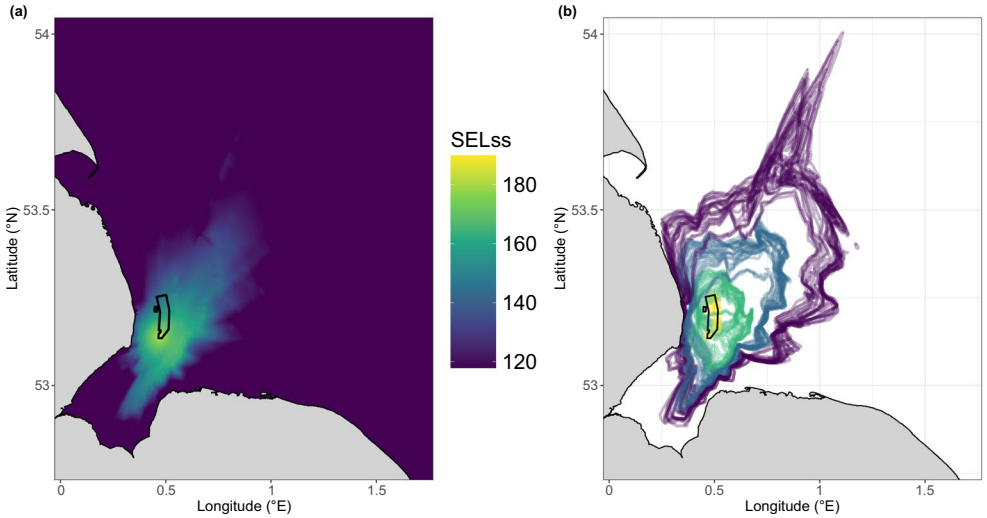

FIGURE 2 | Predicted piling sound levels (single-strike sound exposure levels, SELss, dB re 1 μPa²·s) across the study area. (a) Full predicted sound levels for one of the piling locations (turbine LS22), and (b) for illustration of variability across piling locations, summarised contours of sound levels in 20 dB increments across all 27 turbines. Shown are the median SELss across all modelled depth bins at the reference piling strike energy of 1000 kJ. Predicted SELss below the estimated ambient noise level of 118 dB re 1 μPa²·s were set to 118 dB re 1 μPa²·s.

between successive GPS locations. The metrics calculated (see Supporting Information) were: (1) horizontal speed over ground ($m\,s^{-1}$); (2) acceleration (absolute value of change in horizontal speed; $m\,s^{-2}$); (3) heading variability (0 to 1, where similar angles result in values near 0); and (4) radial avoidance rate (relative change in radius from the wind farm per km travelled by the seal; km^{-1}; where values range from $\frac{-1}{\text{radius}}$ to $\frac{1}{\text{radius}}$). Metrics were chosen following a review of literature documenting behavioural responses to sound disturbance in marine mammals (e.g., Antunes et al. 2014; Kastelein et al. 2006; Southall et al. 2021), alongside consideration of whether these metrics may be biologically informative for this particular species and type of data. Responses may include one or more of the metrics (1–4) chosen, on the assumption that the following behavioural changes can be indicative of a response: (1) higher or lower swim speeds; (2) sudden changes in speed; (3) more directed movement; (4) changes in heading direction relative to the wind farm.

2.6 | Specifying Baseline

To compare seal behaviour between piling and non-piling periods, it was necessary to specify a subset of the tracking data which could be considered as baseline. As piling took place intermittently, baseline data were pooled from intermittent periods across the study duration. Data collected between 6 h pre-piling and 24 h post-piling were excluded from the baseline, to conservatively remove any potentially altered behaviour.

2.7 | Identifying Behavioural Responses

The four movement metrics were summarised into a single variable representing the overall difference in movement behaviour, using the multivariate measure Mahalanobis distance (M-distance). This was implemented by applying a moving time window across the time series of each individual, and comparing this to a fixed time window across the baseline period (Figure 3; DeRuiter et al. 2013). The M-distance $MD_{(\boldsymbol{x},\boldsymbol{y})}$ between each pair of time windows was calculated by

$$MD_{(\mathbf{x},\mathbf{y})} = \sqrt{(\mathbf{x}-\mathbf{y})^T \mathbf{S}^{-1}(\mathbf{x}-\mathbf{y})} \quad (1)$$

where $\boldsymbol{x} = (x_1, x_2, x_3, x_4)$ is a vector containing means of each of the movement metrics in the moving time window, $\boldsymbol{y} = (y_1, y_2, y_3, y_4)$ is a vector containing means of the same movement metrics across the baseline, and $\boldsymbol{S}^{-1}$ is the inverse covariance matrix of the data (calculated from the baseline period only). The resulting M-distance is a measurement of how far apart the observations in the two time windows are, accounting for the variability and correlations of the dataset. All comparisons were within each individual, using 20 min time windows which moved in 10 min increments (Whyte 2022). This produced, for each individual, a time series of M-distance values (one value per 20-min moving window) characterising the overall difference in movement behaviour relative to average baseline conditions.

To identify unusual behaviour changes, M-distance values observed during piling were compared to those in baseline by randomisation tests (Figure 3). For each piling bout, individuals that were estimated to have a received level of piling above ambient sound were considered to be an 'encounter'. For each encounter, responses were then investigated within the pile driving period plus a 30 min buffer afterwards (allowing at least one M-distance time window immediately post-piling). This buffer was important as the irregular timing of GPS locations and the time required for an individual to change its behaviour in a significant way meant that responses towards the end of piling would only be detectable after piling had ended. For each encounter, 1000 randomly sampled 'mock exposure periods' were taken from the baseline for that individual

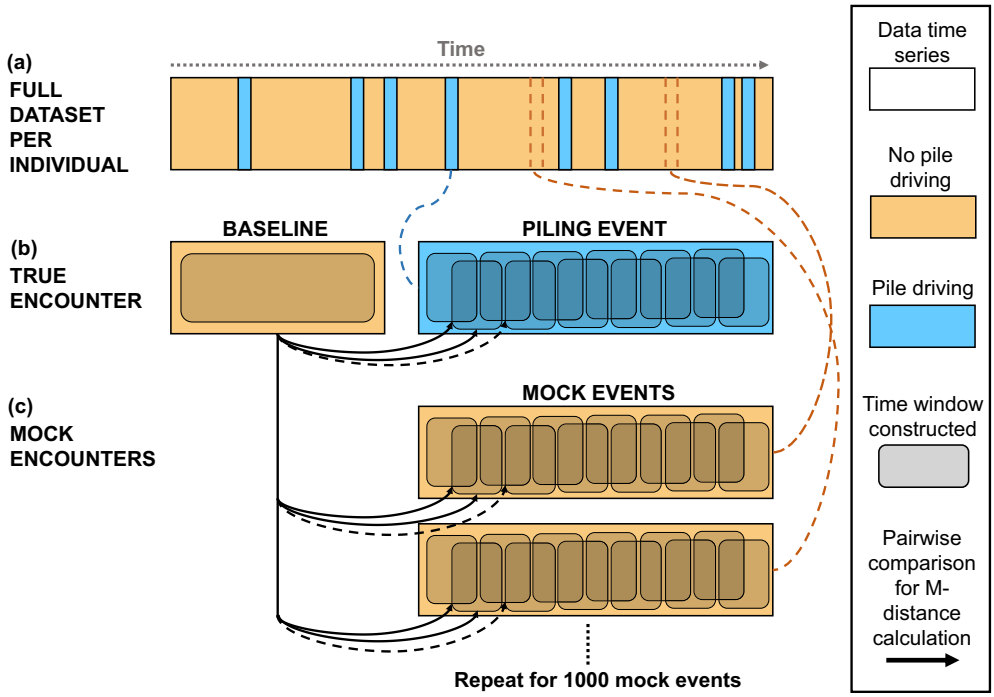

FIGURE 3 | Overview infographic of approach used to identify behavioural responses. (a) For each individual, there is a time series of GPS data (and corresponding movement metrics), which consists of periods of piling and non-piling. (b) All non-piling periods are aggregated to produce a baseline, over which a single fixed time window is constructed. For a given piling event, moving time windows are constructed across the duration, and pairwise comparisons of movement are calculated against the baseline (via M-distance; see Equation 1). (c) A mock event of the same duration as the true piling event is randomly selected from the baseline, and pairwise comparisons are similarly calculated. This process is repeated to produce M-distance values for 1000 mock events. Observed values between true and mock events can then be compared to identify responses.

(Figure 3); mock exposures were the same duration as the piling bout (plus buffer). The maximum M-distance MD_{max} observed in each of the mock exposures was then compared to the M-distance values observed in the true exposure encounter. The 95th percentile of the MD_{max} samples across the mock exposures was used as a threshold MD_{th}, above which it is considered unlikely that behaviour changes of this magnitude will occur by chance. M-distances exceeding this threshold in the piling encounter are considered to be a likely response to the piling itself, as they occur with low probability ($< 5\%$) in the baseline. All analyses were conducted in R (R Core Team 2020). Characteristics of pile driving encounters were compared across males and females using summary statistics. Identified responses were then also inspected visually to categorise the different behavioural reactions, based on movement characteristics before, during and after the response.

2.8 | Modelling Response Thresholds

A Bayesian hierarchical model (based on Miller et al. 2014) was used to estimate the relationship between piling sound level and likelihood of behavioural response, using information from all encounters. The model is structured around the concept that each seal i has a sound level $t_{i,j}$ at which they will respond in an encounter j with piling, and individuals that do not respond on that occasion have simply not exceeded their response threshold (i.e., the individual sound level which elicits a response). Response thresholds can vary between individuals and between encounters (within individual), and depend on individual-level and encounter-level covariates. Non-response encounters are considered to be right-censored (Miller et al. 2014); the model assumes that the true response threshold $t_{i,j}$ is greater than the maximum received piling sound.

Response thresholds are assumed to be normally distributed, and each individual i is assumed to have a mean response threshold μ_i,

$$\mu_i \sim \mathrm{N}\left(\mu + \boldsymbol{z}_i^{\mathrm{T}}\boldsymbol{\alpha}, \phi^2\right) \quad (2)$$

where μ is the mean response threshold (in dB re $1\,\mu Pa^2{\cdot}s$) for the population, $\boldsymbol{z}_i$ is a vector of individual-level covariates, $\boldsymbol{\alpha}$ is a vector of model parameters, and ϕ^2 is the variance between individuals. The model is hierarchical in that the true (but unobserved) response threshold $t_{i,j}$ for a given individual i and encounter j, is also assumed to be normally distributed around the mean response threshold μ_i for each individual i, with exposure-level covariates and variance between encounters. Additionally, to account for uncertainty in the estimated acoustic dose eliciting the response, it was assumed that the true response threshold $t_{i,j}$ is observed with some normally-distributed error.

Models were fit in JAGS and `rjags` (version 4.3.0; Plummer 2019) using 4 chains of 100,000 iterations each (a conservative approach to ensure full convergence; initial model testing indicated rapid and consistent convergence). A suite of potential covariates was also considered in the dose–response model (Table S1), which included individual-level covariates (sex, age class) obtained during seal tagging, and exposure-level covariates (initial distance to piling, piling

bout length, day or night, exposure history, behavioural state) which were measured or estimated for each piling encounter. Gibbs variable selection (O'Hara and Sillanpää 2009) was used to assess the level of support for including each of these covariates within the final dose–response model, using an indicator variable to estimate the posterior probability that this term is present in the true model. Full descriptions of model structure, fitting, and evaluation are provided in Supporting Information.

Posterior samples from the model were used to estimate a dose–response curve (i.e., the overall relationship between sound level and the probability of response), by constructing a cumulative distribution function in 1 dB increments. The mean dose–response function was estimated by taking the mean values of these cumulative distribution functions across all samples, and 95% credible intervals from the 2.5% and 97.5% quantiles.

2.9 | Effective Response Range

In practice, dose–response relationships are applied over space to estimate the total numbers of animals likely to be affected. Due to spreading of sound from a source, the spatial area that has low-moderate levels of sound is much larger (and contains more individuals) than the area with the highest levels of sound. Using a p_{50} estimate (threshold at which half of animals respond) can lead to underestimation of the numbers of animals affected (Tyack and Thomas 2019), and can ignore the most sensitive individuals. The effective response range (ERR) is the estimated distance at which the number of animals responding beyond this distance is equal to the number not responding within this distance, and the effective received level (ERL) is the equivalent sound level at which this occurs (Tyack and Thomas 2019). ERRs (or other methods) can be used to inform effective deterrence ranges (EDRs), which are policy recommendations based on published ranges where the majority of effects have been detected (JNCC 2020). To increase the utility and interpretability of the results, here we compared the mean dose–response function to the predicted SELss (for each piling location), to predict response probability across the study area and estimate the ERR and ERL (assuming uniform animal density as in Tyack and Thomas 2019). The median ERR was compared to harbour seal density estimates (Carter et al. 2022) to illustrate the total number of seals potentially affected (see Supporting Information).

3 | Results

3.1 | Seal Responses

In total, 20 out of 24 (83%) tagged seals had piling encounters, that is were estimated to have received SELss above ambient sound levels. The mean number of encounters per seal was 11 (min = 1, max = 36), with initial distances between seals and piling ranging from 4.2 to 45.1 km.

Out of 216 encounters between seals and pile driving activity, 15 responses (across nine individuals) were identified by the M-distance randomisation tests (i.e., encounters that were above the threshold used; Table S4). Initial distances of seals in these identified responses ranged from 5.0 to 28.6 km, and the maximum values of M-distance appeared to decline with distance (Figure 4). Estimated median received SELss (across depths) at the identified time of response ranged from 119 to 169 dB re 1 $\mu Pa^2 \cdot s$.

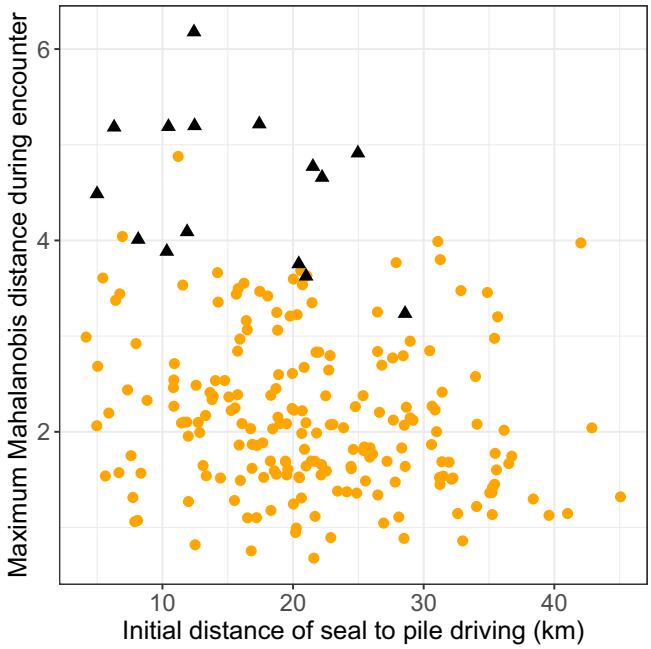

FIGURE 4 | Maximum Mahalanobis distance during all encounters between tagged seals and pile driving. By randomisation test, each encounter was identified as either a detected response (black triangles) or a non-response (orange circles).

Overall, the behavioural responses identified could be divided into three broad categories (Figures S5–S19). First, encounters in which seals moved at unusually high speeds ($n = 6$; Figure 5). Seals either increased speed while already travelling away from the wind farm, or turned around and then moved faster away from the wind farm. Second, encounters where seals decelerated suddenly and reduced movement during piling ($n = 6$). Third, encounters in which seals suddenly initiated fast and directed movement ($n = 3$), after a substantially long (3–12 h) period of remaining stationary.

3.2 | Dose–Response

The models showed rapid convergence of the MCMC chains, with a Gelman-Rubin of 1.0. Gibbs variable selection indicated a low level of support for including covariates within the dose–response model, estimating probabilities of 6%–48% that each of the covariates were drivers (Table S5).

As overall there was not sufficient evidence to support inclusion of covariates, the reduced model (no covariates) was chosen to produce the final dose–response function (Figure 6; Table S6). The mean estimated population response threshold μ was 186 (95% CI: 169–199) dB re 1 $\mu Pa^2 \cdot s$, with a standard deviation between individuals ϕ of 14 dB re 1 $\mu Pa^2 \cdot s$ and between encounters

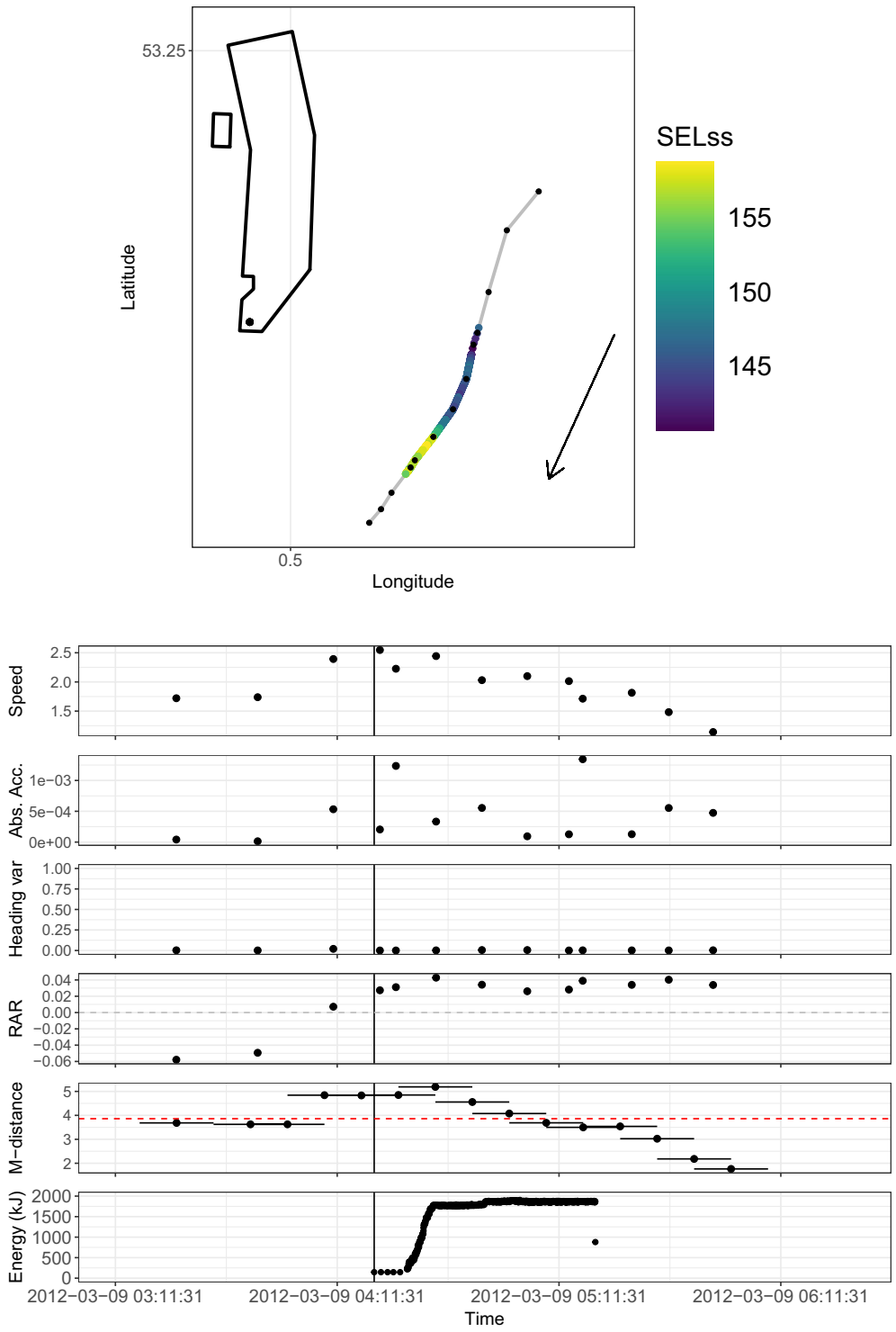

FIGURE 5 | Example track and metrics from one of the identified behavioural responses (seal pv42-162, initial distance 10.5 km). Top panel: GPS locations (black dots) of seal moving south-west past Lincs wind farm (black outline) during piling at pile LS75 (black dot within Lincs). Estimated received SELss (dB re 1 $\mu Pa^2 \cdot s$; median across depth) for each piling blow are also shown (coloured dots). Bottom panel: Horizontal speed ($m\,s^{-1}$), absolute acceleration (i.e., change in speed, $m\,s^{-2}$), heading variation, and radial avoidance rate (RAR) for each observed GPS location (black dots). Mahalanobis distances for each overlapping 20-min time window (horizontal lines), with the midpoint of each time window (black dots) and the threshold used to identify responses (red dashed line). Also shown are the recorded piling blow energies during the piling event, with the timing of the first piling blow highlighted (vertical black line). Tracks and metrics show 1 h pre-piling to 1 h post-piling.

σ of 24 dB re 1 $\mu Pa^2 \cdot s$. The estimated p_{50} (dose at which there is a 50% response probability) for the final model was 175 (95% CI: 166–181) dB re 1 $\mu Pa^2 \cdot s$.

Only 20 of the 216 encounters were in males, and the number of encounters per individual was higher in females (median = 7, SD = 13) than males (median = 1, SD = 2). Encounters in males tended to be

at further initial distances from piling (median = 28.4 km) than in females (median = 20.2 km). This may have been driven by sex-related differences in seal distribution across the study area.

3.3 | Effective Response Range

The ERR estimated for each piling location ranged from 7.75 to 9.00 km, with a median of 8.75 km (SD = 0.35 km; Figure 7). It should be noted that this uncertainty only accounts for variation in response probability across piling locations (and not uncertainty in the estimated dose–response). This ERR is equivalent to an ERL of ~160 dB re 1 $\mu Pa^2 \cdot s$. The average density of harbour seals within 50 km of Lincs wind farm was estimated to be 0.75 per 1 km squared (Carter et al. 2022; 4160 seals total). If a median ERR of 8.75 km is assumed, this corresponds to, on average, 180 seals exhibiting responses to piling (estimated population size within England is ~4900; SCOS 2025). These calculations give an indication of the potential count of at-sea seals affected; however, the density estimates are snapshots (averaged across tidal cycle), and do not account for potential turnover of individuals in the area during a piling event.

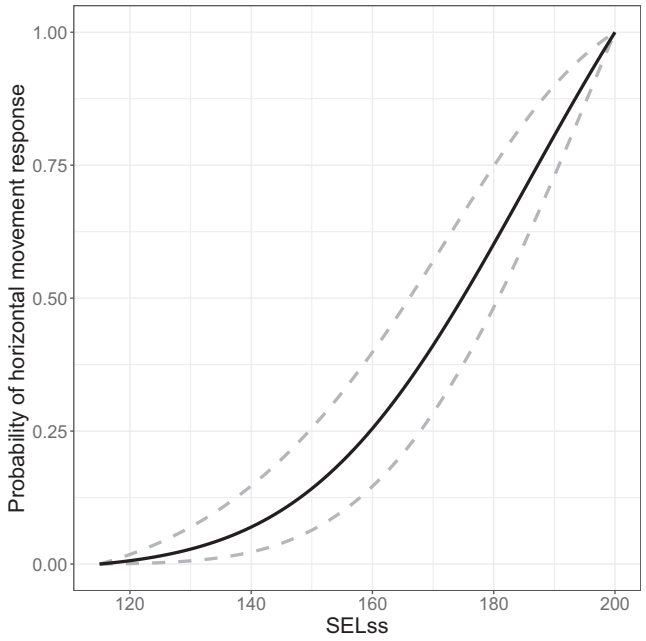

FIGURE 6 | Estimated dose–response relationship for horizontal movement responses in harbour seals as a function of single-strike sound exposure level (SELss in dB re 1 $\mu Pa^2 \cdot s$; median across depth) of pile driving. The mean estimated function (black) and the 95% credible intervals (grey dashed) are shown.

4 | Discussion

This study addressed a key knowledge gap in understanding the impact of pile driving on pinnipeds. Specifically, we quantified the relationship between piling sound exposure and behavioural changes in individual seals, and observed that seals responded by altering their movement behaviour in one of three ways: increasing speed, reducing movement, or suddenly initiating movement. Twenty (83%) of the seals were estimated to be exposed to piling sounds at levels above ambient, and in nine of those seals (45%) a response was detected at least once. Overall, the mean estimated population response threshold was at a SELss of 186 dB re 1 $\mu Pa^2 \cdot s$, with high variability between (SD = 14) and within (SD = 24) individuals. There was limited evidence to support inclusion of covariates in the dose–response relationship; however, the number of times individuals were exposed to piling sounds differed between males (median per individual = 1) and females (median per individual = 7). The median effective response range (ERR) was estimated at 8.75 km, equivalent to approximately 180 harbour seals responding to pile driving.

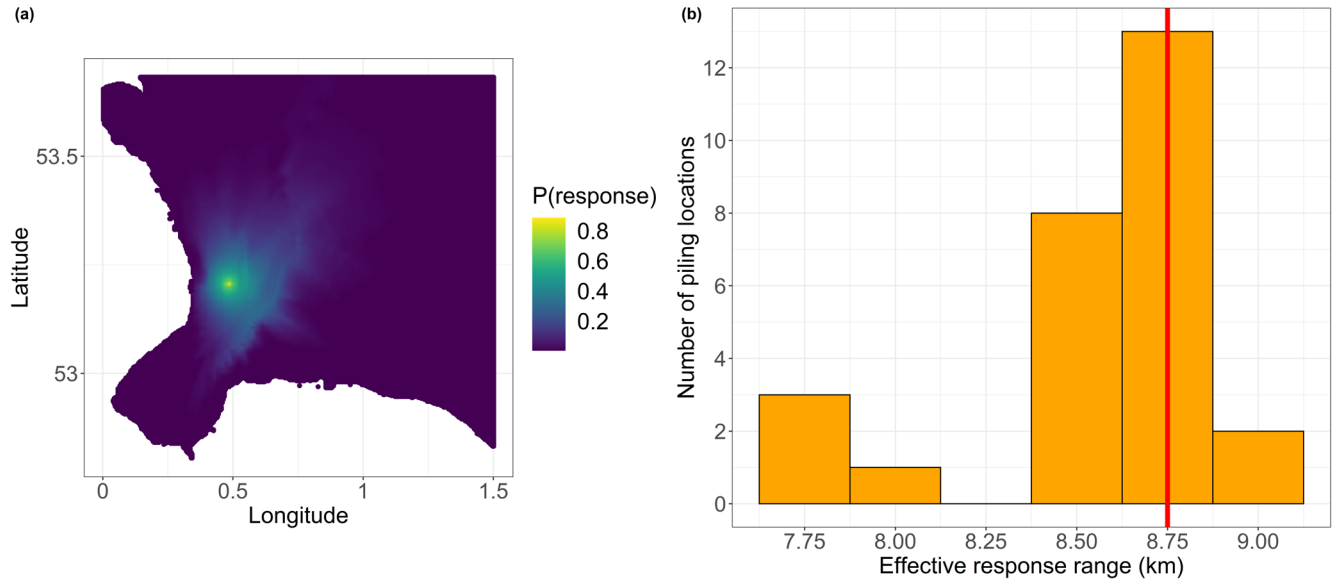

FIGURE 7 | (a) Predicted response probability across the study area for one piling location (pile LS22) using the mean dose–response relationship. (b) Histogram of effective response ranges (ERRs) for each of the 27 piling locations; red line denotes the median ERR.

A multivariate approach, that is all movement metrics were considered together, was used to identify times when individuals exhibited their most unusual movements. In the detected responses, three broad types of unusual behaviour were observed: (1) unusually high travel speeds, (2) sudden deceleration and reduced horizontal movement, or (3) initiation of travel after a long stationary period. Seals responding by approach (1) or (3) can increase distance from the piling source (reducing noise exposure) and may theoretically be reducing risks of hearing damage, perceived threats or nuisance sounds. The burst of speed sometimes observed could be an initial startle response, as has been observed in captive playback studies (Götz and Janik 2011). Seals responding by approach (2) may be assessing the potential threat, or waiting to resume an intended behaviour once disturbance has ended. Changes in dive behaviour were not examined here, but would be valuable to consider to further understand behavioural effects and potential impacts. Overall, data on movement responses of free-ranging pinnipeds to underwater sounds are relatively limited. Gordon et al. (2019) observed some increases in speed and heading changes in tagged harbour seals exposed to acoustic deterrent device playbacks; however, these were part of a targeted exposure experiment, rather than the in situ disturbance events observed here. Considered together, these initial findings of individual seal responses to sound disturbance are broadly consistent with studies of harbour porpoise, where changes in horizontal movement behaviour (Mikkelsen et al. 2017; van Beest et al. 2018) have been observed in response to seismic airgun and acoustic deterrent sounds.

Here, relatively few unusual responses were observed (~7% of encounters). As multiple randomisation tests were carried out, it is possible that some were false positives or false negatives (Whyte 2022). The approach used provided a mechanism to identify the most unusual instances of movement, and it was assumed these were related to the sound level of piling. Responses could also be driven by the (perceived) distance from a sound source (Southall et al. 2019; Wensveen et al. 2025), and its interaction with sound level. Here, we did not consider distance as it was highly correlated with received sound level; however, comparing the relative effects of both drivers would be valuable in an experimental setup. The consistency and types of reactions observed, alongside visual inspection of the observed seal tracks during each encounter, support the explanation that these behavioural changes were related to piling. The relatively low number of detected responses is likely because, from the available data, the measurements of movement during disturbance are not highly extreme, when compared to a long baseline duration (weeks–months). In the data used here, there were few close-range encounters (< 10 km) between seals and piling. Furthermore, the baseline data may have included other potential disturbances (e.g., shipping, predator/competitor encounters). By this approach, only prolonged changes would be detectable in the data, and some responses (e.g., subtle/short movement changes, altered frequency of behaviours, porpoising) would not be detected, but are worthy of further investigation. Additionally, low-level responses at large distances, which could contribute to barrier effects, would not be detectable but may reduce overall sound exposure for seals. Indeed, as seals leave the SAC haulout (< 40 km from Lincs), they may respond by staying within the embayment rather than foraging offshore; such responses would not be detectable here.

The detected responses here provide likely mechanisms for the seal density changes described in Russell et al. (2016) and Whyte et al. (2020), with individual reactions contributing to altered movement speeds and directions as seals move around the wind farm. In any case, applied to the population level, the dose–response curve suggests that a substantial number of seals (~180) would respond per piling event. Such responses may alter energetic expenditure, or delay important behaviours such as foraging or resting. The construction of a single wind farm requires multiple piling events across multiple turbines, and so it is reasonable to expect that some individuals will be exposed to pile driving multiple times (as was observed in this study). Similarly, with current widescale wind farm development (WindEurope 2023), multiple wind farms are increasingly likely to be constructed within the habitat of a species across a multi-year period. This cumulative exposure to piling sounds has the potential to cause an increase in the occurrence of behavioural changes such as those observed here, contributing to changes in individual health, vital rates, and ultimately population success. The population-level impact of such responses will also depend on the turnover of individuals. Turnover is important as it determines whether a smaller group of individuals are affected multiple times or a larger group of individuals are singularly affected across piling events, which is determined by both short and long-term movement of individuals through their environment. The metapopulation that the study SAC is part of holds the majority of eastern Atlantic harbour seals and is in decline for unknown reasons, with prey availability a candidate factor. As such, the impacts of widespread wind farm development, considered cumulatively with other potential impacts, should be a research priority.

In estimating the acoustic exposure of seals, there were potential sources of uncertainty. Sound levels can vary during the 20-min intervals used in analyses as a result of the seal's depth and piling hammer energy; however, in practice, sound did not vary highly within this interval (maximum SD of 2.18; Table S4) and was strongly determined by the seal's initial location. The median sound level across all water depths was used, representing the acoustic dose available at a given location (reflecting information typically available in impact assessments), but not necessarily the associated sound level received by the seal. Incorporating information on dive behaviour or using biologgers which record acoustic information (Mikkelsen et al. 2019) would enable further examination; however, sample size and study longevity of high-resolution acoustic tags is typically more limited. Uncertainty in the acoustic model predictions may also contribute to uncertainty in estimated doses (estimated mean error = 4 dB re 1 $\mu Pa^2 \cdot s$; Whyte et al. 2020).

A Bayesian hierarchical model was used to estimate the distribution of response thresholds across the population (between individual $\phi = 14$; between encounter $\sigma = 24$ dB re 1 $\mu Pa^2 \cdot s$), and quantify the dose–response relationship (Figure 6). Other studies using this approach have estimated similar variability in pilot whale ($\phi = 18$; $\sigma = 21$; Antunes et al. 2014) and killer whale ($\phi = 17$; $\sigma = 26$; Miller et al. 2014) responses to sonar. Overall, the results highlight high variability in the levels of sound contributing to behavioural responses in seals. Responses are likely dependent on individual variability and the ecological, behavioural, social, and exposure context (Ellison et al. 2012;

Hooker et al. 2015; Isojunno et al. 2017) of the encounter; considering the relative role of these factors are important areas of future research. Individuals may also differ in hearing ability (Lucke et al. 2016), which could affect their likelihood of response. Here, a suite of candidate covariates were included in the dose–response model to assess additional drivers of response thresholds; however, there was insufficient evidence to support their inclusion (GVS p scores of 0.09–0.48). Similar studies that have examined covariates have not identified GVS support above 0.54 (Antunes et al. 2014; Miller et al. 2014).

In this study, tagged female seals were exposed to piling more often than males. Females, in general, appeared to spend more time close to the wind farm, compared to males which were further offshore. We did not examine behaviour during the breeding season, when sex-related differences may be expected to be more extreme (Thompson et al. 1994; van Parijs et al. 1997). Sex-related differences in activity budgets of grey and harbour seals have been described (Russell et al. 2015); however, Sharples et al. (2012) found that sex was a relatively poor predictor of trip duration and distance in harbour seals, compared to geographic region or time of year. Further investigation into sex-related differences in habitat use is critical to understand how this may influence predictions of noise exposure and population-level consequences. If males and females are affected to varying degrees by pile driving activity, this difference could contribute to sex-related differences in individual health, and increasing uncertainty in population trajectories depending on how each sex is affected. Hypothetically, sex-related differences may also develop post-construction in the use of offshore structures and foraging on aggregated fish (Bicknell et al. 2026) if, for example, wind farms are built in areas which typically have different usage across sexes. As harbour seals are not a highly sexually-dimorphic species, sex-related differences in impact may be more pronounced in other pinniped species.

The dose–response curve produced in this study (Figure 6) can be used in assessments to predict the probability of overt movement responses for a given piling sound exposure level, and the provided credible intervals (Table S6) should be used to account for uncertainty. The dose–response relationship should be combined with spatial estimates of seal density to estimate of the number of seals that may respond behaviourally to a piling event. These estimates can then be incorporated into models (e.g., iPCoD; King et al. 2015) which consider survival and reproduction effects to predict population-level consequences. These results can therefore support conservation and management decisions related to both seal populations and offshore activities. This dose–response curve was produced based on harbour seals from the key English haulout at a particular time of year (January–May; see Supporting Information for discussion on representativeness). A vital area of future research is to examine responses in other populations, in particular those where (1) seals are likely to be more naïve to anthropogenic sounds, and (2) those with different geographies (e.g., here, seals had to pass near the wind farm to enter and leave the haulout). The responses were to a single monopile type and future designs (which may be larger) may produce differing responses; however, these observations remain relevant to fixed and floating wind farms where piling can be required to install turbine anchors. Furthermore, future research investigating the interaction of piling sounds with other sound types, for example more continuous sounds from shipping, fishing and construction vessels (e.g., Benhemma-Le Gall et al. 2021), will be valuable to contribute to a more holistic understanding of the effects of noise and appropriate mitigation strategies.

For the purposes of management, recent policy recommendations for marine mammals can include the use of effective deterrence ranges (EDRs; JNCC 2020). EDRs are a threshold value used in the management of marine activities, and are based on determination of a fixed distance at which the majority of effects on a species have been detected (collating information across studies). The EDR-based approach is currently used in England and Wales (UK); however, it is comparable to single-value threshold approaches used in other countries (e.g., in the United States for acoustic harassment; Darias-O'Hara et al. 2025). Whilst we recommend use of the full dose–response curve (Figure 6, Table S6) to most accurately estimate the number of seals potentially affected, account for uncertainty, and accommodate location-specific noise propagation conditions (Sinclair et al. 2023), some management situations may require a single-value threshold such as an EDR. The ERRs estimated here could be used in decision-making for establishing pinniped EDRs. In doing so, our ERRs should be considered a minimum distance, as only one type of potential impact (overt movement responses) were examined. Additionally, the observations of all detected responses (Table S4) should be considered in these decisions, as responses were observed up to 28.6 km from piling.

This study examined seal behaviour during piling, adapting and implementing an approach for identifying unusual movements, and applying this to pinnipeds for the first time. The methods and frameworks outlined here are applicable to analyses on the effects of piling on other pinniped species, and indeed for understanding disturbance effects on animal movement in any taxa. In applying these approaches, future studies principally need to consider: (1) appropriate metrics of movement to calculate; (2) how baseline periods will be defined; and (3) the spatial and temporal scales on which they expect behavioural changes to occur and be detectable. The observed responses in this study contribute towards key knowledge gaps on pinniped responses to underwater noise in the wild, an area of limited data in general. Considering potential differences across species, harbour seals may be more (sensitisation) or less (habituation) responsive than other pinnipeds, driven by their highly coastal distribution. Across different potential sources of disturbance, responses may show broad similarities; however, the impulsive nature of piling sounds may elicit more extreme responses than other sound types (e.g., shipping; Jones et al. 2017).

The behavioural responses observed here improve understanding of how individual seals react to in situ anthropogenic sounds and, in particular, provide vital insights for the renewable energy sector on how seals move during exposure to pile driving. This information supports consent-related decisions for offshore wind farm construction, by (1) characterising the nature of movement responses, helping in mitigation and management-related decisions, and (2) quantifying the relationship between behavioural changes and sound level, enabling more accurate predictions of potential impact. The behaviours observed here can also be used in informing

simulation-based approaches of movement (Chudzinska et al. 2021; Nabe-Nielsen et al. 2018) and dynamic energy budget models (Harwood et al. 2020), which are increasingly being used in environmental impact assessments. The framework developed and outlined here to quantitatively identify potential disturbance events is widely applicable to biologging data across different taxa and contexts. Overall, this study provides a key contribution in estimating a direct link between predicted sound exposure, behavioural changes, energetic consequences, and ultimately population-level effects of sound disturbance.

Author Contributions

K.F.W., D.J.F.R., G.D.H. and C.E.S. conceived the ideas and designed methodology; D.J.F.R. and G.D.H. led the supervision of K.F.W.; B.B. developed the acoustic models; K.F.W. analysed the data; K.F.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Ethics Statement

All capture and handling protocols were carried out under UK Home Office Licence 60/4009 in accordance with the Animals Scientific Procedures Act 1986, with additional licence approval from the University of St Andrews Animal Welfare and Ethics Committee. Seals were captured under licence from the Marine Management Organisation. All appropriate permissions with regard to designated sites, with any necessary mitigation measures in place, were obtained from the relevant authority.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h79q4.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** acv70102-sup-0001-Supinfo.pdf.