Target-specific acoustic predator deterrence in the marine environment

T. Götz & V. M. Janik

Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, UK

Abstract

Acoustic deterrent devices (ADDs) have often been considered a benign solution to managing pinniped predation. However, ADDs have also been highlighted as a conservation concern since they can inflict large-scale habitat exclusion in toothed whales (odontocetes). We tested a new method that selectively inflicted startle responses in harbour seals (*Phoca vitulina*) at close ranges to the loudspeaker but not in a non-target species, the harbour porpoise (*Phocoena phocoena*), by using a frequency range where porpoise hearing was less sensitive than that of phocid seals. The sound exposure consisted of isolated 200 ms long, 2–3 octave-band noise pulses with a peak frequency of 1 kHz, which were presented at a source level of ~180 dB re 1 μPa. Field tests were carried out within a 2-month period on a fish farm on the west coast of Scotland where marine mammal behaviour was observed within three distance categories. Seal numbers dropped sharply during sound exposure compared with control observation periods within 250 m of the sound source but were unaffected at distances further away from the farm. A Poisson regression model revealed that the number of seal tracks within 250 m of the device decreased by ~91% during sound exposure and was primarily influenced by sound exposure with no evidence for a change in the effect of treatment such as habituation, throughout the experiment. In contrast to seals, there was no shift in the number of porpoise groups in each distance category as a result of sound exposure and porpoises were regularly seen close to the device. We also sighted six common minke whales during sound exposure while only one was seen during control periods. Our data demonstrate that the startle method can be used to selectively deter seals without affecting porpoises.

Introduction

Pinniped predation on fish farms and fisheries is a worldwide problem and has led to substantial pressure on regulators and politicians to allow targeted shooting or population control (Nash, Iwamoto & Mahnken, 2000; Würsig & Gailey, 2002). Acoustic deterrent devices (ADDs) have often been considered a benign way of solving this problem. However, the main issues with ADDs appear to be lack of long-term efficiency and unintended effects on other marine wildlife (Jefferson & Curry, 1996; Würsig & Gailey, 2002; Götz & Janik, 2013). While some studies found prolonged effectiveness of ADDs (Fjälling, Wahlberg & Westerberg, 2006; Graham et al., 2009), others showed that ADDs had little effect on seals and sea lions around haul-out sites or fish farms (Norberg, 2000; Jacobs & Terhune, 2002). In these cases, animals may either tolerate or habituate to high noise levels (i.e. as the result of food motivation) and may consecutively suffer hearing damage, which would

further reduce responsiveness (Götz & Janik, 2013). Rapid habituation to recorded sounds from commercially available ADDs has been found in a captive study on phocid seals where food was presented close to the speaker (Götz & Janik, 2010). Furthermore, ADDs can potentially cause damage to the hearing system of target and non-target species (Taylor, Johnston & Verboom, 1997; Götz & Janik, 2013) and cause long-term habitat exclusion of toothed whales (odontocetes). Harbour porpoises (*Phocoena phocoena*) in Canada were excluded from an area of up to 645 m from an Airmar ADD device and numbers were lower than in control periods up to a distance of 1.5 km (Johnston, 2002). A similar study showed that porpoise sightings dropped to 10% at ranges up to 3.5 km from an operating ADD (Olesiuk et al., 2002). Morton & Symonds (2002) observed a drop in killer whale (*Orcinus orca*) sightings in Canada (Johnston Strait) after the introduction of ADDs on fish farms and a recovery of sighting rates after fish farms stopped using ADDs. Their study suggests that

killer whales did not habituate to ADDs. In the same area Morton (2000) observed a decline in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), which seemed to correlate with the introduction of ADDs. One likely reason for this is that odontocete hearing is much more sensitive than pinniped hearing (Richardson *et al.*, 1995) in the frequency range between 10 and 40 kHz where most ADDs operate (Götz & Janik, 2013).

For fish predators, a successful acoustic deterrent will have to cause sufficient 'perceived risk' to override the benefits obtained from foraging on the anthropogenic food source (Schakner & Blumstein, 2013). Current ADDs transmit loud sounds often aimed at inflicting pain in the target animal. An alternative is to use signals based on biological concepts of aversiveness like eliciting the acoustic startle reflex (Götz & Janik, 2013). This reflex consists of a contraction of flexor muscles (flinch), is mediated by an oligosynaptic reflex arc in the brainstem and can be elicited by pulsed sounds with a short rise time (Koch & Schnitzler, 1997). Captive grey seals (*Halichoerus grypus*), which were repeatedly exposed to startling stimuli, have been shown to sensitize to the stimulus, resulting in sustained flight responses and place avoidance behaviour (Götz & Janik, 2011). The startle threshold mirrors the audiogram at a level of 80–90 dB above the hearing threshold (Pilz, Schnitzler & Menne, 1987), and therefore, differences in hearing abilities across species could be exploited to reduce effects on non-target species. Since phocid seal auditory sensitivity at low frequencies is higher than that of toothed whales, it should be possible to elicit the startle reflex in seals entering a confined zone around the loudspeaker while other less sensitive taxa would be unaffected.

In this study, we investigated the effectiveness of a low-frequency pulsed sound on a typical ADD target species, the harbour seal, *Phoca vitulina*, and on non-target species such as harbour porpoises and common minke whales *Balaenoptera acutorostrata* around a salmon farm.

Methods

Study site

Our study site was located in the Sound of Mull on the west coast of Scotland/UK. Experiments were conducted on a fish farm (Scottish Sea Farms Ltd), which was stocked with five cages (up to 15 m deep). The fish farm reported seal predation before the experimental period but had not used a deterrent system in the past.

Playback equipment and stimuli

The playback system consisted of a Lubell 9162 underwater loudspeaker (Lubell Labs, Columbus, OH, USA), a Cadence Z9000 power amplifier (Cadence Acoustics, Ltd., Industry, CA, USA), a Panasonic SL-S120 CD player (Panasonic Corporation, Osaka, Japan) and a car battery installed in a waterproof box. The box was placed on one of the cages (Fig. 1) with the transducer being deployed at ~17 m depth (~2 m below the deepest part of the cage). The playback sounds were band-limited noise pulses synthesized in Cool Edit Pro 1.2 (Syntrillium Software Corporation, Scottsdale, AZ, USA). The sound stimulus was 200 ms long, extended over 2–3 octave-bands in frequency with a peak at 950–1000 Hz, had a rise time of <5 ms and was played at a source level of ~180 dB re 1 μPa (rms) at 1 m. This noise pulse was within 10 dB of its maximum output between ~700 Hz and 1500 Hz. Pulses were played at irregular, pseudorandom intervals ranging from 2 to 40 s with an average of 0.04 pulses per second (duty cycle: 0.8%).

Experimental design

Experiments were carried out in sea states of less than 3 in June and July 2007. Sound exposure and control observation periods were carried out on 16 days respectively, (sound: 58 h, control: 55 h) with the average length of an observation period being ~3.5 h. The following list represents the sequence of all 32 observation periods giving the calendar day from the start of the experiment (days 1 to 43) and experimental condition (C, control; S, sound exposure). The time in the middle of the observation period is represented as a decimal point with the decimal representing a fraction of 24 h (e.g. 1.5 would means the first day at 12:00): 1.5 (C), 2.5 (C), 4.7 (C), 6.7 (C), 8.6 (C), 9.7 (C), 10.5 (C), 11.5 (C), 17.6 (S), 18.5 (S), 19.5 (S), 20.7 (S), 21.6 (S), 22.5 (C), 23.5 (S), 24.5 (S), 25.5 (S), 26.5 (C), 27.5 (S), 28.5 (S), 31.5 (C), 31.6 (S), 32.4 (C), 32.5 (S), 34.5 (S), 36.6 (S), 37.5 (S), 38.5 (S), 40.4 (C), 41.4 (C), 42.4 (S), 43.4 (S).

Visual observations were conducted by two observers from shore using the naked eye, Carl Zeiss Jena 10 × 50 binoculars (Carl Zeiss AG, Jena, Germany) and a Topcon DT-102 digital theodolite (Topcon Positioning Systems, Inc., Livermore, CA, USA). The position of the theodolite station was measured with a Garmin GPS12 XL (Garmin, Schaffhausen, Switzerland) receiver on 2 separate days. The horizontal theodolite angle was set to zero using a reference point at Rubha nan Gall lighthouse. The bearing from the theodolite station to the lighthouse was calculated using the position of the theodolite and the lighthouse. The altitude of the theodolite station was calculated using two trigonometric points and the known height of the lighthouse. Visibility allowing, the vertical and horizontal angle to these points was measured daily and averaged. The mean altitude of the theodolite station was 73.5 m above OS survey datum.

During observations, one observer was typically scanning by eye while the other observer used binoculars. If one observer detected an animal, consecutive surface positions were logged with the theodolite resulting in a track. If animals did not resurface for 15 min, a track was ended. The other observer continued to scan the area and would indicate any new sightings to the tracker who would then track both animals alternately. If animals of the same species were within 20 m of each other, they were considered to be one group and were tracked as one.
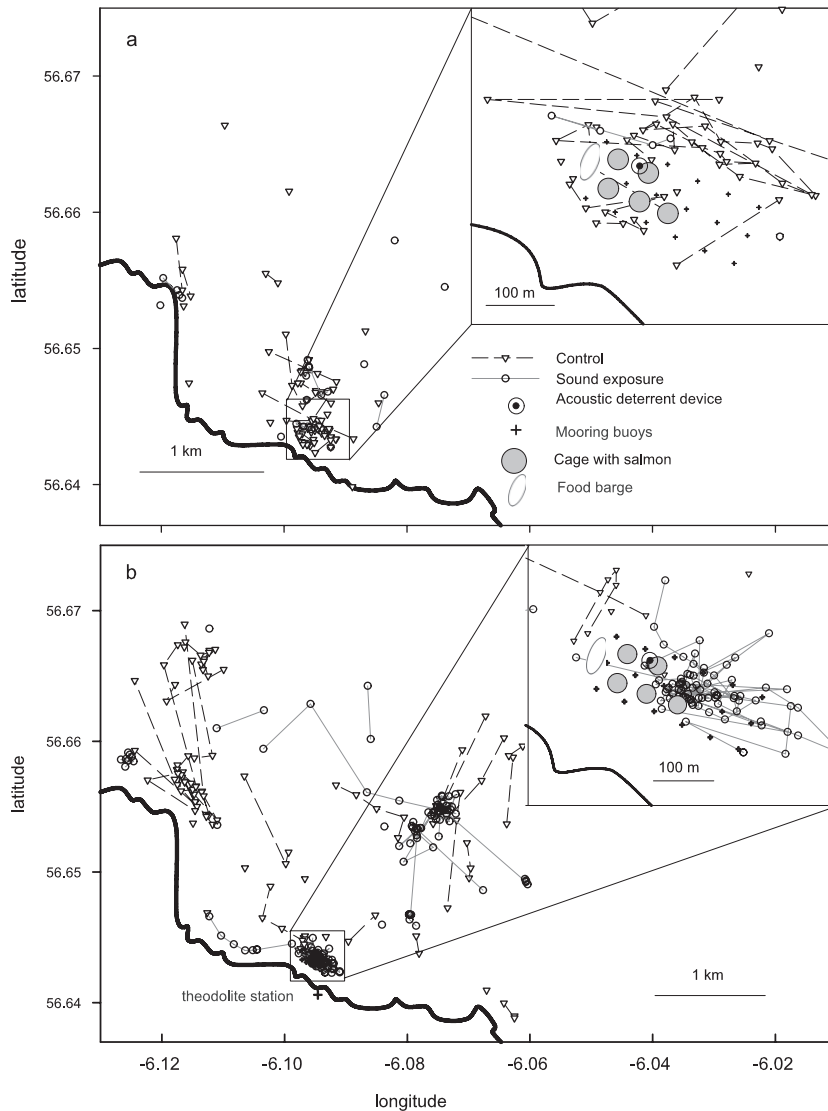
Figure 1 Seal (a) and porpoise (b) tracks for the overall observation area (large maps) and in the vicinity of the fish farm (inset maps).

All data were processed in Pythagoras 1.2.15 (Gailey & Ortega-Ortiz, 2002). A tide height table for Tobermory Bay was exported from POLTIPS 3.2 (Proudman Oceanographic Laboratory, Liverpool, UK) and uploaded to Pythagoras. The surface positions were then calculated in Pythagoras taking tide height into account. These positions were exported and distances between the surface positions and the transducer were calculated using the Vincenty formula (Vincenty, 1975).

Sound field measurements

The sound field and source level were measured using a calibrated B&K 8103 hydrophone and a B&K 2635 charge amplifier (Brüel & Kjær, Nærum, Denmark) with a calibrated sound card of a Toshiba laptop computer (Tokyo, Japan) as in Götz & Janik (2010). Source level measurements were taken at sea in water 20 m deep, with the transducer and

hydrophone at 2 m depth and 1.7 m apart. The source level was calculated as the average of 20 measured pulses adding the transmission loss back to a reference distance of 1 m. The measurements of the sound field around the fish farm were also conducted with the hydrophone at 2 m depth. Measurement locations were in part chosen based on sighting hotspots. Locations covered a representative part of the whole area and were in line of sight of the farm, both on the seaward and landward sides including some locations between cages. Real distances to the transducer were calculated using Pythagoras' theorem. The hydrophone position was measured with the theodolite for distances of up to 1000 m and a GPS receiver for longer distances.

Data analysis and sample size

Data were analysed in distance bins of 0–250 m, 250–1500-m and more than 1500-m. The 250-m bin was chosen

to roughly cover the area around the fish farm while the 1500-m bin was based on a study that showed adverse effects of ADDs on harbour porpoise (Johnston, 2002) Closest observed approaches per track and the average distance from the transducer within a track were measured for seals and porpoises. Seals were mostly solitary, but porpoises often appeared in groups. Therefore, both number of porpoise groups and number of individual porpoises were used as the unit of analysis.

All statistical analysis was carried out in R 3.0.2 (R Development Core Team, 2013) with the exception of the sound propagation model (SigmaPlot 8.0, SPSS Inc., Chicago, IL, USA). Log-linear models (Poisson GLMs, see Fox & Weisberg, 2011) were used to analyse the contingency tables (see Fig. 2) containing the cumulative count of all tracks/individuals within each distance bin for the 16 sound exposure and control observation periods. The model tested the effect of the interaction term of 'distance bin' and 'treatment' (unordered factors) with contrasts being set as 'sum to zero' (see Fox & Weisberg, 2011). The cumulative observation effort for sound exposure (55 h) and control (58 h) observation periods was included as a logarithmic offset.

Analysis of deviance tables were used to assess significance levels of all model terms using the analysis of variance (ANOVA) function in the 'car' package for R (Fox & Weisberg, 2011). The 'lsmeans' function from the 'lsmeans' package for R was used to compute pairwise comparisons (contrasts) between sound exposure and control observation periods for each distance bin. P-values were adjusted to account for multiple testing using the Tukey method in the 'lsmeans' package (Lenth, 2013).

In order to test for changes in animal abundance and the effect of treatment over the course of the experiment, a Poisson regression model (logarithmic link function) was calculated using the generalized linear modelling function (glm) in R. The model used the number of tracks during each 'observation period' within less than 250m from the loudspeaker as a unit of analysis. A number of potential candidate models were assessed and the model with the lowest Akaike information criterion (AIC) was selected. The number of animals during each observation period was used as the response variable, the logarithm of the duration of the respective observation period (effort) was used as an offset and treatment was always included as a factor (control vs.
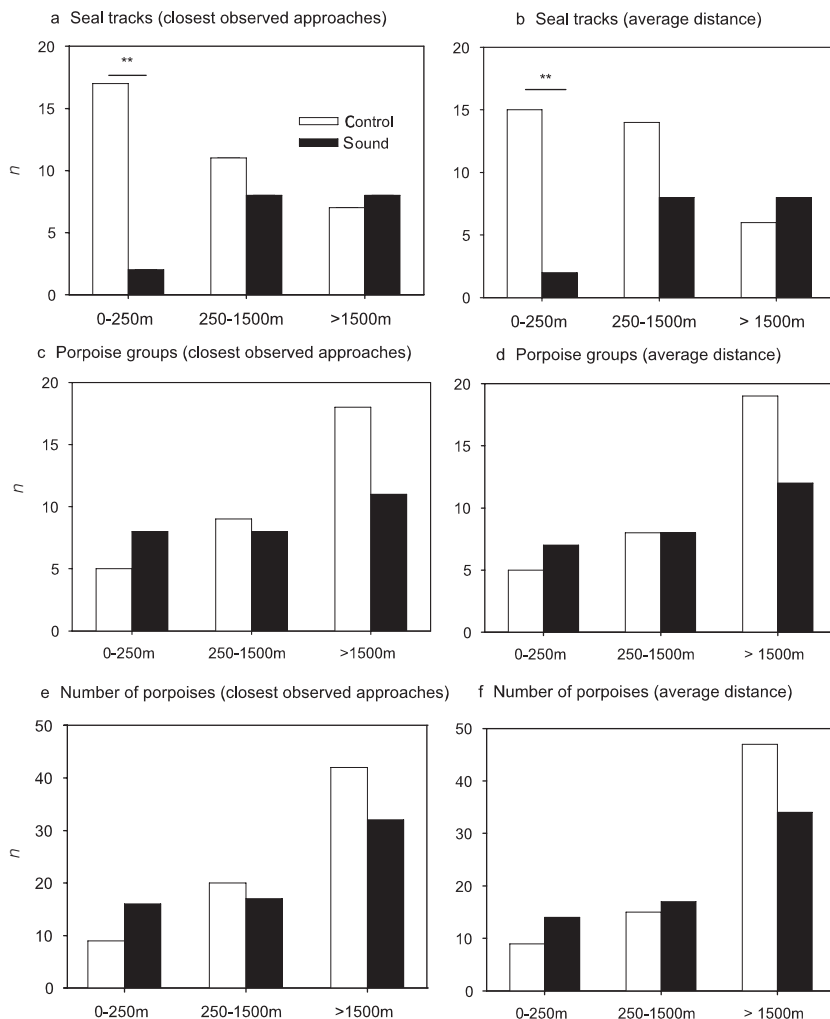

Figure 2 Seal and porpoise tracks observed during control periods (white bars) and sound exposure (black bars): (a, b) seal tracks, (c, d) number of porpoise groups (d, e) overall number of individual porpoises. The bars represent the cumulative number of tracks within a respective distance bin (based on average distance or closest observed approaches) counted across all observation periods. Pairwise differences were computed for each distance bins and are depicted by asterisks (*$P < 0.05$, **$P < 0.01$).
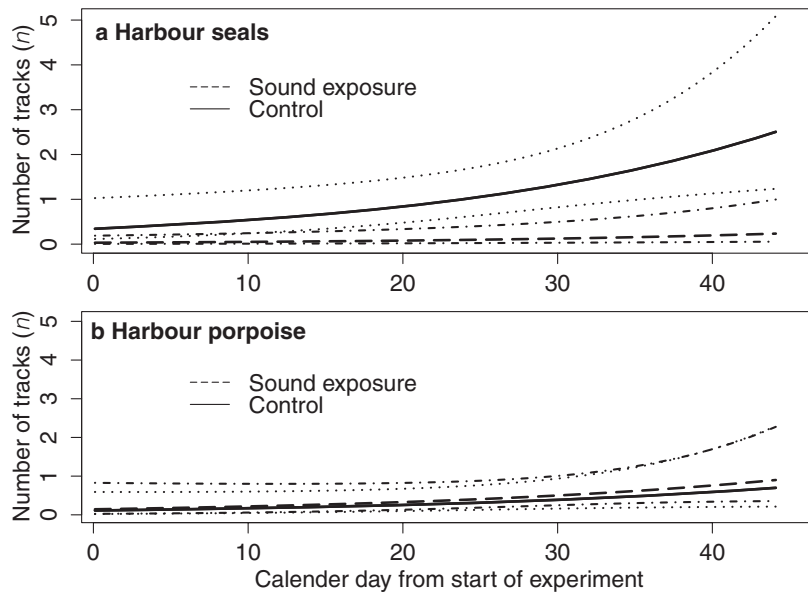
Figure 3 Predicted number of (a) seal and (b) porpoise tracks (< 250 m distance) with 95% confidence intervals (CI) for control (solid line, CI: dotted line) and sound exposure periods (dashed lines, CI: dash-dotted lines) obtained from the Poisson regression models.

sound). A set of additional predictor variables was assessed during the model selection process: calendar/Julian day on which the observation period was carried out (starting from the first observation day with time being reflected by decimal points), number of playback period with control periods set to 0 and sea state (factor). The term 'number of playback period' would have indicated a change in the response to sound exposure during consecutive playback periods such as habituation or sensitization ('habituation term'). The final, selected model only included treatment and calendar day for both, seals and porpoise. The effect of model predictors is reported based on the results from an analysis of deviance (ANOVA function, 'car' package, Fox & Weisberg, 2011). Model coefficients, confidence intervals and P-values based on the model summary are presented in Supporting Information Appendix S1. A goodness of fit test carried out for the two final selected models was not significant, indicating reasonable model fit (seals: $P = 0.44$, porpoise: $P = 0.15$). The Durbin–Watson statistic showed that there was no significant autocorrelation of the residuals (seals: DW = 1.77, P-value = 0.15, porpoise: DW = 1.74, P-value = 0.13). Predicted values shown in Fig. 3 are based on the average observation period of 3.5 h. Confidence intervals for predicted values were calculated from standard errors obtained from the predict function.

Results

Harbour seals

The tracking maps (Fig. 1a) for seals showed less seal tracks during sound exposure compared with control observation periods close to the farm. The overall number of seal tracks dropped sharply during sound exposure within 250 m of the transducer but remained relatively unaffected at higher distances (Fig. 2a–b). The log-linear model used to analyse the

contingency tables of distance bin and treatment (Fig. 2) showed that sound exposure had a significant effect on the number of seal tracks, for both closest observed approaches (COA) ($\chi^2 = 4.68$, $P = 0.03$) and average approach distance (AD) per track ($\chi^2 = 4.68$, $P = 0.03$). The significant interaction term between treatment and distance bin showed that sound exposure had a different effect within each of the respective distance bins (COA: $\chi^2 = 8.54$, $P = 0.014$, AD: $\chi^2 = 7.65$, $P = 0.022$). The factor distance bin was not significant (COA: $\chi^2 = 0.62$, $P = 0.73$; AD: $\chi^2 = 1.83$, $P = 0.40$). Post-hoc testing using model contrasts revealed that the number of seal tracks was significantly lower in the closest distance bin only (Fig. 2, COA: $P = 0.005$, AD: $P = 0.009$). The number of tracks was unaffected by sound exposure at distances between 250 m and 1500-m (COA: $P = 0.57$, AD: $P = 0.25$) and more than 1500-m (COA: $P = 0.72$, AD: $P = 0.53$). The effect of sound exposure on the number of seal tracks (model estimate) in each distance is provided in Supporting Information Appendix S1.1.

The number of animals within less than 250 m of the loudspeaker was modelled using Poisson regressions (generalized linear model, Fig. 3, Supporting Information Appendix S1.2). The most parsimonious model (lowest AIC) only contained treatment and calendar day as predictors but did not contain the 'habituation term'. The model for seals revealed a highly significant effect of sound exposure ($\chi^2 = 16.89$, $P < 0.0001$) and calendar day ($\chi^2 = 7.21$, $P = 0.0072$) on the number of seals in the vicinity of the farm. The predicted values show that the number of seal tracks during control observation periods increased towards the end of the experiment. However, during sound exposure seal numbers remained low throughout the whole experimental period (Fig. 3a). The model coefficient for treatment showed that sound exposure led to a 90.6% (10.68-fold) reduction in the number of seal tracks within 250 m of the device (Supporting Information Appendix S1.2).

Harbour porpoises

The map of all harbour porpoise tracks showed a roughly similar pattern of distribution for control and sound exposure periods at distances of more than 200–300 m (Fig. 1b). The log-linear models used to analyse the number of tracks within the distance bins (Fig. 2c–f) during the two treatments only returned distance bin as a significant factor. This was the case irrespective of whether number of porpoise groups or overall number of animals was used as the unit of analysis (COA: $\chi^2 = 27.7$, $P < 0.001$ AD: $\chi^2 = 40.5$, $P < 0.001$). Post-hoc tests (model contrasts) confirmed that there was no significant difference between sound exposure and control in any of the distance bins (see Fig. 2, $P > 0.05$). Hence, while more porpoise tracks were logged in the distance bins further away (reflecting increasing area) the numbers in each respective bin were unaffected by sound exposure. Model coefficients and 95% confidence intervals showing the effect of sound exposure on the number of porpoise tracks in each distance bin are provided in Supporting Information Appendix S1.1.

The Poisson regression model (GLM, Fig. 3b, Supporting Information Appendix S1.2) with the lowest AIC only retained calendar day as an additional explanatory variable. The model showed that sound exposure did not influence porpoise abundance around the farm ($\chi^2 = 0.197$ $P = 0.657$). The covariate calendar day approached significance which may indicate that porpoise numbers increased slightly towards the end of the experiment ($\chi^2 = 2.73$, $P = 0.099$). The fact that the 'habituation term' was not retained in the final model indicates that porpoise behaviour during sound exposure did not change throughout the experimental period.

Common minke whales

Sighting rates for minke whales were low with six tracks logged during sound exposure periods and only one during a control period (Fig. 4). The closest observed approach for a common minke whale was 1109 m during sound exposure and 2808 m during the one control period with a minke whale approach. The closest observed approach was directed into the bay where the fish farm was located. The average COA distance for all tracks was 2391 m for sound exposure periods.

Sound field

Figure 5 shows measured received levels at various distances from the transducer as well as a waveform and spectrogram of a typical pulse recorded during the source level measurement.

A logarithmic regression line based on the equation

$$RL = SL - a * \log_{10} (\text{distance from transducer})$$

was fitted to the measured values for the rms received levels (RL = received level, SL = source level at 1 m distance,
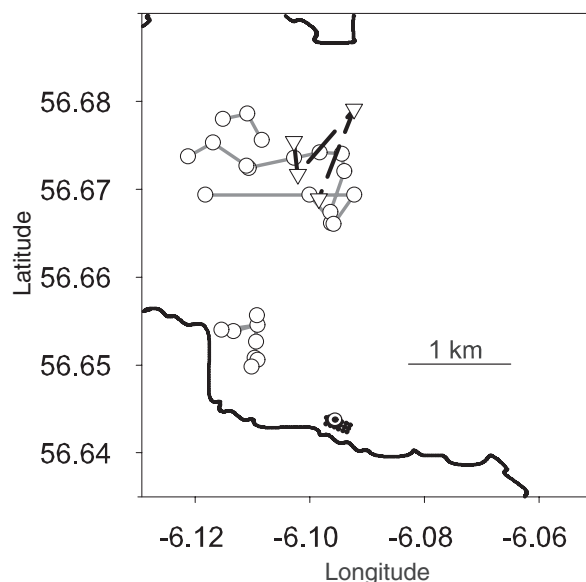

Figure 4 Common minke whale tracks during control periods (triangles) and sound exposure periods (circles). The farm gird is depicted with dots and the location of the sound source is shown by a black circle.

a = fitted parameter). Parameter a was estimated to be 18.3 indicating that transmission loss was between spherical and cylindrical (Fig. 5, $r^2 = 0.95$).

Discussion

Effectiveness as a deterrent

At our study site, seals seemed to use the area close to the fish farm more extensively than areas beyond 250 m from it. This was indicated by the fact that we found no difference in seal numbers between the much smaller area around the farm when compared with the much larger distance bin further away. This pattern was not observed for porpoises, which were seen more often in the larger distance bins, indicating a roughly equal use of both areas. The analysis by distance bin (Fig. 2a–b) and the tracking maps (Fig. 1a) show that the deterrence effect on seals was limited to the vicinity of the fish farm while porpoises were not deterred (Figs 1b and 2c–f). The sound field measurements confirmed that received levels decreased logarithmically with increasing distance from the sound source (Fig. 5). The limited deterrence range for seals is therefore likely to be a result of received levels dropping below an avoidance threshold. Previous experiments on captive grey seals (*Halichoerus grypus*) showed that the average pure tone startle threshold at 1 kHz is about 159 dB re 1 μPa, (Götz & Janik, 2011). Two animals in those experiments could not be startled even with higher levels, which was assumed to be an indication of previous hearing loss and higher startle thresholds in those animals. Startle thresholds measured with broadband noise stimuli are approximately 14 dB lower than pure
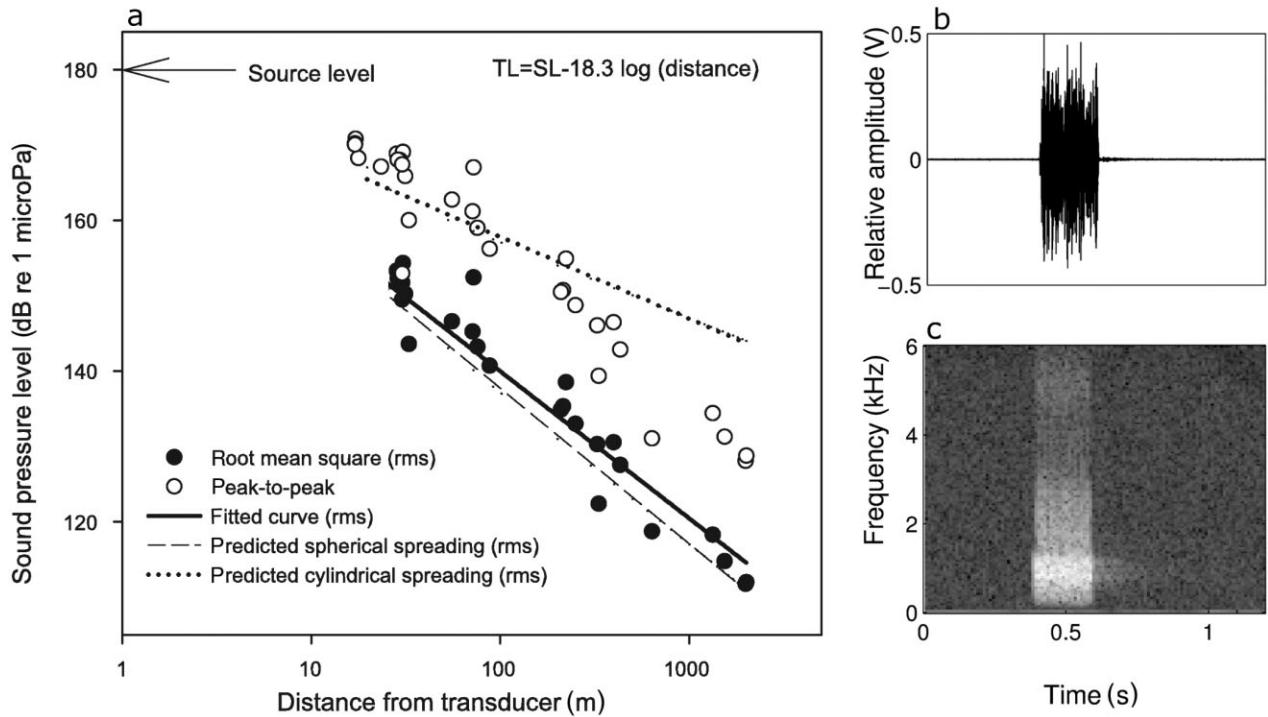
Figure 5 Measured sound transmission loss around the fish farm and acoustic properties of the band-limited noise pulse (spectrogram: Hanning window, frequency resolution: 47 Hz). The fitted curve for rms values is based on SPL = SL-18.3 log (distance). Spherical and cylindrical spreading were calculated as SPL = SL-20 log (distance in m) and SPL = SL-10 log (distance in m).

tone thresholds (see Fig. 2b in Stoddart, Noonan & Martin-Iverson, 2008). Hence, the noise pulse used in our study is likely to elicit startle responses at a received level of approximately 145 dB re 1 μPa. When applying the sound propagation model based on our measurements (Fig. 5), startle responses would be expected to occur at distances of up to 82 m around the transducer. The significant drop of animals within the zone of 250 m could theoretically be explained in two different ways. Seals that approached the cages underwater would eventually be exposed to sound pulses exceeding the startle threshold. These animals were likely to sensitize and exhibit flight responses causing them to leave a wider area around the cage (see Götz & Janik, 2011). Alternatively, some of the avoidance responses within 250 m may not be mediated by the startle reflex but by a general avoidance behaviour caused by novel sound stimuli. Captive harbour seals avoid noise pulses at frequencies between 8 and 45 kHz at sound pressure levels between 131 and 141 dB re 1 μPa (Kastelein *et al.*, 2006), which is close to the measured received levels at 250 m distance (135 dB re 1 μPa, see Fig. 5). Similarly, avoidance thresholds in wild grey seals exposed to non-startling sounds were found to be between 135 and 140 dB re 1 μPa (Götz & Janik, 2010). Harbour seals in the Hebrides show haul-out site fidelity and average foraging trip distances are only between 25 and 35 km (Sharples *et al.*, 2012). It is therefore likely that the same seals visited the farm repeatedly and were exposed to the stimulus several times. Thus, we would

have expected a habituation effect over time, if novelty had caused the initial avoidance response (see Götz & Janik, 2010). However, the Poisson regression model showed that sound exposure retained a strong effect on seal numbers around the farm during the whole experimental period (Fig. 3a). Models that contained a 'habituation/ sensitization term' were rejected during model selection (AICs). Therefore, at least part of the avoidance behaviour appeared to be caused by the startle reflex and responses did not habituate within the exposure period (~3.5 h) or across the 16 sound exposure periods tested in this study (see Götz & Janik, 2011). Future studies should explore seal reactions to this method during permanent exposure. The fact that two seal tracks occurred within 250 m of the transducer could be explained by received levels not exceeding the startle threshold within the entire area or animals tolerating the sound, that may be, because of compromised hearing which would reduce the deterrence range.

Impact on harbour porpoises

There was no statistical difference between the control and sound treatment for any of the response variables for harbour porpoises. Therefore, the startle method can be used to deter seals but not affect harbour porpoises. In contrast, Johnston (2002) reported a significant decrease in porpoise sightings around an Airmar ADD (10 kHz signal) in an observation area extending up to 1500-m from the

device. In their study, the closest observed approach distance of 645 m during sound exposure correlated with a modelled received level of 128 dB re 1 μPa. The received level of the stimulus tested in our study at the same distance (modelled by equation (1)) is also 128 dB re 1 μPa. This shows that porpoises respond very differently to sounds of the same received level depending on the frequency band and duty cycle used. The harbour porpoise hearing threshold at the peak frequency of our sounds (1 kHz) is approximately 82 dB re 1 μPa while the threshold at the peak frequencies of the Airmar ADD (10 kHz) is 53 dB re 1 μPa (averaged values: Kastelein et al., 2002; Andersen, 1970). Therefore, in the study by Johnston (2002) the sensation level in dB above the hearing threshold at the edge of the exclusion zone is 75 dB (obtained by subtracting 53 dB from the RL of 128 dB). The closest observed approach of a porpoise group during sound exposure in our study was 8 m (measured RL of 154 dB re 1 μPa) resulting in a sensation level of 72 dB (82 dB subtracted from 154 dB). This shows that sensation levels explain the lack of avoidance responses in porpoises in our study and are important when predicting responses to noise (Götz & Janik, 2013).

Kastelein et al. (2012) investigated changes in swim direction and speed in porpoises exposed to frequency-modulated signals. They interpreted these responses as 'startle' and found a response threshold of ~133 dB re μPa to 1–2 kHz sweeps. However, the sounds used by Kastelein et al. (2012) had long rise times (50 ms), which strongly reduces their startle potency (Fleshler, 1965). Hence, the stimuli would have needed to be louder than what was used by Kastelein et al. (2012) to elicit the startle reflex (Fleshler, 1965; Pilz et al., 1987). Furthermore, Kastelein included movement responses that were initiated after the 1 s long stimulus ceased. These would have been unrelated to startle as response latencies of the reflex are significantly shorter (Pilz et al., 1987). Thus, Kastelein et al. (2012) seems to have used the term 'startle' in a more colloquial rather than neurophysiological sense (see Koch & Schnitzler, 1997).

Unintended effects on target and non-target species

While we have only limited data on common minke whales, our study provides no evidence for any impacts at distances of more than 1000 m. Longer minke whale tracks were observed in sound exposure periods when compared with treatment periods and track directions showed that animals were not leaving the area. However, the received level at the distance of the closest observed approach (1109 m) was relatively low (125 dB re 1 μPa) and it cannot be ruled out that common minke whales would be affected at closer distances.

Hearing abilities in fish vary across taxa but many species have poor sensitivity to sound pressure at frequencies above 700–800 Hz (Popper & Fay, 1993). However, some species (e.g. herring) have at least moderate sensitivity up to several kHz (Enger, 1967). We provide a detailed discussion on any potential side effects of the suggested deterrence method on

fish, seals and cetaceans in Supporting Information Appendix S2 but conclude that adverse effects are less likely unless animals are very close to the device (<100 m) for long periods of time.

Conclusions

Our study demonstrated that startling noise pulses presented at low duty cycles are effective in reducing the number of seals in an area up to 250 m around a transducer. The advantages of using the startle reflex in acoustic deterrence are that short isolated pulses can be used, avoidance responses are limited to a defined area and noise pollution can be minimized by using a low duty cycle (0.8%). Additional applications include temporary exclusion of animals from marine installations (e.g. tidal turbines) or industrial activities which may cause hearing damage (pile driving). In these applications, the startle pulse could be centred within a different frequency band depending on the auditory sensitivity of the species that have to be deterred.

We showed that inter-species differences in frequency-dependent hearing sensitivity hold some potential for developing deterrent devices, which target one taxon while not affecting others. Adverse impacts of current acoustic deterrent devices on harbour porpoise, such as prolonged habitat exclusion shown in previous studies can be mitigated. Future studies will have to test whether startle stimuli are capable of reducing predation losses. Our data showed that the described method has the potential to address conservation concerns related to acoustic deterrent devices and therefore extend the range of management tools available to the industry.

Acknowledgements

References

Andersen, S. (1970). Auditory sensitivity of the harbour porpoise. *Investigations on Cetacea* **2,** 155–159.

Enger, P. (1967). Hearing in herring. *Comp. Biochem. Physiol. A* **22,** 527–538.

Fjälling, A., Wahlberg, M. & Westerberg, H. (2006). Acoustic harassment devices reduce seal interaction in the

Baltic salmon-trap, net fishery. *ICES J. Mar. Sci.* **63,** 1751–1758.

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

Fox, J. & Weisberg, S. (2011). *An {R} companion to applied regression.* 2nd edn. Thousand Oaks, CA: Sage Publication. URL: socserv.socsci.mcmaster.ca/jfox/Books/Companion.

Gailey, G. & Ortega-Ortiz, J.G. (2002). A note on a computer-based system for theodolite tracking of cetaceans. *J. Cetacean Res. Manag.* **4,** 213–218.

Götz, T. & Janik, V.M. (2010). Aversiveness of sound in *phocid* seals: psycho-physiological factors, learning processes and motivation. *J. Exp. Biol.* **213,** 1536–1548.

Götz, T. & Janik, V.M. (2011). Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behavior and induces fear conditioning. *BMC Neurosci.* **12,** 30.

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

Graham, I.M., Harris, R.N., Denny, B., Fowden, D. & Pullan, D. (2009). Testing the effectiveness of an acoustic deterrent device for excluding seals from Atlantic salmon rivers in Scotland. *ICES J. Mar. Sci.* **66,** 860–864.

Jacobs, S.R. & Terhune, J.M. (2002). The effectiveness of acoustic harassment devices in the Bay of Fundy, Canada: seal reactions and a noise exposure model. *Aquat. Mamm.* **28,** 147–158.

Jefferson, T.A. & Curry, B.E. (1996). Acoustic methods of reducing or eliminating marine mammal-fishery interactions: do they work? *Ocean Coast. Manag.* **31,** 41–70.

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

Kastelein, R.A., Bunskoek, P., Hagedoorn, M., Au, W.W.L. & de Haan, D. (2002). Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals. *J. Acoust. Soc. Am.* **112,** 334–344.

Kastelein, R.A., van der Heul, S., Terhune, J.M., Verboom, W.C. & Triesscheijn, R.J.V. (2006). Deterring effects of 8–45 kHz tone pulses on harbour seals (*Phoca vitulina*) in a large pool. *Mar. Environ. Res.* **62,** 356–373.

Kastelein, R.A., Steen, N., Gransier, R., Wensveen, P.J. & De Jong, C.A.F. (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 harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* **131,** 2325–2333.

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

Lenth, R.V. (2013). lsmeans: least-squares means. R package version 1.10-2. http://cran.r-project.org/web/packages/lsmeans/

Morton, A. (2000). Occurrence, photo-identification and prey of pacific white-sided dolphins (*Lagenorhyncus obliquidens*) in the Broughton Archipelago, Canada 1984–1998. *Mar. Mamm. Sci.* **16,** 80–93.

Morton, A.B. & Symonds, H.K. (2002). Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES J. Mar. Sci.* **59,** 71–80.

Nash, C.E., Iwamoto, R.N. & Mahnken, C.V.W. (2000). Aquaculture risk management and marine mammal interactions in the Pacific Northwest. *Aquaculture* **183,** 307–323.

Norberg, B. (2000). Looking at the effects of acoustic deterrent devices on California sea lion predation pattern on a commercial salmon farm. National Marine Fisheries Servive (Ed.). Seattle: Northwest Regional Office.

Olesiuk, P.F., Nicol, L.M., Sowden, M.J. & Ford, J.B. (2002). Effects of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbour porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. *Mar. Mamm. Sci.* **18,** 843–862.

Pilz, P.K.D., Schnitzler, H.U. & Menne, D. (1987). Acoustic startle threshold of the albino-rat (*Rattus norvegicus*). *J. Comp. Psychol.* **101,** 67–72.

Popper, A.N. & Fay, R.R. (1993). Sound detection and processing by fish: critical review and major research questions. *Brain Behav. Evol.* **41,** 14–38.

R Development Core Team (2013). *R: a language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL: http://www.R-project.org/.

Richardson, W.J., Greene, C.G. Jr., Malme, C.I. & Thompson, D.H. (1995). *Marine mammals and noise.* San Diego: Academic Press.

Schakner, Z.A. & Blumstein, D.T. (2013). Behavioral biology of marine mammal deterrents: a review and prospectus. *Biol. Conserv.* **167,** 380–389.

Sharples, R.J., Moss, S.E., Patterson, T.A. & Hammond, P.S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PLoS ONE* **7,** e37216.

Stoddart, C.W., Noonan, J. & Martin-Iverson, M.T. (2008). Stimulus quality affects expression of the acoustic startle response and prepulse inhibition in mice. *Behav. Neurosci.* **122,** 516–526.

Taylor, V.J., Johnston, D.W. & Verboom, W.C. (1997). Acoustic harassment device (AHD) use in the aquaculture industry and implications for marine mammals. *Proc. Inst. Acoust.* **19,** 167–274.

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

Würsig, B. & Gailey, G.A. (2002). Marine mammals and aquaculture: conflicts and potential resolutions. In *Marine aquaculture*: 45–59. Stickney, R.R. & McVey, J.P. (Eds). Wallingford, UK: CAB International.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Additional statistical information.
Appendix S2. Potential effects on target and non-target species.