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Behavioral Responses of a Harbor Porpoise (*Phocoena phocoena*) to a Series of Four Different Simulated Low-Frequency Sonar Sounds (1.33-1.43 kHz)

Ronald A. Kastelein, Amy Verhoeven, and Lean Helder-Hoek

Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands
E-mail: researchteam@zonnet.nl

Abstract

Low-frequency sonar systems that produce sound in the 1.33 to 1.43 kHz frequency band are deployed from navy helicopters (HELRAS [Helicopter Long Range Active Sonar]) and vessels to detect submarines, and the sounds vary in spectrum, duration, and inter-pulse interval depending on the detection tasks. The sounds produced may affect the behavior of harbor porpoises (*Phocoena phocoena*) within a certain distance from the sound source. The goal of this study was to determine whether sonar sounds with four different harmonic contents and amplitude envelopes had different effects on harbor porpoise behavior. The sounds all had the same duration (1.25 s) and source level (107 dB re 1 μPa), and were produced in a series with regular inter-pulse intervals (14.4 s; duty cycle: 8%). A porpoise in a 12 × 8 m quiet pool was exposed to a 30-min series of each of the four sonar sounds (115 sounds/30 min). Mean received sound pressure level (SPL) in the pool was ~97 dB re 1 μPa for all exposures. During test sessions with each of the four sounds, the porpoise's mean distance to the transducer remained the same, and his swimming speed and number of surfacings (respirations) were only slightly higher than during baseline sessions without sounds. The downsweep caused a smaller behavioral effect than the continuous wave sounds. It is important to realize that the spectrum and SPL received by an animal determine whether it responds to a sound or not, and not the spectrum and SPL near a source.

Key Words: anthropogenic noise, behavioral response, disturbance, mitigation, naval sonar, odontocete

Introduction

Knowledge of the hearing systems and behavior of many marine mammals is limited, but sound is particularly important for them, as it may be used for orientation, communication, and the location of prey, conspecifics, and predators (Richardson et al., 1995). Therefore, marine mammals are likely to be disturbed by sound in their environment, and sound in the oceans may have negative physiological, auditory, and/or behavioral effects on marine mammals (National Research Council [NRC], 2003).

Background noise in the oceans consists of natural and anthropogenic sound. Navies worldwide cause part of the anthropogenic sound by employing shipping, causing explosions during exercises and removal of ammunition, and using sonar systems. Various types of sonar systems are used by navies to accomplish different detection tasks (Funnell, 2009). For example, some NATO navies use Helicopter Long Range Active Sonar (HELRAS) systems to detect submarines. These and some low-frequency ship-mounted sonar systems produce series of sounds generally between 1.33 and 1.43 kHz with different sound types, durations, and duty cycles at source levels (SLs) up to 217 dB re 1 μPa-m (L3 Ocean Systems, 2007).

Some marine mammal species are highly responsive to certain anthropogenic sounds, either generally or under particular conditions, and this can result in strong and sometimes large-scale avoidance of noisy areas. The harbor porpoise (*Phocoena phocoena*) is such a species (Southall et al., 2007). Information on the response of the harbor porpoise to sonar sounds is of particular interest because this odontocete species has a large geographic range in the Northern Hemisphere and has functional hearing over a very wide frequency range (Kastelein et al., 2017). Harbor porpoises are also known to be relatively easily deterred by certain anthropogenic underwater noises such as those produced by ships (Amundin & Amundin, 1973; Polacheck & Thorpe, 1990), acoustic alarms to prevent unwanted bycatch in gillnet fisheries (Laake et al., 1998; Kastelein et al., 2000, 2001, 2008a, 2008b; Culik et al., 2001; Johnston, 2002; Olesiuk et al., 2002; Barlow & Cameron, 2003; Teilmann et al., 2006), offshore wind turbines (Koschinski et al., 2003), underwater data communication systems (Kastelein et al., 2005), and simulated low- and mid-frequency ship-mounted naval sonar systems (Kastelein et al., 2014). Behavioral response threshold levels of harbor porpoises have been determined for noise bands around 12 kHz, a continuous 50 kHz tone, continuous and pulsed 70 and 120 kHz tones (Kastelein et al., 2005, 2008a, 2008b), 1 to 2 kHz and 6 to 7 kHz up- and downsweeps (Kastelein et al., 2012), 1.33 to 1.43 kHz helicopter dipping sonar (124 to 144 dB re 1 µPa depending on the sound type; Kastelein et al., 2013a), pile-driving sound playbacks (Kastelein et al., 2013c), an impulsive sound (Kastelein et al., 2013b), and 25-kHz sonar sounds (Kastelein et al., 2015b). These studies show that the spectrum, received sound pressure level (SPL), kurtosis, and duty cycle of an underwater sound play important roles in the effect the sound has on the behavior of porpoises.

Kastelein et al. (2011a) found that the 50% hearing thresholds of a harbor porpoise for five different low-frequency sonar sounds (HELRAS) were similar: 76 dB re 1 µPa (broadband SPL, averaged over the sound's duration). The hearing thresholds were similar to those found in the same porpoise for tonal sounds in the 1 to 2 kHz range (Kastelein et al., 2010). The harmonics occurring in three of the five HELRAS sonar sounds that were tested contained enough energy to influence the sounds' audibility. Kastelein et al. (2013a) showed that startle responses (i.e., short-duration responses occurring shortly after the onset of a sound) in harbor porpoises occur at relatively low received levels for complex HELRAS sounds with relatively strong harmonic contents. Producing individual HELRAS sounds similar to those used in the present study at various levels caused a 50% startle response rate in the same harbor porpoise at mean received SPLs (averaged over the 90% energy duration of the sound, and averaged over all 231 measurement locations in the pool) of between 124 and 144 dB re 1 µPa, depending on the signal type. Of the sounds that were tested, the downsweep without harmonics (a sound that was not tested in the present study) required the highest level to produce startle responses in 50% of the emissions (Kastelein et al., 2013a). Harmonics can have a strong effect on harbor porpoises' behavioral responses, so the detection level and number of decibels (dBs) above the hearing threshold of the harmonics causing behavioral effects need to be differentiated.

The goal of this study was to determine whether the structure of low-frequency sonar sounds, produced at a duty cycle in the range used in naval operations (115 sounds/30 min) during 30-min exposures, play a role in the effect these sounds have on sustained harbor porpoise behavior (as opposed to startle behavior). To achieve this, a harbor porpoise in a pool was subjected to four series of simulated low-frequency sonar sounds with the same signal duration and mean exposure SPL, but differing in harmonic content and amplitude envelopes.

Methods

Study Animal

The male porpoise (identified as Porpoise M02, 4.5 y, 37 kg, 143 cm) used in this study had participated in previous psychoacoustic hearing threshold studies and behavioral response studies (Kastelein et al., 2009, 2010, 2012, 2013a, 2013b, 2013c, 2015a, 2015b). His hearing is similar to that of five other harbor porpoises (Kastelein et al., 2017) and is considered to be typical for young harbor porpoises.

Study Area

The study was conducted at the SEAMARCO Research Institute, the Netherlands, in a remote and quiet location that was selected for acoustic research. The study animal was kept alone in a pool complex specifically built for acoustic research, which consisted of an outdoor pool (12 m × 8 m, 2 m deep) connected via a channel (4 m × 3 m, 1.4 m deep) with an indoor pool (8 m × 7 m, 2 m deep; Figure 1). The study was conducted in the outdoor pool. The pool walls were made of plywood covered with polyester. To reduce reflections of sound in the pool, the walls were covered with 3-cm-thick coconut mats with their fibers embedded in 4-mm-thick rubber (reducing reflections mainly above 25 kHz), and the bottom was covered with a 20-cm-thick layer of sloping sand. The coconut mats extended to 10 cm above the water level to reduce the splashing noise of waves.

The water level was kept constant by means of skimmers. The seawater was pumped directly from the nearby Oosterschelde, a tidal inlet of the North Sea, into the open system; 80% recirculation through sand filters ensured year-round water clarity.

The water circulation system and the aeration system for the biofilter were made as quiet as possible. This was done by choosing "whisper" pumps, mounting the pumps on rubber mats, and connecting the pumps to the circulation pipes with very flexible hoses. The water temperature during the study varied between 4° and 10°C; the salinity was around 34‰. There was no current in the

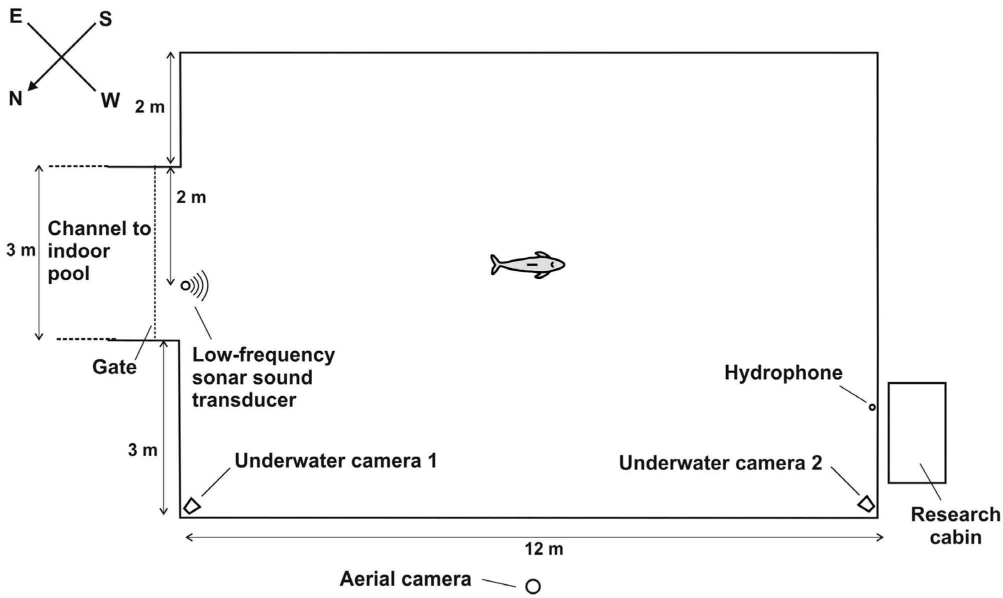


Figure 1. Top scale view of the outdoor pool at the study facility, showing the study animal, the location of the aerial camera, the two underwater cameras, the underwater transducer emitting the sonar sounds, and the listening hydrophone. Also shown is the research cabin that housed the equipment and the operator.

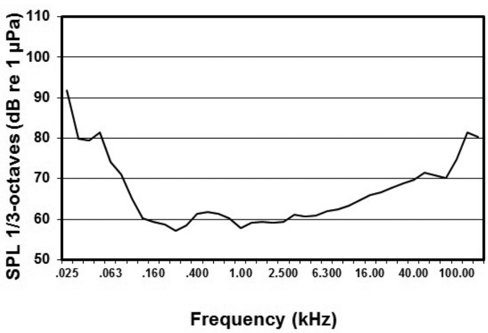


Figure 2. The background noise level in the outdoor pool during test conditions. Above 10 kHz, the noise measurements were influenced by electronic noise.

pool during the experiments, as the water circulation pump and the air pump of the adjacent biofilter were shut off 30 min before each session and during each session. As a result, by the time a session started, no water flowed over the skimmers so that there was little or no flow noise (Figure 2).

Video and Audio Equipment

The equipment used to produce the sounds was housed out of sight of the study animal in a research cabin adjacent to the pool (Figure 1). The digitized test sounds (WAV files; sample frequency 48 kHz) were played back by a laptop computer (Model D250-0DK, Acer – Aspire One) to an audio power amplifier (Model HQ VPA2200MBN), the output of which was controlled with a custom-built, digitally controlled attenuator (1 dB steps). After going through an isolation transformer (Model AC202; Lubell Labs, Columbus, OH, USA), the sounds were projected under water via a directional balanced tonpilz piezoelectric acoustic transducer (Model LL916, Lubell Labs) suspended 1 m below the water surface at the northeastern end of the pool near the entrance of the channel to the indoor pool (Figure 1). The output of the sound system to the transducer was monitored by means of an oscilloscope (Model 2201; Tektronix, Madison, WI, USA), a voltmeter (Model 34401A; Agilent Technologies, Santa Clara, CA, USA), and a spectrum analyzer (Model PCSU1000; Velleman, Gavere, Belgium).

The animal's behavior was filmed from above via a waterproof camera (Model 750940; Conrad Electronics, Hirschau, Germany), with a wide-angle lens and a polarized filter to prevent saturation of the video image by glare from the water surface. The camera was placed on a pole 9 m above the water surface on the northwestern side of the pool (Figure 1). The entire surface of the pool was captured on the video image. The output of the camera was fed through a video multiplexer (Model 8, MX) that added the time and date to the images. Thereafter, the output was digitized with an analog-to-digital converter (EZ Grabber, Model Vista version) and stored on a laptop computer (Model MD96780; Medion, Essen, Germany). The animal was also filmed by two underwater video cameras (Model Delta Vision B/W; Ocean Systems Inc., Everett, WA, USA) in two corners of the pool (Figure 1). The images from the underwater cameras were visible to the operator on two screens in the research cabin.

The audio part of the background noise and the test sounds were recorded via a custom-built hydrophone and a custom-built pre-amplifier. The output of the pre-amplifier was digitized via the analog-to-digital converter and recorded on the computer in synchrony with the video images. The output was also fed to an amplified loudspeaker so that the operator in the research cabin could monitor the background noise and the test sounds during sessions.

Test Stimuli

Sonar Sounds—The harbor porpoise's response to four simulated sonar sounds was tested (Table 1). Sounds produced by HELRAS consist of a series of tonal signals with durations of 0.313 to 10 s; at nominal frequencies of 1,311, 1,380, or 1,449 Hz, with various amplitude envelopes; or frequency-modulated (FM) signals, with durations of 0.156 to 5 s and bandwidths of 50 to 300 Hz. Three sounds, provided by the manufacturer of HELRAS (L3 Communications, Ocean Systems Division, Sylmar, CA, USA) as representative, were manipulated to make them of consistent duration (1.25 s, which falls within the range used for HELRAS and is likely to be used in shallow coastal waters). One additional sound (a continuous wave [CW]), similar to the original recordings but without the harmonics, was synthesized.

The four simulated sonar sounds were created as WAV files using *Cool Edit Pro* (NCH Software, Canberra, Australia). The sounds were defined as CWht (a 1,380-Hz continuous wave with a cosine squared amplitude taper and harmonics), CWh (a 1,380-Hz continuous wave with harmonics and 50-ms cosine tapers at start and end), DSh (a 1,430- to 1,330-Hz FM downsweep with harmonics), and CW (a 1,380-Hz CW with 50-ms cosine tapers at start and end). Waveforms and sonograms of the four sonar sounds are shown in Figures 3 & 4, respectively. The first three sounds (CWht, CWh, and DSh) exhibit a 3rd and 5th harmonic that are 11 to 30 dB below the level of the fundamental frequency (Table 1).

Series of Sonar Sounds—The four 1.25-s simulated sonar sounds were transmitted in series with a regular inter-pulse interval (the silence period between two sounds) of 14.4 s, resulting in a duty

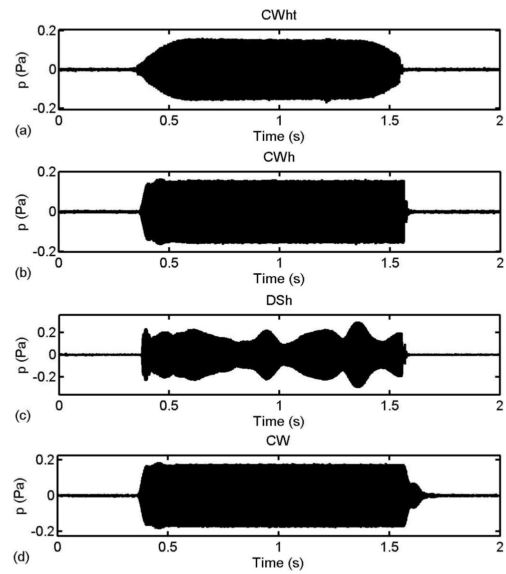


Figure 3. The waveforms of the simulated sonar sounds that were used in the behavioral response study with a harbor porpoise (*Phocoena phocoena*): (a) CWht, (b) CWh, (c) DSh, and (d) CW

Table 1. The characteristics of the four sonar sounds that were used in the behavioral response study with a harbor porpoise (*Phocoena phocoena*)

Sound	Description	Relative level of 3rd harmonic	Relative level of 5th harmonic
CWht	1,380-Hz continuous wave with harmonics and cosine squared tapers	-16 dB	< -30 dB
CWh	1,380-Hz continuous wave with harmonics	-15 dB	< -30 dB
DSh	1,430- to 1,330-Hz downsweep with harmonics	-11 dB	< -30 dB
CW	1,380 Hz continuous wave	No harmonics	No harmonics

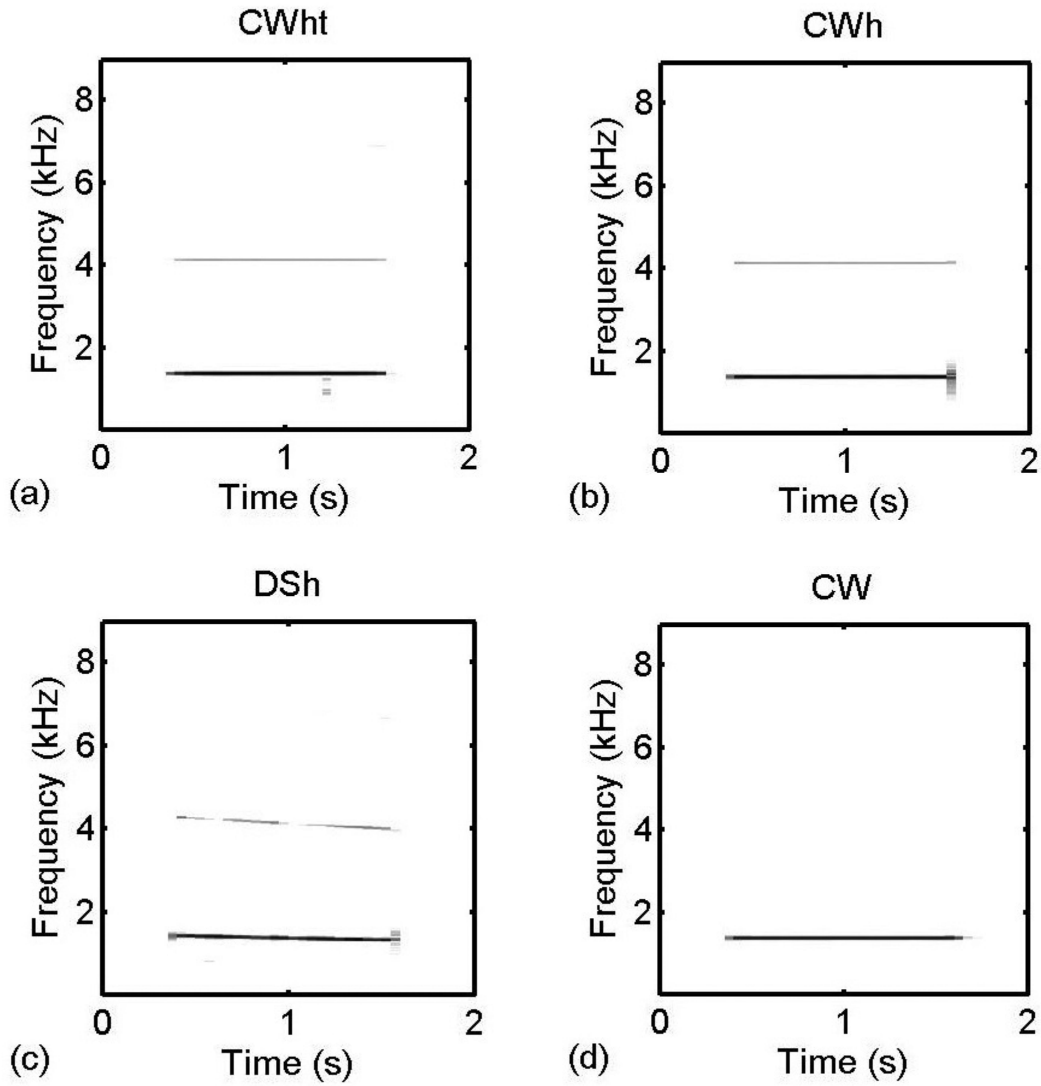


Figure 4. Sonograms of the four simulated sonar sounds that were used in the behavioral response study with a harbor porpoise: (a) CWht, (b) CWh, (c) DSh, and (d) CW.

cycle of 8%, falling within the duty cycle range used in normal navy operation in which the duty cycle of the HELRAS system varies between 5 and 10%.

Determination of the Source Level Used in the Tests—During a pretest, the SL of the CW sound was gradually increased until, in response to it, the harbor porpoise moved slightly away from the transducer, and his respiration rate increased noticeably. The SL at which this occurred (107 dB re 1µPa) was used for all four sonar test sounds during the study.

SPL Distribution Measurements—To determine the sound distribution in the pool, the SPL (dB re 1 µPa) for each of the test sounds was measured at 77 locations (on a horizontal grid of 1 m × 1 m). The SPL was measured at three depths per location on the grid (0.5, 1.0, and 1.5 m below the water surface). Thus, 231 measurements were made for each of the four sonar sounds (Table 2; Figure 5). The SPLs were based on a recording of one sound per location, and the analysis was done in the time domain. The duration of the sound (t_{90} in s) was defined as the time between the moments when the cumulated sound exposure reached 5 and 95% of the total exposure—that is, when it contained 90% of the total energy in the sound (see Table 2). The SPL was determined by subtracting 10 times the logarithm

Table 2. The source level (SL) and the mean received level in the pool (dB-averaged over all measurement locations in the pool; $n = 231$), and the mean sound pressure level (SPL) per depth ($n = 77$ per depth) of the four simulated sonar test sounds

Sonar sound	SL (dB re 1µPa @ 1m)	Mean (± SD) received SPL in pool (dB re 1 µPa)	SPL range in the pool	t_{90} (s)	Mean received SPL for each measurement depth (dB re 1 µPa)		
					0.5 m	1.0 m	1.5 m
CWht	107	96 ± 6	84-108	0.946	96 ± 7	98 ± 3	93 ± 6
CWh	107	96 ± 6	83-108	1.047	96 ± 7	99 ± 3	93 ± 6
DSh	107	98 ± 4	87-108	1.061	98 ± 5	100 ± 3	95 ± 4
CW	108	97 ± 6	82-110	1.071	97 ± 7	100 ± 4	94 ± 6

of the t_{90} duration from the sound exposure level (SEL). Figure 5 shows the SPLs of the sounds as a function of the distance (slant range) between the transducer and the hydrophone. The received levels of the tonal sonar sounds at different positions in the pool are affected by interference between direct and reflected sound transmission paths from the transducer to the location of the hydrophone. Variation is greatest for hydrophone positions that are closest to the water surface and the bottom of the pool (0.5 and 1.5 m deep). In general, up to about 6 m from the transducer, the received levels drop due to spreading loss; at greater distances, the received levels are more independent of distance due to the reverberation in the pool. The mean received SPL reported in this study is averaged over all 231 measurement locations in the pool. As expected, the SPL range for the downsweep was smallest, as the signal's frequency changed during signal presentation, and this reduced the chance of standing waves (Finneran & Schlundt, 2007).

Experimental Procedure

Each test consisted of a 30-min baseline session (no sound emission), followed immediately by a 30-min test session (sonar sound emission, 115 sounds/30 min). The transducer producing the sonar sounds was positioned in the pool 30 min before the baseline session started (Figure 1). Usually one but occasionally two tests were conducted per day, normally 5 d/wk, beginning between 1000 and 1500 h. To prevent reactions by the harbor porpoise to stimuli other than the sonar test stimuli, only personnel conducting the tests were allowed within 10 m of the pool during the tests.

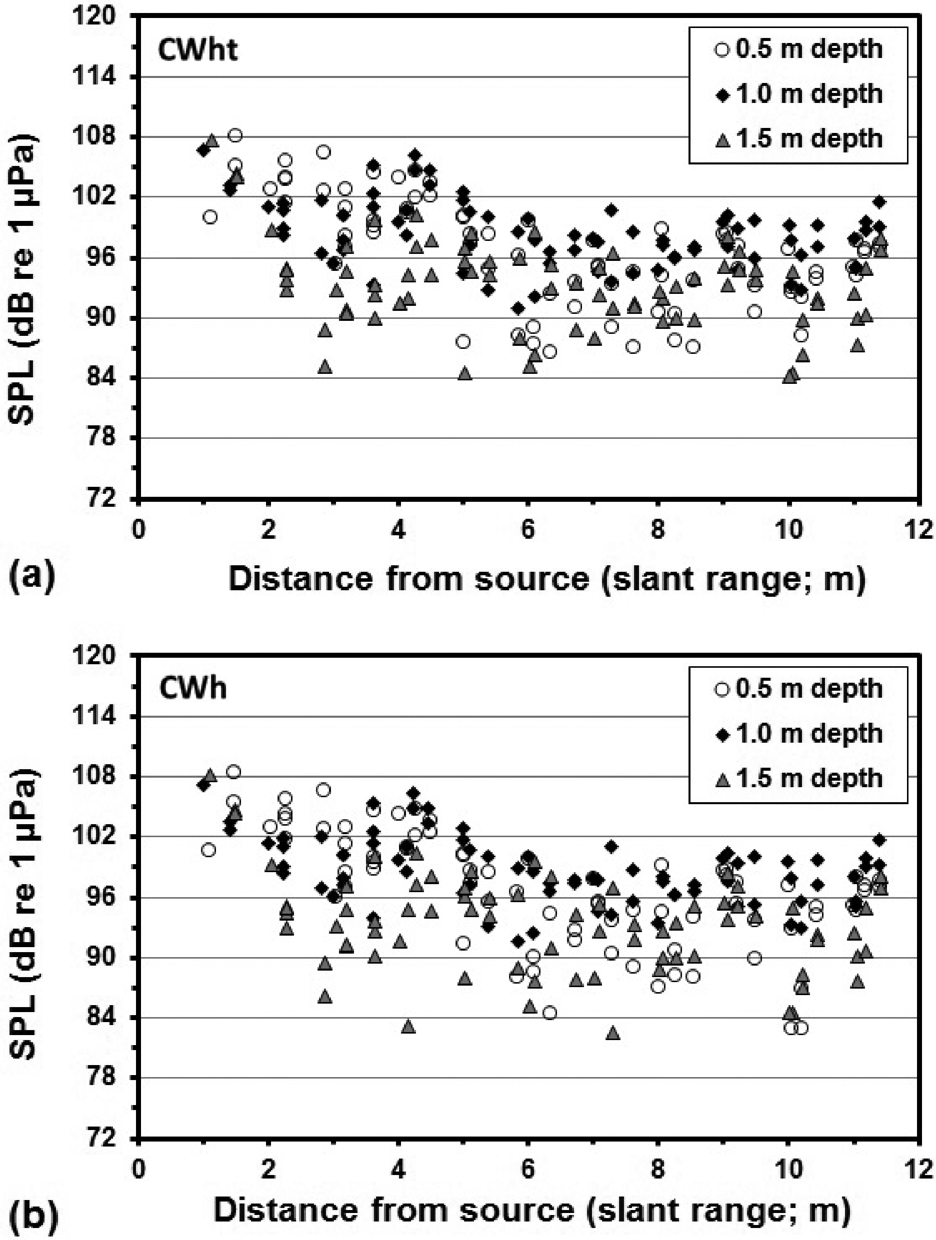
One sonar sound was tested per session; and for each sound, six tests were conducted in total. During each 30-min test session, a sound was presented 115 times. The four sonar sounds were tested in random order. To ensure low ambient noise, tests were not carried out during rainfall or when wind speeds were above Beaufort 4. The data were collected over a period of 2 mo (March-April 2010).

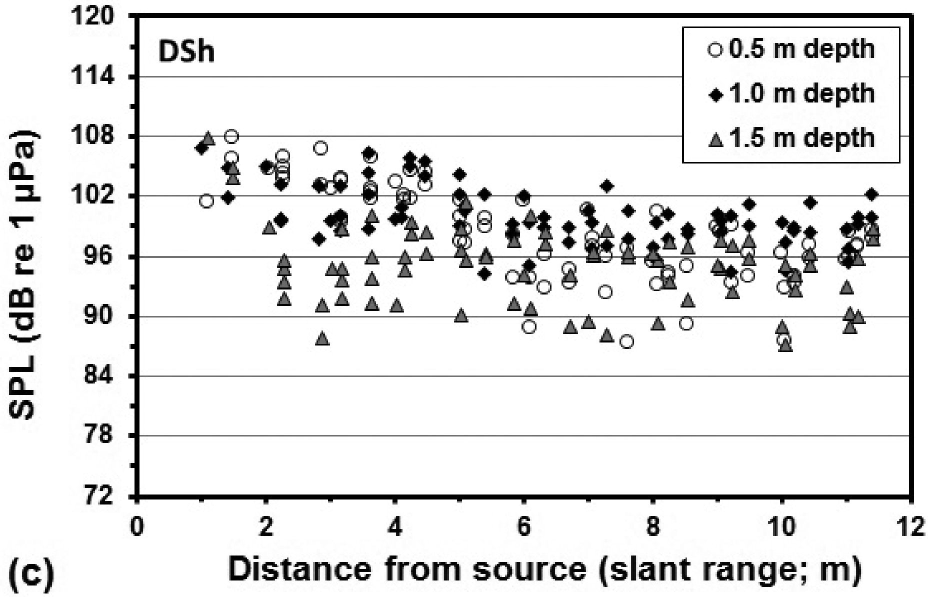
Response Parameters and Behavioral Data Recording

Two objective behavioral parameters were used to quantify the harbor porpoise's responses to the sonar sounds: (1) his surfacing location in the pool relative to the transducer and (2) the number of times he surfaced (surfacings coincided with respirations; this could be heard). These parameters were quantified and compared for baseline and test sessions, with each 30-min session being further subdivided into 10-min periods.

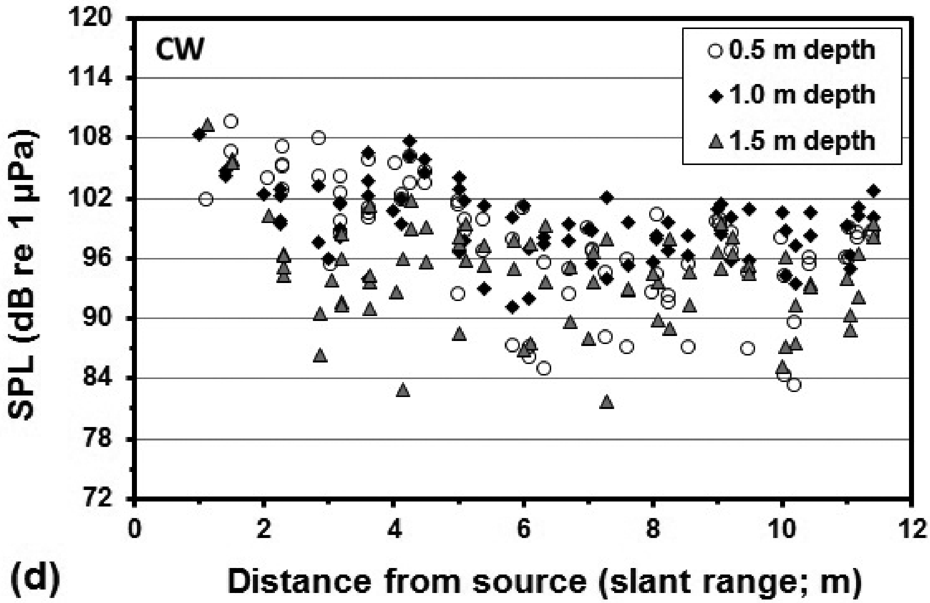
The distance between the transducer and the location where the animal surfaced was quantified to determine whether the harbor porpoise responded to the sounds by swimming away from the sound source. This was done as follows: from video camera recordings, the locations where the porpoise surfaced during the baseline and test sessions were recorded on a grid superimposed on the computer screen. The grid corresponded to a pool grid of 1 m × 1 m and was made by connecting lines drawn onto the computer screen between physical 1 m markers on the pool's sides. The grid square in which the porpoise surfaced was determined from the video recordings, and the center point of the grid square was used to calculate the distance between the porpoise's surfacing location and the transducer via triangulation. The water was always clear; and when light conditions were such that the bottom of the pool was visible and the porpoise could be seen well below the water surface, he generally did not swim far away from the surfacing locations. Hence, the surfacing locations were a good indication of the porpoise's general swimming area. To determine whether the porpoise responded to the sounds by increasing his surfacing rate (and, thus, his breathing rate), the number of surfacings in the baseline sessions was compared with the number during the test sessions.

In addition to the two objective behavioral parameters (distance from the transducer and number of surfacings), the animal's relative swimming speed was quantified subjectively. For this, the test sessions were divided into three 10-min periods. In each, swimming speed was classed relative to the swimming speed during the previous baseline period as a number between one and zero. Greatly increased speed was classed as one (~maximum speed observed in the pool, causing ~10 cm high waves; only possible for short periods of time); increased speed was classed as a score of 2/3 (sustainable, causing ~5 cm waves); slightly increased speed was classed as a score of 1/3 (faster than usual, causing no waves); and no change in swimming speed compared to the speed in the baseline (the usual swimming speed) was classed as zero. The average of the three numbers per test session was used to quantify the change in swimming speed (maximum value: one).





(c)



(d)

Figure 5. The SPL distribution (dB re 1 µPa, averaged over the 90% energy duration of the sounds) of the four simulated sonar sounds as a function of the distance (slant range) between the transducer and the hydrophone: (a) CWht, (b) CWh, (c) DSh, and (d) CW. As expected, the SPL range per distance is smaller for the DSh sound (c) than for the CW sounds (a, b & d).

Analyses

To ensure consistency, all the video recordings were analyzed by one person who was not aware of the type of sonar sound that had been emitted. Two separate analyses were conducted for different purposes as explained below: (1) an analysis of covariance (ANCOVA) and (2) paired tests (parametric and non-parametric versions). To investigate habituation and differences between the effects of the sonar sounds, one ANCOVA was conducted for each parameter (relative distance to the transducer and relative number of surfacings) with "sonar sound" and "10-minute period" as factors, and "session number" as the covariate. For both relative distance from the transducer and relative number of surfacings, analyses were conducted on the differences between baseline and associated test session (calculated as test minus baseline for each 10-min period). The session number and the 10-min period were included as different measures of habituation.

To investigate the effect of each sonar sound individually, paired *t* tests were carried out for distance to the transducer and number of surfacings (to compare the 30-min baseline and associated test sessions). Similarly, Wilcoxon signed rank tests (Zar, 1999) were carried out to compare the animal's relative swimming speed to zero (zero being indicative of no change between baseline and test). For all analyses, data conformed to the assumptions of the tests used, and the level of significance was 0.05 (Zar, 1999).

Results

During the 30-min baseline sessions, the harbor porpoise usually swam large clockwise ovals in the pool. The distance to the transducer was consistent (mean = 5.9, SD ± 0.2 m, $n = 24$), and the porpoise rarely jumped out of the water. The mean number of surfacings (= respirations) varied between 43 and 127 (mean = 85, SD ± 11, $n = 24$). The animal generally showed a regular dive pattern consisting of long dives alternated with shorter dives.

Comparing each baseline session with its associated test session revealed that, on average in test sessions (of all four sounds taken together), the harbor porpoise increased his distance to the transducer only slightly by 0.11 m (mean increase, SD ± 0.37, $n = 24$; to put this number into perspective: total pool length = 12 m) and his number of surfacings by 16 (mean increase, range = 6 to 32, SD ± 4, $n = 24$). His swimming speed was scored as 0.3 (mean, SD ± 0.06, $n = 24$; a score of zero would indicate no difference between baseline and test, and a score of one would be the maximum score).

The ANCOVAs showed that, collectively, the four sonar sounds affected the harbor porpoise significantly in terms of his relative distance to the transducer and relative number of surfacings (Table 3; Figure 6). Tukey tests showed that, for relative distance, the porpoise responded more strongly (by swimming slightly further away) to sonar sound CW than to the other sounds; and for relative numbers of surfacings, he responded less strongly (by exhibiting a slightly lower relative number of surfacings) to DSh than to the other three sonar sounds. There was no evidence of habituation to the sounds, either within each 30-min session or over the entire study period (evidenced by no significant effect of 10-min period or session number; Table 3).

Subsequent paired *t* tests of the effects of each sound separately, ignoring the nonsignificant effects of session number and 10-min period, showed that all four sonar sounds caused the animal to swim faster and surface more frequently during test sessions than during baseline sessions (Table 4), but the sounds had no significant effect on relative distance.

Table 3. Results of the ANCOVAs on (a) relative distance from the transducer and (b) relative number of surfacings (both calculated as test minus baseline) for the covariate "session number" and the factors "sonar sound" and "10-minute period." *df* = degrees of freedom, Adj. ms = adjusted mean squared, * = significant, NS = not significant, F = F-statistic, and *p* = probability.

(a) Relative distance from the transducer (m)				
Source of variation	*df*	Adj. ms	F	*p*
Session	1	2.78	3.54	0.064 NS
Sonar sound	3	2.29	2.92	0.041*
10-min period	2	0.16	0.20	0.818 NS
Error	65	0.78		
Total	71			
(b) Relative number of surfacings				
Source of variation	*df*	Adj. ms	F	*p*
Session	1	2.07	0.11	0.743 NS
Sonar sound	3	76.8	4.03	0.011*
10-min period	2	10.8	0.57	0.571 NS
Error	65	19.1		
Total	71			

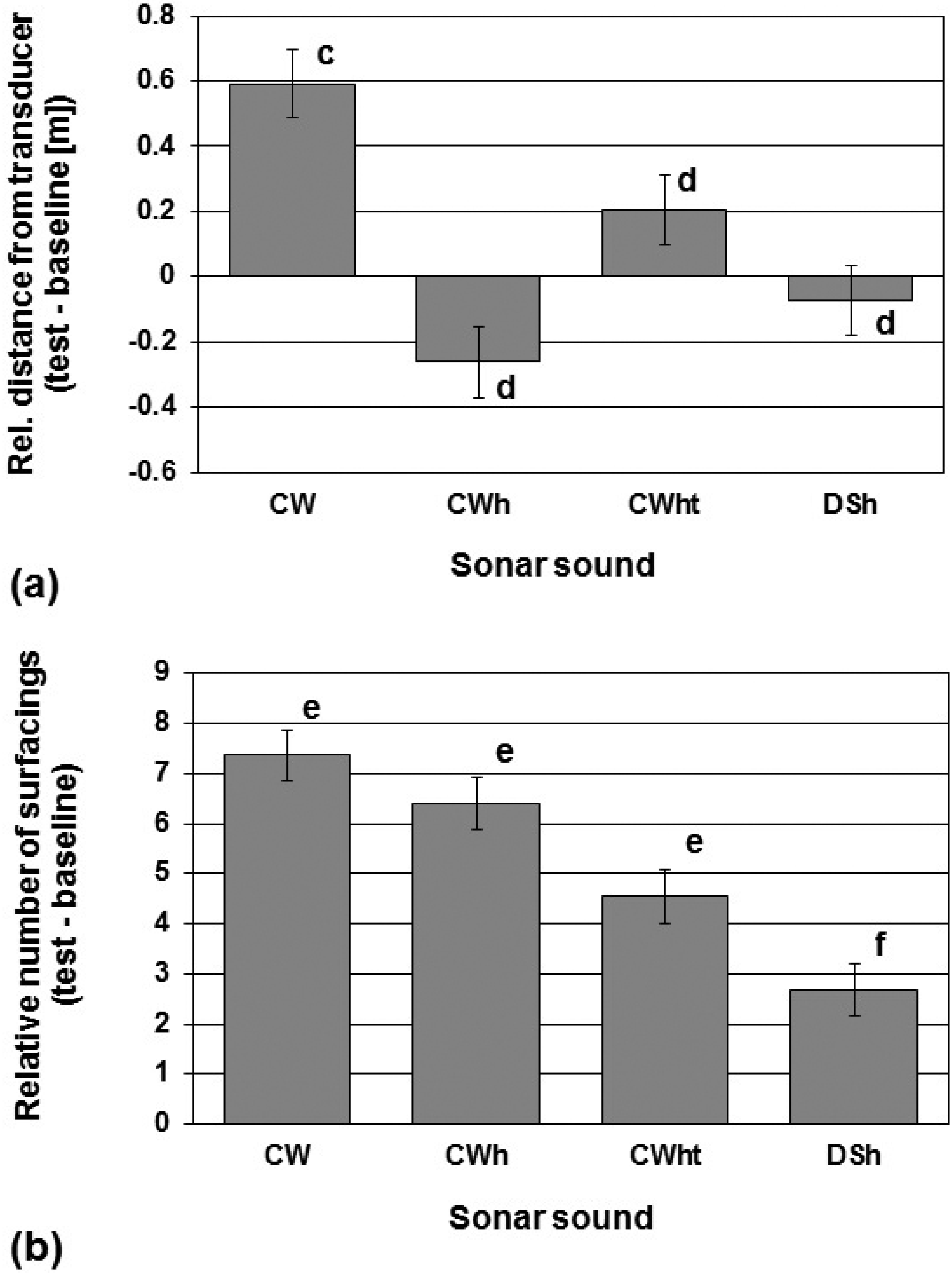


Figure 6. The effect of the four sonar sounds, at a mean received SPL of ~ 97± 6 dB re 1 μPa, on the harbor porpoise's behavior, adjusted for the covariate, and shown as means (bars are standard errors; *n* = 6): (a) the relative distance to the transducer (total pool length: 12 m) and (b) the relative number of respirations per 10-min period. The effect of the sounds on distance from the transducer was small but greater for the CW sound than for the others. The effect of the sounds on the number of surfacings was smaller for DSh than for the others. Bars with the same letter (c-f) do not differ from one another statistically. The four sounds all had the same duration (1.25 s) and almost the same source level (SL), and the series of sounds had the same regular inter-pulse interval (14.4 s; duty cycle: 8%); *n* = 6 for each sound. Baseline and test sessions lasted 30 min each. In each test session, 115 sonar sounds were produced.

Table 4. Results of paired *t* tests for distances to the transducer and numbers of surfacings, and Wilcoxon signed rank tests for swimming speed, in baseline and test sessions, for each of the sonar sounds separately. The factors "session number" and "10-minute period" are not taken into account. Only significant *p* values are shown; NS = not significant. The sample size for each analysis is six. In all cases, the number of surfacings was significantly higher, and the swimming speed faster, in test sessions than in baseline sessions.

Sonar sound	Distance to transducer	Number of surfacings	Swimming speed
CWht	NS	0.008	0.036
CWh	NS	0.004	0.036
DSh	NS	< 0.001	0.036
CW	NS	0.002	0.036

Discussion

Behavioral responses to sounds are context-dependent; they vary with location, time of day, season, social setting, and ongoing behavior such as foraging or migrating. They also depend on the background noise level. The effects observed in the present study occurred under very low background noise and in unmasked conditions. Under higher background noise conditions, the effect may be even smaller, as was observed in the same harbor porpoise for 6 to 7 kHz upsweeps transmitted under controlled ambient noise conditions resembling those of various sea states (Kastelein et al., 2011b).

Evaluation

The hearing of the study animal was representative of that of harbor porpoises of his age and was very similar to that of other porpoises of similar age (Kastelein et al., 2017). Still, it cannot be said whether the study animal's response was representative of its species. Therefore, the present study should be repeated with other porpoises if possible, as responses may vary between individuals (Kastelein et al., 2000, 2001, 2008b).

Casual observation showed that after each session, when the sonar sound exposure had stopped, the animal's behavior returned to normal immediately. He cooperated in a psychoacoustic test only minutes after the test sounds had ceased. Therefore, after exposure to the sonar sounds at a mean received broadband SPL of ~97 ± 6 dB re 1 µPa for 30 min at a duty cycle of 8%, there were no post-exposure effects on the animal's behavior. A similar quick return to baseline behavior was seen in previous acoustic alarm (pinger) studies with harbor porpoises (Kastelein et al., 2000, 2001, 2006, 2008a, 2008b) and was the reason for not including a post-test observation period in this study, as was done in the first pinger study (Kastelein et al., 2000).

Kastelein et al. (2013a) showed that 50% startle response threshold levels to the sonar sounds used in the present study occurred at mean received levels well above the level used in the present study (124 to 140 dB re 1 µPa, depending on the signal type); the low levels used in the present study resulted in no observable startle responses. This suggests that repetitive exposures to low-level sounds that do not produce startle responses may result in more sustained, but weak, behavioral responses. In the free field, increases in respiration rate due to sound exposure are expected to decrease as distance to the source increases (because the received SPL decreases with distance) when animals swim away from a sound source. However, reverberations due to the acoustic characteristics and limited size of the pool used in the present study meant that it was not possible to investigate the relationship between respiration rate and distance to the transducer (Figure 5). Understanding this relationship would increase our insight into the ecological and behavioral effects of sound exposures on harbor porpoises.

Comparison of Levels Used in the Behavioral Study with Hearing Thresholds

The 50% hearing thresholds (broadband SPL, averaged over the signal duration) of the harbor porpoise used in the present study for the four different sonar sounds were similar (76 dB re 1 µPa; Kastelein et al., 2011a). The mean received broadband level in the present study was ~97 ± 6 dB re 1 µPa. Thus, the mean broadband sensation level (i.e., the number of dB above the 50% hearing threshold) of the harbor porpoise for the sounds in the present study was ~21 dB (see Tougaard et al., 2014, for context). In the detection levels reported by Kastelein et al. (2011a) for HELRAS sounds, the harmonic content played no role, and, thus, the 50% hearing thresholds depended on the fundamental frequency (1.33 to 1.43 kHz). In the present study, the content of the 3rd harmonic was close to the detection threshold of 4 kHz, and the 5th harmonic was very weak and below the detection threshold. Thus, the porpoise in the present study probably responded to the fundamental frequency of the sonar signals. To elicit a startle reflex in harbor porpoises, the SPL of the HELRAS sound had to be higher, which caused harmonics. Kastelein et al. (2013a) concluded that the 50% startle response threshold SPL for HELRAS sounds was probably affected by the harmonic content of the sound. Therefore, the broadband SPL cannot always be used as an absolute value to predict behavioral responses, but the sound's spectrum (including harmonics) should be compared to the hearing thresholds of the species as a first step in estimating the behavioral effects of a sound.

Use of Sonar by Navies

The hearing of the harbor porpoise is relatively insensitive for frequencies below 4 kHz (it is a high-frequency hearing specialist, with most sensitive hearing around 125 kHz; Kastelein et al., 2017). Therefore, levels of anthropogenic low-frequency sonar sounds need to be relatively high for porpoises to hear them, and even higher for the animals' behavior to be affected.

In the present study, sonar sounds with sensation levels of ~21 dB (and 8% duty cycle) hardly displaced the harbor porpoise and only led to a slight increase in respiration rate and a small increase in swimming speed. The effect on the study animal's behavior did not continue after the sound exposure stopped. Thus, if porpoises at sea are exposed to sonar signals at SPLs similar to those experienced by the porpoise in the present study, the effects are expected to be minimal.

The sonar sounds tested in this study did not have high-SPL, high-frequency harmonics; however, other studies have shown that relatively high-level harmonics of low-frequency sonar sounds may greatly increase the effect of the sounds on harbor porpoises, especially if the sensation level of the harmonics is higher than that of the fundamental frequency (Kastelein et al., 2012, 2013a, 2014). Thus, in the design of new sonar systems, the level of harmonics should be reduced as much as possible to reduce the impact of the systems on the behavior of harbor porpoises and possibly other odontocete species. Higher harmonics are likely to be more prominent when the SL is pushed to its maximum. Operators of sonar systems should identify the SLs above which strong harmonics are produced and understand how spectra change over distance from the sound source. Fortunately for harbor porpoises, the higher frequencies of harmonics are attenuated to a greater extent than the lower fundamental frequencies, as water acts as a low-pass filter. In addition, sound duration and amplitude modulation are influenced by reverberations. Therefore, it is important to consider the spectrum and SPL received by an animal, and not the spectrum and SPL near the source, when estimating the potential impact of a sound on an animal.

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