Vol. 672: 223–241, 2021
https://doi.org/10.3354/meps13757

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 19

Behavioural reactions of harbour porpoises *Phocoena phocoena* to startle-eliciting stimuli: movement responses and practical applications

Helen M. Hiley[1,2], Vincent M. Janik[1,*], Thomas Götz[1]

[1]Sea Mammal Research Unit, Scottish Oceans Institute, School of Biology, University of St. Andrews, St. Andrews, Fife KY16 8LB, UK

[2]*Present address:* Scottish Association for Marine Science, Scottish Marine Institute, Dunstaffnage, Oban, Argyll PA37 1QA, UK

ABSTRACT: Acoustic deterrent devices are frequently used as a mitigation method to exclude harbour porpoises *Phocoena phocoena* from areas of potential harm, such as wind farm construction sites. However, there is increasing evidence that the devices themselves have the capacity to cause hearing damage. Here, we investigated the response of harbour porpoises to a 15 min sequence of 200 ms sound (peak frequency 10.5 kHz, range 5.5–20.5 kHz, 27 sounds total), which elicits the acoustic startle reflex. We used a duty cycle (0.6%) and sound exposure level that were significantly lower than in conventional acoustic deterrent devices. Harbour porpoises were exposed to startle sounds from a small vessel, and groups were visually tracked during 13 sound exposure sequences and 11 no-sound control trials. Porpoises showed a significant avoidance reaction during exposure, travelling a mean distance of 1.78 km (max. 3.21 km). In all cases, they left the area within 1 km of the sound source in the first 15 min after the start of the startle sequence. No avoidance was exhibited during control trials. Results are consistent with the startle reflex mediating this behaviour at low response thresholds. Our method can be used for mitigating collision risk and the risk of hearing damage from renewable energy installations, their construction and the deterrence device itself.

KEY WORDS: Acoustic startle · Acoustic deterrent · Anthropogenic noise · Harbour porpoise · Noise mitigation · Startle-eliciting stimuli

1. INTRODUCTION

In terrestrial and aquatic environments, sound has been used to deter animals and reduce the effects of human–wildlife conflict (Bomford & O'Brien 1990, Götz & Janik 2013). In most cases, aversive sounds are employed to protect a human interest, but on occasion, they are used to protect the animals themselves (Brandt et al. 2013a, Dawson et al. 2013). Acoustic deterrent devices (ADDs) have been used to deter pinnipeds from Scottish fish farms since the 1980s (Götz & Janik 2013, Coram et al. 2014). Seals can cause damage to fish farm pens and fish through depredation, so in a bid to reduce economic loss by non-lethally deterring animals, ADDs have been adopted routinely on fish farms and are often considered benign control methods. ADDs, however, can have unintended effects on other wildlife such as causing hearing impairment or masking sounds for communication or predator detection (Götz & Janik 2013). Disturbance from ADDs can also result in large-scale habitat exclusion of non-target species from areas important for foraging, resting or reproducing (Gill et al. 1996, Johnston 2002, Morton & Symonds 2002, Olesiuk et al. 2002). This has the potential to have substantial effects on both the fit-

*Corresponding author: vj@st-andrews.ac.uk

ness of individuals and the survival of populations. On the west coast of Scotland, ADDs have become a widespread source of noise pollution (Findlay et al. 2018) and are likely to affect both target and non-target species due to the high densities of both seals and cetaceans in this area. Despite their prevalence in the aquaculture industry, few studies have proven the long-term effectiveness of ADDs as a pinniped deterrent (Jefferson & Curry 1996, Götz & Janik 2013), but many have now shown that they are highly effective at deterring harbour porpoises *Phocoena phocoena* (Johnston 2002, Olesiuk et al. 2002, Brandt et al. 2013a, Mikkelsen et al. 2017). This has resulted in the adoption of ADDs by the renewable energy industry as a way to deter harbour porpoises from areas prior to pile driving for the construction of offshore wind farms.

The average size of offshore wind farms under construction has almost doubled in the last decade, and there are now 110 offshore wind farms in 12 European countries (Walsh 2019), with the North Sea alone accounting for 77% of all offshore wind capacity in Europe. With the global offshore wind capacity projected to increase 15-fold over the next 20 yr (IEA 2019), it is extremely important to effectively mitigate the impact of construction and operation on marine mammals.

Due to its high sensitivity to anthropogenic noise, the harbour porpoise has been regarded as an indicator species in noise impact evaluations (Southall et al. 2007, 2019, Tougaard et al. 2015). During wind farm construction, piles are driven into the seabed, which results in high levels of impulsive noise (Tougaard et al. 2009, Bailey at al. 2010, Brandt et al. 2013a, Hastie et al. 2019). It has been demonstrated that porpoises react to piling at considerable distances (Tougaard et al. 2009, Brandt et al. 2011, 2013b), and both single and multiple exposures to impulsive noise have been shown to cause temporary threshold shifts (TTSs) in harbour porpoises at lower noise levels than in other odontocetes (Lucke et al. 2009, Kastelein et al. 2016).

Harbour porpoises are abundant in the North Sea (Reid et al. 2003, Hammond et al. 2017), with shallow areas thought to be important for calving and nursing (Koschinski 2001, Gilles et al. 2016). Therefore, with the expected increase in wind capacity, the potential for impact on harbour porpoises during wind farm construction is high. Tidal resources are also being exploited as another source of renewable energy, and with a number of tidal turbine projects now in their early stages, the risk of injury or death to marine mammals due to collision is of particular concern (Wilson et al. 2007, Malinka et al. 2018). Harbour porpoises are afforded protection under Annexes II and IV of the EU Habitats Directive, which prohibits significant disturbance, and the UK has now established extensive Special Areas of Conservation for this species (JNCC 2016).

The traditional approach to mitigation for offshore wind farm construction is to determine an exclusion zone within which animals are deemed to be at risk and then monitor the area visually and with passive acoustics to ensure that no animals are present before pile driving takes place (JNCC 2010). This can, however, be expensive and is often limited in success (especially during poor weather or at night). Therefore, producing sound to exclude animals from an area to mitigate the risk of injury is becoming more widely used (Bundesministerium für Umwelt 2014).

Most countries use noise exposure criteria recommended by Southall et al. (2019) as well as NOAA criteria (NMFS 2016, 2018) to assess the impact of man-made noise on marine mammals, though details of noise criteria set in place still vary between countries (Erbe et al. 2019, Stöber & Thomsen 2019). In addition, there are national differences in what kinds of effects are seen as acceptable. In Germany, for example, a temporary hearing threshold shift is considered an injury, whereas in the rest of the EU and in the USA, only a permanent shift is considered an injury (Bundesministerium für Umwelt 2014, Erbe et al. 2019).

A variety of ADDs are available commercially, with the majority of them operating at a range of 5 to 40 kHz and a source level of 184 dB re 1 µPa or above (Lepper et al. 2014, Findlay et al. 2018). This frequency range overlaps with the most sensitive hearing range of harbour porpoises (Kastelein et al. 2010, Götz & Janik 2013). The most commonly used devices in the aquaculture industry in Scotland are the Ace Aquatec, Terecos and Airmar ADDs (Northridge et al. 2010, Götz & Janik 2013, Findlay et al. 2018) and recently the Otaq ADD (an Airmar variant); however, it is the Lofitech ADD which has been tested most extensively for use as a mitigation device (Brandt et al. 2013a,b). This device device emits 0.5 s long pulses at 14 kHz, with weak harmonics, at a source level of 189 dB re 1 µPa and a duty cycle (DC; the fraction of time a device is producing sound) of 12% (Brandt et al. 2013a).

While these ADDs appear effective at deterring harbour porpoises (Johnston 2002, Brandt et al. 2013a), they also have the capacity to cause hearing impairment (Schaffeld et al. 2019). Theoretical calculations show that an exposure of around 12 min to the noise produced by an Airmar dB plus ll operating at its 50% DC would lead to a TTS in harbour porpoises within 345 m of the device (Götz & Janik 2013). A single exposure to an ADD signal similar to that of the Lofitech (peak frequency 14 kHz) also has the potential to induce TTS in harbour porpoises at distances of up to 5.9 km (Schaffeld et al. 2019). It is therefore necessary to consider alternatives and to develop devices that can successfully deter animals without causing unintended detrimental effects.

An alternative method to traditional deterrence devices is to deter marine mammals using sounds that elicit the autonomous reflexes associated with the flight response. Götz & Janik (2011, 2015, 2016) have utilised the acoustic startle response to develop a target-specific acoustic predator deterrence system which is able to deter pinnipeds and reduce predation on fish farms without affecting harbour porpoises. The acoustic startle response is characterised by a rapid contraction of facial and skeletal muscles (flexor muscles) which is mediated by an oligosynaptic pathway located in the lower brainstem (Koch & Schnitzler 1997). By exploiting the different hearing abilities of pinnipeds and non-target species (odontocetes are less sensitive to sounds below 5 kHz), the startle response can be elicited in seals without affecting other species (Götz & Janik 2015, 2016).

The startle reflex has also been found to be present in odontocetes (Götz et al. 2020, Elmegaard et al. 2021). With the forecasted future increase of renewable energy developments and a clear need for a deterrent device which has the potential to target both porpoises and pinnipeds in mind, we tested the effectiveness of the acoustic startle technology on harbour porpoises. By changing the peak frequency of the startle signal, this enabled us to target harbour porpoises, while ensuring that the signal would also have the potential to deter pinnipeds. The study aimed to determine how harbour porpoises react to the startle-eliciting stimuli and assess whether the device could be used as an alternative mitigation method for excluding porpoises from potential areas of harm, at a sound level and DC lower than those produced by currently available devices.

2. MATERIALS AND METHODS

2.1. Study sites

The study took place at 3 field sites (Fig. 1) on the west coast of Scotland over 3 yr (2017–2019). In 2017, our study site was located in Shuna Sound, Loch Shuna, the Sound of Luing and the body of water west of Scarba and the Grey Dogs tidal race. Tracking stations were located on the islands of Luing, Arsa and Scarba. In 2018 and 2019, 1 site was located around the Isle of Raasay, in Loch Arnish and the adjacent sound of Raasay, while the other site was located in Coalas Mòr next to the Crowlin Islands. Tracking stations were located at 2 sites on the Isle of Raasay and 2 on Eilean Mòr. Sites were chosen based on areas of predicted high density of harbour porpoises based on data from Scottish Natural Heritage.

2.2. Sound exposure device and stimuli

The sound exposure system consisted of a Lubell 9161 underwater transducer, a Cadence Z9000 power amplifier and a Tascam DR-40 audio player. The tested sound signal consisted of 0.2 s long band-limited noise signals (Fig. 2). The projected signals had a peak frequency of approximately 10.5 kHz and a −40 dB bandwidth of 15 kHz; within this, the frequencies at which power was 40 dB below the peak

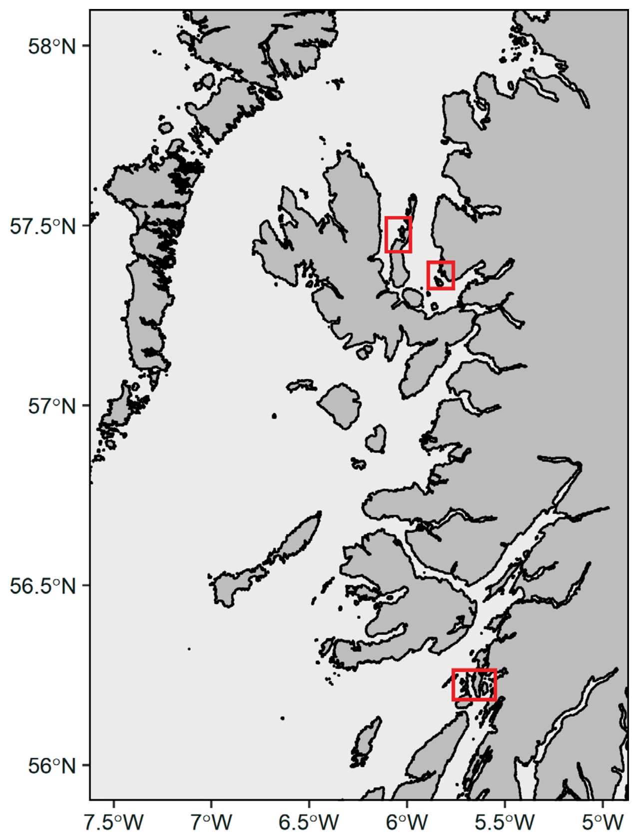

Fig. 1. West coast of Scotland with 3 field sites marked in red boxes. The 2017 field site (bottom box) was located around the islands of Shuna, Luing and Scarba in Argyll; 2018 and 2019 field sites were located around Raasay (top box) and the Crowlin Islands (middle box) near the Isle of Skye

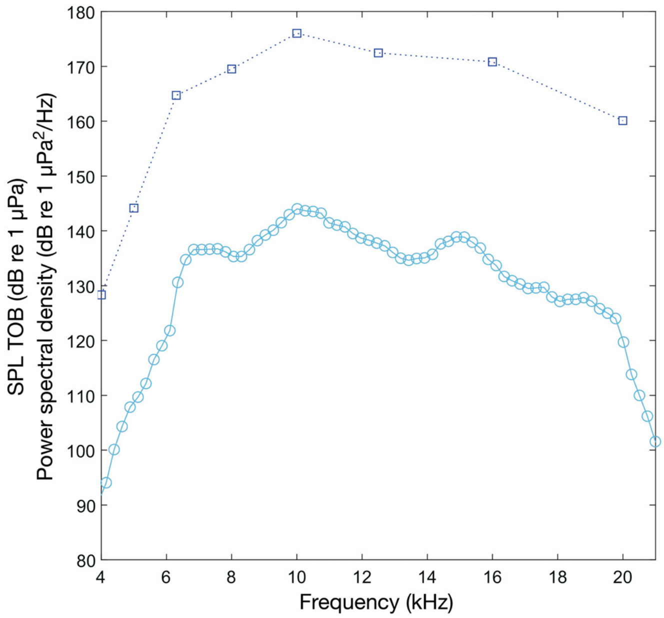

Fig. 2. Sound pressure level (SPL; squares, dotted line) in one-third octave bands (TOBs) and power spectral density (circles, continuous line) for the startle signal tested in this study

were 5.5 and 20.5 kHz (Fig. 2). The rise time of the projected signal at 2 m distance was approximately 2 to 3 ms. The signal was generated with band-pass filters from white noise (stochastic noise). The frequency band was chosen to fall within a sensitive hearing range of odontocetes. A broadband signal was chosen to optimise the probability of eliciting a startle response (Stoddart et al. 2008). In addition, the sound pressure level (SPL) in one-third octave bands (and the associated TTS risk) is lower in a broadband signal compared to a pure tone of the same broadband source level. In an exposure sequence, 27 signals were emitted within a 15 min period, resulting in an overall DC of 0.6%. Signals within a sequence were emitted at randomised intervals ranging from 9.4 to 59.4 s.

Our recording system consisted of a calibrated Reson 4013 hydrophone and either a National Instruments card or a SAIL DAQ card and a laptop computer using PAMGuard software (Gillespie et al. 2008). Data analysis was conducted in MATLAB. The sound output of the exposure system was measured in units of SPL, defined as SPL = 20 × $\log_{10}(p/p0)$, with p being the sound pressure in units of Pascal and p0 being the reference pressure (1 µPa). In our measurements, the SPL was calculated as SPL = |Hs| – gain + 20log V, with |Hs| being the absolute of the hydrophone's voltage sensitivity (in dB re 1V/µPa), gain being any gain amplification in the recording system (pre-amplifier gain in addition to the settings of the DAQ card) and V being the voltage or digital units. For determining the source level of the exposure system, the hydrophone was attached to the transducer frame with a rigid pole (to ensure consistent on-axis measurements), at a distance of 1.5 or 2 m in at least 4 to 5 m water depth, and the received level (SPL measured by the hydrophone) was measured. The source level was then back-calculated assuming spherical spreading, which, due to the recording geometry and water depth, was most likely over the first 2 m. The source level was checked at least once each field season in the absence of animals before experiments commenced using this method. The exposure system was adjusted to operate at a broadband source level (SPL) of 180 dB re 1 µPa for each individual signal. The source level (SPL) in the one-third octave band with the highest SPL for 1 signal was 176 dB re 1 µPa. The broadband sound exposure level (SEL) of a single 0.2 s signal was 173 dB re 1 µPa^2 s, while the highest SEL over a 1 s time window (SEL 1 s) in one-third octave bands was 169 dB re 1 µPa^2 s at the peak frequency. During the control treatment, the transducer was lowered into the water, but no signal was played.

2.3. Visual tracking

Visual observations were conducted from shore-based vantage points (ranging from 21.5 to 93.4 m above the sea surface) overlooking the trial locations. These vantage points provided a good overview of the study sites, allowing porpoise groups to be tracked in the area. A photogrammetric approach was employed to carry out focal follows. Observations were carried out by a maximum of 4 observers, from a maximum of 2 tracking stations, using the naked eye and 7 × 50 binoculars mounted on a custom-built frame above a Canon EOS 80D DSLR with a Sigma 500 mm lens or a Canon EOS 1300D using a Canon EF 70 to 300 mm lens. The positions and altitude of the tracking stations were measured with a Garmin GPS12 eTrex Summit on each day of the study.

A Sokkia SET5E theodolite was used to measure reference points from each observation site. The horizontal theodolite angle was set to zero using a known landmark from each site. The bearing from the theodolite to the zero landmark was calculated using the geographical position of the theodolite and the landmark. Vertical and horizontal bearings from each tracking station to each reference point were also measured. With both the location and height of the tracking station known, and the known locations of reference points captured in the videos, the geographic positions of porpoises at the sea surface were determined using a triangulation method (Leaper & Gordon 2001, Gillespie et al. 2008).

A tide height table for tidal stations near the study sites was exported from POLTIPS-3 software and uploaded into PAMGuard (Gillespie et al. 2008). This enabled the inclusion of tide height in the calculation of animal positions.

2.4. Experimental protocol

A trial consisted of the initial tracking of 1 group of porpoises followed by a 15 min sound exposure or control observation period and the subsequent tracking of the same animals for another 90 min or until they were out of sight. Before the start of each trial, all watches, cameras and GPS times were synchronised to ensure all land-based tracking and boat-based teams were working on the same time frame. All teams were in radio contact throughout each trial, allowing for the coordination of locating and tracking porpoise groups and the sharing of information important to the trial. During trials, observers scanned for harbour porpoises using both the naked eye and binoculars. If an observer detected a group of animals, the camera was switched on, and the video was used to record consecutive surface positions as the observer tracked the animals using the binoculars for a minimum of 15 min. The land-based spotting team informed the other teams of the time that the tracking period began and the location of the focal group in relation to the boat. Every time an animal surfaced, the observer provided an acoustic cue on the video to aid video processing. If animals did not resurface for 15 min, the video was turned off, and scanning for new animals commenced. If a new group was located, a new tracking period was started. When porpoises were first sighted, the boat-based team remained at the edge of the study area, scanning for porpoises with the naked eye and awaiting directions from a land-based team. If multiple porpoise groups were seen in the area and 2 tracking teams were in place, the 2 teams coordinated to track different focal groups. If only 1 focal group was present, then both stations tracked the same group.

After the initial 15 min of tracking, the land-based observers directed the boat to approach the focal group. The mean distance between the boat and the last recorded surface position of a porpoise group as measured by photogrammetry before the start of the treatment was 124 m (range 30–520 m). For controls, the mean distance was 90 m (range 30–196 m); for sound exposures, it was 152 m (range 26–520 m). Once the boat had finished the approach to the focal group, the engine was switched off, the transducer was lowered into the water and the treatment period (sound exposure or control) of 15 min began. During this time, the land-based trackers were blind to the treatment type and were continuously tracking and recording the animals.

After the 15 min treatment period had finished, a further 90 min of tracking was carried out. If animals were lost during this time, tracking stopped, and the land-based observers scanned the area for different animals. If new animals were detected, tracking began again, ensuring all surface positions were recorded. When 2 trials were completed within a day, there was a minimum interval of 60 min between the end of one trial and the start of another. Thus, there was always a minimum of 2.5 h between treatment periods. Environmental conditions (sea state, wind direction) were monitored throughout and recorded whenever they changed. Sea state was estimated following the Beaufort wind scale.

2.5. Video analysis

Videos were analysed using the video range module in PAMGuard. The video footage was played until an individual porpoise or group of porpoises was visible at the water surface (this was made easier by the acoustic cue given by the observer each time an animal surfaced). Using a mouse click for each minimum of 2, known reference points were selected along with the porpoise location at the surface of the water. The location of the porpoise at the sea surface was then determined by PAMGuard using a trigonometric relationship based on the height and position of the tracking station, the location of the reference points and tidal height (Gillespie et al. 2008). Boat location was determined in each trial using the same method. These locations were then used to measure distance from the animal to the exposure boat using the Vincenty formula (Vincenty 1975).

2.6. Data analysis

2.6.1. General approach

All statistical analysis was conducted in R 3.6.1 (R Core Team 2019). The purpose of the surfacing count analysis was to determine the number of surfacings within 500 m of the source boat in 15 min time bins for each treatment, while the aim of the mean distance analysis was to determine the distance of porpoises to the source boat averaged across 15 min time bins for sound exposure and control trials. Surfacing count data and mean distance to source data were analysed with generalised linear mixed models (GLMMs) (logarithmic link function) using the glmmTMB package (Brooks et al. 2017). The third approach was to model porpoise group distance to the exposure boat for control and sound exposure trials as a function of time. This was done using a time series approach within a generalised additive mixed model (GAMM) framework using the mgcv package (Wood 2017). A range of error distributions were tested using the generalised extensions of the linear and additive models, accommodating different data distributions and allowing for zero inflation to be modelled. Random effects (factors which may cause variation in the data but are not of primary interest in this study) were also considered.

To determine the best fit model, a 3-step model selection process was performed using Akaike's information criterion (AIC), in which the models with the lowest AIC were selected (Zuur et al. 2009). In an initial step, a fully populated model was tested to determine both the optimal error distribution and whether the zero-inflation argument should be included in the model. In a 2nd step, the optimal combination of fixed effects was determined. Candidate predictor variables were chosen based on theoretical considerations and study design and are described below for each model. In the final step, the previously determined optimal combination of random effects was carried forward, and the optimal combination of fixed effects was determined. Crossed random effects were also considered to address correlation in the model.

To assess for normality, quantile-quantile plots and histograms of the residuals were inspected. Homogeneity was assessed by plotting the residuals against the fitted values, and model fit was assessed by comparing the fitted values with the observed values. Autocorrelation in the model was assessed by inspecting autocorrelation function (ACF) plots. Further model diagnostics were carried out using the DHARMa package (Hartig 2020). Pairwise comparisons were implemented using the emmeans package (Lenth 2020). Exponentiated model coefficients (e^{β}) are presented on the scale of the response variable to allow an intuitive interpretation of effect size. CIs (95%) and exponentiated coefficients were obtained from the confint function.

2.6.2. Mean distance in 15 min time bins (GLMM)

The response variable for the mean distance data was mean distance to source in 15 min time bins. Treatment by time was included as the fixed effect variable, and a Gamma error distribution was found to be the best fit model. The random effects assessed were trial, sea state and site. No random effects were retained in the model, but time by trial was included as a crossed random effect to address autocorrelation. Predicted values for distance of porpoise groups to the boat and CIs were obtained from emmeans (Lenth 2020).

2.6.3. Surfacing count data (GLMM) within 500 m

The number of surfacings within 500 m represented the response variable in the surfacing count model. Gamma, negative binomial 1 and negative binomial 2 error distributions were tested, and negative binomial 1 was retained. The fixed effect variable was treatment by time; 30 min time bins were used, with the exception of the 15 min for the exposure period. As there were no sightings within 500 m in the 15 min post sound exposure, the data were pooled with the consecutive 15 min time bins to prevent model convergence problems (zero data in 1 time bin). Despite this, data analysis did not indicate that the inclusion of an offset term was warranted. The single random effects assessed were trial, sea state, number of tracking stations and site. Site was retained in the model with the lowest AIC, and time by trial was included as a crossed random effect.

2.6.4. Time and distance as continuous variables (GAMM)

To assess the effect of treatment on the movement of the porpoises, the distances of sightings to the position where the source boat was at the start of the treatment were analysed throughout the trials with GAMMs using the bam function within the mgcv package (Wood 2017). Due to the non-linear and non-monotonous relationship between time and distance, and a skewed distribution in the data, an additive model with a generalised extension was chosen. To allow for the inclusion of random effects in the model, a GAMM was used (Wood 2017).

The primary purpose of the distance to source analysis was to estimate the behavioural response of porpoises to the sound; therefore, treatment (sound exposure or control) by time (included as a continuous predictor) was included as a fixed effects factor in the model. The continuous response variable was distance to the position of the source boat at the start of the treatment. Due to a lack of independence associated with temporal data, temporal autocorrelation had to be addressed in the model. Initially, a simple model (with only fixed effects included or with an autocorrelation structure) was fitted, but inspection of ACF plots showed strong temporal autocorrelation. Based on this inspection, an autoregressive correlation structure (AR1 error model) was included in the GAMM to reduce the effects of autocorrelation. This structure considers that correlations will be highest between immediately adjacent points in the time series and then decrease with increasing distance between data points in the time series. The bam function (in the mgcv package) also allows the starting points for each group within the time series to be marked.

The final model used a log link function with a Gamma error distribution. Random effects factors that were assessed in the model included sea state, site, wind direction, number of tracking stations and trial. Only trial was retained as a random effect in the final model. Knots were determined using generalised cross-validation within the mgcv package. The predicted values on the scale of the response variable and CIs were determined using the predict.gam function within the mgcv package.

2.6.5. Assessing TTS

We assessed the likelihood of the startle signal and conventional ADDs causing TTS in harbour porpoises in a typical mitigation context using noise exposure guidelines by Southall et al. (2019). ADDs have typically been modelled as non-impulsive sound sources (Lepper et al. 2014). While Southall et al. (2019) did not provide a definition for impulsive noise, associated guidelines by NMFS (2018, p. 39) state '…the terms non-impulsive or steady-state do not necessarily imply long duration signals, only that the acoustic signal has sufficient duration to… reach a steady-state condition'. The signal tested in the present study (and used in GenusWave's targeted acoustic startle technology [TAST] system) reaches a steady state condition (for approximately 195 ms), while signals in conventional ADDs are often shorter (<10 ms, see Lepper et al. 2014). In addition, a short rise time has sometimes been suggested as being indicative of impulsive sounds. Lepper et al. (2014) showed rise times of approximately 0.5 ms for the Ace Aquatec device and less than 0.1 ms for the Airmar system (which is emulated by Otaq) compared to 2–3 ms in the tested signal in this study. However, what matters most for TTS is to what extent a sound exposure protocol and signal carry a high or low risk of causing TTS. Kastelein et al. (2014) showed that at the same SEL, the risk posed by a sound exposure protocol with long inter-pulse intervals (as the one tested here) is almost zero, while a short inter-pulse interval device such as used in other ADDs carries a high risk (particularly at pulse intervals of <1 s). In conclusion, regarding TTS risk, the startle signal and sound exposure protocol tested in our study carries a lower TTS risk than conventional ADDs and is therefore being modelled as non-impulsive. In our assessment, we calculated the exposure function using Eq. (3) from Southall et al. (2019), which determines the weighted TTS onset threshold as a function of frequency for a number of functional marine mammal hearing groups:

$$E(f) = K - 10\log_{10}\left\{\frac{(f / f_1)^{2a}}{[1+(f / f_1)^2]^a[1+(f / f_2)^2]^b}\right\}$$

where $E(f)$ is the exposure function amplitude (in dB) at frequency f (in kHz), K defines the vertical position of the function and a and b determine the shape of the function (for full details, see Southall et al. 2019). As a first step, the SEL in one-third octave bands was calculated for a 1 s long time window (SEL-1 s) during an emission for each device. Data on the acoustic properties of the Ace Aquatec and the Airmar dB Plus II were taken from Lepper et al. (2014), in units of SEL; data for the Lofitech device were taken from Brandt et al. (2013a) and for the Fauna Guard Porpoise Module (FG-PM) from Kastelein et al. (2017). In cases where an SPL was stated in the literature, the SEL-1 s was calculated by adding $10 \times \log_{10}$ (signal duration) if the stated duration was less than 1 s or by using the SPL if the signal was continuous over a 1 s time window (in the latter case, SEL and SPL are numerically the same).

Consecutively, the cumulative SEL was calculated for the respective exposure time (single emission, 15 and 30 min) based on the DC of the device and the SEL-1 s. The DC is the percent of time the device produces an emission. This was achieved by adding the term $10 \times \log_{10}$ (exposure time (s) × DC) to the 1 s SEL. The onset TTS thresholds (SEL) were then subtracted from the cumulative SEL values in each one-third octave band, and the band with the maximum difference was selected. This value constitutes the maximum transmission loss (maxTL) required before the received level (SEL) drops below the onset TTS threshold (exposure function). To estimate the corresponding impact zone, we created a vector of distance values (at 0.01 m increments) and calculated both geometrical and absorption losses for each distance. Geometrical losses were assumed to be 18 × $\log_{10}$ (*dist*), which has been found to be a good approximation for long distances in coastal waters similar to the sites in this study (see Götz & Janik 2015 for a sound propagation model using a similar signal). Absorption was calculated as 0.758 dB km^{-1} at 10 kHz, 1.55 dB km^{-1} at 14.9 kHz and 23.85 dB km^{-1} at 80 kHz (Fisher & Simmons 1977). The impact zone was determined by selecting the distance value that corresponded to the maxTL value. More detail is provided in the Supplement at www.int-res.com/articles/suppl/m672p223supp.pdf.

2.6.6. Swim speed

Swim speed during trials was calculated using the difference in porpoise distance to sound source at the start of the trial and at the end of the trial (or the last distance recorded before porpoises were lost from view) divided by the time elapsed. This approach was chosen as we were interested in how quickly porpoises moved away from a simulated area of potential harm.

2.7. Sample size

Twenty-four trials were conducted over a total of 22 d in September 2017, August to September 2018 and July 2019, with 5110 (817 during exposure) surfacing events recorded. Of these, 13 were sound exposure trials, and 11 were no-sound control trials. To assess the effect of sound exposure on the animals, only trials with sightings after the exposure started were included in the distance to exposure source and mean distance analyses. In 3 of the exposure trials, porpoises were lost from sight immediately after sound exposure began. These trials were excluded from the distance analyses but retained in the count data analysis. In the remaining 10 sound exposure trials and 11 control trials, porpoises were observed multiple times (≥6) following the start of the treatment, allowing for a full evaluation of their responses.

3. RESULTS

3.1. Porpoise tracks

In 10 of the sound exposure trials, focal porpoise groups moved clearly away from the transducer, increasing their distance until lost from view. Porpoises remained close to each other and moved away as a cohesive group. In the remaining 3 sound exposure trials, porpoises were lost from sight immediately after the onset of exposure for the remainder of the trial. In the 11 control trials, the porpoises either stayed in the study area for the whole trial or continued moving in the same direction of travel exhibited before the start of the treatment (Table 1). Swimming speed was estimated to be on average 2.2 m s^{-1} (range: 1.2 to 2.8) during sound exposure and 0.46 m s^{-1} (range: 0.1 to 1.6) during controls. Porpoises were observed returning to the study area in 7 of the 13 exposure trials at an average time of 31 min after the end of the exposure period (46 min after the start of the exposure period).

The number of animals in the tracked groups during sound exposures ranged from 2 to 8 individuals (mean 3.8). Porpoises responded to exposure by performing an initial prolonged dive (mean time 2 min 28 s) and travelled an average of 333 m (range: 188–694 m) before the first surfacing event post exposure onset. Although this first surfacing event may have been missed in some cases, this prolonged dive was consistent throughout all trials. Once the porpoises were at this distance, they then surfaced at regular intervals while travelling away from the sound source. The porpoises generally travelled away from the exposure as a group, sometimes slightly spreading out as they initially travelled away but then coming together and travelling as 1 cohesive group. When multiple groups were present, these would often follow a similar track out of the area to groups which preceded them.

Eight trials are shown as examples in Fig. 3. In the 4 control trials, the focal porpoise groups remained in the study area for the duration of the trial (Fig. 3). In the first example (Fig. 3a), the focal group was travelling southwest before the start of the treatment. They were at a distance of 60 m at the start of the treatment, and the group continued moving on an unaltered course during the treatment period. The group then moved back and forth in the same area for the remainder of the trial. They remained within 865 m of the boat, with the closest observed approach (COA) of 97.66 m during the post-treatment period. In the second example (Fig. 3c), the porpoises remained within 511 m of the boat after the start of the treatment, with a COA of 11 m. There was no obvious change in behaviour or movement during or after the onset of the treatment period. In the third control example (Fig. 3e), the focal group stayed within 398 m of the boat during the treatment period

Table 1. Details of the 24 trials that were carried out during the study. (–) No data available (either because a group was lost or because a group did not leave the initial site)

Trial no.	No. of observation stations	Date	Site	Distance to source before sound exposure (m)	First sighting after start of exposure (m)	Distance at end of exposure period (m)	Treatment	Avoidance	Time of return after end of treatment (min)
1	1	7 Sep 2017	Argyll	26	–	–	Sound exposure	Group lost	No return
2	1	8 Sep 2017	Argyll	44	49	1006	Control	No	–
3	1	12 Sep 2017	Argyll	276	282	1372	Sound exposure	Yes	No return
4	1	13 Sep 2017	Argyll	133	–	–	Sound exposure	Group lost	No return
5	1	16 Sep 2017	Argyll	51	138	110	Control	No	–
6	1	17 Sep 2017	Argyll	60	115	606	Control	No (animals continued travelling on same path)	–
7	1	17 Sep 2017	Argyll	113	412	2410	Sound exposure	Yes	29.5
8	1	18 Sep 2017	Argyll	27	262	738[a]	Sound exposure	Yes	No return
9	1	18 Sep 2017	Argyll	90	133	601	Control	No (animals continued travelling on same path)	–
10	1	27 Aug 2018	Raasay	171	493	1249	Sound exposure	Yes	No return
11	2	30 Aug 2018	Raasay	31	48	218	Control	No	–
12	2	30 Aug 2018	Raasay	53	747	1386	Sound exposure	Yes	22.9
13	2	31 Aug 2018	Raasay	145	171	244	Control	No	–
14	2	1 Sep 2018	Raasay	38	298	1414	Sound exposure	Yes	52.2
15	2	3 Sep 2018	Raasay	54	47	427	Control	No	–
16	2	3 Sep 2018	Raasay	64	253	1806	Sound exposure	Yes	23.4
17	2	6 Sep 2018	Crowlin Islands	95	99	252	Control	No	–
18	2	7 Sep 2018	Crowlin Islands	207	147	1495	Sound exposure	Yes	48.0
19	1	8 Sep 2018	Crowlin Islands	167	165	2035	Sound exposure	Yes	20.0
20	2	14 Jul 2019	Raasay	187	–	–	Sound exposure	Group lost	No return
21	2	15 Jul 2019	Raasay	197	195	281	Control	No	–
22	2	15 Jul 2019	Raasay	520	905	1270	Sound exposure	Yes	21.2
23	2	19 Jul 2019	Raasay	127	270	70	Control	No	–
24	2	24 Jul 2019	Crowlin Islands	97	86	253	Control	No	–

[a]Last position recorded before the end of the exposure period

and within 836 m during the whole trial. The COA for the trial was 15 m. In the last hour of the trial, more porpoises moved into the area from the south. In the final control example (Fig. 3g), the focal group stayed within Loch Arnish and within 661 m of the boat for the whole trial. The COA was 20 m.

In the 4 examples of sound exposure trials (Fig. 3b,d,f,h), the focal porpoise groups clearly moved away from the transducer during the exposure treatment period, moving away from the boat in a direct manner, increasing their distance until lost from view. In the first example (Fig. 3b), the focal group moved southeast after exposure onset, headed for the opposite (eastern) shoreline in Loch Shuna and left the area to the south (last logged position 2951 m from the source boat). The animals were tracked for the entire 15 min exposure period and during part of the consecutive post-exposure period until lost from view. Another group of porpoises (a mother and calf pair) then appeared during the final hour of the trial, 29.4 min after exposure stopped. In the second example (Fig. 3d), the focal group moved away from the sound exposure speaker and left Loch Arnish (last logged position 1094 m from the source boat). No porpoises were present during the remainder of the trial. The focal group in the third example (Fig. 3f) moved south, away from the sound exposure boat (last logged position 3209 m from the boat) and out of the study area. Another group of porpoises then came into the area 13.2 min after the sound exposure had ended. In the final example (Fig. 3h), the porpoises moved away to the northwest, headed out of the loch and then

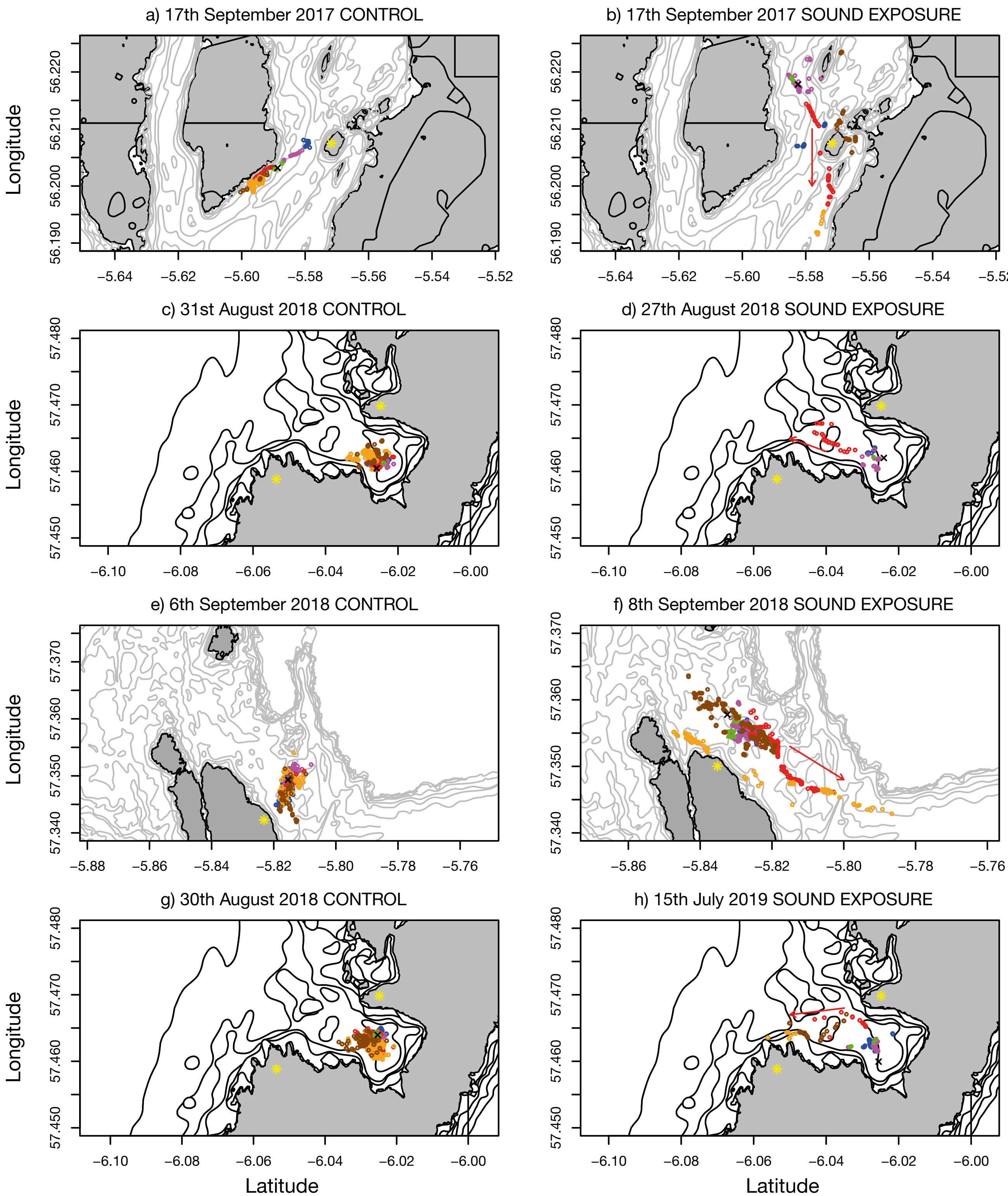

Fig. 3. Harbour porpoise positions during 8 trials (4 control and 4 playback). (a,b) Trials located in Loch Shuna, with a tracking station (✳) on Eilean Arsa. (c,d,g,h) Trials based in Loch Arnish, with tracking stations located on the Isle of Raasay. (e,f) Trials located in Coalas Mor, with tracking stations located on Eilean Mòr of the Crowlin Islands. Red arrow shows direction of travel during exposure periods. Blue dots: porpoise positions in the first 15 min of the trial (Time −30 to −15); magenta dots: porpoise positions in the 15 minutes before the onset of the treatment (Time −15 to 0); green dots: the last 5 porpoise positions before the onset of the treatment; red dots: porpoise positions during the exposure/control treatment period (Time 0 to 15); orange dots: porpoise positions for the 30 min post treatment (Time 15 to 45); brown dots: porpoise positions during the final hour of the trial (Time 45 to 105). Black cross: the boat at the start of the treatment

moved south down the Sound of Raasay (last logged position 1270 m from the source boat). Porpoises were seen again in the final hour of the trial, 21.2 min after the exposure stopped.

3.2. Surfacing count data (GLMM) within 500 m

A significant reduction in the number of harbour porpoise surfacings within 500 m of the boat ($p < 0.001$) during the sound exposure trials was identified by the model. During the pre-treatment 30 min (−30 to 0 min), the number of harbour porpoise surfacings was similar across sound exposure and control trials ($e^{\beta} = 0.779$, CI: 0.4619/1.313, $p = 0.3443$), where e^{β} is the exponentiated model coefficient (Fig. 4). The model coefficient during the treatment period (0–15 min) of the playback exposure trials indicated an 82.6% reduction in the number of surfacings ($e^{\beta} = 0.174$, CI: 0.069/0.436, $p = 0.0003$) during sound exposure (0–15 min). In the 30 min after the exposure (15–45 min), the model estimated a 99.27% reduction in the number of surfacings in the exposure trials (estimate = 0.00732, CI: 0.001/0.069, $p < 0.0001$). In the final hour (45–75 and 75–105 min) of the exposure trials, as porpoises returned to the study area, porpoise numbers were not significantly different from the control (47–75 min: $e^{\beta} = 0.2592$, CI: 0.0579/1.159, $p = 0.0767$; 75–105 min: $e^{\beta} = 0.1717$, CI: 0.0228/1.296, $p = 0.0869$); however, porpoise surfacings still remained somewhat lower in exposure trials than in control trials.

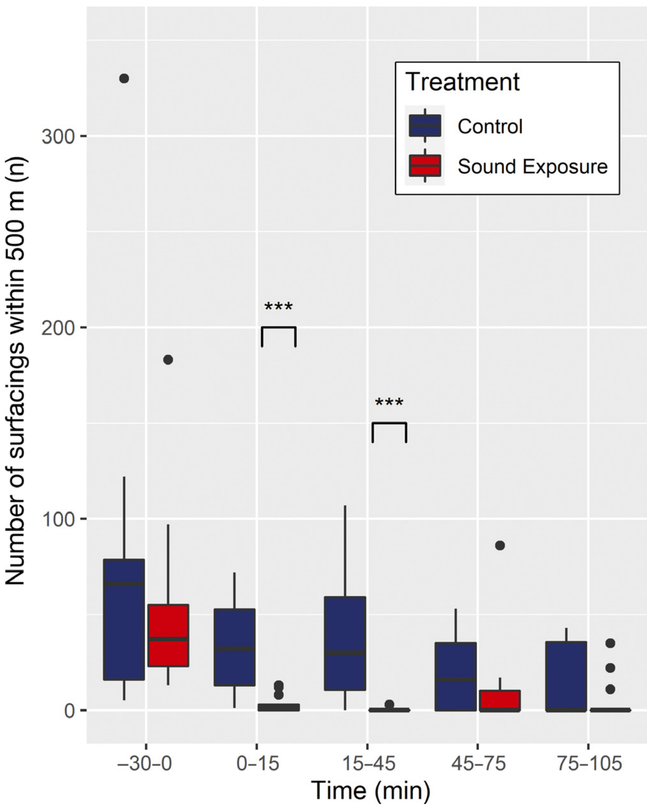

Fig. 4. Mean number of porpoise surfacings within 500 m of the control and sound exposure source. All periods were 30 min long, with the exception of the treatment period, which was 15 min (Time 0–15). Boxes show medians and interquartile ranges (IQRs). Lower whisker = smallest observation ≥25% quartile − 1.5 × IQR, and upper whisker = largest observation ≤75% quartile + 1.5 × IQR. Outliers are represented by dots. Significance values are derived from model results. ***$p < 0.001$

3.3. Mean distance in 15 min time bins (GLMM)

Overall, a significant increase in mean distance (within the specified time bins) from the speaker was also shown between the 2 treatments ($e^{\beta} = 1.725$, $p = 0.037$) (Fig. 5). In the first 30 min of trials (baseline tracking and boat approach), there was no significant difference in mean distance between the sound exposure and control trials (first 15 min: $e^{\beta} = 1.117$, CI: 0.612/2.04, $p = 0.717$; second 15 min: $e^{\beta} = 1.381$, CI: 0.767/2.49, $p = 0.279$). During the sound exposure treatment period, animals significantly increased their mean distance from the boat (994 m, CI: 656/1507), with animals moving away 4 times further than during the control (247 m, CI: 165/368), ($e^{\beta} = 4.029$, CI: 2.262/7.18, $p < 0.0001$). In the 15 min following sound exposure, the model indicated that animals were 4.2 times further away than during the control ($e^{\beta} = 4.235$, CI:2.43/8.0, $p < 0.0001$), with a predicted mean distance of 389 m (CI: 264/575) during controls and 1650 m (CI: 998/2727) during exposure trials.

During the fourth 15 min time period (15–30 min post exposure), predicted values from the model showed animals 2 times further away ($e^{\beta} = 2.05$, CI: 1.098/3.82, $p = 0.025$) at 918 m (CI: 568/1484) in sound exposure trials and 448 m (CI: 301/667) in controls. From 45 to 60 min after the start of the exposure, porpoise distance had decreased, and although porpoises were still further away than during a control, this was not significant ($e^{\beta} = 1.37$, CI: 0.728/2.59, $p = 0.3245$). The predicted mean distances from the model were similar (for 60 and 90 min post treatment, respectively) between exposure (504 and 624 m) and control (508 and 616 m) trials during 60 to 90 min after the onset of the treatment period (60–75 min: $e^{\beta} = 0.992$, CI: 0.53/1.86, $p = 0.98$; 75–90 min: $e^{\beta} = 1.013$, CI: 0.512/2.01, $p = 0.9698$). Although the final 15 min of the trial differed slightly between the 2

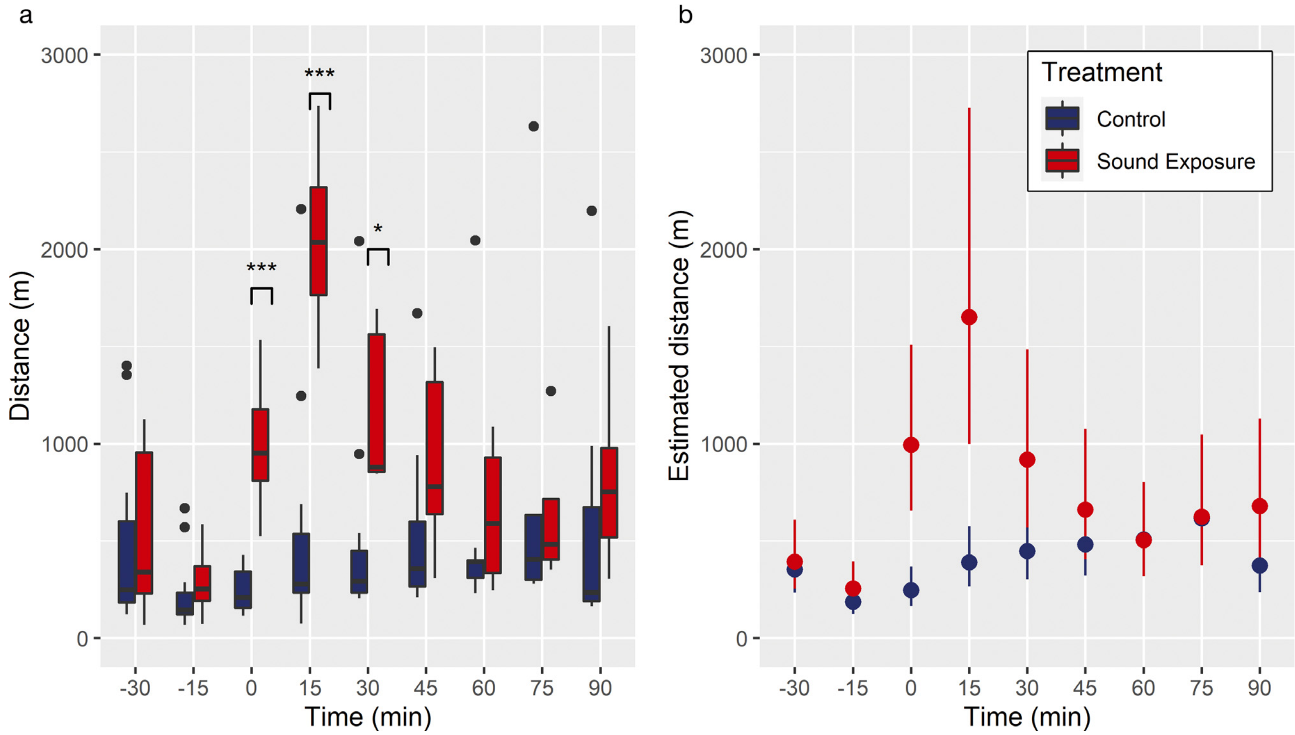

Fig. 5. Box plots showing (a) mean distance per trial (based on the raw data) and (b) predicted mean distance and 95% CIs (derived from generalised linear mixed models) to sound source during sound exposure (red) and control (blue) trials. All periods were 15 min long, and time marks the beginning of each 15 min period. Time 0 (0–15 min) is the treatment period. Box plots as in Fig. 4. Significance values are derived from model results. $^*p < 0.05$, $^{***}p < 0.001$

treatments, this effect was not significant ($e^{\beta} = 1.819$, CI: 0.92/3.6, $p = 0.0847$).

3.4. Porpoise distance to boat as continuous function of time (GAMM)

The smoothers for the treatment periods and the random effect trial were all significant at the 5% level (6.708, $p < 0.001$; 8.469, $p < 0.001$; 16.772, $p < 0.001$). A pseudo R-squared of 0.754 (deviance = 67.8%) indicated that the predictor variable explained the variance of the response variable reasonably well.

At the beginning of the trial, the predicted distance to source boat was similar for sound exposure trials (362.4 m, CI: 176.1/548.8) and control trials (322.4 m, CI: 166.3/478.5). The predicted values from the GAMM indicated that prior to the start of the treatment period, animals were slightly further away from the boat during sound exposure trials than during the control trials, but there was significant variation and CIs overlapped (Fig. 6). The average distance between the boat and porpoises then decreased before the start of the treatment period as the boat approached the focal group. Immediately after the start of the sound exposure treatment, there was a sharp increase in distance as the focal porpoise groups moved away from the boat, with a maximum average distance of 2.07 km at 15 min after the exposure started. At the end of the exposure period, the CI extended from 1.11 to 3.03 km (Fig. 6). The raw data and upper bound of the CI both showed that in 4 of the sound exposure trials, animals continued moving away from the sound source after the exposure for over 2.5 km, 500 m more than the predicted values suggested, with a maximum distance of 3.21 km recorded in one trial.

The CIs of both treatments parted at the onset of the treatment period. During the control treatment period, there was only a slight and variable increase in distance, and predicted values showed that porpoises stayed within 341 m of the boat (an increase from 195 m at the start of the treatment). After the treatment period had ended, the predicted distance in sound exposure trials began to decrease again as porpoises returned or new groups gradually moved into the area. CIs of the exposure and control results began to overlap again at approximately 24 min after the onset of the treatment (Fig. 6). Distance in exposure trials continued to decrease until 1.2 h into the trial as CIs crossed. The predicted distances for exposure trials returned to levels of control trials at just

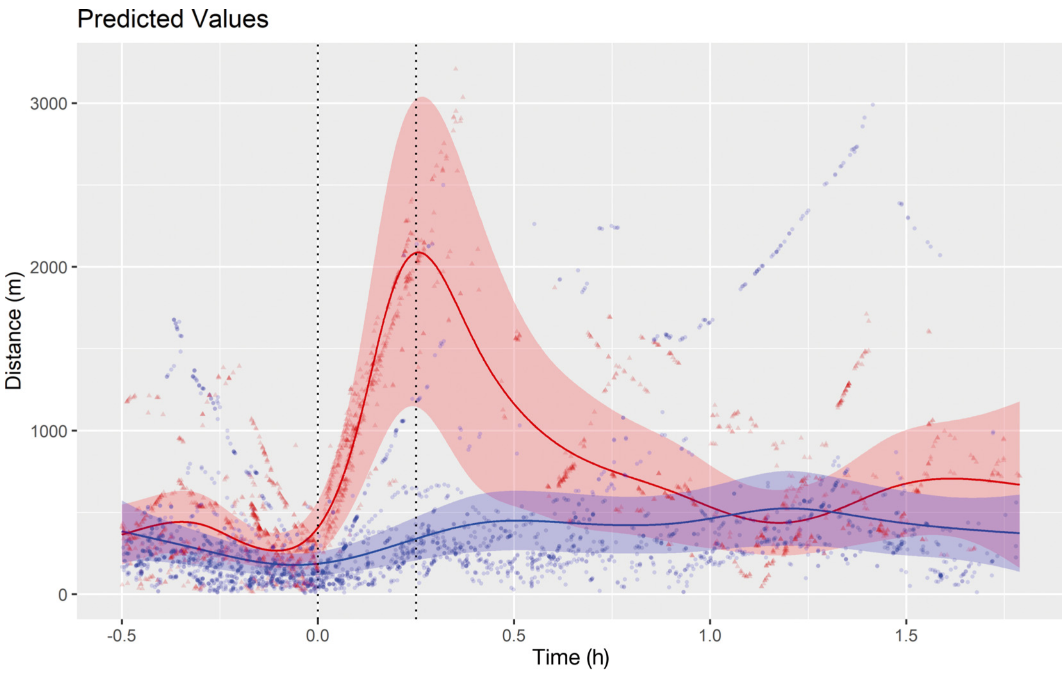

Fig. 6. Predicted distances to boat (solid lines) of porpoises with 95% CIs for control (blue) and sound exposure (red) periods obtained from generalised additive mixed models. Real data have also been fitted to the graph, with control trials represented by blue dots and sound exposure trials represented by red dots. Start of the treatment is at Time 0.0 (first vertical dotted line), and the end is at Time 0.25 (second vertical dotted line)

over 1 h after the start of the treatment period to approximately 488 m. Predicted distances during exposures then increased slightly before a final slight decrease, with distances at the end of the trial predicted at 666 m (CI: 150/1182). The predicted distances during control trials were at their highest at 1.2 h at approximately 528 m (CI: 294/761) before a final decrease to 376 m (CI: 134/617) at the end of the trial. CIs for both remained overlapping until the end of the trials.

3.5. Assessing TTS

The risk of TTS was assessed for 3 different exposure scenarios: (1) a single emission from the deterrent device, (2) 15 min of exposure and (3) 30 min of exposure. The corresponding TTS impact zones are shown in Table 2. When applying the protocol tested in this study, exposure to a single emission (i.e. one 0.2 s signal) would only cause TTS at less than 4 m. TTS onset would occur at 9 m during 15 min exposure to the signal sequence, and at 13 m if a sequence lasted for 30 min. In comparison, exposure to a single emission from the Ace Aquatec, Airmar, Lofitech and FG-PM could result in TTS at distances of 31, 27, 48 and

Table 2. Temporary threshold shift (TTS) risk for different acoustic deterrent devices (ADDs) and our method. Cumulative sound exposure level (SEL) is shown for the one-third octave band that exceeds the weighted onset set TTS threshold (exposure function) the most (1st column). The right column shows the impact zone within which the onset of TTS is predicted to occur if a harbour porpoise is exposed to a single emission, a 15 min or a 30 min time period. ADD source characteristics were taken from this study, Lepper et al. 2014 (Ace Aquatec and Airmar dB Plus II), Brandt et al. 2013a (Lofitech) and Kastelein et al. 2017 (FG-PM). FG-PM: Fauna Guard Porpoise Module

Device	Cumulative SEL (dB re 1 µPa^2 s)	TTS impact zone
This study	Single emission: 169 15 min: 176 30 min: 179	Single emission: 3.6 m 15 min: 9.1 m 30 min: 13.4 m
Ace Aquatec (Silent Scrammer)	Single emission: 186 15 min: 199 30 min: 202	Single emission: 31.4 m 15 min: 154.6 m 30 min: 225.7 m
Airmar dB Plus II	Single emission: 185 15 min: 208 30 min: 211	Single emission: 27.0 m 15 min: 489.2 m 30 min: 704.2 m
Lofitech	Single emission: 186 15 min: 207 30 min: 210	Single emission: 48.4 m 15 min: 586.1 m 30 min: 822.0 m
FG-PM	Single emission: 185 15 min: 200 30 min: 203	Single: 40.6 m 15 min: 182.32 m 30 min: 230.99 m

41 m, respectively. TTS onset during 15 and 30 min exposure would occur at 155 and 226 m in response to the Ace Aquatec, 489 and 704 m in response to the Airmar, 586 and 822 m in response to the Lofitech and 182 and 231 m in response to the FG-PM.

4. DISCUSSION

4.1. Movement responses

In this study, we demonstrated that harbour porpoises react with avoidance to startle-eliciting stimuli, moving in a directed manner away from the sound source to distances of up to 3.21 km (mean 1.78 km). All porpoise sightings within 500 m of the sound source decreased significantly during sound exposure, with no porpoises sighted within 1000 m, 15 min after the sound exposure started. Although we cannot rule out the possibility of porpoises being missed on occasion, this result indicates that porpoises were generally excluded from an area of at least 1 km within 15 min.

The mean distance to the sound source at the start of the exposure trials (152 m) was higher than that of the control periods (90 m). Despite porpoises being further away during exposure trials, an extreme and significant avoidance reaction was exhibited, whereas no avoidance was seen during control trials. This indicates clearly that it was the sound stimuli that deterred the animals rather than the presence and approach of the boat. A smaller distance to the boat at the start of the control trials may have accounted for the slight increase in distance to the boat seen during control treatment periods, but this was not significant. Porpoises are highly mobile animals and have been shown to react to vessels (Oakley et al. 2017) and vessel noise (Dyndo et al. 2015), so it is expected that they might move away following a boat approach. This increase in distance was small; in the 15 min preceding the start of the treatment, porpoises were at an average distance of 192 m from the vessel, and during the control period they were at an average distance of 247 m from it, just an average of 55 m further. Porpoises remained within an average of 444 m during the entire post-treatment period. In 2 control trials (Table 1, trials 6 and 9), the porpoises appeared to increase their distance from the boat during the control period. In both cases, the boat was positioned in the line of a travelling group of porpoises; they showed no change in behaviour after the start of the control and continued travelling in the same direction, passing and then moving away from the boat.

The results from control trials stand in stark contrast to the sound exposure trials, when a clear avoidance reaction was exhibited, with an increase in the average distance during the exposure period from 361 m pre-exposure to 1102 m during and 961 m after the start of the sound for the entire trial. Mean distance at the start of the exposure treatment period was 152 m. This corresponds to a received SPL of approximately 141 dB re 1 µPa. The minimum distance at the start of the exposure was 26 m, which corresponds to a received level of 155 dB re 1 µPa, and the maximum was 520 m, which would result in a received level of 131 dB re 1 µPa. Even at that distance, porpoises still reacted with avoidance to the signal.

With the exception of 3 sound exposure trials in which we lost the porpoises immediately, the animals could be tracked moving away from the exposure location until they reached a distance at which they were no longer detectable by the tracking stations. Mean distance when porpoises were lost from sight across those exposure trials was 1.78 km, with a maximum of 3.21 km in 1 trial and a minimum of 738 m in another (Table 1). In the latter, these porpoises were lost from view 8 min into the exposure, and no porpoises were subsequently seen, suggesting that the animals continued moving away from the sound source and left the area altogether.

In the UK, it is recommended that there should be no marine mammals within 500 m of a construction site before the start of pile driving (JNCC 2010). Our results showed that using our method, porpoises travelled to distances triple that required in only 15 min, showing a significant exclusion effect. Recent work has also suggested that porpoises must move to at least 2 km to avoid TTS from pile-driving activities (Kastelein et al. 2016, Schaffeld et al. 2020). Our results indicate that the presented method can provide such deterrence. Harbour porpoises were deterred to a mean distance of 1.78 km (GLMM, Fig. 5b) and a predicted distance of 2.07 km in the GAMM (Fig. 6). These values correspond to the distance at which porpoises were lost from view, not the maximum deterrence distance, and Fig. 6 shows that porpoises moved away further in some trials when they could be tracked to greater distances. The complex coastlines of the study sites also meant that porpoises were, in some cases, able to disappear from view behind headlands or neighbouring islands. It is likely, as exhibited by the maximum deterrence distance of 3.21 km recorded in this study and the upper CI bounds for the GAMM model, that porpoises continued moving away from the sound source to distances of more than 2 km.

The results of the mean distance GLMM, which modelled distance of porpoises to the boat averaged across 15 min time bins (Fig. 5), and the GAMM, which modelled distance to the exposure boat as a function of time (Fig. 6), showed slightly different results regarding the predicted maximum distances that the porpoises travelled after the onset of the sound. The mean distance GLMM indicated that the predicted mean distance from the sound source that porpoises travel is 1650 m, which they reach between 15 and 30 min after the onset of the sound, whereas the GAMM predicted that porpoise distance to sound source peaks at 2040 m at the end of the exposure period (15 min after the onset of the sound). These differences are likely because time and distance were treated as continuous variables in the GAMM, whereas the GLMM used mean distance in 15 min time bins. The average time after the start of sound exposure that harbour porpoises disappeared from sight was 12.8 min, though some porpoises were tracked for up to 22 min after the sound exposure started. Porpoises moved out of sight during the sound exposure period in 6 of 10 sound exposure trials. In the remaining 4, all of the porpoise surface positions recorded in the 15 min after the end of the exposure were over 1000 m from the exposure source. It is therefore reasonable to expect the maximum distance in the GLMM at the end of the 15 min exposure period or later. In summary, the models showed a maximum deterrence range between 1650 m (GLMM) and over 2070 m (GAMM), either by the end of the sound exposure period (GAMM) or during the 15 min after the exposure stopped (GLMM).

4.2. Swim speed

Porpoises travelled at a mean speed of 2.2 m s^{-1} during sound exposure (2.3 m s^{-1} during first prolonged dive); this is faster than their average swimming speed of 0.9 m s^{-1} found by Otani et al. (2000) but slower than their maximum swimming speed of 4.3 m s^{-1}. Brandt et al. (2013a) reported swimming speeds of between 1.3 and 3.2 m s^{-1} during exposure to seal scarers, and Kastelein et al. (2018) found that captive porpoises increased their swim speed from 1.2 up to 1.98 m s^{-1} when played pile-driving sounds. Although it is hard to compare swim speeds of free-ranging porpoises with swim speeds of a porpoise in a pool, swim speeds reported during sound exposures in both captive and free-ranging studies are in line with what we found.

4.3. Return times

Porpoises were sighted again in 7 of the 13 sound exposure trials. We could not tell whether these were the same animals or different ones. Of the 6 trials in which no animals returned, 3 were trials during which no porpoise sightings occurred after the onset of the sound exposure. Porpoises have been found to disappear immediately after the onset of sound exposure in previous noise studies (Brandt et al. 2013a, Mikkelsen et al. 2017). The immediate loss of porpoises occurred in 6 of 7 trials when a Lofitech ADD was tested on harbour porpoises (Brandt et al. 2013a) and in 3 cases when a sound similar to the Lofitech's was played (Mikkelsen et al. 2017). Both studies concluded that the animals left the area using a fast movement underwater. It is likely that this also occurred in our study. When animals were lost from view immediately, it is reasonable to assume that porpoises moved sufficient distances underwater not to be seen by the tracking stations (or were missed by observers) and then moved away and out of sight before they could be located again.

The average time after the onset of the sound exposure for sightings to re-occur after animals had left was 31 min, though sightings did not occur within 500 m until roughly an hour after the onset of the exposure. No significant difference in the number of surfacings was detected after 45 min from the start of exposure when compared to the control. This return of porpoises to within 500 m of the sound source with a comparable number of surfacings indicates that there was no long-term exclusion effect caused by the device. This is an important aspect when considering a mitigation method.

4.4. Startle reflex

Götz et al. (2020) first showed the presence of the startle reflex in odontocetes. The general physiological characteristics of the reflex were found to be the same as in terrestrial mammals, indicating that the evolutionary development of the startle reflex occurred early in the mammalian lineage. In rodents and humans, the stimuli must meet 2 criteria for the startle reflex to be elicited acoustically; it must be 60 to 90 dB above the auditory threshold (Fleshler 1965, Blumenthal & Berg 1986, Ouagazzal et al. 2006), and it must have a rise time of equal to or less than 50 ms (Fleshler 1965, Blumenthal & Berg 1986). In bottlenose dolphins *Tursiops truncatus* and a false killer whale *Pseudorca crassidens*, the average sensation level capable of eliciting a startle was 82 dB (Götz et al. 2020). Elmegaard et al. (2021) clearly demonstrated the startle reflex in harbour porpoises. Their animals startled 50% of the time at levels of 130 dB re 1 µPa, which was approximately 85 dB above the harbour porpoise hearing threshold at the frequency of 40 kHz. In our study, the lowest estimated received level at the start of a sound exposure trial was 126 dB re 1 µPa. Our results are therefore consistent with the startle reflex being the mediating mechanism of the behavioural avoidance responses observed in this study. They also point towards consistency in sensation levels capable of eliciting startle across mammalian taxa.

Startle-like movement responses have also been described in harbour porpoises (Kastelein et al. 2012) in response to 1–2 and 6–7 kHz up-sweeps and down-sweeps, though the sounds had a comparatively long rise time. This may give some support to the notion of lower startle thresholds but may also be due to generic movement responses being interpreted as startle (unequivocal evidence for startle responses requires determining response latency). The results of our study further support the possibility of targeting specific species by using startle-eliciting stimuli with the aim of deterrence. Porpoises did not react when exposed to low-frequency (peak frequency ~1 kHz) pulsed sounds around a salmon farm, while movement (and likely startle responses) was elicited in harbour seals (Götz & Janik 2015, 2016). In our study reported here, porpoises were exposed to a sound centred around 10 kHz and showed a significant avoidance reaction.

4.5. Mitigation application

To effectively protect harbour porpoise hearing from the effects of pile driving or other noisy activities, the animals must move to a distance at which they are no longer in danger of suffering either temporary or permanent hearing damage. Pile driving can generate underwater SELs in excess of 215 dB re 1 µPa (Ainslie et al. 2012). Although the level of sound created by pile driving depends on both the type and size of the monopile and the topography of the site, it has been found that pile-driving strikes during the construction of a wind farm in the German North Sea had the potential to cause TTS at distances of up to 5.6 km (Schaffeld et al. 2020). TTS onset in harbour porpoises has also been exhibited in animals exposed to single strikes (at 164 dB re 1 µPa^{2}s) (Lucke et al. 2009) and multiple strikes (onset of 175 dB re 1 µPa^{2}s) (Kastelein et al. 2016). In light of these findings, it is concerning that Graham et al. (2019) found that the porpoise response to pile driving diminished over time during the construction of the Beatrice Offshore Windfarm, putting the animals at considerable risk of hearing damage.

Our study, as well as previous studies, showed that acoustic deterrent methods offer an effective solution. Brandt et al. (2013a) tested the Lofitech seal scarer (frequency 14 kHz, source level 189 dB re 1 µPa) and found that porpoise sightings within 1 km of the device significantly decreased and that porpoises within 1.9 km of the device always avoided it. Mikkelsen et al. (2017) also played sounds similar to that of the Lofitech seal scarer but at a reduced peak-to-peak source level of 165 dB re 1 µPa. Harbour porpoises reacted with avoidance at distances of several hundred metres. Johnston (2002) assessed the effects of an Airmar dB Plus II operating at a fundamental frequency of 10 kHz and a source level of 180 dB re 1 µPa and found a significant reduction in porpoise numbers within 1500 m of the device in trials when the ADD was active when compared to an inactive state. A COA of 645 m was found, corresponding to a received level of 128 dB re 1 µPa. In a study on captive harbour porpoises, Kastelein et al. (2015) also found that the Lofitech and Ace Aquatech would be likely to deter porpoises at ranges of 0.2 to 1.2 km.

In our study, as in those mentioned above, porpoises reacted to the sound by moving away from or avoiding an area, but our findings indicate a reaction at a DC of only 0.6% (at least 1 order of magnitude lower than those of conventional ADDs) and at a significantly lower SEL than in any other studies. Our study used the equivalent of 5.4 s of continuous sound within the 15 min exposure period. Using our method allows a significant reduction in the noise dose animals need to be exposed to in order to achieve a similar movement response. This has now been implemented in the GenusWave TAST for odontocetes and is available for general use.

The effectiveness of our method offers a mitigation strategy for hearing damage in a variety of applications such as pile driving and marine construction, and it can also lower collision risk around marine turbines or potentially reduce bycatch of porpoises in fishing nets. In these cases, the source level of the signal could be reduced, as it is only necessary to exclude animals from the immediate area of a turbine or net rather than from the large areas required for pile-driving mitigation. Although the required source level cannot be determined from this study due to the limited variability of received level at the start of our trials, there is the possibility for further work to measure the response to our signals to specifically determine the received and sensation levels at which a response occurs. This would allow for the method to be more finely adjusted depending on the deterrence range required and further minimise risks for porpoises.

When considering the effects of conventional ADDs on harbour porpoises, Schaffeld et al. (2019) concluded that a significant TTS was caused by an ADD (using auditory-evoked potentials) with an onset SEL of 142 dB re 1 μPa^{2}s at 20 kHz and SEL of 147 dB re 1 μPa^{2}s at 28 kHz. These authors also estimated that an ADD signal at 193 dB re 1 μPa can result in TTS at distances of up to 211 m in deep water (spherical spreading) and 5.9 km in shallow water (cylindrical spreading).

Our study was initially designed to adhere to the sound exposure criteria suggested by Southall et al. (2007), within which TTS would be caused by an SEL of ~183 dB re 1 μPa^{2}s for harbour porpoises. Based on those guidelines, the onset of TTS would only have been induced if a porpoise had remained within 3.2 m of our transducer for 20 min. Although a scenario where porpoises remain stationary for 20 min is highly unlikely, no trials were carried out if a porpoise was within 10 m of the sound source. Since the end of our field period, further sound exposure criteria have been published by Southall et al. (2019). When considering the Southall et al. (2019) criteria, onset of TTS caused by a single 200 ms emission in our study would only occur if a porpoise was within 3.6 m of the sound source. As no porpoises were within 10 m of the sound source during trials, no TTS was induced for any porpoises throughout the duration of our study. In comparison, based on the same criteria, a single emission from conventional ADDs would cause the onset of TTS at distances of 27 to 48 m. One device (FG-PM) also operates at a much higher frequency (60–150 kHz) compared to all other ADDs. This overlaps with the peak frequency of harbour porpoise echolocation (~130 kHz), and can lead to masking effects at a time when communication between individuals (e.g. mother–calf pairs), and navigating safely is important. The onset of TTS can be caused by a single emission of this device at a distance of up to 40.6 m.

If the mitigation method itself causes an impact equal to, or indeed exceeding, the impact it should be mitigating, then it negates the effectiveness of the device (Mikkelsen et al. 2017). The acoustic startle method offers the potential to target both odontocetes and pinnipeds, drastically reducing the possibility of detrimental effects on hearing.

5. CONCLUSIONS

We have shown that harbour porpoises exhibit a medium- to large-scale movement response when exposed to the startle-eliciting acoustic stimuli used in this study. This was achieved at a very low DC (0.6%) and a lower source level (max. one-third octave band SPL of 176 dB re 1 μPa) as well as a much lower SEL (single signal, max. one-third octave band of 169 dB re 1 μPa^2 s) compared to existing devices. We suggest that the startle reflex is the underlying physiological mechanism mediating these responses. Our method could be used as an alternative to conventional ADDs to mitigate the risk of hearing damage during marine renewable energy installation and operation. It could also be used to mitigate collision risk with marine renewable energy installations (tidal turbines) or for bycatch reduction (if signals were played at a lower source level).

Acknowledgements. We thank Gabriel Melo-Santos, Sally Tapp, Rowan Prown, Annabel Westell, Monica Arancibia-Colgain, Nina Hildebrandt, Madalina Matei, Clair Evers, Fiona McNie, Will Brown, Patrick Keith, Sam Walmsley, Aidan Maccormick, Calum MacArthur, Denish Risch, Jamie Macaulay and Simon Moss for their assistance and advice. This study was conducted under SNH licence 102785 and was funded by Bankers LLC. V.M.J. and T.G. are involved in a commercialisation project to develop a targeted acoustic startle method to deter marine mammals sustainably.

LITERATURE CITED

Ainslie MA, de Jong CAF, Robinson SP, Lepper PA (2012) What is the source level of pile-driving noise in water? Adv Exp Med Biol 730:445–448

Bailey H, Senior B, Simmons D, Rusin J, Picken G, Thompson PM (2010) Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. Mar Pollut Bull 60:888–897

Blumenthal TD, Berg WK (1986) Stimulus rise time, intensity, and bandwidth effects on acoustic startle amplitude and probability. Psychophysiology 23:635–641

Bomford M, O'Brien PH (1990) Sonic deterrents in animal damage control: a review of device tests and effectiveness. Wildl Soc Bull 18:411–422

Brandt MJ, Diederichs A, Betke K, Nehls G (2011) Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. Mar Ecol Prog Ser 421:205–216

Brandt MJ, Höschle C, Diederichs A, Betke K, Matuschek R, Nehls G (2013a) Seal scarers as a tool to deter harbour porpoises from offshore construction sites. Mar Ecol Prog Ser 475:291–302

Brandt MJ, Höschle C, Diederichs A, Betke K, Matuschek R, Witte S, Nehls G (2013b) Far-reaching effects of a seal scarer on harbour porpoises (*Phocoena phocoena*). Aquat Conserv 23:222–232

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Bundesministerium für Umwelt (2014) Concept for the protection of harbour porpoises from sound exposures during the construction of offshore wind farms in the German North Sea. 21st ASCOBANS Advisory Committee Meeting AC21/Inf.3.2.2.a (P), 29 September–1 October 2014, Gothenburg. https://www.ascobans.org/sites/default/files/document/AC21_Inf_3.2.2.a_German_Sound_Protection_Concept.pdf (accessed July 2021)

Coram A, Gordon J, Thompson D, Northridge S (2014) Evaluating and assessing the relative effectiveness of acoustic deterrent devices and other non-lethal measures on marine mammals. Scottish Government, Edinburgh

Dawson SM, Northridge S, Waples D, Read AJ (2013) To ping or not to ping: the use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. Endang Species Res 19:201–221

Dyndo M, Wisniewska DM, Rojano-Donate L, Madsen PT (2015) Harbour porpoise react to low levels of high frequency vessel noise. Sci Rep 5:11083

Elmegaard SL, McDonald BI, Teilman J, Madsen PT (2021) Heart rate and startle responses in diving, captive harbour porpoises (*Phocoena phocoena*) exposed to transient noise and sonar. Biol Open10:bio058679

Erbe C, Dähne M, Gordon J, Herata H and others (2019) Managing the effects of noise from ship traffic, seismic surveying and construction on marine mammals in Antarctica. Front Mar Sci 6:647

Findlay CR, Ripple HD, Coomber F, Froud K and others (2018) Mapping widespread and increasing underwater noise pollution from acoustic deterrent devices. Mar Pollut Bull 135:1042–1050

Fisher FH, Simmons VP (1977) Sound absorption in sea water. J Acoust Soc Am 62:558–564

Fleshler M (1965) Adequate acoustic stimulus for startle reaction in the rat. J Comp Physiol Psychol 60: 200–207

Gill JA, Sutherland WJ, Watkinson AR (1996) A method to quantify the effects of human disturbance on animal populations. J Appl Ecol 33:786–792

Gilles A, Viquerat S, Becker EA, Forney KA and others (2016) Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. Ecosphere 7:e01367

Gillespie D, Mellinger DK, Gordon J, McLaren D and others (2008) PAMGUARD: semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. In: Conference on underwater noise measurement, impact and mitigation 2008. Proc Inst Acoustics, Vol 30, Part 5, Southampton, 14–15 October 2008. Curran Associates, Red Hook, NY

Götz T, Janik VM (2011) Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. BMC Neurosci 12:30

Götz T, Janik VM (2013) Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. Mar Ecol Prog Ser 492: 285–302

Götz T, Janik VM (2015) Target-specific acoustic predator deterrence in the marine environment. Anim Conserv 18:102–111

Götz T, Janik VM (2016) Non-lethal management of carnivore predation: long-term tests with a startle reflex-based deterrence system on a fish farm. Anim Conserv 19:212–221

Götz T, Pacini AF, Nachtigall PE, Janik VM (2020) The startle reflex in echolocating odontocetes: basic physiology and practical implications. J Exp Biol 223:jeb208470

Graham IM, Merchant ND, Farcas A, Barton TR, Cheney B, Bono S, Thompson PM (2019) Harbour porpoise responses to pile-driving diminish over time. R Soc Open Sci 6:190335

Hammond PS, Lacey C, Gilles A, Viquerat S and others (2017) Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys. https://synergy.st-andrews.ac.uk/scans3/files/2017/05/SCANS-III-design-based-estimates-2017-05-12-final-revised.pdf (accessed July 2021)

Hartig F (2020) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.7. https://CRAN.R-project.org/package=DHARMa (accessed July 2021)

Hastie G, Merchant ND, Götz T, Russell DJF, Thompson PM, Janik VM (2019) Effects of impulsive noise on marine mammals: investigating range-dependent risk. Ecol Appl 29:e01906

IEA (International Energy Agency) (2019) Offshore wind outlook 2019. IEA, Paris. https://iea.blob.core.windows.net/assets/495ab264-4ddf-4b68-b9c0-514295ff40a7/Offshore_Wind_Outlook_2019.pdf (accessed July 2021)

Jefferson TA, Curry BE (1996) Acoustic methods of reducing or eliminating marine mammal-fishery interactions: Do they work? Ocean Coast Manage 31:41–70

JNCC (2010) Statutory nature conservation agency protocol for minimising the risk of injury to marine mammals from piling noise. Joint Nature Conservation Committee, Aberdeen

JNCC (2016) Harbour porpoise (*Phocoena phocoena*) possible Special Area of Conservation: southern North Sea draft conservation objectives and advice on activities. Joint Nature Conservation Committee, Aberdeen

Johnston DW (2002) The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. Biol Conserv 108:113–118

Kastelein RA, Hoek L, de Jong CAF, Wensveen PJ (2010) The effect of signal duration on the underwater detection thresholds of a harbor porpoise (*Phocoena phocoena*) for single frequency-modulated tonal signals between 0.25 and 160 kHz. J Acoust Soc Am 128:3211–3222

Kastelein RA, Steen N, Gransier R, Wensveen PJ, de Jong CAF (2012) Threshold received sound pressure levels of single 1–2 kHz and 6–7 kHz up-sweeps and down-sweeps causing startle responses in a harbour porpoise (*Phocoena phocoena*). J Acoust Soc Am 131:2325–2333

Kastelein RA, Hoek L, Gransier R, Rambags M, Claeys N (2014) Effect of level, duration, and inter-pulse interval of 1–2 kHz sonar signal exposures on harbor porpoise hearing. J Acoust Soc Am 136:412–422

Kastelein RA, Hoek L, Gransier R, De Jong CAF, Terhune JM, Jennings N (2015) Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) for playbacks of seal scarer signals, and effects of the signals on behavior. Hydrobiologia 756:89–103

Kastelein RA, Helder-Hoek L, Covi J, Gransier R (2016) Pile driving playback sounds and temporary threshold shift in harbor porpoises (*Phocoena phocoena*): effect of exposure duration. J Acoust Soc Am 139:2842–2851

Kastelein RA, Huybrechts J, Covi J, Helder-Hoek L (2017) Behavioral responses of a harbor porpoise (*Phocoena phocoena*) to sounds from an acoustic porpoise deterrent. Aquat Mamm 43:233–244

Kastelein RA, Van de Voorde S, Jennings N (2018) Swimming speed of harbour porpoise (*Phocoena phocoena*) during playbacks of offshore pile driving sounds. Aquat Mamm 44:92–99

Koch M, Schnitzler HU (1997) The acoustic startle response in rats: circuits mediating evocation, inhibition and potentiation. Behav Brain Res 89:35–49

Koschinski S (2001) Current knowledge on harbour porpoises (*Phocoena phocoena*) in the Baltic Sea. Ophelia 55:167–197

Leaper R, Gordon J (2001) Application of photogrammetric methods for locating and tracking cetacean movements at sea. J Cetacean Res Manag 3:131–141

Lenth R (2020) emmeans: estimated marginal means, aka least-squares means. R package version 1.4.4. https://CRAN.R-project.org/package=emmeans

Lepper PA, Gordon J, Booth C, Theobald P, Robinson SP, Northridge S, Wang L (2014) Establishing the sensitivity of cetaceans and seals to acoustic deterrent devices in Scotland. Scottish Natural Heritage Commissioned Report No. 517

Lucke K, Siebert U, Lepper PA, Blanchet MA (2009) Temporary shift in masked hearing thresholds in a harbor porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. J Acoust Soc Am 125:4060–4070

Malinka CE, Gillespie DM, Macaulay JDJ, Joy R, Sparling CE (2018) First *in situ* passive acoustic monitoring for marine mammals during operation of a tidal turbine in Ramsey Sound, Wales. Mar Ecol Prog Ser 590:247–266

Mikkelsen L, Hermannsen L, Beedholm K, Madsen PT, Tougaard J (2017) Simulated seal scarer sounds scare porpoises, but not seals: species-specific responses to 12 kHz deterrence sounds. R Soc Open Sci 4:170286

Morton AB, Symonds HK (2002) Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. ICES J Mar Sci 59:71–80

NMFS (National Marine Fisheries Service) (2016) Technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing: underwater acoustic thresholds for onset of permanent and temporary threshold shifts. NOAA Tech Memo NMFS-OPR-55

NMFS (2018) Revisions to: technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing (version 2.0): underwater thresholds for onset of permanent and temporary threshold shifts. NOAA Tech Memo NMFS-OPR-59

Northridge S, Gordon J, Booth C, Calderan S and others (2010) Assessment of the impacts and utility of acoustic deterrent devices. Project code SARF044. Scottish Aquaculture Research Forum, Pitlochry

Oakley JA, Williams AT, Thomas T (2017) Reactions of harbour porpoise (*Phocoena phocoena*) to vessel traffic in the coastal waters of south west Wales, UK. Ocean Coast Manage 138:158–169

Olesiuk PF, Nichol LM, Sowden MJ, Ford JKB (2002) Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoises (*Phocoena phocoena*) in retreat passage, British Columbia. Mar Mamm Sci 18:843–862

Otani S, Naito Y, Kato A, Kawamura A (2000) Diving behavior and swimming speed of a free-ranging harbor porpoise, *Phocoena phocoena.* Mar Mamm Sci 16:811–814

Ouagazzal AM, Reiss D, Romand R (2006) Effects of age-related hearing loss on startle reflex and prepulse inhibition in mice on pure and mixed C57BL and 129 genetic background. Behav Brain Res 172:307–315

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Reid JB, Evans PGH, Northridge SP (2003) Atlas of cetacean distribution in north-west European waters. JNCC, Peterborough

Schaffeld T, Ruser A, Woelfing B, Baltzer J and others (2019) The use of seal scarers as a protective mitigation measure can induce hearing impairment in harbour porpoises. J Acoust Soc Am 146:4288–4298

Schaffeld T, Schnitzler JG, Ruser A, Woelfing B, Baltzer J, Siebert U (2020) Effects of multiple exposures to pile driving noise on harbor porpoise hearing during simulated flights — an evaluation tool. J Acoust Soc Am 147: 685–697

SMart Wind (2019) Hornsea offshore wind farm environmental statement project 2. https://infrastructure.planninginspectorate.gov.uk/wpcontent/ipc/uploads/projects/EN010053/EN010053-000241-121005_EN010053_Scoping%20Report.pdf

Southall BL, Bowles AE, Ellison WT, Finneran JJ and others (2007) Marine mammal noise exposure criteria: initial scientific recommendations. Aquat Mamm 33:411–521

Southall BL, Finneran JJ, Reichmuth C, Nachtigall PE and others (2019) Marine mammal noise exposure criteria: updated scientific recommendations for residual hearing effects. Aquat Mamm 45:125–232

Stoddart CW, Noonan J, Martin-Iverson MT (2008) Stimulus quality affects expression of the acoustic startle response and prepulse inhibition in mice. Behav Neurosci 122: 516–526

Stöber U, Thomsen F (2019) Effect of impact pile driving noise on marine mammals: a comparison of different noise exposure criteria. J Acoust Soc Am 145:3252–3259

Tougaard J, Carstensen J, Teilmann J, Skov H, Rasmussen P (2009) Pile driving zone of responsiveness extends beyond 20 km for harbour porpoises (*Phocoena phocoena* (L.)). J Acoust Soc Am 126:11–14

Tougaard J, Wright AJ, Madsen PT (2015) Cetacean noise criteria revisited in the light of proposed exposure limits for harbour porpoises. Mar Pollut Bull 90:196–208

Vincenty T (1975) Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. Surv Rev 23:83–93

Walsh C (2019) Offshore wind in Europe: key trends and statistics 2019. WindEurope, Brussels. https://windeurope.org/data-and-analysis/product/?id=61 (accessed July 2021)

Wilson B, Batty RS, Daunt F, Carter C (2007) Collision risks between marine renewable energy devices and mammals, fish and diving birds. Report to the Scottish Executive. Scottish Association for Marine Science, Oban

Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC, Boca Raton, FL

Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA
Reviewed by: T. Schaffeld, L. Favaro and 1 anonymous referee

Submitted: November 27, 2020
Accepted: May 17, 2021
Proofs received from author(s): August 2 , 2021