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Effect of Pile-Driving Playback Sound Level on Fish-Catching Efficiency in Harbor Porpoises (*Phocoena phocoena*)

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Abstract

The foundations of offshore wind turbine parks are often constructed by means of percussion pile driving. Broadband impulsive sounds generated by pile driving may disturb and distract marine mammals such as harbor porpoises (*Phocoena phocoena*); their concentration may be reduced, affecting the skills they need for foraging (e.g., timing and precision) or reducing their ability to catch prey and, thus, their foraging efficiency. The resulting reduction in fitness may eventually lead to population declines. Therefore, it is important to understand the effects of these anthropogenic sounds on the ability of harbor porpoises to catch fish. Two captive harbor porpoises (porpoise F05 and porpoise M06) performed a fish-catching task (i.e., retrieving dead fish from a net feeding cage) while they were exposed to low ambient noise (quiet conditions) and impulsive pile-driving playback sounds at three (porpoise M06) or four (porpoise F05) mean received single-strike sound exposure levels (SELss) between 125 and 143 dB re 1 $\mu Pa^2 s$. The two study animals differed in their fish-catching success rate at all noise levels, including under quiet conditions: Porpoise F05 was less likely to catch fish than porpoise M06. They also responded differently to increasing SELss: Only porpoise F05 was significantly more likely to terminate trials and less likely to catch fish as SELss increased above 134 dB, but her trial failure rate remained unaffected by increasing SELss. The time taken to catch a fish did not vary with SELss but was slightly longer for porpoise F05 than for porpoise M06. Results suggest that high-amplitude pile driving sounds are likely to negatively affect foraging in some harbor porpoises by decreasing their catch success rate and increasing the termination rate of their fish-catching attempts; the severity of the effects is likely to increase with increasing pile driving SELss. However, individual differences in responses to sound, termination rates, and fish-catching success (even in ambient conditions) may complicate the quantification of the impacts of pile driving sounds on harbor porpoises.

Key Words: anthropogenic sound, distraction, behavior, foraging, harbor porpoise, odontocete, marine mammal, individual variation, pile driving, wind park

Introduction

In the coming decades, many wind turbine parks will be built in the North Sea and in nearby waters (https://www.actu-environnement.com/media/pdf/news-29718-scenario-2020-eolien-Europe-WindEurope.pdf) within the geographic range of the harbor porpoise (*Phocoena phocoena*; Rice, 1998). Impulsive sounds are produced during the construction of offshore wind turbines by means of percussion pile driving (so far, the most commonly used method). It may take several thousand blows (depending on the pile diameter and length, and the composition of the substrate) to drive one pile into the sea floor in a time period of 2 to 3 h. Typically, one pile is placed per day, and the construction of an entire offshore wind park may take months. The broadband high-amplitude sounds produced during offshore percussion pile driving have most of their energy below 1 kHz (Bailey et al., 2010; Gabriel et al., 2011; Norro et al., 2013), so they are not expected to mask the high-frequency echolocation signals used by harbor porpoises (around 125 kHz, narrow band; Møhl & Andersen, 1973). However, at certain received levels, percussion pile driving does affect the behavior of harbor porpoises (Carstensen et al., 2006; Tougaard et al., 2009; Bailey et al., 2010; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014).

Apart from the most commonly used percussion pile driving method, vibratory pile driving is sometimes used, which also produces broadband high-amplitude sounds. The effect of vibratory pile driving sounds on echolocation vigilance has been investigated in another odontocete, the bottlenose dolphin (*Tursiops truncatus*; Branstetter et al., 2018). The vibratory sounds have energy up to 80 kHz, so their spectra overlap with those of the echolocation signals of bottlenose dolphins. While the echolocation performance of two of the five dolphins used in the study was unaffected, the remaining three almost completely stopped echolocating during their first exposure to the highest sound level, suggesting that these dolphins were distracted by the sounds (Branstetter et al., 2018). Wild bottlenose dolphins exposed to vibratory pile driving sounds (with energy in the 0 to 80 kHz range) may temporarily stop echolocating and, thus, stop foraging (Branstetter et al., 2018).

Pile driving sounds are unlikely to mask the echolocation signals of harbor porpoises, but they may distract foraging harbor porpoises since porpoises use echolocation to find, track, and catch prey items (DeRuiter et al., 2009; Miller, 2010; Wahlberg et al., 2015). When closing in on their prey, usually small to medium-sized fish (Sveegaard et al., 2012; Wisniewska et al., 2016), harbor porpoises produce very rapid echolocation click sequences (DeRuiter et al., 2009). They catch a fish by grabbing it with their teeth or by sucking it into their mouth cavity by withdrawing their tongue (Kastelein et al., 1997b). This requires precision and good timing, skills that may be impaired if the porpoise is distracted by underwater anthropogenic sounds. Such effects of sound have been observed in fish; they made more prey-handling errors in the presence of intermittent sound (Purser & Radford, 2011; Shafiei Sabet et al., 2015).

Harbor porpoises are relatively small and inhabit the cold temperate waters of the Northern Hemisphere (Rice, 1998), so their thermoregulation imposes energetic challenges (Lockyer, 2007). Because of their high relative heat loss and rapid life history, harbor porpoises have been referred to as "aquatic shrews" (Kanwisher & Sundnes, 1965). To sustain their high metabolic rates, harbor porpoises must spend a large portion of their time feeding (Wisniewska et al., 2016, 2018; Hoekendijk et al., 2017); and if their foraging is interrupted, they are susceptible to starvation (MacLeod et al., 2007). Although the resilience of harbor porpoises to anthropogenic disturbances is debated (Wisniewska et al., 2016, 2018; Hoekendijk et al., 2017), distraction of foraging harbor porpoises by pile driving sounds may have particularly detrimental impacts because of the species' biological traits. If exposure to sounds produced during wind park construction routinely affects harbor porpoise foraging and animals cannot compensate, then in the long term, the population dynamics of the species may be affected.

Policymakers need to assess to what extent acoustic disturbances are likely to affect the population dynamics of marine mammals in order to make informed wildlife management decisions. Several theoretical models are being developed, such as the Population Consequences of Acoustic Disturbance model (PCAD; National Research Council, 2005), and model principles have been implemented in mathematical frameworks such as the Interim Population Consequences of Disturbance model (iPCoD; King et al., 2015) and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea model (DEPONS; Nabe-Nielsen et al., 2014, 2018). These models require input parameters such as the number of animals that will be significantly affected by a noise disturbance, the energetic needs of a species (DEPONS), the relevant food availability (DEPONS), and other parameters affecting the vital rates (birth and death rates). So far, most of the information that is needed is lacking for most marine mammal species, though estimates for input parameters for the iPCoD model have been made via an expert elicitation method (Donovan et al., 2016).

The goal of this study was to contribute towards a more accurate assessment of an input parameter for models of acoustic disturbances for the harbor porpoise. The effect of pile-driving playback sounds on the efficiency (success rate and speed) of attempts by harbor porpoises to catch fish in a controlled environment is quantified.

Methods

Study Animals

The two harbor porpoises that participated in the study, an adult female and a subadult male, had both been found stranded on the North Sea coast and had been rehabilitated. The long duration of their rehabilitation deemed the porpoises unsuitable for release, and they were therefore made available for research. The female (identified as porpoise F05) was ~11 mo old when she stranded; the male (identified as porpoise M06) was ~7 mo old. At the time of the study, both animals were healthy and in good physical condition. Porpoise F05 had reached her maximum body length (154 cm) and was 7 years old. Her weight varied between 43 and 46 kg during the study period. Porpoise M06 was 4 years old and still growing (130 cm). His weight varied between 30 and 34 kg during the study period.

Food Consumption
The harbor porpoises were normally fed four to five times a day on a diet of thawed sprat (*Sprattus sprattus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and squid (*Loligo opalescens*). Vitamin supplements (Akwavit; Arie Blok Animal Nutrition, Woerden, The Netherlands) were added to the thawed fish. Fish were fed to the porpoises at a temperature of ~4°C. The fish were weighed digitally (5 g accuracy), and the mass of each fish species eaten during each meal was recorded. During experimental fish-catching sessions, only thawed sprats were used (~15 cm long). Before a session began, the sprats were dropped into a bucket of sea water, and only those that sank were used (i.e., those which did not contain gas).

Study Area
The study was conducted at the Sea Mammal Research Company (SEAMARCO) Research Institute in the Netherlands. The animals were kept in a pool complex consisting of an outdoor pool (12 × 8 m; 2 m deep; Figure 1) connected via a channel (4 × 3 m; 1.4 m deep) to an indoor pool (8 × 7 m; 2 m deep). The bottom was covered with a 20-cm-thick layer of sloping sand on which aquatic vegetation grew and invertebrates lived. Skimmers kept the water level constant. Sea water was pumped directly from the Eastern Scheldt, a lagoon of the North Sea, into the water circulation system; partial recirculation through biological and sand filters ensured year-round water clarity and quality.

The pool water temperature was measured once per day and varied between 2 and 15°C during the study period. The minimum and maximum air temperatures over each 24-h period were also recorded. The mean daily air temperature ranges (2.3 to 16.9°C in winter and 5.7 to 26.9°C in summer) and salinity (~3.4%) experienced during the study period by the captive study animals were similar to those experienced by wild conspecifics in the North Sea (occurring ~200 m away on the other side of the dyke in the Eastern Scheldt).

Net Feeding Cage
To quantify fish-catching efficiency, fish were offered to the harbor porpoises under water in a custom-built net feeding cage (Figure 2). The cage was made of monofilament transparent twine net with a mesh size of 12 cm. The entire back of

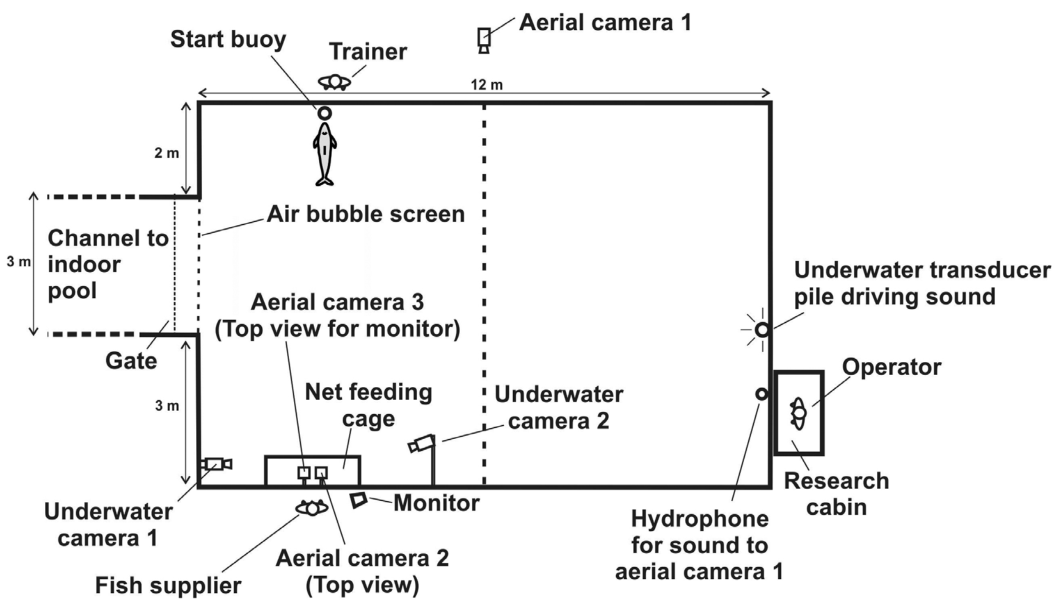

Figure 1. The outdoor pool used for the study, showing the location of the test harbor porpoise (*Phocoena phocoena*) at the start buoy, the net feeding cage, the underwater transducer, and the various aerial and underwater cameras. Also shown is the research cabin which housed the sound-producing, sound-monitoring, and video-recording equipment and the operator. During the sessions, the test porpoise remained to the left of the dashed central imaginary demarcation line. An air-bubble screen reduced the high-frequency components of the impulsive broadband pile driving sound that could reach the indoor pool where the non-test porpoise was housed while the test porpoise participated in the study.

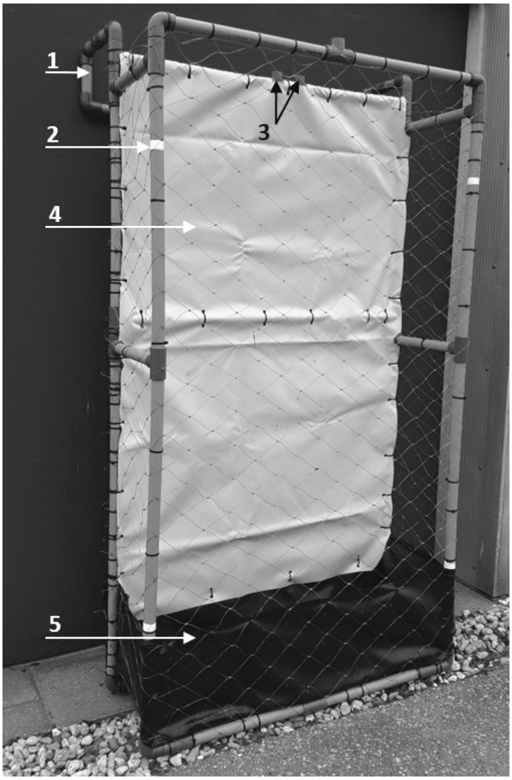

Figure 2. The net feeding cage (104 cm wide, 188 cm high, and 36 cm deep) which was placed in the water and attached to the side of the pool by the suspension system (1) when in use. The white markings (2) indicate the water level during fish-catching trials. Top view camera mounting locations are shown (3; aerial cameras #2 and 3; see Figure 1). The back of the net feeding cage (4) was covered with white pond liner so that fish remained in the cage. Fish that were not caught by the harbor porpoise fell into the drop box (5) made of black pond liner.

the cage was covered with white pond liner so that the fish could not swirl through the meshes at the back and get stuck between the cage and the side of the pool. The lower sides and front of the net cage were covered with black pond liner (36 cm high) so that the porpoises could not access a fish once it had reached the bottom of the net cage within this so-called drop box.

Background Noise and Stimulus Measurements

Unless stated otherwise, acoustic terms and definitions follow *ISO 18405 Underwater Acoustics – Terminology* (ISO, 2017). The background noise and pile driving sounds were measured via three hydrophones (Brüel & Kjaer [B&K] – 8106) with a multichannel high-frequency analyzer (B&K PULSE – 3560 D) and a laptop computer with B&K PULSE software (*Labshop*, Version 12.1; sample frequency used: 524,288 Hz). Before analysis, the recordings were high-pass filtered (cut-off frequency 100 Hz; 3rd order Butterworth filter; 18 dB/octave) to remove low-frequency sounds made by water surface movements. The system was calibrated with a pistonphone (B&K – 4223). The received sound pressure of the impulsive pile driving sounds was analyzed in terms of unweighted single-strike sound exposure level (SELss) in dB re 1 $\mu Pa^2 s$.

Fish-catching sessions were not performed under unfavorable weather conditions such as rain or hard wind (i.e., Beaufort wind force 6 or more). Raindrops falling on the water surface may distract the harbor porpoises or distort the images made by the top view cameras. Strong wind may move the water surface, thereby changing the random swirling pattern of fish in the net feeding cage. In addition, when the wind came from the south, sessions were not performed if the Beaufort wind force was 4 or more, as under these conditions; the fish always moved towards the back of the net cage where the porpoise could not reach them. Only the people involved in the tests were allowed within 15 m of the pool during sessions, and they were required to stand still. During test conditions without pile driving sounds, the background noise in the pool was below that typical of sea state 0 (see Kastelein et al., 2012).

Pile-Driving Playback Sound

The sound intended to distract the harbor porpoises consisted of playbacks of a series of offshore percussion (impulsive) pile driving sounds recorded at 800 m from a 4.2-m diameter pile being driven into the sea bed as the foundation for a wind turbine for the Dutch offshore wind farm "Egmond aan Zee" in the North Sea. No mitigation, such as bubble screens, was used. The strike rate was 2,760/h. A WAV file was made of a series of consecutive pile-driving strike sounds. The original recordings were sampled at 65 kHz and band-pass filtered between 50 Hz and 32.5 kHz. For the generation of the WAV files used in the study, signals were resampled to 88.2 kHz.

A random section of five strikes from the digitized original recording of a series of pile driving sounds (WAV file) was played back repeatedly by a laptop computer (ASUS PC 1001 PXD) with *Adobe Audition*, Version 3.0, to a digitally controlled attenuator. The output went through a custom-built variable passive low-pass filter (set to 125 kHz), after which it went to a power amplifier (East & West Inc. – LS5002), which drove the transducer (Lubell – LL1424HP) through an isolation transformer (Lubell – AC1424HP). The transducer was placed at the southwestern end of the pool at 2 m depth (~10 m away from the net feeding cage; Figure 1). The linearity of the transmitter system used for the pile-driving playback sound deviated at most by 1 dB within a 42 dB range.

The sound distribution was measured both in the general area where the harbor porpoises swam during the sessions (6 × 7 m, 1-m grid on the left side of the central dashed line in Figure 1; 42 locations) and up to 1 m from the net feeding cage (four locations). The SELss was measured at three depths per location (0.5, 1.0, and 1.5 m below the surface). Three strikes were recorded per depth and location over a 10-s period. The analysis of a single strike was done for a 500-ms time window. The average received SELss (dB re 1 µPa^{2}s) of the played back impulsive sound, as experienced by the harbor porpoises when they were near the net feeding cage, was calculated as the power average of all 12 individual measurement positions (four locations, three depths at each). There were only small differences in SELss per position, showing that the sound field near the net feeding cage was fairly homogeneous (Table 1).

Both study animals were tested during exposure to pile driving sounds at SELss = 125 dB, 134 dB, and 143 dB re 1 µPa^{2}s. Porpoise F05 responded differently (she showed a profound reaction by increasing swimming speed) to the highest level than porpoise M06, so exposure to SELss = 137 dB re 1 µPa^{2}s was added to show a response gradient. Porpoise M06 was not exposed to pile driving sound at SELss = 137 dB re 1 µPa^{2}s because his pattern of behavior remained constant at the highest and lower levels. Therefore, based on the study animals' behavior, the pile driving sounds were played back at three levels for porpoise M06 and at four levels for porpoise F05. The highest amplitude was the maximum level that could be produced by the sound emitting system: a mean SELss of 143 dB re 1 µPa^{2}s in the swimming area of the porpoise (the waveform is shown in Figure 3a). The background noise level in the pool, converted to SELss based on a t_{90} pulse duration of 151 ms, was measured to be in the range between 50 and 65 dB re 1 µPa^{2}s in the one-third octave bands between 100 Hz and 10 kHz. The spectrum and level of the playback sound in the pool (Figure 3b) resembled the spectra of pile driving sounds recorded in shallow water at 7 km from a North Sea pile driving site (Remmers & Bellmann, 2016). Below 600 Hz, the energy at sea could not be replicated in the pool due to the characteristics of the transducer and the dimensions of the pool.

Experimental Procedure

Before each session, the harbor porpoises were not fed for approximately 2 h to ensure that their motivation to feed was strong and consistent. While they were in the indoor pool, the transducer and the net feeding cage were lowered into the outdoor pool, and the video cameras were activated (Figure 1). Then, the test porpoise for that session was asked to swim into the outdoor pool. The non-test porpoise was kept in the indoor pool and was tested once the session with the first animal had been completed. The air-bubble screen (Figure 1) was lowered during each session; this reduced the high-frequency components of the pile driving sound in the indoor pool so that the non-test animal was not disturbed by it.

The fish-catching task required skill, concentration, and prior training (which had taken 2 wks). Once the test porpoise had stationed at the start buoy near the trainer, 8 m from the net feeding cage (Figure 1), the fish supplier held a fish just under the water surface in the middle of the top of the net cage (always in the same position; the fish was held horizontally, parallel to the pool wall, with its ventral side pointing downwards; Figure 4). The trainer counted out loud from one to three, then gave a hand signal and the vocal command "search" to send the porpoise to the net cage. The fish supplier released the fish

Table 1. The four mean (± standard deviation [SD]) exposure levels (expressed as SELss and peak level) and t_{90} of the pile-driving playback sound in the area where the harbor porpoises (*Phocoena phocoena*) swam during the fish-catching sessions ("Overall"; n = 126 locations) and in the 1 m area around the net feeding cage ("Cage"; n = 12 locations).

	Mean SELss (dB re 1µPa^{2}s) ± SD		Mean t_{90} (ms) ± SD		Mean peak level (dB re 1 µPa^2) ± SD	
Porpoise	Overall	Cage	Overall	Cage	Overall	Cage
F05 & M06	125 ± 2	123 ± 1	151 ± 11	158 ± 11	148 ± 2	146 ± 1
F05 & M06	134 ± 2	132 ± 1	151 ± 11	158 ± 11	157 ± 2	155 ± 1
F05	137 ± 2	135 ± 1	151 ± 11	158 ± 11	160 ± 2	158 ± 1
F05 & M06	143 ± 2	141 ± 1	151 ± 11	158 ± 11	166 ± 2	164 ± 1

when the trainer began counting with the word "one." After releasing the fish, the fish supplier sat down and was not visible to the porpoise. During each session, the porpoise and net feeding cage were filmed simultaneously by five cameras (Figure 1): one underwater camera on each side of the net cage (Rollei Actioncam 300), one aerial top view camera (Rollei Actioncam 300) on a 1.5 m high pole, and one aerial camera on a 6-m-high pole for a top view of the swimming tracks (GoPro Hero 3; Figure 1). Another aerial camera (Conrad), connected to a monitor (camera 3 in Figure 1), allowed the fish supplier to see whether the fish was caught or not without distracting the porpoise.

As the harbor porpoise swam towards the net feeding cage (usually taking ~3 s for the 8 m distance), the fish slowly swirled down through the water column (mean swirling time between surface and drop box, where the fish was no longer accessible to the porpoise: 30 s; SD: 6 s; range: 14 to 40 s; n = 30). Once the porpoise reached

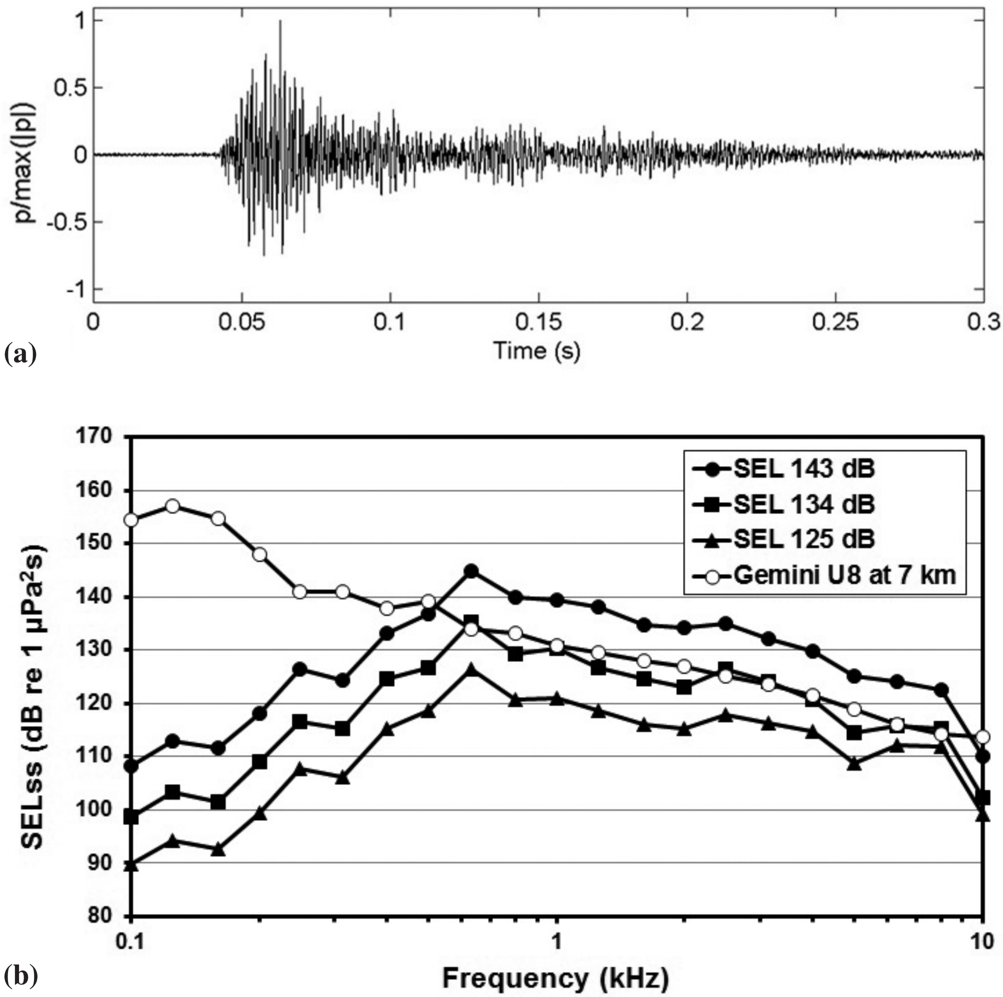

Figure 3. (a) The waveform of a pile-driving playback sound in the pool, measured at a distance of 2 m from the source and at a depth of 1.5 m; and (b) the one-third octave (base-10) band spectra of a pile-driving playback sound in the pool measured at the same location (at source levels corresponding to a mean SELss in the pool part used by the porpoises during the sessions of 125, 134, and 143 dB re 1 µPa²s), and, for comparison, the one-third octave band spectrum of a pile driving sound recorded at 7 km distance from a North Sea pile driving site (Remmers & Bellmann, 2016).

the net cage, it (1) sucked or grabbed the fish through the net and ingested it ("catch" or "success"), (2) tried to catch the fish but was unable to so the fish ended up in the drop box ("failure"), or (3) abandoned any attempt to catch the fish before the fish reached the drop box ("termination"; in some cases, no attempt to capture the fish was made, but the porpoise always swam towards the net cage).

To catch a fish before it fell into the drop box, the harbor porpoise had to be in the right place (vertically and horizontally), and the fish had to be near a hole in the net. The position of the fish was partially determined by chance as it swirled down through the water, but it could be manipulated by currents created by the mouth of the porpoise (suction) or by movement of its entire body. After each trial, the porpoise returned to the trainer at the start buoy and was then sent back to the net feeding cage for the next trial.

Each session consisted of 20 trials per harbor porpoise, and both porpoises were tested in random order once a day, usually in the afternoon. Sessions were conducted either in the low background noise level of the pool or during playbacks of the pile driving sound at three or four (depending on the animal) source levels. Sessions were conducted in random order; during sessions with pile driving sound, the sound was played back throughout the session (one strike every 1.2 s; 47 strikes/min). Data collection took place between October 2017 and March 2018.

Data Collection and Analysis

The outcome of each trial (success, failure, or termination) was recorded by the fish supplier at the net feeding cage. A separate nominal logistic regression (Hosmer & Lemeshow, 2000) was used for each animal to assess the effects of the factor SELss on the outcome of each trial, with successful fish capture as the reference event and the quiet condition as the reference level of SELss.

Video recordings of successful trials were analysed to quantify the catch time—the time between the moment a fish was released (when the trainer at the buoy said "one") and when the fish was caught. All catch times were quantified by the same person, mostly using the video recordings made by top view aerial camera #2 mounted on the net cage (Figures 1 & 2). On the rare occasions when a trial outcome was not clearly visible on these video images, the video recordings from underwater cameras #1 and 2, mounted on either side of the net cage, were used. A general linear model (Zar, 1999) was used to evaluate the effect of the factors "porpoise" and "SELss" on the catch time (which was log transformed to bring it close to normal distribution). Assumptions of general linear models were checked for and mostly met. Some slight departures from homogeneity of variances and normality occurred in the data, but models are robust to such departures. All statistical analysis was conducted with *Minitab 18*; the significance level was set at 5% (Zar, 1999).

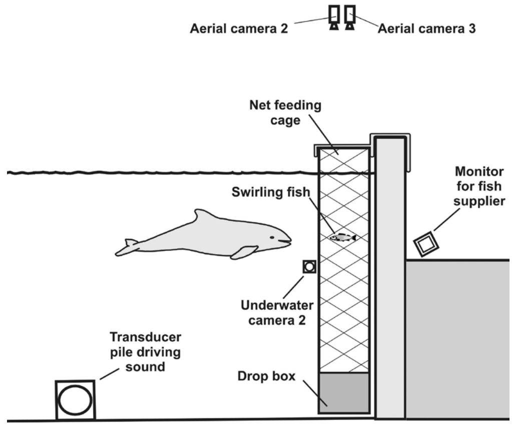

Figure 4. A schematic representation (lateral view) of the experimental set-up used for the fish-catching task.

Results

In all, 1,640 trials were conducted in 57 sessions: 1,060 trials with porpoise F05 and 580 with porpoise M06. The sample size for porpoise M06 was lower than for porpoise F05, mainly because only three SELss were tested. Overall, 991 trials resulted in a successful fish catch, 373 trials resulted in failure, and 276 trials were terminated. Responses differed greatly between the two study animals: Compared to porpoise F05, porpoise M06 was much more likely to capture fish successfully, less likely to fail to catch a fish, and less likely to terminate trials (Figure 5). The harbor porpoises also used different fish-catching techniques. Porpoise F05 approached the net feeding cage forcefully, swimming fast, slowing down at the last moment, and sometimes swimming on her back (i.e., with her dorsal fin pointing down), thus causing water displacement; she then used a biting technique to grab the fish. Porpoise M06 used either this biting and grabbing technique or the suction technique (i.e., sucking the fish into his oral cavity by quickly withdrawing his tongue; Kastelein et al., 1997b). Porpoise F05 was observed to increase her swimming speed at SELss above 134 dB dB re 1 μPa^2s, whereas porpoise M06 maintained a constant swimming speed.

For porpoise F05, the nominal logistic regression model revealed a statistically significant

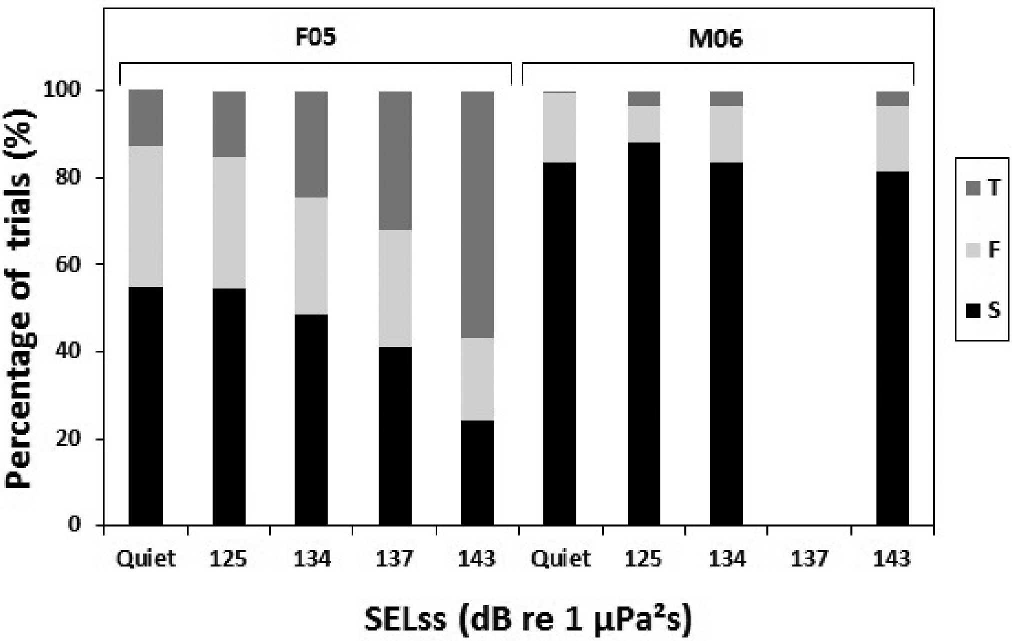

Figure 5. The outcomes of fish-catching trials, shown as percentages of the number of trials for each SELss (in total, there were 1,060 trials with porpoise F05 and 580 with porpoise M06). Outcomes are shown as T = termination, F = failure, and S = successful fish capture. Porpoise M06 had a higher overall success rate than porpoise F05. For porpoise F05 only, success rate declined with increasing SELss (from 134 dB re 1 µPa^{2}s), as failure rate remained approximately constant and termination rate increased. Porpoise M06 was not tested during exposure to pile driving sound at 137 dB re 1 µPa^{2}s because his pattern of behavior remained constant even at the highest level (143 dB re 1 µPa^{2}s). Porpoise F05 did behave differently at the highest level, so the 137 dB re 1 µPa^{2}s SELss was added to show a response gradient.

correlation between the outcome of the trials and the terms in the model ($G = 96.8_8$; $p = 0.000$). Trials were significantly more likely to be terminated when the SELss was 134 dB dB re 1 µPa^{2}s or above (Logit 1, comparing termination with success; Table 2); SELss had a significant effect on trial outcome in Logit 1 ($\chi^2 = 79.2_4$; $p = 0.000$) but not in Logit 2 (comparing failure with success, $\chi^2 = 1.98_4$; $p = 0.739$). The odds of termination were ~10 times higher when SELss was 143 dB re 1 µPa^{2}s than in quiet conditions (odds ratio = 9.79, $p = 0.000$). Thus, as the SELss increased, there was an increasing likelihood of trial termination, but the trial failure rate was not affected by SELss (Logit 2; Table 2).

For porpoise M06, the nominal logistic regression model revealed that there was no statistically significant correlation between the outcome of the trials and the terms in the model ($G = 7.25_6$; $p = 0.298$).

The mean catch time in successful trials was 11.7 ± 4.2 s ($n = 985$). Analysis of the log-transformed catch times showed that they were not affected by SELss but were affected by porpoise (Table 3); porpoise F05 had slightly longer catch times than porpoise M06 (untransformed and uncorrected means ± SD: F05, 12.0 ± 4.2 s, $n = 495$; M06, 11.5 ± 4.1 s, $n = 490$).

Discussion and Conclusions

Substantial individual variation in the responses of the two captive harbor porpoises to underwater sound was seen in the present study, which was in line with results of research on bottlenose dolphins (Branstetter et al., 2018). The fish-catching ability of porpoise F05 was negatively influenced by pile driving sounds, while porpoise M06's performance remained constant in the presence of the playback sound. Porpoise M06's capture success rate was higher than porpoise F05's in general and was unaffected by the pile-driving sound playbacks, even at the highest SELss. As the noise level increased above SELss = 134 dB re 1 µPa^{2}s, fish-catch success declined for porpoise F05, and she was more likely to terminate trials, especially

Table 2. Results of the nominal logistic regression model to assess the effects of SELss on the outcome of each trial (success, failure, or termination) for porpoise F05. The reference outcome is S (successful catch). Logit 1 relates S to T (termination) and shows that trials were significantly more likely to be terminated when the SELss was 134 dB or above. The odds of termination were ~10 times higher when SELss was 143 dB dB re 1 µPa^{2}s than in quiet conditions (odds ratio = 9.79). Logit 2 relates S to F (failure) and shows that SELss had no significant effect on the trial failure rate.

Predictor	Coefficient ± SE	Z	*p*	Odds ratio	95% CI (Lower-upper)
Logit 1: (T/S)					
Constant	-1.4 ± 0.2	-7.49	0.000		
SELss = 125 dB	0.2 ± 0.3	0.62	0.536	1.18	0.70-1.99
SELss = 134 dB	0.7 ± 0.2	2.99	0.003	2.11	1.29-3.43
SELss = 137 dB	1.2 ± 0.3	4.66	0.000	3.26	1.98-5.36
SELss = 143 dB	2.3 ± 0.3	7.80	0.000	9.79	5.52-17.38
Logit 2: (F/S)					
Constant	-0.5 ± 0.1	-3.81	0.000		
SELss = 125 dB	-0.1 ± 0.2	-0.37	0.715	0.92	0.63-1.38
SELss = 134 dB	-0.1 ± 0.2	-0.38	0.706	0.92	0.62-1.39
SELss = 137 dB	0.1 ± 0.2	0.48	0.630	1.11	0.72-1.72
SELss = 143 dB	0.3 ± 0.3	0.94	0.346	1.34	0.73-2.47

Table 3. Results of the general linear model on the dependent variable "catch time" (log transformed) in successful trials only to evaluate the effects of the factors "porpoise" and "SELss." Source = source of variation, *df* = degrees of freedom, Adj SS = adjusted sum of squares, and Adj MS = adjusted mean squares.

Source	*df*	Adj SS	Adj MS	*F* value	*p* value
SELss	4	0.1664	0.04160	2.02	0.090
Porpoise	1	0.0915	0.09147	4.44	0.035
Error	979	20.1856	0.02062		
Total	984	20.4332			

at the highest SELss (Figure 5). This suggests that her ability to catch fish was negatively affected by the increasing sound levels, most of all by decreasing her motivation to complete a trial. In addition, as porpoise F05 was observed to increase her swimming speed at SELss above 134 dB, she might have increased the task's difficulty (and thus decreased the chance of success) in some trials herself by displacing more water than usual (see below) and pushing the fish temporarily out of reach. During such trials, which only rarely occurred, a decreased motivation might have led porpoise F05 to decide not to wait for the fish to come within reach again before it reached the drop box.

The decline in fish-catch success and the increase in trial termination seen in porpoise F05 when unweighted broadband SELss increased above 134 dB suggest that some harbor porpoises may experience a *distraction threshold* for percussion pile driving sounds, approximately between 125 and 134 dB re 1 µPa^{2}s. *Distraction* is defined herein as the involuntary diversion of attention from one stimulus or set of stimuli to another. In this case, the decrease in success rate for porpoise F05 suggested that the (auditory) stimuli of playback pile driving sounds diverted her attention from the fish-catching task. Since actual echolocation activity was not measured in this study, we can only speculate that the decrease in fish-catch success rate exhibited by porpoise F05 was caused by a decrease in vigilance behavior similar to that in the bottlenose dolphins tested by Branstetter et al. (2018). Besides distraction, *aversive stimuli*, such as loud sounds, may influence motivation-related behaviors, as has been shown for grey seals (*Halichoerus grypus*; Götz & Janik, 2010). For instance, avoidance behavior may be induced, and foraging behavior may be suppressed. The latter seems to be the case for porpoise F05: at the highest SELss, she terminated over half of all trials, even though hunger was the intrinsic motivation for both porpoises to perform the task. This decrease in motivation is also consistent with the findings by Branstetter et al. (2018). Finally, the increase in swimming speed observed in porpoise F05 for the highest SELss is consistent with the behavioral response of captive harbor porpoises to pinger-like sounds observed by Teilmann et al. (2006). In their study, Teilmann et al. also measured a concurrent increase in heart rate, indicating stress. The concept of stress, however, is difficult to define, and more accurate measurements of stress in relation to sound exposure would require a physiological approach (e.g., Romano et al., 2004). Regardless, stress could have been a factor contributing to distraction from and/or a decrease in motivation to perform the fish-catching task.

Surprisingly, the catch times in successful trials remained stable for porpoise F05 with increasing SELss. When the same harbor porpoises involved in the present study were asked to perform a fish-searching task while exposed to various intermittent and continuous sounds at two different levels in another behavioral response study, search times were also found to be stable (Kok et al., 2018).

Individual differences in the harbor porpoises' approach to the fish-catching task also became apparent: porpoise F05 terminated trials more readily than porpoise M06 (Figure 5), and she took slightly longer to catch fish in successful trials. In a study of prey-searching behavior by the same porpoises, Kok et al. (2018) found that porpoise M06 spent less time searching than porpoise F05.

The two harbor porpoises certainly had different fish-catching techniques. Porpoise M06 approached the net feeding cage relatively slowly and used either the biting and grabbing technique or the suction technique. He sometimes pushed himself as far as possible into the net to reach the fish. Porpoise F05 did not use the suction technique and did not push into the net cage. She sometimes rotated horizontally and grabbed the fish through the net while swimming with her dorsal fin pointing down. It is not known whether this twisting maneuver is normal during prey capture by harbor porpoises, as it is for lunge-feeding blue whales (*Balaenoptera musculus*; Goldbogen et al., 2013) and for squid-hunting sperm whales (*Physeter macrocephalus*; Miller et al., 2004). Using electronic tags, Akamatsu et al. (2010) observed rolling dives in finless porpoises (*Neophocaena phocaenoides*) in which the porpoises often rotated their bodies more than 60° around the body axis in a dive bout. This behavior occupied 31% of the dive duration, and the rolling dives were associated with extensive searching effort. The authors suggest that the finless porpoises searched extensively for targets and rolled their bodies to enlarge the search area by changing the narrow beam axis of their biosonar. Though echolocation was not recorded, occasional checks with a hydrophone and a bat detector showed that the harbor porpoises in the present study did use echolocation in addition to vision when approaching the net cage with the fish.

The suction technique in harbor porpoises was described in detail by Kastelein et al. (1997b). The biting and grabbing technique and the suction technique have also been observed in harbor seals (*Phoca vitulina*; Marshall et al., 2014). In the setting of the present study, porpoise F05 was a less effective forager than porpoise M06. Porpoise F05 approached the net cage at higher speeds than porpoise M06 and, because of her speed and because she was bigger than porpoise M06, she displaced more water and produced more waves, which sometimes pushed the fish towards the back of the net cage, thus making it more difficult to retrieve the fish.

Measurements in shallow parts of the North Sea (34 m deep) show that the spectrum of the playback sound at a broadband SELss = 134 dB re 1 μPa^2s in the present study resembles the spectrum of pile driving sounds recorded at 7 km from a pile driving site at frequencies above about 500 Hz (Remmers & Bellmann, 2016). The corresponding unweighted broadband SELss measured in the field was 163 dB re 1 μPa^2s. However, harbor porpoises can probably sense the distance to a sound source due to reverberations, which may affect their reaction to a sound apart from the received SELss. Porpoises have a low hearing sensitivity for low-frequency sounds, so pile driving sounds with a frequency content below 500 Hz, which could not be reproduced in this playback study, are unlikely to be relevant for their behavioral response (Tougaard et al., 2015). However, individual differences in both fish-catching success (even in ambient conditions) and termination rates may complicate the quantification of the impacts of percussion pile driving sounds on harbor porpoises. Individual differences in responses to sound found in both bottlenose dolphins (Branstetter et al., 2018) and in harbor porpoises (present study) could be due to differences in a wide range of factors that may, or may not, be quantifiable, such as sex, motivation, age, history, reproductive state, body condition, degree of need for food, or character.

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