Aria of the Dutch North Sea

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4.2. MOVEMENT BEHAVIOUR INFLUENCES POPULATION LEVEL EXPOSURE TO UNDERWATER SOUND: IMPACT OF EXPLOSIONS ON HARBOUR POPOISES

This section[3] is submitted as [G. Aarts, A.M. von Benda-Beckmann, K. Lucke, H.Ö. Sertlek, R. van Bemmelen, S. Geelhoed, S. Brasseur, F.P. Lam, H. Slabbekoorn, R. Kirkwood, Movement behaviour influences population level exposure to underwater sound: Impact of explosions on harbor porpoises,under review by Journal of Animal Ecology]

Abstract: Anthropogenic sound in the marine environment can have negative population-level consequences for marine species. Estimating how many individuals are impacted by sound remains challenging though, as this is dependent on their mobility. The objective of this study is to reveal how animal movement influences how many and how often animals are impacted by sound. In a dedicated study we investigated the impact of sound from underwater detonations of recovered ordnance (mostly WWII aerial bombs) on harbour porpoise (*Phocoena phocoena*) in the Dutch North Sea. Geo-statistical distribution models were fitted to data from four marine mammal aerial line-transect surveys and used to simulate the distribution and movement of porpoises. Based on derived dose-response thresholds for temporary or permanent threshold shift (i.e. TTS and PTS), we estimated the number of animals affected was estimated. When individuals were free-roaming, 1200 and 24,000 unique individuals would suffer PTS and TTS, respectively. In contrast, when individuals were completely site-faithful, 1100 and 15,000 unique individuals would receive PTS and TTS, respectively. As explosions occurred more frequently in one region, the southern Dutch North Sea, high site-fidelity increased the probability of repeated exposures. Free-roaming

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[3] My contribution to this section concerns providing sound maps and source model of the underwater explosions. This section is included as illustration of a biological application of the sound maps during my PhD project.

movement, resulted in more individuals being exposed, but reduced the number of repeated exposures. Since most anthropogenic sound-producing activities operate continuous or are intermittent, snap-shot distribution estimates alone tend to underestimate the number of individuals exposed, particularly for mobile species. This study shows that an understanding of animal movement is needed to estimate the impact of underwater sound, or other human disturbance.

4.1.1 INTRODUCTION

Human activities in the marine environment such as offshore pile driving, seismic surveys, and detonation of explosives often produce impulsive sounds of high amplitude (Ainslie et al. 2009). Extreme levels of these anthropogenic sounds have the potential to disturb and/or damage marine mammals (Richardson et al. 1995, Southall et al. 2007, Nowacek et al. 2007). Particularly population-level consequences of sound are of great concern (National Research Council 2003). However, the first step of estimating the total number of individuals exposed to specific sound sources is challenging: Often only a fraction of the population is observed, and then, most marine mammals move large distances, changing the exposure probability, and consequently affecting the cumulative number of individuals exposed.

A general framework, labelled Population Consequences of Disturbance (PCoD) or Population Consequences of Acoustic Disturbance (PCAD) has been proposed to assess the impact of sound from anthropogenic activities at sea (e.g. offshore pile driving, seismic surveys, naval activities, shipping) at a population level (e.g. National Research Council 2003; Thompson *et al.* 2013b; New *et al.* 2014; King *et al.* 2015). The framework's first step in a chain of several steps requires an estimate of the number of individuals exposed to a level with detrimental impact. Frequency-specific sound source levels and sound propagation models are used to derive maps of sound exposure levels (SEL) or sound pressure levels (SPL). Published dose-response relationships describe the received level at which hearing impairment or behavioural responses are expected to occur (e.g. Southall *et al.* 2007; Lucke *et al.* 2009; Kastelein *et al.* 2012; Tougaard, Wright & Madsen 2014). The sound maps are then overlaid with marine mammal distribution estimates, to estimate the number of individuals exposed to sound levels above behavioural or auditory thresholds.

This method to estimate the number of individuals impacted can be used for single sound exposures, with the timescale of the exposure being small compared to the distance travelled by those individuals. However, it is deficient for the majority of situations, where continuous or intermittent sounds are produced over longer periods. These represent the majority of situations. With ongoing and intermittent sounds, individuals that are unaware of the event may (re-)enter an area of impact in-between the sound emission events. Consequently, a larger number of individuals could be exposed than would be expected based on 'snap-shot' density estimates. Moreover, individuals that have not vacated the area may receive multiple exposures during a sound production period.

Each type of anthropogenic sound-source has unique acoustic characteristics in terms of intensity, frequency range and repetition rate, and may change in location over time. Underwater explosions (e.g. controlled underwater detonations of recovered bombs, mines, and torpedoes from WWII) are unique as they represent single sound events, with the peak sound pressures of the blast wave being one of the highest anthropogenic noises produced in the marine environment (Ainslie et al. 2009, Koschinski 2011). Such detonations are conducted on the Dutch Continental Shelf (DCS) by the Royal Dutch Navy in a controlled manner, to reduce the risk of uncontrolled explosions, which could be dangerous to human life and infra-structure (Koschinski 2011, von Benda-Beckmann et al. 2015). Each year, approximately 100 detonations occur on the DCS. To marine mammals, the sound produced by these explosions could cause acute and chronic stress (Reeder & Kramer 2005), trigger behavioural reactions (Southall et al. 2007, Nowacek et al. 2007), and may lead to temporary or permanent hearing impairment or other physical injury (Ketten 2004, Lucke et al. 2009, Kastelein et al. 2012). Since the detonations appear to occur irregularly in time and space (von Benda-Beckmann et al. 2015), animals may be unable to anticipate and avoid them.

In the North Sea, the harbour porpoise (*Phocoena phocoena*) is the most abundant marine mammal, with approximately 230,000 individuals in 2005 (Hammond et al. 2013). In the southern North Sea, harbour porpoises were virtually absent for several decades but, since 1990, numbers have grown exponentially, presumably as a result of large-scale movement southwards (Camphuysen 2011, Hammond et al. 2013). Coastal sightings and aerial survey data suggest that most harbour porpoises reside in the southern North Sea in winter, and many migrate northwards along the Dutch and German coast in March and April (Scheidat et al. 2012). Due to their small size and a high metabolism in a cold environment, harbour porpoises require a higher daily food intake than most other Odontoceti (Kastelein 1997). Any impairment of their foraging efficiency, such as displacement in response to anthropogenic sound or impaired echolocation ability, could reduce the animal’s fitness.

Benda-Beckmann *et al.* (2015) investigated potential impacts of naval explosive clearance activities on the harbour porpoise on the DCS and concluded that these likely resulted in hundreds to thousands of PTS *events* annually. However, the total number of individuals exposed could not be estimated.

Here, we extend the study of Benda-Beckmann *et al*. (2015) by applying individual-based models to investigate the effects of hypothetical movement strategies of harbour porpoise (random dispersal and site fidelity), and thereby deriving improved population-level estimates. We base our analyses on one year of distribution data of harbour porpoise in the North Sea, and the time-line and amplitude levels of detonations in the same period. The first general question we aim to answer is ‘how does the interaction between the spacing and timing of explosions, and movement behaviour of the harbour porpoises, influence the exposure probability?’ And secondly, we attempt to estimate the total number of porpoises exposed to annual detonations of underwater explosions on the DCS. Although the study focusses on one species, one sound source and a finite region, the results are applicable to broader investigations of marine mammal (and potentially other marine fauna) responses to underwater anthropogenic sound.

4.1.2 METHODS

Pilot simulation: How does movement of the animal and the sound source influences the number of animals exposed?

Not only animals, but also sound sources tend to move through space, influencing how many and how often individual animals are exposed to sound. The sound source can be either fixed, moving randomly at high speed, or everything in-between. For illustrative purposes, we here adopt a simplified simulation to illustrate the extremes with respect to movement of the animal and the sound source, and how it affects the number of porpoises exposed, and exposure repeatability. A stationary sound source (e.g. underwater explosion or pile-driving event) was assumed to be either at a single location or at a different, randomly selected locations each day. It was active at one instance each day over a duration of 100 days. Porpoise movement was simulated on a 100 x 100 km grid, and those present within an arbitrarily chosen distance of 10 km from the source were assumed to be negatively impacted (e.g. auditory damage or severe panic response). The initial distribution of porpoises was randomly uniform, after which individuals moved according to different rules. One group of 1000 *site-faithful* porpoises remained at their initial location, and the other group of 1000 porpoises were *free-roaming*, making steps in random directions every 10 min., and moving at a high speed of 1.4 m/s (Otani et al. 2001). More realistic individual-based movement models for harbour porpoises that incorporate resource dynamics in space and time have been developed (Nabe-Nielsen et al. 2013). However, the necessary porpoise movement data and a representation of the food landscape were not available to parameterize this model for the southern North Sea. Another harbour porpoise movement model has been developed by Haelters *et al.* (2015), but this models applies to porpoises actively avoiding a pile-driving event. Here, we aim to simulate movement under more natural, undisturbed conditions.

Harbour porpoise aerial survey data

The defined one year study period was 15 March 2010 to 15 March 2011; data on explosions and harbour porpoise numbers on the DCS were analysed for this period. Here we use data from four aerial surveys of porpoise abundance, conducted in March, July and October-November 2010, and March 2011 on the DCS (Scheidat, Verdaat & Aarts 2012; Geelhoed *et al.* 2013). Surveys were conducted in weather conditions safe for flying and suitable for porpoise surveys, i.e. no heavy or freezing rain, visibility >3 km and expected sea state ≤3 bft. A high-winged, twin-engine aircraft (Partenavia 68) was used, flying at an altitude of ca. 183 m (600 feet) with a speed of 185 km/h (100 knots). Observers at bubble windows (allowing observations beneath the plane) on either side of the aircraft relayed details on environmental conditions (i.e. sea state, turbidity, cloud cover, precipitation and 'subjective' conditions) and sightings to a navigator. Conditions were reported at the beginning of each transect and whenever conditions changed. The subjective conditions (ranked as poor, moderate or good) represented the observer's perception of the likelihood of seeing a harbour porpoise should one be present, taking into account all environmental conditions. Only data collected under good and moderate conditions were used in the analysis. Sightings data included: species, inclination angle (to estimate distance), group size, presence of calves, behaviour, swimming direction and cue (e.g. body at surface, under water, splash).

Accounting for incomplete detection

To estimate absolute porpoise density, it is necessary to correct for the number of undetected porpoises (e.g. those well below the surface or not noticed by the observer). Here, detection probabilities were based on 'racetrack' calibrations and 'distance sampling' carried out in German and Danish waters using the same survey procedures and type of aircraft (Scheidat et al. 2008). The racetrack method estimates the proportion of animals re-sighted after flying a circle and resurveying part of the transect line (Hiby & Lovell 1998). The distance sampling method estimates the decrease in detection probability as a function of distance from the transect, using data on flight height and inclination of the porpoises from the aircraft (Buckland et al. 2004). The effective strip width (ESW) was calculated for each side of the aircraft. Published one-sided ESWs are 76.5 m (SE = 37.2 m) for good sighting conditions and 27 m (SE = 13.9) for moderate sighting conditions (Scheidat et al. 2008).The effective area surveyed is the distance travelled multiplied by the two-sided ESW.

Geo-statistical modelling of porpoise density

Estimating the number of individuals impacted by sound, requires species distribution estimates that can be overlaid with sound maps (e.g. McCarthy *et al.* 2011; Thompson *et al.* 2013). Not all types of species distribution models are suited for this purpose. For example, presence-absence models (e.g. Thompson *et al.* 2013; Bailey, Hammond & Thompson 2014) can yield biased estimates, because they do not differentiate between high and low density grid cells. In contrast, models based on count data provide estimates which are proportional to density (Aarts et al. 2012). To estimate the *absolute* number of individuals exposed, it is furthermore necessary to account for those individuals present, but not detected. This was achieved by incorporating the effective survey area, which accounts for the number of undetected individuals (see Hiby & Lovell 1998, Buckland *et al.* 2004).

In this study, porpoise density for the entire study area was derived from the survey data. First, a regular 10 km x 10 km grid was created, and the surveyed area and number of porpoise sightings within each grid cell were calculated. Grid cells with no survey effort resulted in missing values. Next a Bayesian spatial model was fitted to the data using Integrated Nested Laplace Approximation (INLA, Rue *et al*. 2009). The number of sightings (Y) in each grid cell '*i*' were treated as Negative Binomial distributed counts (with a dispersion parameter of τ) and the log of the effective area surveyed (A_i) was treated as an offset. A_i included the detection probability. Spatial correlation in the residuals (u) was treated as a latent Gaussian random field using a two-dimensional autoregressive correlation function of order-1:

$$\begin{aligned} Y_i &\sim NegBin(\lambda_i, \tau) \\ \lambda_i &= \exp\left(\beta_0 + \ln(A_i) + u_i\right) \end{aligned} \tag{1}$$

where λ is the expected count and β_0 is the model intercept. Bayesian prior distributions for the parameters β_0, τ and ρ_x and ρ_y (the correlation parameters in x and y direction, respectively) were defined as Gaussian distributed variables with mean 0 and precisions 0.0001. The model was used to estimate porpoise density for each grid cell within the DCS. We fitted models for each survey season to account for large seasonal differences in abundance and distribution. Linear interpolation between seasonal porpoise density estimates was used to estimate porpoise density at the date of each explosion.

Underwater sound field estimates

Information on the underwater explosions during 2010 and 2011, their location, timing, and sound propagation properties, are detailed in von Benda-Beckmann *et al.* (2015). We considered all 88 explosions on the DCS between 15 March 2010 and 15 March 2011, which concerned the period for which porpoise density estimates were available. Briefly, the acoustic property of the explosive is a short, expanding shock-wave comprising an almost instantaneous rise in pressure followed by an exponential decay, leaving behind expanding and contracting bubbles (Weston 1960), which then is transferred into a more complex waveform due to shallow water propagation (von Benda-Beckmann et al. 2015). Underwater sound propagation of the explosions was modelled using the software module SOPRANO (Sertlek et al., Sertlek & Ainslie 2014), which takes into account frequency dependent reflection losses due to surface and bottom interactions, and attenuation by the water. Input data for estimating sound propagation includes spectral source level energy and depth of the explosion, bathymetry maps (resolution: 0.125 x 0.125 minutes longitude and latitude, respectively, source: EMODNET database, http://www.emodnet-hydrography.eu/), geo-acoustical properties of the seabed (source: DINO database,http://www.en.geologicalsurvey.nl), and wind speed. Broadband sound exposure levels were calculated for the near-surface layer (1 m from the surface), and the near-bottom layer (1 m from the bottom). It was assumed that 50% of the porpoises were near the surface (between 0-2m depth – Teilmann *et al.* 2013) and 50% near the sea floor at the time of the explosion.

Hearing loss thresholds

The (masked) TTS onset level (estimated based on measured auditory evoked potentials for a harbour porpoise exposed to single airgun transients) was at SEL of 164 dB re 1 μPa^2s (Lucke et al. 2009). Potential frequency dependent effects of underwater explosions on TTS were assumed to be similar to the airgun transients, and therefore, it was considered unnecessary to apply frequency weighting to the SEL when estimating TTS risk. No precise data are available on PTS-onset levels in marine mammals, instead, following (Southall et al. 2007), PTS-onset was defined as 164 dB re 1 μPa^2s + 15 dB = 179 dB re 1 μPa^2s, and considered a lower limit below which PTS is unlikely to occur. Experimental exposure of fresh dead carcasses to underwater explosives (Ketten 2004) showed that ear trauma can occur at peak over-pressures between 10 – 25 psi (or 69 – 172 kPa), which approximately corresponds to SEL 190 – 203 dB re 1μPa^2s for explosions in shallow water environment (von Benda-Beckmann et al. 2015). It was therefore assumed that explosion sound would very likely cause PTS at the lower limit at which ear trauma occurs (i.e. SEL >190 dB re 1μPa^2s), which is the PTS threshold used in this study.

Number of animals affected by single detonations

For single impulsive sound sources, the porpoise density estimates can be directly overlaid with SEL (or SPL) maps, to estimate the number of individuals exposed to sound levels above the previously defined TTS or PTS thresholds. For each explosion, we defined for which grid cells the SEL was above the defined auditory threshold, and used the porpoise density estimates to estimate the number of porpoises present in those cells.

The effect of animal movement on the exposure to underwater explosions

To estimate the total number of unique individual porpoises exposed, and how often each individual was exposed, we simulated their movement for two extreme scenarios.

1. *Site faithful*. Porpoise density estimates for each survey season were treated as a probability density surfaces from which independent realizations of individual points (i.e. porpoises) were generated (see e.g. Fig. 5). At the mid-point between two successive surveys, each simulated individual from one survey was linked to the nearest individual from the subsequent survey. Since the absolute abundance between seasons differed, some individuals could not be linked, and those were considered to be temporarily outside the study area. The SEL sound maps of each explosion were then linked to the realized distribution of individual animals derived from the aerial survey closest in time.

2. *Free roaming/high mobility.* Although in this simulation we only considered the impact of explosions on porpoises within the DCS, we allowed porpoises to move freely within the entire North Sea. The total North Sea population size was defined as the sum of the geographic areas B, H, J, L, M, T, U, V and Y of Hammond et al. (2013), which equates to 232,450 animals. Since no information was available on inter-annual changes in abundance, the population size was assumed to remain constant between 2010 and 2011. Although these 232,450 individual animals were allowed to move freely within the entire North Sea, the total abundance and distribution of animals within the DCS corresponded to our absolute, seasonal porpoise density estimate. This was achieved by assigning to each grid cell outside the DCS, but within the North Sea, a sampling probability of (N_s -232,450)/G, where N_s is the total abundance within the DCS for season s, and G is the total number of grid cells in the entire study area.

For the first explosion, the simulated distribution of porpoises was based on the nearest survey in time, similar to scenario 1 above. Between the explosion at time t_1 and the subsequent explosion at time t_2, the individual animal was allowed to move at an average cruising speed of v = 1.4 m/s over a maximum distance of $m = v(t_2\text{-}t_1)$. Here v is the speed at which the energetic cost of transportation is at its minimum (1.3 – 1.5 m/s), which lies in-between the mean (experimentally derived) swim speed (i.e. 0.76–0.91 m/s) and maximum observed swim speed (4.2 m/s) (Otani et al. 2001). For each individual porpoise at t_1, the porpoise density map corresponding to the explosion at t_2 was used to generate a new point location, with the constraint that it was within the maximum travel distance m.

These two simulations allowed us to trace how individual animals (i.e. points) were exposed to multiple explosions in time. No data are available on how porpoises respond to exposure of underwater explosions, and it is even questionable whether they are capable of estimating the distance or direction of the source. Hence, no attempt was made to study in detail the effect of avoidance.

4.1.3 RESULTS

Pilot Simulation: The effect of movement on exposure probability of fixed and moving sound sources.

If the sound source remains at a fixed location and porpoises are site-faithful (Fig. 1d), only those individuals living directly within the impact zone (here <10 km from the source) will be negatively impacted (Fig. 2a), however, they will be exposed each time the sound source is active (Fig. 2b). In contrast, when porpoises are free roaming and not avoiding the impact area, nearly all individuals are exposed at least once (on average 937 of 1000 individuals), but on average each individual is only exposed 3 times within the 100 day study period. The total number of impact events remains the same, regardless of whether individuals are site-faithful or roam freely.

When simulating a sound source which is randomly moving in space (Fig. 1c, d), different movement behaviours have little effect on either numbers of individuals exposed or numbers of multiple exposures. Over time, approximately all individuals could be exposed at least once.

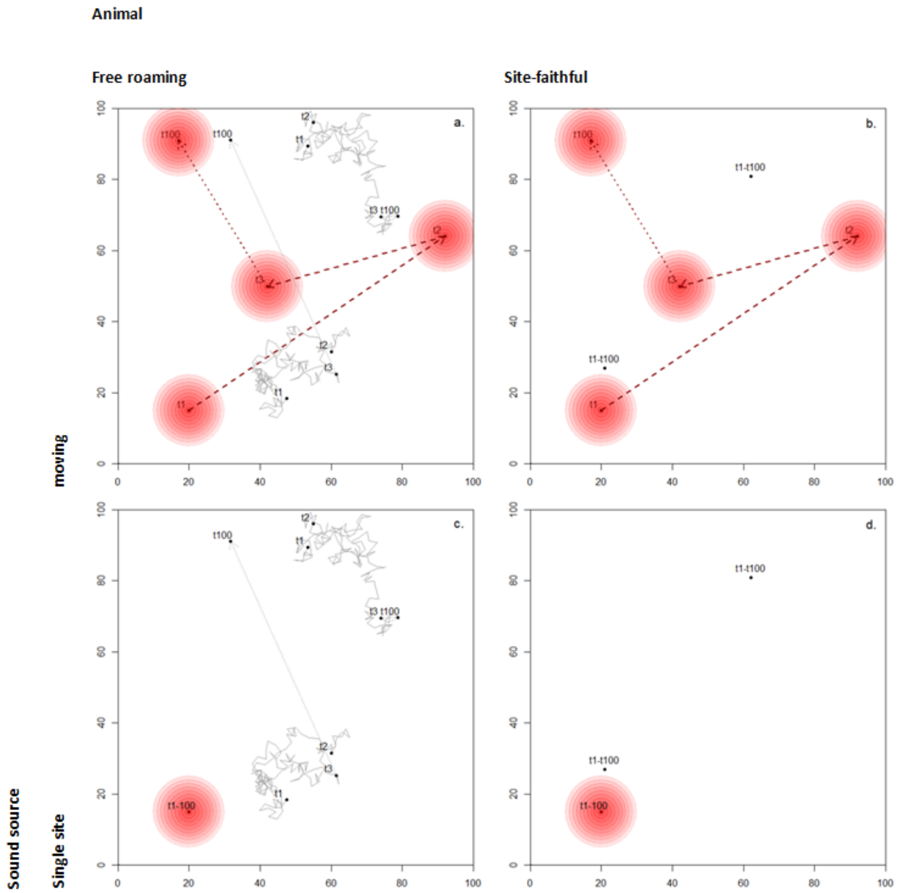


Figure 1. Illustrating the simulation of the movement by the animal and the sound source. The sound source (red circle) either moves randomly through space (a, b) or occurs at a single site (c, d). Animals (grey track and black dots) either move at a speed of 1.4 m/s randomly through space (a, c) or are site-faithful (b, d). t1-t100 represent day 1 through day 100. Only the track of the first three and final location of the animal and sound source are shown.

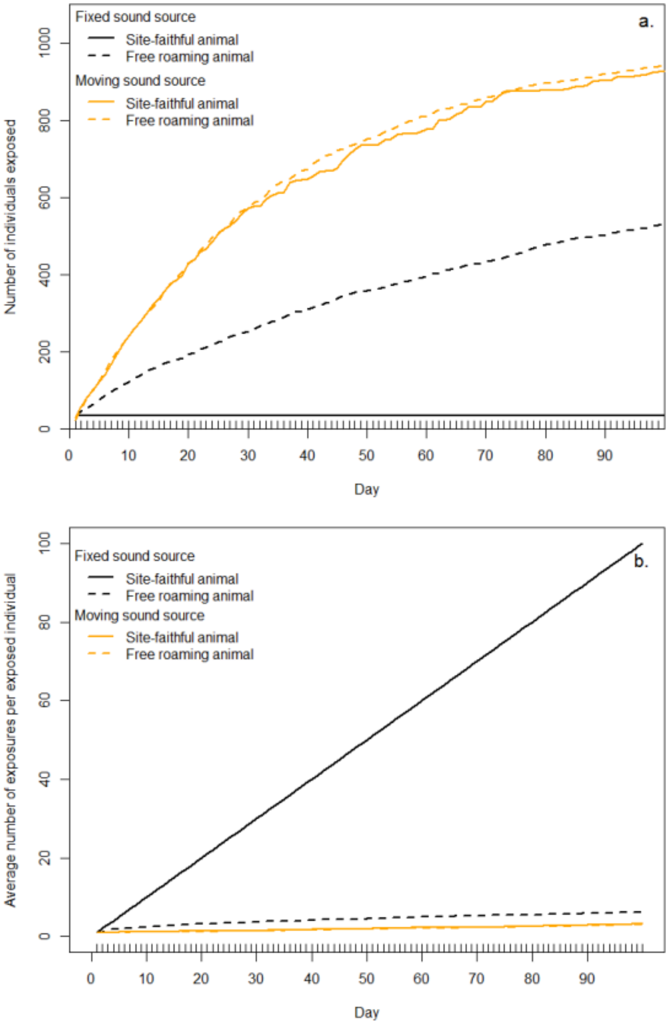


Figure 2. Simulation illustrating the effect of movement by the animal and the sound source on the exposure probability. When an organism is free roaming and the sound source is at a predictable (i.e. fixed) location, the cumulative number of individuals impacted is much larger than when the organism is site-faithful (a), however the number or repeated exposures is reduced (b). If the location of the source is completely unpredictable in space, movement does not reduce the number of individuals exposed (a) nor the average exposure probability (b).

Spatiotemporal distribution of underwater explosions in the DCS

Explosives were mostly detonated at their site of discovery, with the highest density in the southern part of the DCS (Fig. 3) as most of the explosives were dropped in this area during WWII (OSPAR Commission 2010). The detonations occurred in all months of the year, with a peak in March. There were 88 explosions on the DCS between 15 March 2010 and 15 March 2011.

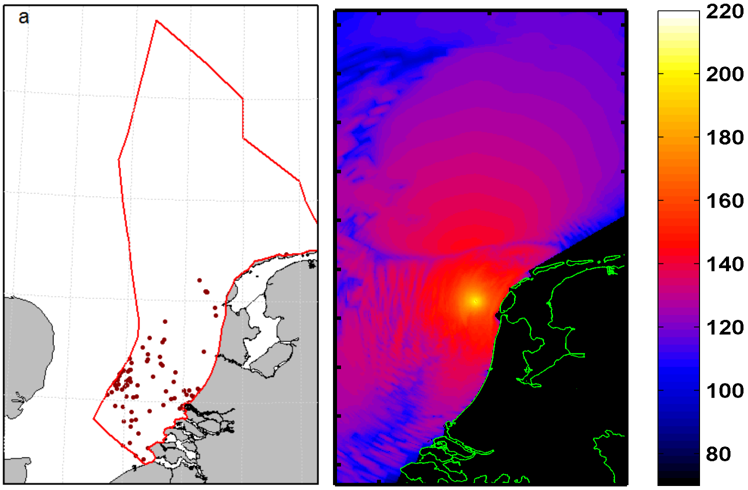


Figure 3. a. Distribution of explosives detonated by the Dutch Royal Navy for 1 year (15 March 2010 to 15 March 2011). b. Estimated unweighted broadband SEL of a single example explosion (263 TNT eq. charge mass) received at a depth of 1m above the sea floor. See Benda-Beckmann et al. (2016), Sertlek and Ainslie (2014) and Sertlek et al. (in prep.) for more details.

Spatiotemporal distribution of harbour porpoises in the DCS

Harbour porpoise distribution over the DCS changed between each survey (Fig. 4, see table S2 for summary of fitted models). In March 2010 (Fig. 4a), the average porpoise density was 1.09km^{-2}, with the highest density in the central DCS, and the lowest density in the southern DCS. There was no survey effort in the most northern Dogger Bank region, so those density estimates were extrapolated from densities in the adjacent region B. In July 2010 (Fig. 4b), porpoises were present in low numbers, averaging 0.60 km^{-2}. In October/November 2010 (Fig. 4c), overall density was again low (0.63 km^{-2}). In March 2011 (Fig. 4d), the overall density was high again (i.e. 1.34 km^{-2}). The model-based estimates of harbour porpoise numbers on the DCS were 64,851 (March 2010), 35,754 (July 2010), 37,574 (Oct/Nov 2010) and 79,318 (March 2011). These estimates were within the 95% confidence intervals of the original stratified survey estimates of Geelhoed *et al.* (2013).

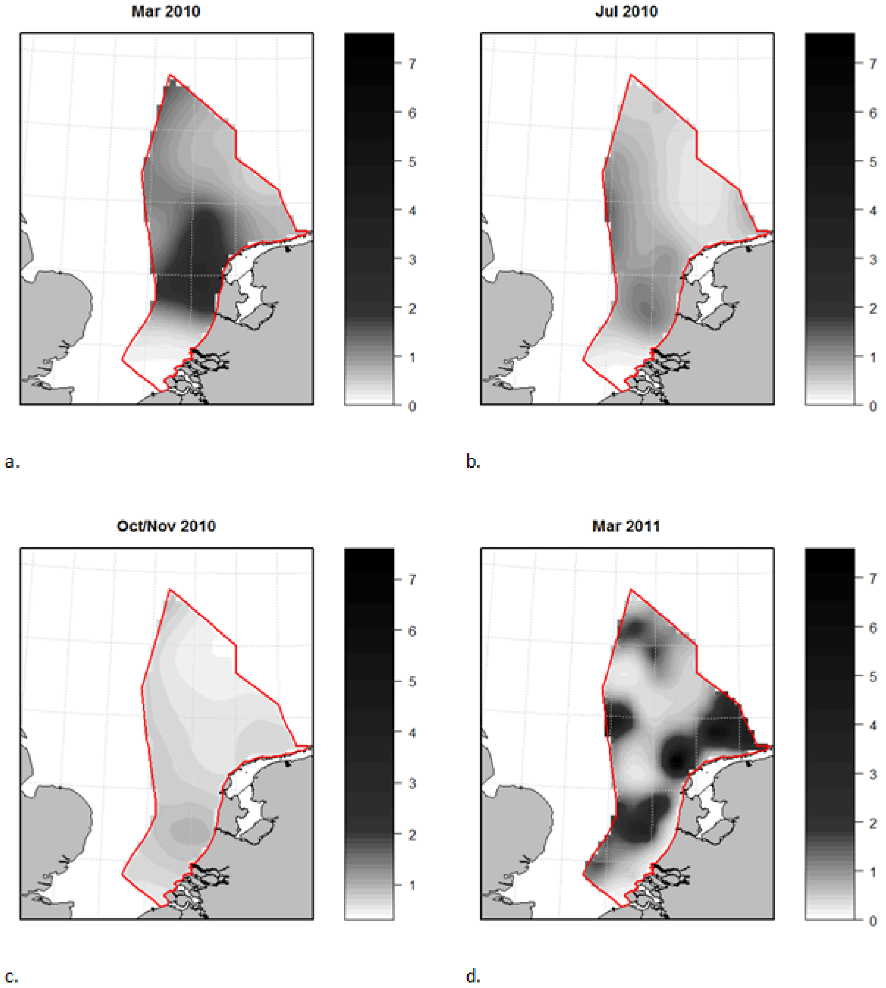


Figure 4. Seasonal model-based estimates of harbour porpoise density (grey scale) within the Dutch Continental Shelf (red polygon) for March (a), July (b) and October-November (c) 2010, and March 2011 (d).

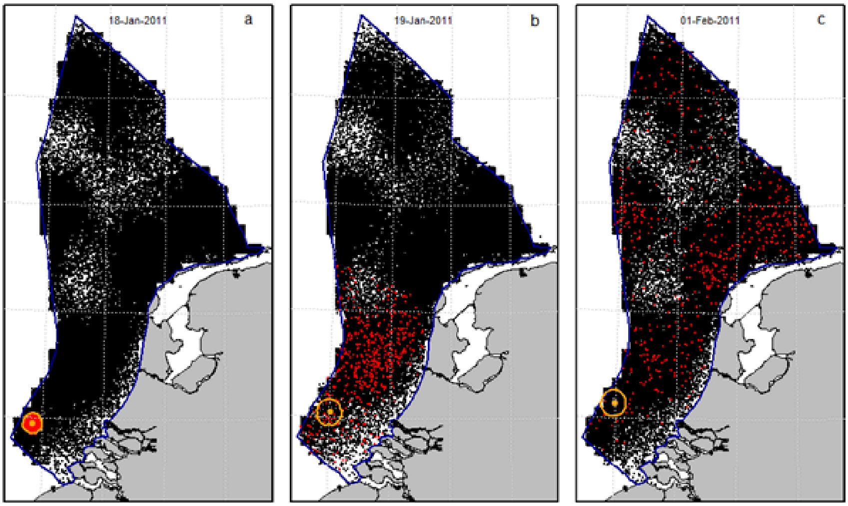
Estimated number of porpoises affected by single explosions

There was considerable variation in the number of harbour porpoises affected by each explosion. These estimates were influenced by the assumed position of harbour porpoises in the water column: if near the sea floor the exposure was approximately 8-times larger compared to near the surface (Table S1, Benda-Beckmann *et al.* 2015). On average, for each single explosion within the DCS during the survey period, 15 porpoises were estimated to be exposed to an SEL of ≥190 dB re 1µPa^{2}s and hence, assumed to suffer PTS (Table S1). At the lower threshold limit of the range at which PTS becomes increasingly likely (i.e. SEL ≥ 179 dB re 1µPa^{2}s), each explosion resulted in an average of 62 porpoises suffering PTS (**Table S1**). On average, following each explosion, 319 porpoises were estimated to have been exposed to a SEL of ≥164 dB re 1µPa^{2}s and, therefore, to have suffered a TTS (Table S1).

Estimated number of porpoises affected by multiple explosions: The effect of movement

The average time between explosions was 3.8 days (median = 0.8, SD = 6.6), during which individuals were often able to redistribute. For the continuous roaming scenario, assuming a maximum average cruising speed of 1.4 m/s (Otani et al. 2001), individuals were theoretically capable of travelling 120 km within a single day (i.e. 24 hours). Assuming non-directional, random movement in-between successive explosions, some individuals remained in the proximity of the explosion site of the previous explosion, while others relocated to regions tens of kilometres away. If the time-window between successive explosions was sufficiently large, individuals were capable of relocating to any site within the DCS or even beyond (Fig. 5a-c). In contrast, site-faithful individuals (by definition) remain at their initial fixed location (Fig. 5d-f), and are exposed to successive explosions when the upcoming explosions were in the vicinity.

Free roaming



Site Faithful

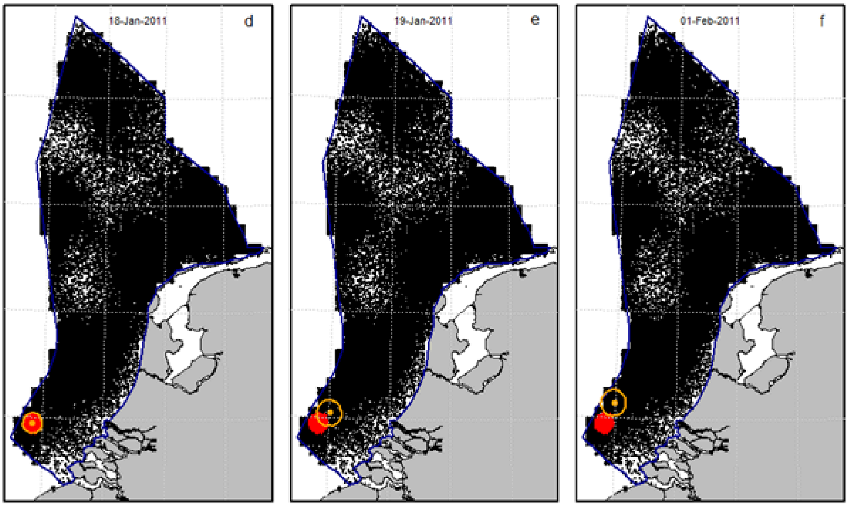


Figure 5. Example showing the effect of movement (a, b, c: free roaming, d, e, f: site-faithful) on repeated exposure probability to successive underwater explosions. The 79,000 black and red points represent all individual porpoises; their distributions are derived from the seasonal density surface estimates. Red points are those individuals exposed to an SEL ≥164 dB re 1µPa^{2}s, i.e. received TTS (orange circle), from an explosion on 18 January 2011. Free-roaming individuals were capable of dispersing to other regions. With explosions occurring near to each other, amongst individuals affected by the first explosion, free-roaming individuals had less chance of multiple-exposures than did site-faithful individuals.

For a single year (March 2010 – 2011), there were 1283 estimated PTS events (i.e. PTS very likely, SEL > 190 dB re 1µPa^{2}s). When porpoises were free roaming throughout the North Sea, 0.5 % of the exposed individuals were exposed at least twice, while for site-faithful individuals it was 6 % (Fig. 6c,d, Table 1).

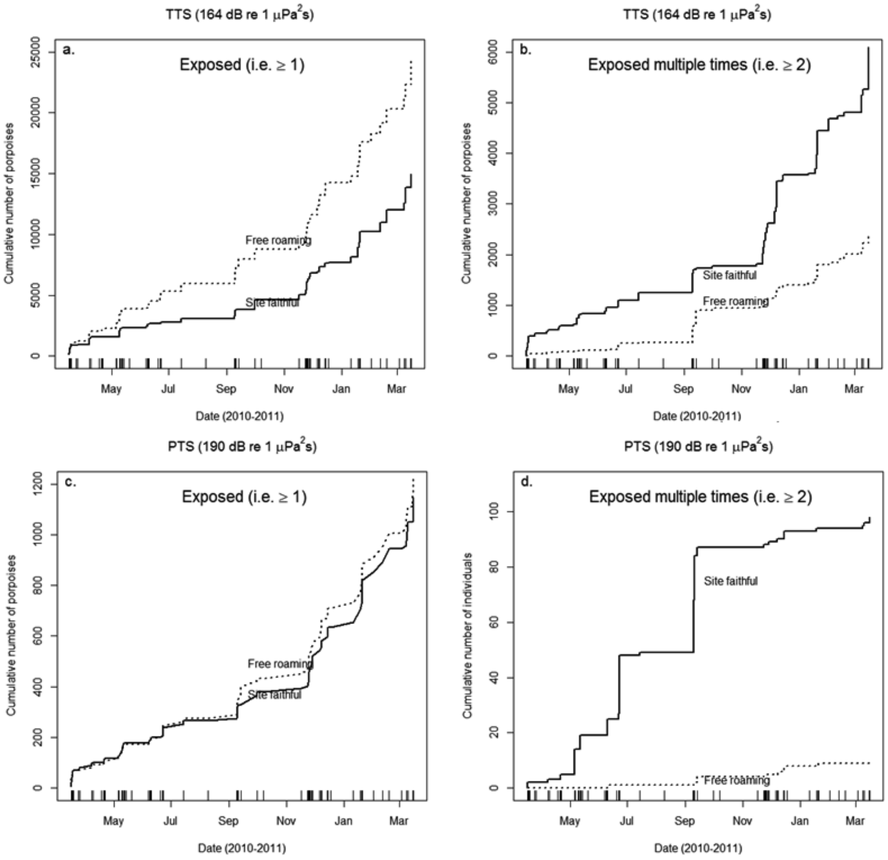


Figure 6. The effect of type of movement (high site-fidelity versus free roaming throughout North Sea) on the number of individuals expected to receive TTS (SEL ≥164 dB re 1µPa^{2}s, a, b) or PTS onset very likely (SEL ≥190 dB re 1µPa^{2}s, c, d) at least once (a, c) and at least twice (b, d). Free roaming movement will lead to more individuals being exposed to levels exceeding TTS (and PTS) thresholds, but high site fidelity leads to more individuals being exposed multiple times.

On average, 28,067 TTS events were estimated to occur on the DCS during the study period. If porpoises roamed freely within the entire North Sea, an estimated 24,272 unique individuals suffered TTS, and approx. 10 % of these suffered TTS on multiple occasions. In contrast, when individuals were site-faithful, only 14,963 suffered TTS, but doing so on multiple occasions (38%, Table 1 and Fig. 6a,b).

Table 1. The estimated number (and 95% confidence interval between brackets) of harbour porpoises suffering hearing loss due to the cumulative effect of 88 explosive clearances on the Dutch Continental Shelf (DCS) between 15 March 2010 and 15 March 2011. Porpoises were assumed to spend 50% of the time near the surface and 50% near the bottom.

		Number of unique porpoises	
Type	**Threshold unweighted SEL [dB re 1μPa^{2}s]**	**Free roaming**	**Site-faithful**
Blast wave ear trauma *Very likely*	203	59 (46-76)	50 (38-66)
Permanent hearing loss *very likely*	190	1217 (1151-1287)	1145 (1081-1213)
Permanent hearing loss *increasingly likely*	179	5204 (5066-5346)	4275 (4152-4401)
TTS *very likely*	164	24,272 (23,985-24,562)	14,963 (14,748-15,180)

4.1.4 DISCUSSION

Effect of movement on the number of individuals exposed to sound from underwater explosions

This study shows that increased movement speed and dispersal rate increases the accumulative number of individuals within a population that will be exposed to a repetitive anthropogenic sound. However, repeated exposure probability is reduced. This effect is strongest if the sound source remains at a fixed location. Since most marine mammal species, including harbour porpoises, are highly mobile, incorporating the effect of movement is important for estimating impacts at the population-level.

Even for underwater explosions, which may appear unpredictable in space and time, the cumulative number of harbour porpoises exposed depends on how individuals move. We estimate that if all individuals were free-roaming and continuously on the move, in a single year on the DCS 1200 individuals were very likely to receive PTS and 24,000 individuals would receive TTS. In contrast, if harbour porpoises were site-faithful, less individuals would receive PTS or TTS (i.e. 1100 and 15,000, respectively), but more would be exposed on multiple occasions. These numbers are probably underestimated, since only porpoises on the DCS were considered here (given the available survey data), and many individuals outside the DCS might also be exposed. In addition, porpoises residing within the DCS might be affected by detonations outside the DCS, for which no complete data on detonation activities were available.

The effect of movement on the total number of animals experiencing PTS is small, because the PTS effect area is small (relatively to that for TTS), and few explosions occur exactly on the same spot. In contrast, the number of individuals exposed to SELs exceeding the TTS threshold in the free-roaming scenario was1.6 times higher than in the site-faithful scenario. While movement alters the balance between the number of individuals exposed and the number of repeated exposures, it does not influence the number of impact events, at least assuming individuals do not actively avoid the region where they were previously exposed.

Site-fidelity increases repeated exposure probability: Avoid and redistribute?

The simulation study shows that if the location of the source is at a fixed location, remaining site-faithful increases the risk of being exposed again to following sound exposures. Conversely, if the location of the source is completely unpredictable, any type of movement, including active avoidance, has no effect on numbers exposed and repeated exposure probability. Even though the distribution of underwater explosions may appear unpredictable, this study shows that site-faithful individuals have an increased risk of suffering TTS or PTS on multiple occasions (Fig. 6). Hence, once exposed to underwater explosions, individual porpoises could reduce the risk of future PTS or TTS by avoiding the site of exposure. This suggests that the approximate location of explosions *is* to some extend predictable. Indeed, in this study explosions were more densely distributed in one region; the southern DCS (Fig. 3). Dense clustering of explosions (or other human sounds) is often likely as they could relate to either the biased distribution of ordnance, or a focus of human activity. For example prior to construction activities (e.g. wind farm development), an area is surveyed for the presence of unexploded ordnances, which are often detonated close in space and time. Such events are apparent in Fig 6, showing a sudden jump in the number of individuals exposed at least twice.

Although not explicitly explored in this study, the porpoise density in the southern DCS (i.e. the region with the highest density of detonations) is on average lower than the rest of the DCS (Fig. 4). This could be caused by natural processes (e.g. food availability) or other anthropogenic activities (e.g. shipping activity near the international harbour of Rotterdam). However, it may also be partly driven by large-scale redistribution resulting from avoidance of underwater explosions. If so, this has direct implications for our results. First, the March 2010 survey took place from 2 – 11 March. Explosions prior to the survey could have already reduced porpoise densities. Hence, the estimated number of exposed individuals might be underestimated for that period. Furthermore, although the possible influence of underwater explosions on porpoise distribution might be partly reflected in the observed porpoise density estimates, the movement simulation ignores direct avoidance and relocation. Avoidance could reduce the number of repeated exposures. However, for PTS the effect of avoidance will be small: Even if porpoises are completely site-faithful, less than 10% are exposed to PTS levels on multiple occasions, and hence relocation will have a minor influence on the total number of PTS events.

Several anthropogenic activities emit repetitive sounds separated by silent periods. During the silent periods, if sufficiently long, acoustically naive marine animals risk entering the area of high risk of auditory (or other physical) damage. This is more likely to occur for highly mobile organisms. Hence, although movement allows organisms to reach other regions with higher survival and reproduction potential, it increases the risk of individuals being exposed to repetitive sound sources.

Whether individuals should avoid an area once exposed to an intense sound source ultimately depends on how well the individual is capable of predicting when and where a new sound will be emitted. Even if the individual would have perfect knowledge of the spatial location and timing the sound event, it is questionable whether avoidance is the best decision. Avoidance may reduce future auditory damage, but it also reduces the time and the amount of habitat available in which to forage or reproduce. Clearly decisions about whether to move and/or avoid certain areas are complex and difficult to predict for species in which high levels of individual variability can be expected, such as for marine mammals.

The importance of movement data for assessing the impact of repetitive sound exposures

Given the importance of movement on the total number of individuals impacted, species distribution models producing a single distribution estimate (see e.g. Fig. 4) might be sufficient for a single event, such as a single explosion, but are insufficient for assessing the impact of longer lasting human activities, including a series of explosions, seismic surveys, pile driving, and shipping operations. Particularly for highly mobile species, the time spent (or population density) at a specific location can be low. Nevertheless, when the sites are vital for the species' survival and reproduction, over time, the cumulative number of individuals using this site might be high (van Horne 1983). Hence, for longer-lasting disturbing activities (e.g. pile driving or seismic surveys), the cumulative number of individuals impacted might far exceed the instantaneous or average population density. The functional form of this accumulation depends on how individuals move. Such individual movement data is often unavailable for marine mammal species (including harbour porpoises in the southern North Sea). As an alternative, simulations can provide information on the magnitude of the effect of movement on the number of individuals exposed and exposure probability to specific anthropogenic sound sources.

The simulation in this study shows that for PTS, the type of movement has little impact on the estimated number of individuals exposed. In contrast, for more moderate exposure impacts with larger impact areas (e.g. TTS – Fig. 6), the type of movement behaviour has a substantial impact on the number exposed. As the initiation of behavioural response could be triggered at larger distances than the PTS and TTS threshold distances, movement behaviour is likely to have an even greater influence on total numbers impacted than suggested by our results. The availability of actual movement data and observations of responses at larger distances is critical to better understanding the magnitude of impacts from anthropogenic sounds.

Further research

Although the framework presented here illustrates how to make population level estimates, and suggests underwater explosions may impact a substantial part of the North Sea harbour porpoise population (Fig 6, Table 2), a number of improvements in the estimates can be made. First of all, various fundamental biological and especially auditory parameters, such as the level and frequencies at which PTS occurs (von Benda-Beckmann et al. 2015) are missing. Furthermore, although this study provides clues about how different movement regimes influence the total number of unique exposed individuals, there is currently no data on harbour porpoise movement within the southern North Sea. Studies in the Kattegat-Skagerrak suggest that porpoises mix local searching/site fidelity movements with larger scale movements (Nabe-Nielsen et al. 2013). Land- and ship-based surveys in coastal habitats, often reveal large tide-dependent variability in occurrence, which suggests that at least in these habitats, porpoises are not extremely site-faithful (Jones et al. 2014, IJsseldijk et al. 2015). In the North Sea, seasonal differences in coastal sighting rates (Camphuysen 2011) and absolute abundance estimates (Geelhoed *et al.* 2013, and this study), suggest that long-distance migrations also occur seasonally. Several direct observations provide further detail on the flexibility in movement by harbour porpoises. In one example, an albino porpoise observed in Den Helder on 25 Feb. 2012 at 11:30, was re-sighted near Juist (Germany) on 28 Feb. 15:30, a distance of 187 km travelled in just 76 hours, implying a minimum average speed of 0.70 m/s (Cees Rebel and Kees Camphuysen pers. comm.). In contrast, a female porpoise with calf was observed to remain present near an offshore oil platform for at least 3-weeks (Camphuysen & Krop 2011), indicating a high level of temporal site-fidelity.

In addition to the lack of data on how porpoises move under 'natural' circumstances, it is unknown how porpoises respond to underwater explosions. Harbour porpoises do respond with avoidance behaviour to persistent sound (Dähne et al. 2013, Tougaard et al. 2014). Behavioural reactions to on-off explosions are unknown. They could involve brief startles, or periods of erratic, fast swimming, followed by directional swimming for long periods (minutes to hours – depending on the strength of the sound and previous experience). Although the animals are unlikely to be capable of determining the source direction for such a single, short duration, sound (Kastelein et al. 2007), persistent swimming over several kilometres by exposed harbour porpoises, may still lead to lower densities within the impact areas.

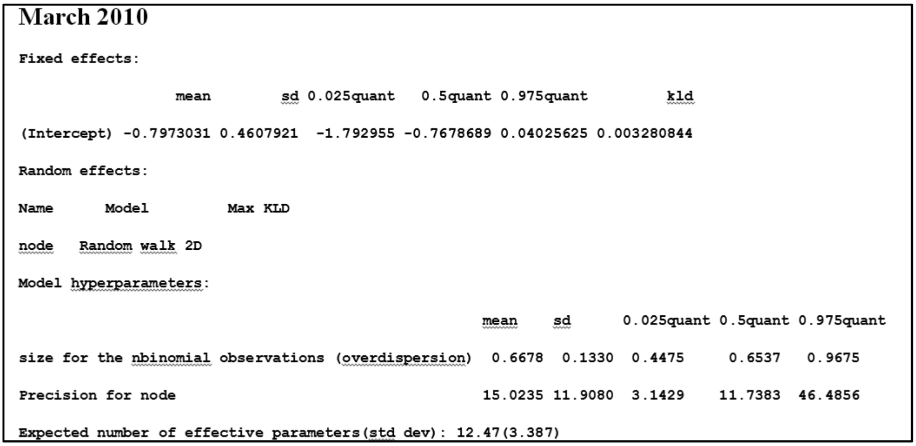
If porpoises in the southern North Sea move large distances on a daily basis and have no spatial knowledge regarding the location of upcoming detonations, impact areas may soon be replenished. Also the study by Thompson *et al.* (2013a) show that after short-term disturbance (by a seismic survey), porpoise density returned to initial values, and it was argued that therefore the activity did not lead to long-term displacement of porpoises. That study, however, was based on passive acoustic monitoring and visual aerial surveys. Without individual movement data, it is not possible to distinguish between a situation where displaced individuals returned, or whether the impacted area was replenished by acoustically naïve individuals. Such individual movement data is vital, particularly for assessing population level consequences of disturbance (PCOD – Rossington *et al.* 2013; King *et al.* 2015) on mobile marine organismes. Movement data reveals whether anthropogenic sound has long-term negative effects on individuals (e.g. reduction of available habitat and increased energetic costs), while observations on population density alone, can be obscured by the behaviour of previously unexposed individuals.

SUPPLEMENTARY MATERIAL

Table S1. The estimated average number of harbour porpoises suffering receiving hearing loss, caused by a single explosive clearance on the Dutch continental shelf (DCS) waters between 15 March 2010 and 15 March 2011. Estimates were made for near the sea surface at 1 m depth, near the bottom (i.e. 1 m above the bottom) and the average of these two. See also Benda-Beckmann et al. (2015) for more details.

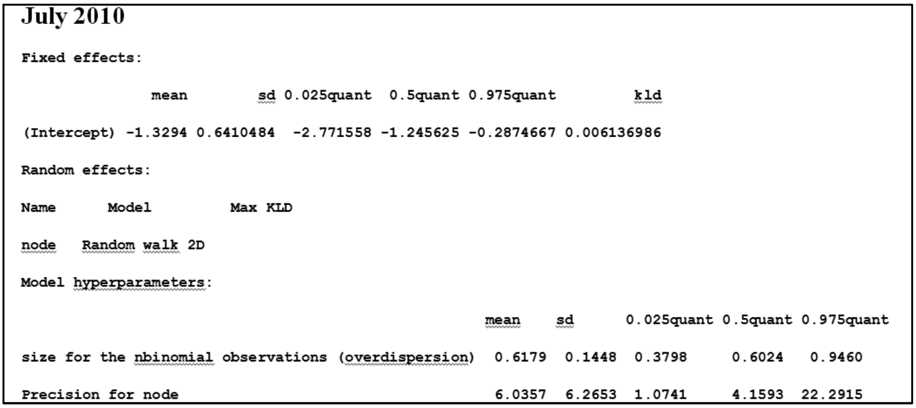
		Number of porpoises		
Type	**Threshold unweighted SEL [dB re 1µPa²s]**	**If all near Surface**	**If all near Bottom**	**If 50% near Surface and 50% near bottom**
Blast wave ear trauma *Very likely*	203	0	1	1
Permanent hearing loss *very likely*	190	2	27	15
Permanent hearing loss *increasingly likely*	179	18	106	62
TTS *very likely*	164	190	448	319

Table S2. Summary of models to the four survey seasons: March, July and October-November 2010 and March 2011. The exponent of the fixed effects estimate of the intercept represents the mean density over the entire square study area. Since this also includes the areas on land and outside the DCS, the absolute value has no biological meaning. The overdispersion parameter represents the overdispersion in the residuals. When the estimate is large, this indicates clustering of individual sightings within the 10 x 10 km grid cells. The inverse of the "precision for node" reflects the variance of the latent Gaussian random field. The expected number of effective parameters is a measure of the complexity of the distribution surface. E.g. for the October-November 2010 survey, when the model estimates a relative homogeneous distribution (see Fig. 3c), the effective number of parameters is 3.1.



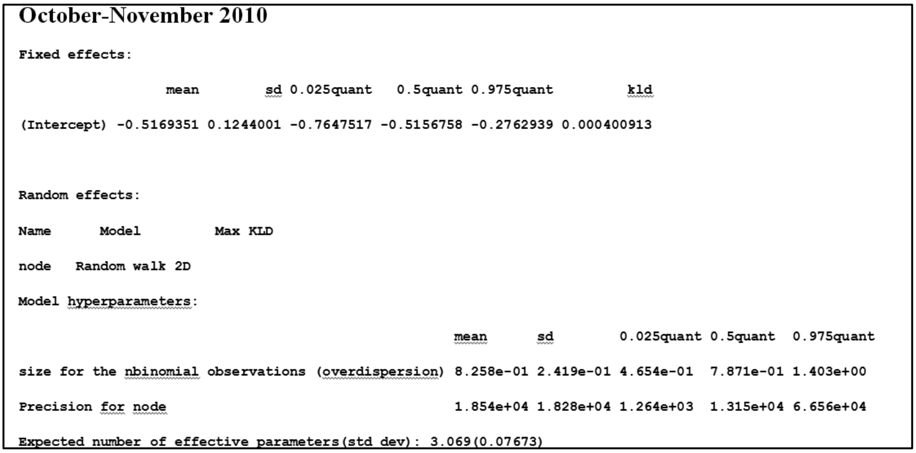
March 2010

```
Fixed effects:
                  mean        sd 0.025quant   0.5quant 0.975quant          kld
(Intercept) -0.7973031 0.4607921  -1.792955 -0.7678689 0.04025625 0.003280844
Random effects:
Name      Model         Max KLD
node   Random walk 2D
Model hyperparameters:
                                                    mean     sd      0.025quant 0.5quant 0.975quant
size for the nbinomial observations (overdispersion)  0.6678  0.1330  0.4475     0.6537   0.9675
Precision for node                                  15.0235 11.9080  3.1429    11.7383  46.4856
Expected number of effective parameters(std dev): 12.47(3.387)
```



July 2010

```
Fixed effects:
              mean        sd 0.025quant  0.5quant 0.975quant          kld
(Intercept) -1.3294 0.6410484  -2.771558 -1.245625 -0.2874667 0.006136986
Random effects:
Name      Model         Max KLD
node   Random walk 2D
Model hyperparameters:
                                                    mean     sd      0.025quant 0.5quant 0.975quant
size for the nbinomial observations (overdispersion)  0.6179  0.1448  0.3798     0.6024   0.9460
Precision for node                                    6.0357  6.2653  1.0741     4.1593  22.2915
```



October-November 2010

```
Fixed effects:
                  mean        sd 0.025quant   0.5quant 0.975quant          kld
(Intercept) -0.5169351 0.1244001 -0.7647517 -0.5156758 -0.2762939 0.000400913


Random effects:
Name      Model         Max KLD
node   Random walk 2D
Model hyperparameters:
                                                    mean      sd        0.025quant 0.5quant  0.975quant
size for the nbinomial observations (overdispersion) 8.258e-01 2.419e-01 4.654e-01  7.871e-01 1.403e+00
Precision for node                                   1.854e+04 1.828e+04 1.264e+03  1.315e+04 6.656e+04
Expected number of effective parameters(std dev): 3.069(0.07673)
```