

Acoustic risk balancing by marine mammals: anthropogenic noise can influence the foraging decisions by seals

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Abstract

1. Avoidance of anthropogenic sounds has been measured in many species. The results, which are typically based on observations in limited exposure contexts, are frequently used to inform policy and the regulation of industrial activities. However, the occurrence and magnitude of avoidance may be a consequence of complex risk-balancing decisions made by animals. The importance of the factors in decision-making, such as perceived risks associated with the sounds or prey quantity and quality during sound exposure, is unknown.
2. Here we address this knowledge gap by measuring the relative influence of perceived –risk of a sound (silence, pile driving, and a tidal turbine) and prey patch quality on decision-making and foraging success in grey seals *Halichoerus grypus*.
3. Seals were given access to two underwater ‘prey patches’ in an experimental pool where fish were delivered at controlled rates to simulate a low-density (LD) and a high-density (HD) prey patch. Acoustic playbacks were made using an underwater speaker above one of the prey patches (randomised during the study), and three decision and foraging metrics (foraging duration, foraging effort allocation between the prey patches, and foraging success) were measured.
4. Foraging success was highest during silent controls and was similar regardless of speaker location (LD/HD). Under the tidal turbine and pile-driving treatments, foraging success was similar to the controls when the speaker was located at the HD prey patch but was significantly reduced (~16%–28% lower) when the speaker was located at the LD prey patch. Foraging decisions by the seals were consistent with a risk/profit balancing approach. Avoidance rates depend on the quality of the prey patch as well as the perceived risk.
5. *Policy implications.* The results suggest that foraging context is important when interpreting avoidance behaviour and should be considered when predicting the effects of anthropogenic activities. For example, sound exposure in different prey patch qualities may result in markedly different avoidance behaviour, potentially leading to contrasting predictions of impact in Environmental Assessments. We recommend future studies explicitly consider foraging context, and other

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contextual factors such as behavioural state (e.g. foraging or travelling) and habitat quality.

KEYWORDS

avoidance, behavioural responses, foraging, marine mammals, pile driving, renewable energy, tidal turbines, underwater noise

1 | INTRODUCTION

Predator survival is fundamentally determined by their ability to effectively find and capture prey; this involves constant decision-making about how to balance time spent foraging with time spent carrying out other behaviours. Such foraging decisions are likely to be affected by a range of internal factors such as hunger level, health condition and reproductive status, and by external factors such as the abundance or availability of prey, intra- and interspecific competition, and predation risk (Lima & Dill, 1990; Stephens et al., 2007).

For marine air breathing predators (e.g. marine mammals), time spent foraging must be offset against time spent at the water surface between dives replenishing oxygen stores, readjusting blood pH and processing metabolites (Kooyman et al., 1981). This therefore requires a series of foraging decisions that are subject to the normal constraints of foraging on patchily distributed prey, but with an additional set of rigid, short-term constraints imposed by the need to feed underwater and load oxygen at the surface (Sparling, Fedak, et al., 2007; Thompson & Fedak, 2001). External factors that compromise decision-making during foraging may have detrimental consequences for foraging success and ultimately individual fitness (Voellmy et al., 2014), and for species such as marine mammals that have rigid physiological constraints, these effects may be particularly acute.

In the last few decades, there has been increasing concern about how anthropogenic noise from sources such as construction, resource extraction and transportation, might affect animals (e.g. Blickley & Patricelli, 2010). There is a growing literature demonstrating that noise can affect the behaviour of animals (e.g. Bruum, 2013; Götz & Janik, 2011; Hastie et al., 2014; Schaub et al., 2008) which can lead to changes in foraging success; studies have reported that anthropogenic noise can reduce the foraging success of terrestrial animals as a result of acoustic masking (Siemers & Schaub, 2011), and a number of studies of birds and mammals have shown decreases in foraging success as a result of increases in vigilance behaviour in response to noise exposure (e.g. Barber et al., 2010; Quinn et al., 2006).

There is increasing evidence that underwater noise can compromise the foraging behaviour of marine species including fish (Purser & Radford, 2011; Voellmy et al., 2014) and invertebrates (Wale et al., 2013). A limited number of studies have investigated the effects of sound exposure on the foraging behaviour (e.g. Aguilar Soto et al., 2006; Blair et al., 2016) and prey capture rates (Kastelein et al., 2019; Wisniewska et al., 2018) of marine mammals, and have inferred that these might have longer-term fitness consequences (e.g. Blair et al., 2016; Williams et al., 2006). Despite this,

experimental evidence on the direct effects of noise on the foraging decisions by marine mammals and how these relate to foraging success is largely lacking. This is a key data gap in our understanding of the true risks of exposure to anthropogenic noise.

In this study, we address this knowledge gap and investigate whether anthropogenic sound affects foraging decisions by grey seals *Halichoerus grypus*. Specifically, we measure the influence of acoustic signals indicative of two offshore activities (pile driving and an underwater tidal turbine) that have previously been shown to elicit avoidance responses by wild seals (Hastie et al., 2018; Russell et al., 2016) on foraging decisions and foraging success within a simulated foraging scenario in a captive environment.

2 | MATERIALS AND METHODS

2.1 | Experimental setup

Experimental trials were carried out with five temporarily captive grey seals (two females and three males) during 2014 at the Sea Mammal Research Unit captive seal facility. For more information on the seals, their capture history, and their experimental trials, see Supporting Information; Appendix S1. Throughout the study, the seals were housed in outdoor seawater pools at ambient temperature and fed a diet of herring, *Clupea harrengus* and sprat, *Sprattus sprattus*, supplemented with vitamins (Aquavits and Ferrous Gluconate, International Zoo Veterinary Group, Keighley, U.K.). All experimental protocols were carried out with UK Home Office approval under project licence number 60/4009, in accordance with the Animals (Scientific Procedures) Act 1986.

During an experimental trial, a single seal was housed within a large experimental pool (42-m long × 6-m wide × 2.5-m deep) for a period of 60 min (Figure 1). Aluminium mesh panels 0.5 m below the water surface covered the majority of the pool, and access to the surface was only available in a clear acrylic breathing chamber situated at one side of the pool. Each seal was trained to swim from the breathing chamber to two 'prey patches' via a series of underwater lanes (Figure 1). To simulate each prey patch, an aluminium-framed conveyor belt was deployed at two of the corners of the pool (approximately 63-m swimming distance from the breathing chamber). These were used to deliver fish underwater at a controlled rate; this setup is described in detail in Sparling, Georges, et al. (2007). It is important to highlight that, for practical purposes, this setup uses horizontal swimming to represent dives; although the consequences of buoyancy, pressure and swimming mode may be different in

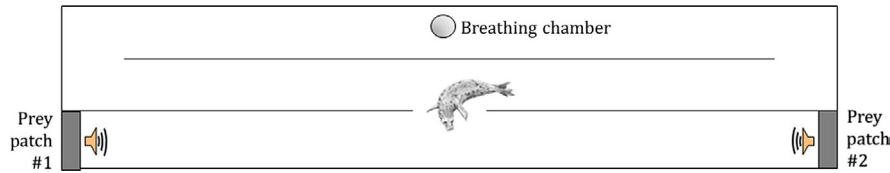


FIGURE 1 Plan view of the experimental pool (42 m long x 6 m wide x 2.5 m deep) showing the location of the breathing chamber, the two simulated prey patches (shaded boxes), and the speaker locations (active or dummy). The figure also shows the configuration of the swimming lanes (shown by the horizontal lines) between the breathing chamber and the prey patches

vertical dives, it is a valid approximation of diving effort in phocid seals (Sparling & Fedak, 2004).

A total of 0.75 kg of sprat (approximately 100 fish) were made available at each of the prey patches during a trial (1.5 kg in total which represented approximately 0.5–0.75 of their daily food); however, the presentation rate of prey varied between the prey patches to simulate a low-density (LD) and a high-density (HD) prey patch during each trial. The prey presentation rate was 36 fish/min at the HD patch and 18 fish/min at the LD patch. These rates were chosen to represent prey patches with contrasting reward levels during the trials; however, it is important to highlight that these are likely to be markedly higher than prey encounter rates observed in wild seals (Bowen et al., 2002; Heaslip et al., 2014). As the seal consumed fish from each patch, the number removed was noted and they were replaced by new fish on the conveyor belt to maintain a consistent patch density; however, once the 0.75 kg of fish had been placed on the conveyor belt, any further fish removed by the seal effectively reduced the prey density at the patch in future dives.

Throughout the trials, seals were permitted to freely dive from the breathing chamber to spend time foraging at either, or both, of the prey patches. Video cameras were mounted above the breathing chamber and at each of the prey patches so that the seals' presence at these locations could be recorded and monitored.

Seals were not fed overnight prior to a trial and each seal carried out a maximum of one trial per day. Up to four trials were completed on any 1 day and the number of days between consecutive trials for individual seals ranged between 1 and 8 days ($M = 2.6$). On days when seals did not carry out a trial, they were housed in a separate holding pool at the facility and fed once or twice a day.

2.2 | Acoustic playbacks

To measure the effects of anthropogenic noise on the foraging behaviour of seals, a series of underwater acoustic playbacks were carried out. The acoustic signals used in the study were (a) a silent control, (b) pile driving and (c) an operational tidal turbine. The pile-driving signal was derived from far-field measurements of pile driving in a shallow water environment scaled to the playback system. Similarly, the tidal turbine signal was generated to show comparative far-field temporal and spectral characteristics of real turbine noise again scaled to the playback system.

Signals were played from a TASCAM DR-40 digital recorder using a Sony XPL0D 1200W power amplifier (model XM-2200GTX) and an underwater speaker (Lubell LL9162T; LUBELL LABS INC.). The frequency response of the system was relatively flat between 250 Hz and 20 kHz \pm 3 dB. Transducer calibrations were made using a Reson 4034 hydrophone with an ETEC A1001 hydrophone amplifier and an NI-PCI 6251 digital acquisition system at sample rates up to 50 kHz.

Both the pile-driving and tidal turbine signal were played at the same RMS source level (148 dB re 1 μ Pa @ 1 $m_{(RMS)}$); however, the peak-to-peak source level of the pile-driving signal was approximately 16 dB higher than the tidal turbine signal. Transmission loss between the prey patches was measured at approximately 17 dB resulting in received levels of 148 and 131 dB re 1 μ Pa $_{(RMS)}$ at the speaker and non-speaker prey patches respectively (for more information see Supporting Information; Appendix S2).

In each trial, the speaker was mounted 1.5 m above either the HD or LD prey patch and one of the three acoustic signals was played continuously throughout the 60-min trial; this resulted in six different treatments. To ensure that seals did not respond to the visual presence of the speaker, a second dummy speaker was mounted above the alternative prey patch during a trial. Further, to exclude the potential influence of preferences by seals to forage at particular ends of the pool, the end of the pool that the HD prey patch was located was alternated for each treatment resulting in a total of up to 12 trials for each seal (Supporting Information; Appendix S1). The order in which the treatments were presented to each seal was randomised throughout the study.

Three foraging metrics were assessed for each trial: (a) Foraging duration (the total time spent at the prey patches as a proportion of the dive duration), to assess whether seals adjusted foraging effort in response to experimental treatment; (b) Allocation of foraging effort to the LD and HD prey patches to assess whether seals were exhibiting a response to the location of the sound source; and (c) Foraging success, to assess the effects of any behavioural responses.

2.3 | Analysis of foraging durations

To measure the foraging durations by seals under each experimental treatment, the combined time spent at the prey patches was analysed on a dive-by-dive basis using Generalised Additive Mixed Models (GAMM) with binomial errors and a logit link

function. The response variable was the total time that the seal spent foraging (i.e. at the prey patches) as a proportion of the dive duration during each dive. The candidate predictor variables were the trial number as a smooth term; and an interaction between start time of each dive during the trial (s) and the experimental treatment. This interaction allowed a different smooth to be fitted for each experimental treatment. Trial number denoted each seals' trial number (1–12) and was included to test whether foraging duration changed over the course of the study. 'Seal ID' was included as a random effect (intercept and slope) to account for the non-independence of data within an individual. GAMM analyses were carried out using the `GAMM` function in the `MGCV` package (Wood, 2011) in the software `R` (R Core Team, 2017) and model selection was carried out using second order Akaike's Information Criterion (AICc) implemented through the `dredge` function in the `MuMIn` package (Barton, 2018).

2.4 | Analysis of foraging allocation

To determine how the experimental treatment affected foraging decisions, we used a Generalised Linear Mixed Model (GLMM) with Gaussian errors and an identity link function to model how the time spent foraging (analysed above) was allocated between the HD and LD prey patches, as a function of experimental treatment. The response variable, foraging allocation, was calculated as the total time spent at HD prey patch over the trial minus the total time spent at the LD prey patch over the trial; thus, if a seal spent equal time at the HD and LD patches during a trial, the foraging allocation would be 0. Candidate predictor variables tested were the experimental treatment, trial number and an interaction between experimental treatment and trial number; 'Seal ID' was included as a random effect (intercept and slope). GLMM analyses were carried out using the `R` package `LME4`, and model selection was carried out using a Wald's Test (Hardin & Hilbe, 2003) to determine the covariates' significance. Confidence intervals around model predictions were based on 1,000 bootstraps from a parametric bootstrapping approach using the `bootMer` function in the `R` package `LME4`.

2.5 | Analysis of foraging success

To compare the foraging success of seals under the different experimental treatments, the total number of fish consumed per trial was analysed using a GLMM with Poisson errors and a log link function. The response variable in the model was the total number of fish consumed (from both prey patches combined) during each trial. Candidate predictor variables were the experimental treatment, trial number and an interaction between experimental treatment and trial number; 'Seal ID' was included as a random effect (intercept and slope). Model selection and the calculation of confidence intervals surrounding predictions was conducted using the same approach as described in 'Analysis of foraging allocation'.

3 | RESULTS

3.1 | Foraging durations

All seals dived to, and foraged at, both of the prey patches during the experimental trials. The proportion of the dive spent foraging (at both feeders combined) varied between 0 and 0.73 ($M = 0.29$, 95% CIs = 0.28–0.30). The foraging proportion varied over the period of the one-hour trials with a general pattern of higher proportions within the first 15–20 min of the trials, after which a steady decline to minimum proportions towards the end of the 1-hr period was evident. The covariates retained (based on AICc) to explain foraging proportion, were the interaction between the time through the trial (s) and experimental treatment; the interaction between experimental treatment and trial number was not retained. Specifically, during the silent control playbacks, predicted mean foraging proportions were generally high until approximately 15 min into the trial, and thereafter showed a steady decline (Figure 2). During the tidal turbine and pile-driving playbacks, predicted foraging proportions showed a similar pattern but were generally lower overall than during the silent controls, particularly during initial dives until approximately 20 min into the trial (Figure 2). Further details of the models are provided in the Supporting Information; Appendix S3.

3.2 | Foraging allocation

Results of the GLMM for foraging allocation showed that the experimental treatment ($\chi^2_5 = 15.481$, $p = 0.009$) and trial number ($\chi^2_1 = 9.231$, $p = 0.002$) were both significant predictors of prey patch foraging allocation; however, the interaction between experimental treatment and trial were not significant predictors and were excluded from the final model.

The final model shows that foraging allocations were similar during both the silent control treatments, regardless of whether the speaker was located at the HD or LD prey patch. In comparison, the foraging allocations during the tidal turbine and pile-driving experimental treatments showed apparent differences depending upon whether the speaker was located at the HD or LD prey patch. Specifically, mean foraging allocations were similar to the silent controls when the speaker was located at the HD prey patch; however, mean foraging allocations were relatively skewed towards the HD prey patch when the speaker was located at the LD prey patch (Figure 3). When the trial number was set to its median value (6), predicted mean foraging allocations for the silent controls were -92.8 s (95% CIs: -325.0 to $+105.6$) and -176.0 s (95% CIs: -431.5 to $+75.4$) when the speaker was located at the LD and HD prey patches respectively. During the tidal turbine playbacks, predicted mean foraging allocations were $+23.0$ s (95% CIs: -195.9 to $+216.0$) and -173.4 s (95% CIs: -383.7 to $+40.7$) when the speaker was located at the LD and HD prey patches respectively. During the pile-driving playbacks, predicted mean foraging allocations were -1.0 s (95% CIs: -203.6 to $+210.8$) and -329.8 s (95% CIs: -529.5 to -122.8) when

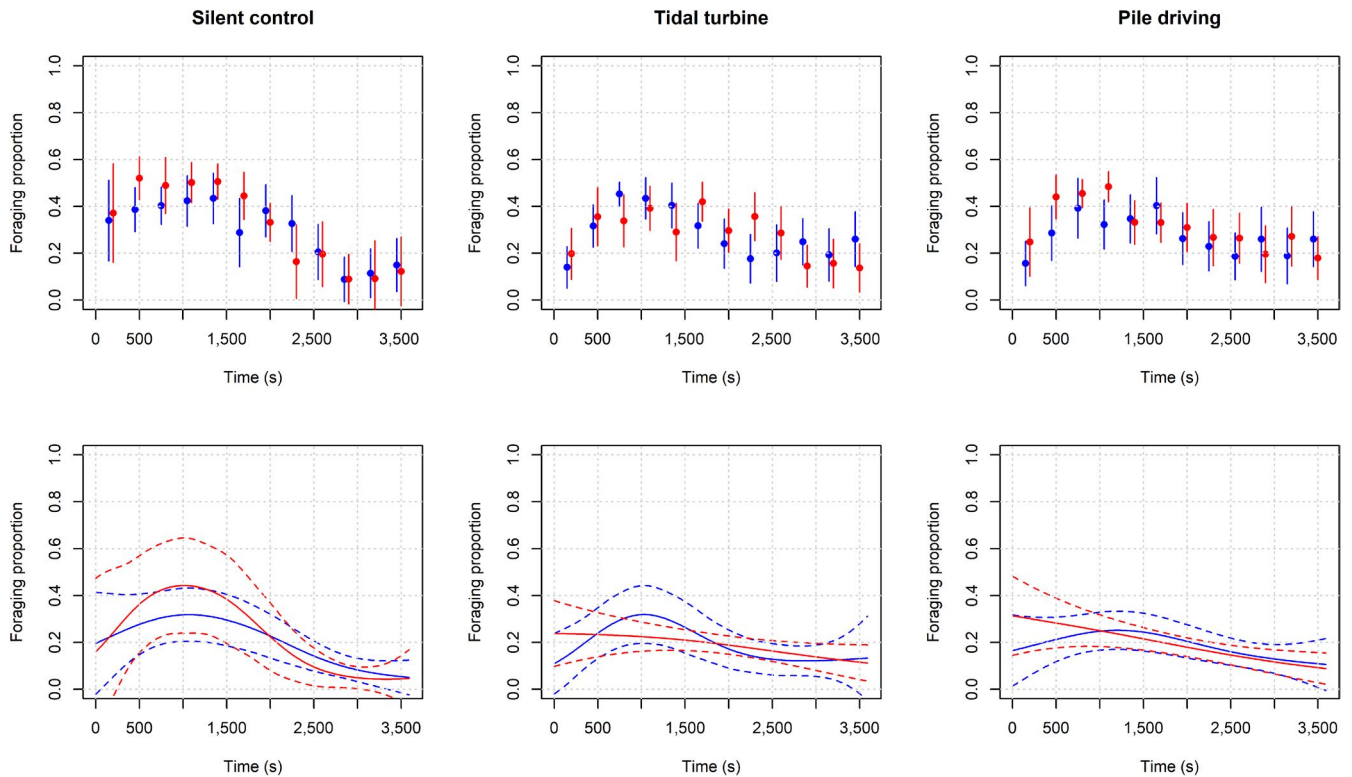


FIGURE 2 The top panels show the mean (\pm 95% CIs) foraging proportions (defined as the combined time in seconds that the seal spent at either of the two simulated prey patches, as a proportion of the dive duration) for all seals during dives under each of the experimental treatments (silent, tidal turbine, and pile driving acoustic playbacks, when the active speaker was located at the HD: red points, or LD prey patch: blue points); data are binned into 5 min intervals by dive start time. The lower panel shows the predicted model functions (\pm 95% CI's) from the best fit GAMM of foraging proportion under each of the experimental treatments (colour coded as described above)

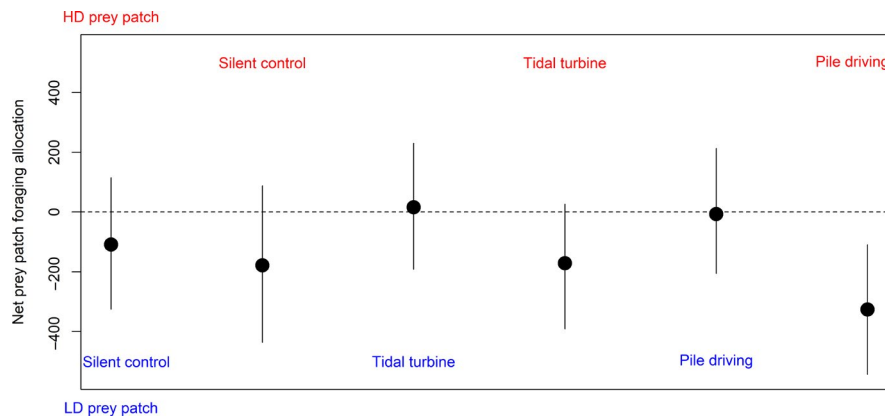


FIGURE 3 The predicted model functions (\pm 95% CIs) from the GLMM that describes the foraging duration at the high (HD) and low-density (LD) prey patches (calculated as the total time at the HD prey patch - total time at the LD prey patch) under each of the experimental treatments. The text in each panel describes the acoustic signal and the location of the speaker relative to the HD or LD prey patches; specifically, the text is located towards the top of the plot and coloured red if the speaker was next to the HD prey patch, and towards the bottom of the plot and coloured blue if the speaker was next to the LD prey patch. For illustrative purposes, the trial number was set to a value of 6

the speaker was located at the LD and HD prey patches respectively (Figure 3). Further details of the models are provided in the Supporting Information; Appendix S4.

Seals also exhibited changes in foraging allocation throughout the duration of individual trials showing a preference for foraging

at the HD prey patch during initial dives before switching to a preference for foraging at the LD prey patch during latter dives; across all trials, mean foraging allocation during the first 1,200 s was +99 s (95% CIs: +59 to +141), and was -138 s (95% CIs: -219 to -56) during the latter 2,400 s. This pattern also appeared to vary markedly

between experimental treatments; during the silent controls, mean foraging allocations changed from +129 to -161 and from +123 to -261 when the speaker was located at the LD and HD prey patches respectively (Figure 4). Similarly, during both the tidal turbine and pile-driving playbacks, when the speaker was located at the HD prey patch, mean foraging allocations changed from +76 to -186 and from +85 to -328 for the tidal turbine and pile-driving playbacks respectively. However, when the speaker was located at the LD prey patch, mean foraging allocations remained positive throughout, changing from +145 to +42 and from +59 to +1 for the tidal turbine and pile-driving playbacks respectively (Figure 4).

3.3 | Foraging success

Fish were consumed on approximately half of the dives (49.8%) and numbers of fish consumed during individual dives ranged from 0 to 38 ($M = 1.9$, 95% CIs = 1.76–2.03). The total number of fish consumed in each trial ranged from 12 to 89 with a mean of 46.8 (95% CIs = 43.1–50.4). When expressed as a proportion of the total number of fish available during each trial, the mean total proportion of fish consumed ranged from 0.12 to 0.87 with a mean of 0.46 (95% CIs = 0.42–0.49). Results of the foraging success GLMMs describing the total number of fish consumed during the trials showed that experimental treatment ($\chi^2_5 = 38.9$, $p < 0.001$) and trial number ($\chi^2_1 = 9.1$, $p = 0.003$) were significant predictors of the total number of fish consumed during a trial. The interaction between experimental treatment and trial number were not significant. Further details of the models are provided in the Supporting Information; Appendix S5.

Inspection of the foraging success model predictions showed that, when trial number was set to its median value (6), the total number of fish consumed was similar regardless of whether the speaker

was located as the LD or HD prey patch during the silent controls; mean number of fish was only around 1% less when the speaker was located at the LD prey patch ($M = 48.6$, 95% CIs = 43.4–53.7) compared to when it was located at the HD prey patch ($M = 49.1$, 95% CIs = 42.4–56.6) (Figure 5). During the tidal turbine playbacks, the

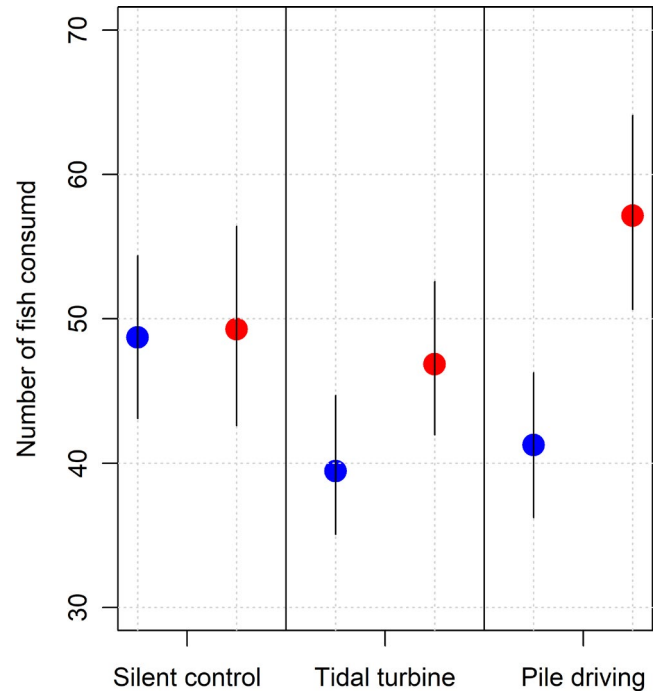


FIGURE 5 The number of fish consumed during the trials for each of the experimental treatments (from left to right: silent control, tidal turbine, and pile driving). The plot shows the model predictions (\pm 95% CI's) from the GLMM describing the total number of fish consumed during each of the acoustic trials. For illustrative purposes, trial number was set to its median (6). The points are colour coded to show whether the active speaker was located at the LD prey patch (blue) or HD prey patch (red)

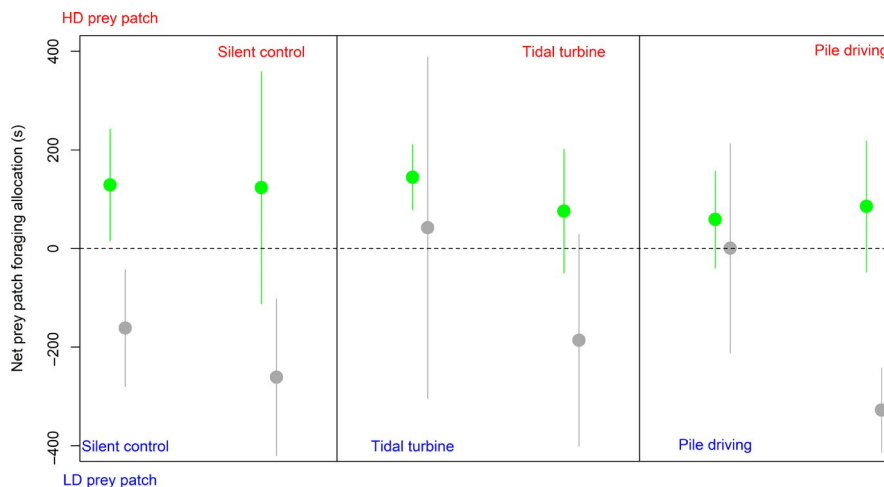


FIGURE 4 Mean prey patch foraging allocations (\pm 95% CIs) measured across all trials during the initial 1,200 s in each trial (green points) and during the latter 2,400 s in each trial (grey points). The text in each panel describes the acoustic signal and the location of the speaker relative to the HD or LD prey patches; specifically, the text is located towards the top of the plot and coloured red if the speaker was next to the HD prey patch, and towards the bottom of the plot and coloured blue if the speaker was next to the LD prey patch

TABLE 1 The number of fish consumed at each of the two prey patches between the experimental treatments. The table shows the mean number ($\pm 95\%$ CIs) of fish consumed from the low-density (LD) and high-density (HD) prey patches for each of the acoustic signals when the speaker was located at the LD or HD prey patch. The percentage difference between the mean number of fish consumed at the HD and LD prey patches is also shown

Acoustic signal	Speaker location	Fish consumed		% difference
		HD prey patch	LD prey patch	
Silent control	LD prey patch	25.0 (22.1–28.0)	25.1 (21.5–28.8)	+0.4
	HD prey patch	25.2 (18.4–32.0)	26.6 (24.2–29.0)	+5.6
Tidal turbine	LD prey patch	22.0 (14.5–29.5)	16.6 (8.9–24.3)	–24.5
	HD prey patch	25.8 (23.4–28.3)	21.2 (14.6–27.8)	–17.8
Pile driving	LD prey patch	22.3 (18.8–25.7)	18.9 (12.1–25.8)	–15.2
	HD prey patch	28.3 (22.4–34.2)	27.8 (22.1–33.4)	–1.8

mean number of fish consumed during trials was approximately 16% less when the speaker was located at the LD prey patch than when located at the HD prey patch; mean number of fish was 39.5 (95% CIs = 35.2–44.1) and 46.9 (95% CIs = 41.8–52.2) when the speaker was located at the LD and HD prey patch respectively (Figure 5). During the pile-driving playbacks, this pattern was more striking with the mean number of fish consumed being approximately 28% lower when the speaker was located at the LD prey patch than when located at the HD prey patch; mean number of fish was 41.2 (95% CIs = 36.6–45.8) and 57.3 (95% CIs = 51.0–63.7) when the speaker was located at the LD and HD prey patch respectively (Figure 5).

The contribution to the total number of consumed fish from each of the two prey patches also showed marked differences between the experimental treatments. During the silent controls, the mean number of fish consumed from each prey patch was similar regardless of whether the speaker was located at the LD or HD prey patch (Table 1). In all the active acoustic treatments, the mean number of fish consumed at the LD prey patch was lower than the number consumed at the HD prey patch. Further, within both the pile-driving and tidal turbine treatments, markedly lower numbers of fish were consumed from the LD prey patch when the speaker was also located at the LD prey patch (Table 1).

4 | DISCUSSION

This study provides the first empirical measures of changes in foraging decisions by a marine mammal as a result of exposure to anthropogenic underwater sounds. The results showed that grey seals exposed to different anthropogenic sounds in a simulated foraging setting exhibited behavioural changes that led to changes in the numbers of prey items acquired. Foraging success was generally highest during the silent control treatments and was similar regardless of whether the speaker was located at the HD or LD prey patch. However, there were differences in foraging success by seals under certain active experimental treatments (tidal turbine and pile-driving sounds); foraging success was similar to the silent controls when the speaker was located at the HD prey patch during the active experimental treatments but was markedly reduced (~16%–28% lower) when the speaker was located at the LD prey patch.

The differences in foraging success shown here appear to be driven, at least in part, by the effect of experimental treatments on

foraging decisions that led to differences in both foraging durations and in how seals allocated their foraging time between the HD and LD prey patches. Foraging durations varied during the one-hour trials with a general pattern of low foraging durations at the start and end of each trial, and a peak approximately 10–15 min into the trial; this pattern showed a number of key differences as a result of exposure to the different acoustic signals (Figure 2). Specifically, the proportion of the dives spent foraging appeared to be generally shorter during the tidal turbine and pile-driving playbacks than during the silent controls. This was particularly apparent during the first 10–20 min of a trial when foraging proportions were markedly less than the silent controls. This indicates that there may have been an initial aversive response to the tidal turbine and pile-driving playbacks that diminished during each trial.

The pattern of how seals allocated their foraging time between HD and LD prey patches also showed significant differences between experimental treatments. For each of the silent control treatments, the patterns were similar with mean foraging allocations skewed towards the LD prey patch (Figure 3). Although seemingly counter-intuitive, this pattern can be explained by seals attempting to maximise their prey consumption at each prey patch with the result that a relatively longer time was required at the LD prey patch than the HD prey patch for the same number of fish, resulting in a negative foraging allocation. A similar allocation pattern was seen during both the tidal turbine and pile-driving playbacks when the active speaker was located at the HD prey patch. However, during the tidal turbine and pile-driving playbacks when the active speaker was located at the LD prey patch, seals spent relatively less time foraging at the LD prey patch (Figure 3).

Between experimental treatments there was also marked differences in how the foraging allocation changed over the period of individual trials. During both the silent control treatments, and the tidal turbine and pile-driving treatments where the speaker was located at the HD prey patch, seals foraged primarily at the HD prey patch during initial dives before switching to forage primarily at the LD prey patch during later dives (Figure 4). However, in the tidal turbine and pile-driving treatments when the speaker was located at the LD prey patch, this switch to foraging at the LD prey patch was far less apparent and seals appeared to continue to forage primarily at the HD prey patch throughout the trials (Figure 4). This apparent avoidance of the LD prey patch when the speaker was co-located there was also observed in the relative contribution of the consumed

fish from each of the two prey patches; for both the tidal turbine and pile-driving playbacks, the lowest numbers of fish consumed were from the LD prey patch when the speaker was also located at the LD prey patch. It appears therefore that seals made foraging decisions within the trials that were based on both the energetic value of the prey patch, and the nature and location of the acoustic signal relative to the prey patches of different value.

Foraging theory predicts that individuals should attempt to maximise their energy gain by foraging at patches with high densities of preferred prey (Stephens & Krebs, 1986). The foraging decisions made here appear to reflect this with seals exhibiting a general preference for the HD prey patch during the initial dives of each trial and switching (presumably when the density of fish at the HD prey patch declined) to a preference for foraging at the LD prey patch during later dives. There is also evidence showing that foraging behaviour can be influenced by the perceived risk of predation (Dill, 1987; Dill & Fraser, 1984; Milinski, 1986; Wirsing et al., 2011) and that animals may reduce time spent foraging when perceived risk increases. Animals faced with a choice between a rewarding prey patch which has a perceived high degree of risk associated with it, and one that is both less rewarding but perceptually less dangerous, may be expected to exhibit foraging decisions that reflect both the degree of risk involved, and the relative energetic advantage (for review, see Lima & Dill, 1990). There are a number of methods by which animals can balance foraging efficiency against perceived risk, including the timing and selection of foraging sites (Heithaus & Dill, 2002; Lima & Dill, 1990; Sih, 1987; Wirsing et al., 2007); risk-balancing hypotheses predict that the effect of risk will depend on an interaction between food availability and perceived risk (Cerri & Fraser, 1983). Such an approach has been shown in many terrestrial and aquatic species. For example, European minnows *Phoxinus phoxinus* (Pitcher et al., 1988), stream mayflies *Baetis tricaudatus* (Scrimgeour & Culp, 1994), sticklebacks *Gasterosteus aculeatus* (Heller & Milinski, 1979) and ants *Lasius pallitarsis* (Nonacs & Dill, 1990) have all been shown to perform a risk-balancing trade-off by avoiding hazard for equal food, but accepting predator risk for higher food rewards.

A growing body of research into disturbance to animals by human activities has begun to embrace the principle that nonlethal disturbance stimuli caused by humans may be analogous to predation risk (Curé et al., 2016; Dorresteijn et al., 2015; Frid & Dill, 2002). The foraging decisions exhibited by the seals during the tidal turbine and pile-driving playbacks may therefore reflect a classic predation risk/profit-balancing approach. In response to a perceived risk associated with the sounds, seals apparently showed avoidance of the tidal turbine and pile-driving signals when the energetic rewards were limited (speaker at LD prey patch) but not when the rewards were higher (speaker at HD prey patch). Particularly relevant to the current study is the concept of balancing foraging at prey patches in which quality varies temporally with perceived risk. Given that the absolute density of prey at each of the patches generally started to decline at some point during the trials as a result of prey capture, the seals potentially combined perceived risk with a progressively

shifting assessment of prey patch quality to form estimates of overall prey patch value.

Clearly, the risk-balancing hypothesis as applied here supposes that the seals both detected the acoustic signals and perceived them as a risk. Whilst we have no direct information on the hearing sensitivity of the individual seals here, comparisons of the measured sound levels to hearing sensitivities of phocid seals suggests that both the signals would have been clearly audible. Although measuring audibility of acoustic signals is highly complex and is dependent on a variety of factors including the width of critical bands, signal duration and receiver integration time, phocid underwater hearing is most sensitive at frequencies between 0.5 and 30 kHz with thresholds of approximately 50–60 dB re 1 μ Pa (Southall et al., 2019); this is well below the measured levels for the signals at both prey patches in the current study (Supporting Information; Appendix S2).

Both tidal turbine and pile-driving signals are underwater sounds that have previously been shown to elicit avoidance responses by seals. Specifically, the tidal turbine signal used here was the same as that used in a series of playbacks to wild harbour seals tagged with GPS tags (Hastie et al., 2018); those seals showed a significant spatial avoidance up to ranges of approximately 500 m to playbacks of the tidal turbine signal (Hastie et al., 2018). The pile-driving signals were based on recordings made during the installation of offshore wind turbine foundations during a study of harbour seal responses to pile driving (Russell et al., 2016); that study (Russell et al., 2016) showed a significant decrease in usage by seals up to 25 km from the pile-driving location. However, it is important to consider that the avoidance of sounds by animals may be associated with factors other than a perception of risk. For example, models based on psychophysical parameters in humans suggest that sounds that have low tonality, high sharpness, high roughness and high loudness are perceived as relatively unpleasant (Zwicker & Fastl, 1990). It is therefore possible that the avoidance shown by seals to pile-driving and tidal turbine signals in this and previous studies (Hastie et al., 2018; Russell et al., 2016) may not be solely due to a perception of risk but may also be related to psychophysical parameters. Nevertheless, the results presented here demonstrate behavioural responses by foraging seals to anthropogenic sounds which is dependent upon both the quality of the prey patch and the aversiveness of the sound.

The results show that, in a simulated foraging scenario within a captive setting, seals appear to make foraging decisions based on both the perceived value of prey patches and on their sound exposure and a perception of relative risks or aversiveness of anthropogenic sounds. From an applied perspective, this has implications for seals exposed to anthropogenic sound in the wild and suggests that exposure to these sounds may have direct consequences for foraging success, particularly in less profitable habitats. The results also highlight the importance of considering habitat quality when interpreting animal responses (or lack of) to anthropogenic activities in the wild. Specifically, the relative importance or value of a foraging area is likely to have a significant influence on whether an individual responds to an aversive stimulus. Importantly, a lack of behavioural response does not preclude the presence of other physiological or

stress responses to activities which could have potential impacts on animal health and vital rates. It is therefore critical to consider contextual variables such as habitat quality when using the results of behavioural response studies in the wild to predict responses in new areas or activities.

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AUTHORS' CONTRIBUTIONS

G.D.H., P.L. and D.T. conceived of the study; G.D.H., C.M. and R.M. participated in the design of the study and carried out the data collection; D.J.F.R. participated in data analysis; G.D.H. drafted the manuscript; all authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.tjqj2bvzv> (Hastie et al., 2021).

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SUPPORTING INFORMATION

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