FEATURE PAPER

Non-lethal management of carnivore predation: long-term tests with a startle reflex-based deterrence system on a fish farm

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Abstract

Carnivore depredation on human livestock is a worldwide problem with few viable solutions. Non-lethal management tools such as acoustic devices show highly varying success and often pose a conservation risk due to noise pollution and habitat degradation. We tested the long-term effectiveness of a deterrence system which harnesses an autonomous reflex (startle) to selectively inflict avoidance responses in a target species (*phocid* seals) by emitting band-limited noise pulses with sharp onset times. Seal predation was monitored at a marine salmon farm (test site) over a full production cycle (19 month) with a multi-transducer deterrent system deployed for the final year. Predation was also monitored for several months at two control sites and additional short-term tests were carried out at sites which suffered higher predation rates. Generalized linear (mixed) models revealed that sound exposure caused a 91% reduction in lost fish when comparing predation levels within the test site and 97% when comparing the test site against both control sites. Similarly, sound exposure led to a 93% reduction in the number of fish lost due to seal damage at a short-term test site. Visual monitoring of marine mammals around the long-term test site showed that the number of seal surfacings within 100 m from the loudspeakers was only slightly lower during sound exposure. Harbour porpoise and otter distribution around the farm was not affected by sound exposure. By adjusting the frequency composition of startle stimuli, our method has the potential to provide solutions for managing human–wildlife conflicts in terrestrial and marine habitats by selectively deterring target species.

Introduction

Carnivore depredation on human livestock is a worldwide problem which occurs in terrestrial and marine habitats (Treves & Karanth, 2003; Quick, Middlemas & Armstrong, 2004). In terrestrial habitats, livestock losses typically range from 0.2% to 2.6% (Graham, Beckerman & Thirgood, 2005), while fish farms have reported losses of up to 10% of the farm gate value (Nash, Iwamoto & Mahnken, 2000). The main depredating terrestrial taxa are *canids*, *felids*, *ursids* and *mustelids*, while *pinnipeds* are of primary concern in the marine environment (Treves & Karanth, 2003; Quick *et al.*, 2004; Baker *et al.*, 2008). Predator control methods include physical barriers, deterrent devices, relocation of animals, lethal removals of problem individuals or population control (Shivik, Treves & Callahan, 2003; Quick *et al.*, 2004; Baker *et al.*, 2008). Physical separation of predator and prey can be effective but costs are

often high and measures are difficult to implement (Quick *et al.*, 2004; Baker *et al.*, 2008). Population control is not always effective since predator density is not necessarily related to the amount of losses (Graham *et al.*, 2005). Culling of individuals may be effective in some cases but removed individuals can also be quickly replaced by new arrivals (Landa *et al.*, 1999). Furthermore, culling may have adverse effects on populations (Thompson *et al.*, 2007), ecosystem functioning (Terborgh *et al.*, 2001) or wildlife stocks of commercial interest (Yodzis, 2001). In addition, shooting of 'charismatic' top predators carries a reputational risk for farmers (Nash *et al.*, 2000).

The main problem associated with many deterrents is a lack of long-term effectiveness which can be the result of habituation, that is a decrease in the responsiveness of an animal as the result of repeated exposure (Jefferson & Curry, 1996; Shivik *et al.*, 2003; Baker *et al.*, 2008; Götz & Janik, 2013). In the marine environment, acoustic

deterrents cause additional problems, namely long-term habitat exclusion in non-target species, large-scale noise pollution and the potential to permanently damage the auditory system of target and non-target species (Götz & Janik, 2013). The population level effects of behavioural disturbance and hearing damage caused by anthropogenic noise pollution are of increasing concern (Boyd *et al.*, 2011). Habitat exclusion by current acoustic deterrent devices (ADDs) has been shown in a range of *odontocete* species and exclusion effects can persist over several years (Morton & Symonds, 2002). These effects are most likely a result of odontocetes being more sensitive than seals at the frequencies used in deterrent devices (Götz & Janik, 2013). Hence, there is a need for deterrent systems which (1) address the habituation problem, (2) do not pose a risk of damaging the hearing of target and non-target species and (3) do not lead to large-scale habitat degradation through displacement of non-target species.

Most ADDs either project loud sound aimed to elicit pain, use predator calls or employ continuous high duty-cycle artificial sounds (Bomford & Obrien, 1990; Götz & Janik, 2013). Inflicting pain is problematic because animals are likely to suffer hearing damage (Campbell & Bloom, 1965), while using predator calls can desensitize animals to natural predators. Animals often habituate quickly to long-duration artificial sounds irrespective of stimulus variation (Götz & Janik, 2010). A new avenue is the use of sounds which are optimized to harness autonomous reflexes associated with flight behaviour. One candidate is the acoustic startle reflex, an oligosynaptic reflex which is triggered by short onset time stimuli (Yeomans *et al.*, 2002). In grey seals *Halichoerus grypus*, repeated elicitation of the startle reflex leads to sensitization of avoidance responses, interruption of foraging behaviour and flight responses (Götz & Janik, 2011). The use of the startle reflex is advantageous because inter-species differences in hearing abilities can be exploited to specifically target a group of species: an initial field test showed that startle eliciting sound pulses could be used to successfully deter pinnipeds without affecting harbour porpoise (Götz & Janik, 2015). However, the applicability of such a method as a conservation tool will depend on its ability to reduce long-term livestock damage.
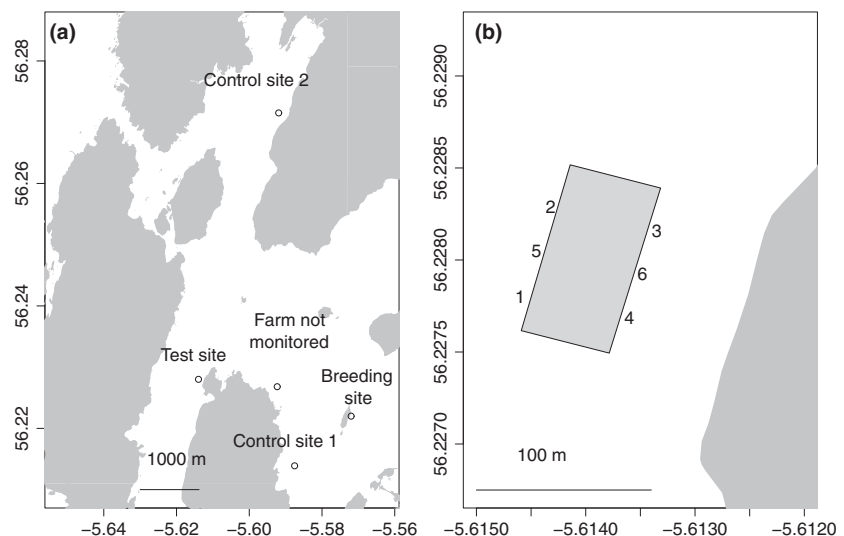
Here, we tested effectiveness of a startle reflex-based deterrence system on predation on fish farms in Scotland using counts of dead fish and visual detection of marine mammals as indicators of functionality.

Materials and methods

Study sites

Experiments were carried out at one long-term and two short-term test sites (Fig. 2). The long-term experiment took place on a marine salmon *Salmo salar* farm on the west coast of Scotland (Fig. 1), which consisted of a 2 × 4 grid of rectangular steel cages. Two salmon farms in spatial proximity to the test site (operated by the same company) were used as control sites. Control site 1 consisted of a grid of two columns of isolated circular cages with a maximum of six cages in each column. Control site 2 consisted of a 2 × 9 grid of cages and was partly stocked. These farms had not previously operated a deterrent system, but seal predation was present in previous production cycles. The test site and control site 1 were stocked in October 2010 and harvested between February and April 2012. Control site 2 was first stocked with large fish shortly before harvest (April–May 2011), was then fallow and consecutively re-stocked with fish which were on the same production cycle as the test site. We used this site as a short-term test site in April and May 2011 when it unexpectedly suffered higher levels of predation. It was consecutively used as control site 2 for the long-term study after it was re-stocked with fish on the same production cycle as the test site. The second short-term test site was located in the Orkney Islands in

Figure 1 (a) Map of site locations at which experiments were carried out (Scotland/UK) and (b) transducer locations used at the main long-term test site (see also Supporting Information Appendix S2).

Kirkwall Bay (N 59.0072, W 2.9848) and contained smolts in four cages.

Acoustic deterrent device

The ADD consisted of 2–4 transducers (Lubell LL 9162T; Lubell Labs Inc., Whitehall, OH, USA.), two stereo Lanzar Vibe 292 (Lanzar Inc., New York, NY, USA) power amplifiers, an Edirol R-44 4-channel recorder, Roland Corporation, Hamamatsu, Japan (used as a sound player), a marine power supply (CTek M200, CTek, Vikmanshyttan, Sweden) connected to the generator of the fish farm and a car battery. The car battery was charged from the power supply whenever the generator was running while the device was running from the battery for the rest of the time. All components were mounted on a metal frame in a watertight case. The control box was deployed in the centre of the farm and transducers were positioned at the respective locations shown in Fig. 1. The two main loudspeaker configurations consisted of speakers running at positions 1, 2, 3, 4 (~4 months) and at positions 1, 2, 6 (~8 months). The breakdown of two power amplifiers, a power supply and cable cuts resulted in off periods. We provide a complete record of ADD operations, loudspeaker configurations and breakdowns (Supporting Information Appendix S1).

The device which was temporarily deployed at control site 2 for the short-term test consisted of a single transducer driven by a Cadence Z 2000 (Cadence Sound, Industry, CA, USA) power amplifier. The Orkney device consisted of two loudspeakers connected to a control Box which contained a Lanzar Vibe 292 power amplifier (in stereo mode), a Sony NWZE453B E player (Sony, Tokyo, Japan) and a car battery.

Sound exposure and experimental protocol

The ADD emitted 2–3 octave-band noise pulses (200 ms duration) with sharp rise times of <5 ms (similar to the ones used by Götz & Janik, 2015). Pulses were emitted at pseudorandom intervals with an overall duty cycle (i.e. time during which sound is emitted) of 0.8–1%, only playing sounds from one transducer at a time. Successive pulses played from different transducers in a pseudorandom sequence. The source level was set in a series of measurements from a pontoon in a harbour using a B&K 8103 hydrophone connected to a B&K 2635 charge amplifier and a M-audio Microtrack II recorder which was calibrated using the charge amplifier's test tone (see Götz & Janik, 2015, 2.3 m distance between hydrophone and speaker, 2 m depth, source level were back-calculated assuming spherical spreading). Broadband source levels were found to be 176–179 dB re 1 µPa [root mean square (rms)] at 1 m distance. The source level of the device used temporarily at control site 1 was ~180 dB re 1 µPa (rms), while the device deployed in Orkney only operated at 174–176 dB re 1 µPa (rms). Loudspeakers were deployed below the main part of the cage to prevent shadow effects (12–14 m depth).

The acoustic deterrent system on the main test site was first installed on 16 January 2011 with two transducers operating but was consecutively expanded to operate with four transducers on 7 February 2011 (see also Supporting Information Appendix S1). On 12 May 2011, one speaker was removed and the system used three transducers for the remaining time. The device was removed after 12.5 months on 1 February 2012. The deterrent device on control site 2 was deployed on 18 May 2011 and operation ceased with completion of the harvest on 31 May 2011. Deployment at the short-term test site in Orkney started on 2 July 2011 and lasted ~2 weeks with the exact date of its breakdown during the storm unknown.

Predation and marine mammal monitoring

Predation monitoring was carried out using a variety of techniques based on industry standards. Data were collected using a combination of sources including questionnaires, logbook entries and specific counts. Seal-related mortalities were identified using bite marks and appearance of the carcass (see Supporting Information Appendix S2 for details). Data have been collected for 18 months on the test site with 2.5 months during pre-deployment, 12.5 months during sound exposure and 3 months post-deployment. Data from control sites were collected for 8 months (control site 1) and 7 months (control site 2) respectively. For the long-term test, predation data were pooled for each month. The short-term test at control site 2 involved data from a 6-week period (2 weeks of sound exposure), while the test in Orkney included data from a 4-week period (1–2 weeks of sound exposure).

A theodolite tracking method was used to determine surface positions of marine mammals in the vicinity of the farm. Visual observations were conducted from the roof of a feed barge and data were only included in the analysis if sea state was less than or equal to 2. Observations were carried out on 19 days during sound exposure and 12 control observation days. The overall observation effort was 25 h 20 min during the pre-deployment/control periods and 76 h 15 min during sound exposure. If sound exposure and control periods occurred on the same day (i.e. due to repairs) surfacings were counted separately for both periods. Grey seal *Halichoerus grypus* sightings (*n* = 2) were pooled with harbour seal *Phoca vitulina* sightings which are presented as 'seals'. Other marine mammals present were harbour porpoises *Phocoena phocoena* and European otters *Lutra lutra*.

Sound field measurements

Sound field measurements were conducted around the long-term test site from a Zodiac inflatable boat at various distances from the three transducers. Recordings were made with a Reson TC4014 hydrophone and a Tascam DR-2d recorder, TASCAM, Montebello, CA, USA (sam-

pling rate = 96 kHz) when the boat was drifting with the engine switched off. The position of the boat was recorded with a GPS transceiver or laser range finder at regular intervals and corresponding times were noted. Only the loudest pulses for which a position was available were analysed in order to only include direct arrivals of pulses from the closest transducer. Sound pressure levels (SPL) were calculated as SPL = $|Mx| - G + 20 \times \log(V)$ with $|Mx|$ being the voltage sensitivity of the hydrophone (in dB re 1 V µPa^{-1}), G being any gain in the recording chain (i.e. the recording gain of the Tascam) and V being the voltage of the signal measured (Au, 1993). Measured received levels (RLs) are presented as rms SPL. The recording depth was used to calculate real distances between the hydrophone and closest speaker using Pythagoras' theorem. A 1/3 octave-band analysis was carried out in Matlab R (MathWorks, Natick, MA, USA) 2011b for pulses recorded at 19–20 m (average of 3) and 100–102 m (average of 4) which were recorded at 5 and 13 m depth respectively. We also calculated 1/3 octave bands for the source level estimate using the data from the previously mentioned sound source calibration conducted prior to the experiment in a local harbour.

Data analysis and statistical modelling

All statistical analysis was conducted in R 3.0.2 (R Core Team 2013). Predation and marine mammal monitoring data were analysed with generalized linear (mixed) models (GLMM) (logarithmic link function) using the glmmADMB package (Skaug et al., 2013). This approach allowed us to test a range of error distributions which can deal with over-dispersed data (e.g. negative binomial), take zero inflation in the data into account when necessary and consider random effects, which account for variation in the dataset but are not of primary interest in the context of this study (Bolker et al., 2009). A stepwise model selection process was carried out and the models with the lowest, second order Akaike information criterion (AICc) were selected. In a first step, the optimal error distribution and the need for using the zero-inflation argument was tested using the fully populated model. In a second step, the optimal combination of random effects was determined while consecutively the optimal fixed effects combination was determined. Model specifications, coefficients, confidence intervals, P values, error distributions and offset terms considered during model selection are presented in the Supporting Information (Appendix S3).

The main purpose of the predation data analysis was to estimate the reduction in predation caused by the device; hence, only sound exposure was included as a fixed effects factor. The response variable was a count of seal-related losses per month (long-term test) or counts since the previous count (short-term tests). Random effects factors assessed in the predation models included 'quarter of the year' (to account for seasons), '2-month period' (long-term test) and cage ID (short-term tests). Four models were calculated to compare (1) pre/post-deployment versus sound exposure period at the main test site (with days per period as offset), (2) test and control sites including all months for which data were available from at least one of the control sites (with days per period as offset), (3) pre-deployment and sound exposure period for short-term test site 1 and (4) pre-deployment and sound exposure for short-term test site 2.

The response variable for marine mammal monitoring data was surfacings per day. 'Moulting season' was assessed as an additional factor in the seal model. It was defined as the 2 months following the date after which harbour seals start to change fur (early August). The only random effect assessed was 'quartal', reflecting the time of the year. Data were analysed in two distance bins for seals (<100 m from the closest transducer and 100–200 m from the closest transducer) and as one bin of all surfacings up to 200 m from the closest transducer for porpoises. All models contained an offset term which represented the number of observation hours (with one decimal point) on any given day.

Sound field measurement data were analysed using a GLM (Gaussian error distribution, linear link function). The logarithm (base 10) of the distance to the closest loudspeaker was included as the main predictor variable while recording depth (5 m or 13 m) and its interaction with distance was evaluated as an additional factor: only distance was retained in the final model with the lowest AIC.

Results

Predation

Seal predation was significantly reduced at the long-term test site during the test period (Fig. 2a). The highest numbers of fish lost to seal attacks occurred in the beginning of the production cycle prior to deployment of the device (Fig. 2a). There was no seal predation in 10 out of the 12.5 months during which the acoustic deterrence system was operating on the main test site. The generalized linear model showed a highly significant reduction in the number of fish lost during sound exposure compared to the pre- and post-deployment phases ($P = 0.0005$). Model coefficients show that the operation of the deterrent device caused a 91% reduction in seal predation (Fig. 3). The GLMM used to analyse losses at the test and the two control sites also showed a highly significant effect of sound exposure on seal predation ($P = 0.0008$). When comparing sites, operation of the acoustic device caused 97% reduction in the number of fish lost to seal attacks (Fig. 3). Control site 1 suffered the highest predation losses from May to August 2011, while control site 2 was mostly affected in August and September (Fig. 2a).

Short-term test site 1 only contained two stocked cages with fully grown fish awaiting harvest. Both cages suffered predation losses prior to deployment of the acoustic deterrent system but predation dropped after the start of
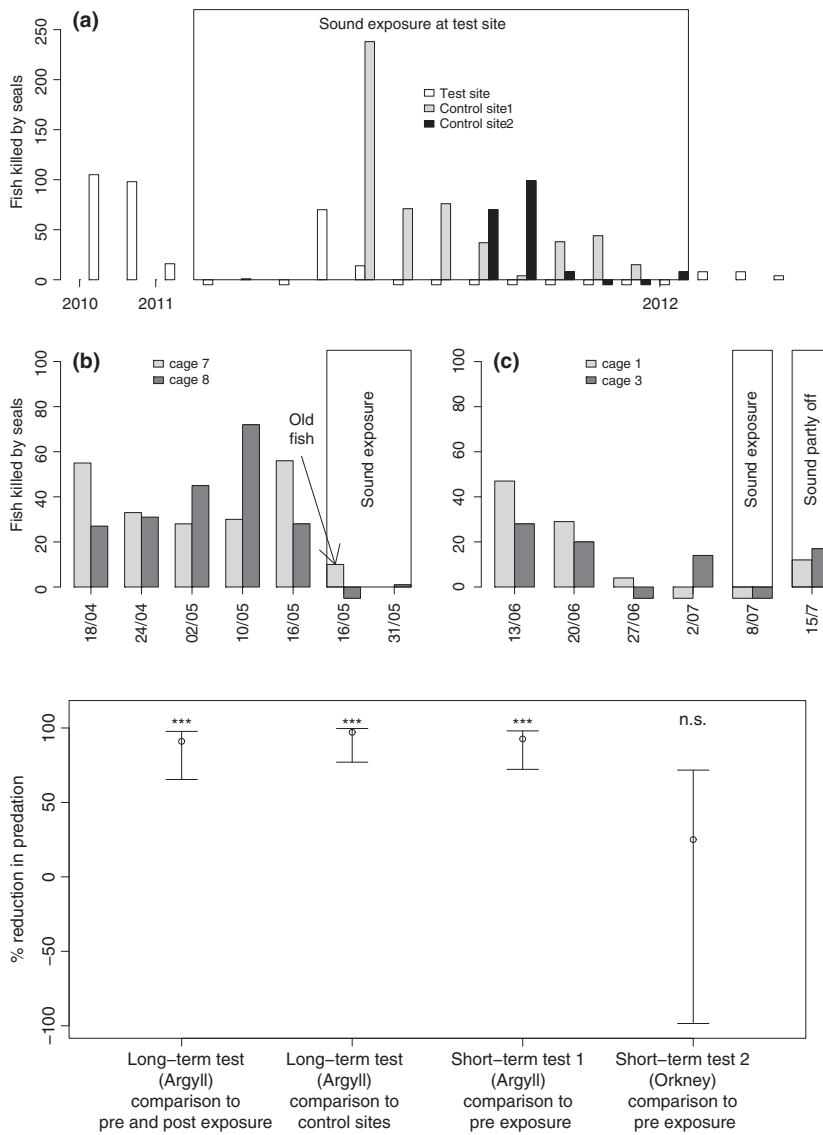
Figure 2 Fish lost due to seal attacks (a) at the long-term test site in comparison to the control sites, (b) at short-term test site 1 and (c) short-term test site 2. Bars with numbers below zero indicate that predation data were available but no losses occurred. Absence of bars indicates that no data were available. The box (a) indicates the time with sound exposure.

Figure 3 Reduction in predation caused by sound exposure at the long-term test site and during the two short-term tests. Asterisks depict the significance level (***$P < 0.001$). The graph shows model coefficients and confidence intervals (5%, 95%) obtained from the generalized linear (mixed) model which are presented as a 'percentage reduction' with zero representing no change and 100% representing absence of predation during sound exposure.

the 2-week sound exposure period (Fig. 2b). Old, decayed fish were retrieved when the net was removed after harvest, but it is uncertain whether these were killed during sound exposure (see Fig. 2b). These fish were included as losses during sound exposure. Nevertheless, the generalized linear model showed a highly significant effect ($P = 0.0001$) of the acoustic deterrent system on the number of fish lost due to seal predation: sound exposure was estimated to have caused a 93% reduction in seal-related losses (Fig. 3).
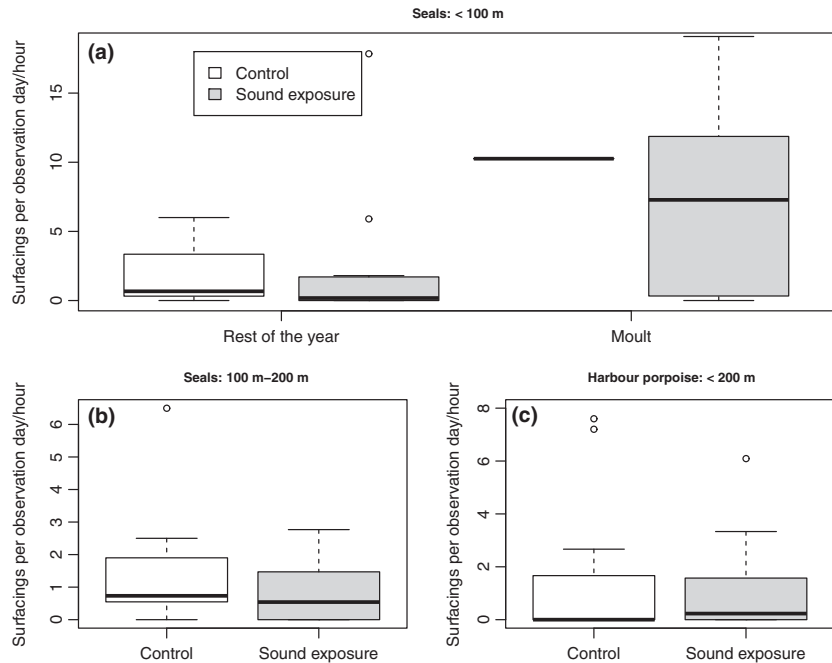
The second short-term test conducted at the site in the Orkney Islands revealed moderate to low predation losses of newly stocked fish (smolts) prior to the operation of the device (Fig. 2c). Predation losses were already declining before the device was switched on. Seal predation was completely absent during the first week of operation of the deterrent device, but predation recurred during the second week. However, the functioning of the device was

compromised due to delayed battery changes and complete destruction in a storm during the second week of operation. Here the effect of sound exposure was not significant ($P = 0.56$). The large confidence interval reflect the uncertainty associated with the estimate (Fig. 3).

Marine mammal monitoring

While sound exposure did not cause a dramatic change in the number of seals observed within 100 m of the closest transducer, distinct seasonal differences in seal abundance were found (Fig. 4a). The model retained 'moulting period' as a significant factor ($P = 0.012$) and indicated that 3.3 times more surfacings occurred during this time period. Many of these seals were pups, presumably from a nearby breeding site (see Fig. 1a). The model coefficient for sound exposure indicates that there might have been a reduction (~57%) in seal surfacings but the

Seals: < 100 m

Figure 4 Seal (a, b) and porpoise surfacings (c) within various ranges from the closest transducer. Seal surfacings within 100 m of the farm during sound exposure and control observation periods are shown separately for the 'moult' and the rest of the year (a). The box shows median and quartiles, the whisker depicts the nominal range of the data inferred from the quartiles with outliers being shown as open circles. [Correction added on 19 May 2016 after first online publication: Figure 4 has been replaced to correct the labelling of the data in Fig. 4A].

effect only approached significance ($P = 0.068$). This is also supported by the strong variability in seal sightings across observation days, both within the sound exposure and control observation period (Fig. 4a). The model for seal sightings between 100 and 200 m distance showed that surfacings were not affected by sound exposure ($P = 0.172$).

Harbour porpoise groups were observed regularly during pre-deployment periods and during operation of the device at various distances from the farm (Fig. 4c). There was no significant effect of sound exposure on the number of harbour porpoise surfacings observed within 200 m from the closest transducer ($P = 0.93$). The median number of surfacings per hour was roughly similar during control and sound exposure periods (Fig. 4c, model coefficient: 1.05).

Otter sightings were rare and only occurred on 2 days during control periods and 5 days during sound exposure. Most sightings were inshore to the southeast of the fish farm. During sound exposure periods, 11 surface positions at distances between 58 and 372 m from the closest transducer were observed, while seven surfacings (54–201 m) were logged during control periods.

Sound field measurements and spectrum

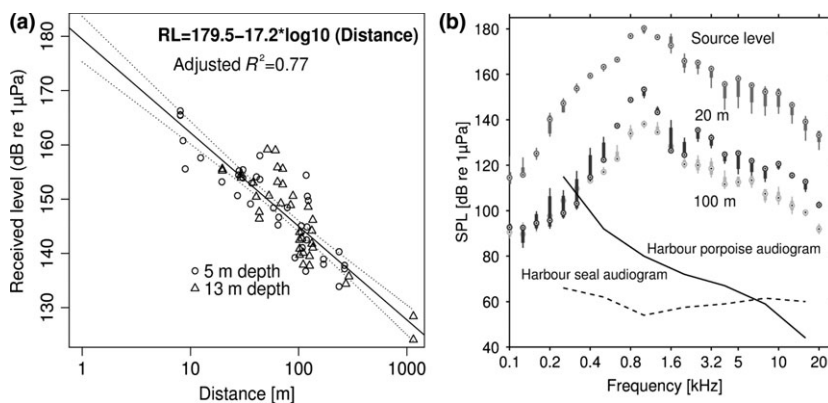Sound field measurements showed a logarithmic drop of RL with increasing distance (Fig. 5a). The only variable

Figure 5 (a) Sound propagation around the fish farm. The graph shows direct measurements at different depths and predictions obtained from a linear regression model (solid line) with confidence intervals (5%, 95%) (dashed lines). (b) Boxplots (median, 25%/75% quantiles & remaining data) show received levels in 1/3 octave bands for averages across 3 and 4 pulses for distances of ~20 and ~100 m respectively. The source level estimate is based on an average of four pulses and was back-calculated assuming spherical spreading. The hearing thresholds (audiograms) for harbour porpoise (Kastelein et al., 2002) and harbour seals (Kastelein et al. 2009) are shown for illustrative purposes.

retained in the final model was the $\log_{10}$ (distance) which was highly significant ($P < 0.0001$). Recording depth was not retained in the model selection process indicating that propagation was roughly similar at the two measured depths (5 and 13 m). The GLM revealed a strong correlation between the logarithm of the distance and the measured RL (adjusted $R^2 = 0.77$). The relationship between the decrease in RL and distance was calculated as:

$$RL = 179.5 \text{ dB re } 1\,\mu Pa - 17.2 \times \log_{10}(\text{distance}),$$

with 179.5 dB being the source level at 1 m distance (model intercept) and 17.2 representing the slope of the regression line. This source level estimate is similar to the close-range measurements carried out while calibrating the device (see Materials and methods section).

The one-third octave band analysis at various distances showed that the central 1 kHz band was transmitted at a back-calculated source level (1 m distance) of almost 180 dB re 1 μPa. Some frequency scatter outside the central band at 1 kHz was present towards higher and lower frequencies (Fig. 5b).

Discussion

Predation

Previous studies on carnivore predation control have shown a lack of long-term effectiveness which can result from various biological processes including hearing damage, habituation or associative learning, sometimes turning the initial deterrent into an attractant (Jefferson & Curry, 1996; Shivik et al., 2003; Baker et al., 2008; Götz & Janik, 2013; Schakner & Blumstein, 2013). Habituation is a common problem in these applications (Shivik et al., 2003; Schakner & Blumstein, 2013) and food motivation can accelerate the process, a phenomenon which has been documented in conventional devices (Götz & Janik, 2010). In order to maintain long-term efficiency, the direct costs and perceived risk inflicted by a deterrent need to exceed the benefits of depredation, therefore causing the animal to adopt a 'natural foraging' mode (Schakner & Blumstein, 2013). The statistical modelling showed that sound exposure reduced predation at the test site by 91–97% (Fig. 3). The effect of the startle device on predation levels seems to be stronger than what has previously been reported for acoustic deterrence methods used in terrestrial (Shivik et al., 2003) and marine applications (Fjalling, Wahlberg & Westerberg, 2006). Predation was limited to 2 out of the 12.5 months sound exposure period. These 2 months (April and May 2010) were close to the beginning of the sound exposure period (Fig. 3a) meaning that predation was not likely to be the result of habituation. The result from the main test site was also supported by short-term test 1 where fully grown fish were predated upon and predation ceased after installation of the device. The decayed fish found at

the bottom of the net during harvest were most likely the result of predation before the sound exposure period (Fig. 2c), but this could not be shown unequivocally. Even though we included these decayed fish as seal-related kills during the sound exposure period, the model indicated a 93% reduction in seal predation. The results from short-term test 2 were ambiguous, but the results were confounded by temporary off periods during the second week (delayed battery change). The difference between short-term test 2 and the other tests could either be the result of differences in seal behaviour or be the result of a seal exploiting the temporary off period. In general, predation events during sound exposure may occur for the following reasons. First, adult seals may have compromised hearing due to previous noise exposure, disease or age-related hearing loss (presbycusis) (see Yamasoba et al., 2013, for humans). Significant age-related hearing loss can lead to a reduction, or in extreme cases disappearance, of the acoustic startle response and would therefore reduce deterrence ranges (Ouagazzal, Reiss & Romand, 2006). Second, elicitation of the startle reflex may not always result in a consistent flight response, that is there may be some form of cognitive control over the follow-up behaviour in some individuals but this may be less likely (Götz & Janik, 2011, 2015). Third, seals may have found a way to exploit acoustic shadow effects around the cages using locations where the RL drops below the startle threshold.

Effect on seal abundance

In the light of the relatively clear results in the predation data, it is puzzling that seal surfacings occurred within 100 m of the transducers (Fig. 4a). The 100 m distance bin was chosen because it reflects the maximum distance at which the modelled RL (145 dB re 1 μPa, Fig. 5) exceeds the startle threshold based on theoretical considerations (see also Götz & Janik, 2015). The result of sightings up to 200 m of the farm stands in contrast to an earlier study which showed a strong reduction in seal tracks within 250 m of a fish farm protected by a single transducer (Götz & Janik, 2015). Captive experiments with grey seals showed that repeated elicitation of the startle reflex leads to a decrease in time spent underwater close to a feeding station (Götz & Janik, 2011). Animals in the current study may have undergone a similar sensitization process which would have led to reduced dive times. Once the head is out of the water, RL would drop below the startle threshold and animals may approach the farm more closely. Increased surface times would also make seals more detectable to observers. However, for a seal to obtain fish from the cage without penetrating the net it needs to form pockets with its flippers or push the net upwards from the bottom. All of these actions require the animal to spend a significant time underwater. These actions would be prevented by the mentioned sensitization process. This is supported by the fact that there was no predation in the month with the highest seal counts in the vicinity of the farm. Animals seen with

the head above the water close to the farm may have experienced a startle response once they dove and consecutively moved further away from the farm.

The highest seals numbers were observed during the moult. A large number of these animals were pups, most likely from a nearby breeding site 3 km from the fish farm (Fig. 1). We often found this haul out to be devoid of seals, except for July to September when 15–30 animals were present. Harbour seal pupping takes place between the end of June and beginning of July and females remain within 2 km of the breeding site during this time (Thompson et al., 1994). Newborn pups can swim from birth, but increase the time they spend in the water during the following 2 weeks (Jorgensen et al., 2001). Female seals begin moulting in early August and spend more time hauled out during this time (Thompson et al., 1989). Since newborn pups do not moult during their first year of life, the adult 'moulting period' coincides with the time when pups begin to increase their ranging patterns. The high number of juvenile seals observed around the farm may be the result of pups exploring this area (Fig. 4a). However, as stated above, this high abundance of seals at the surface did not coincide with increased depredation.

Target specificity of the deterrence method

Conservation concerns have been raised regarding acoustic harassment or deterrent devices commonly used on fish farms. These devices seem to cause large-scale habitat exclusion in non-target species, namely odontocetes with good high-frequency hearing (Morton & Symonds, 2002). Thus, it is important to take the acoustic acuity of affected animals into account when designing repellents (Treves, Wallace & White, 2009; Götz & Janik, 2013). The method presented in our study used an autonomous reflex to selectively inflict startle responses in the target species but not in the non-target species by choosing a frequency band where target species are more sensitive (Götz & Janik, 2013, 2015). We found that porpoise abundance around the fish farm was unaffected by sound exposure (Fig. 4a), a result that is consistent with an earlier study testing shorter exposure periods (Götz & Janik, 2015). The 1/3 octave band analysis at 20 m distance showed that the central band at 1 kHz exceeded the auditory threshold of a seal by 98 dB (sensation level), while none of the 1/3 octave bands exceeded the hearing threshold of a porpoise by more than 72 dB (Fig. 5b, see Kastelein et al., 2002, 2009, for audiograms). The latter sensation level would typically be insufficient for eliciting significant startle responses in mammals (Ouagazzal et al., 2006). The low-frequency components of the signal measured at 20 m distance did not significantly exceed the detection threshold of the farmed fish (see Hawkins & Johnstone, 1978, for audiogram). In previous studies harbour porpoises have been shown to respond to sounds at a relatively low RL at frequencies between 8 and 80 kHz (Johnston, 2002; Kastelein et al., 2005; Brandt et al., 2013). Since harbour porpoises did not respond to

our playbacks, we feel confident that results would be similar with other odontocete species, such as bottlenose dolphins Tursiops truncatus or long-finned pilot whales Globicephala melas, which have a broadly similar hearing sensitivity to harbour porpoises but generally seem to tolerate noise much better (Cox et al., 2004; Antunes et al., 2014). We also observed European otters near the fish farm. While no hearing data are available for this species, American sea otters Enhydra lutris have less sensitive underwater hearing than most pinnipeds (Ghoul & Reichmuth, 2013). If European otter hearing is similar, one would not expect deterrent ranges to exceed those in pinnipeds. A detailed discussion on potential effects of the signals used in our study on mammals, fish and invertebrates has been provided elsewhere (Supporting Information Appendix S2 in Götz & Janik, 2015) and showed that adverse effects are unlikely. In conclusion, target-specific deterrence can be achieved by exploiting taxon-specific differences in hearing abilities and these principles could also be used in terrestrial applications.

Implications for managing carnivore populations

Carnivore predation causes a variety of direct and hidden costs (Barua, Bhagwat & Jadhav, 2013) and requires management solutions. The startle reflex is an evolutionarily ancient reflex arc which is conserved in all mammals studied (Yeomans et al., 2002). The method tested in our study holds the potential to address human–wildlife interactions in a variety of different terrestrial and marine applications and species. The most direct conservation benefits are (1) removing the need for population control or lethal takes which have in some cases been shown to be responsible for population declines (Thompson et al., 2007) or cause additional strain on declining populations (Lonergan et al., 2007), (2) finding solutions in situations where population control is ineffective (Graham et al., 2005), (3) mitigate the risk of secondary ecosystem effects as the result of predator decline (Terborgh et al., 2001). In addition, noise pollution can be significantly reduced by using duty cycles which are at least one order of magnitude lower than in conventional devices (Götz & Janik, 2013). Target specificity can be achieved by choosing a frequency band where hearing sensitivity in target species is higher than in non-target species. Deterrence zones can be limited to an area where the RL exceeds the startle threshold enabling managers to create defined exclusion zones without affecting the wider environment. This method has also promise to deter animals from areas of potential harm, such as tidal turbines in marine mammals or wind turbines in bats.

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Conflict of interest

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Supporting information

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

Appendix S1. Record of seal scarer operation and loud-speaker configurations.
Appendix S2. Predation monitoring.
Appendix S3. Specification and results of generalized linear (mixed) models.