Behavioral Responses of Harbor Seals (*Phoca vitulina*) to Sonar Signals in the 25-kHz Range

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Abstract

The effect of three sonar sound types (around 25 kHz) on the behavior of two harbor seals was quantified in a quiet pool. The behavioral response threshold for each sound type was determined by transmitting at three sound pressure levels (SPLs). Sequences were 50-ms frequency modulated (FM) signals (duty cycle: 2.4%), 600-ms continuous waves (CW; duty cycle: 5.6%), and 900-ms combinations of the two sound types (Combo; duty cycle: 8.3%). Behavioral responses ranged from no reaction to increased time spent at the water surface, numbers of jumps, hauling out, and swimming speed. At the average received sound pressure levels (SPLsav.rec.) ≤ 158 dB re 1 μ Pa, and the duty cycles used, mainly the FM sound type caused significant behavioral responses at SPLsavrec. above 125 dB re 1 µPa. The CW sound type caused minimal response at the SPLsavree. offered. The Combo sound type also caused minimal response, despite the fact that it contained a longer version of the FM sound type and had a higher duty cycle than the FM sound type. However, the inter-pulse interval was longer in the Combo sound type. The possible effects of signals with different parameters (e.g., duty cycles, signal durations, frequencies, waveforms) are unknown. but the results suggest that, for harbor seals, during peace time exercises and in fisheries, the use of CW and Combo signals is preferred to the use of FM signals (at the signal duration and duty cycles used in the present study).

Key Words: disturbance, fisheries sonar, naval sonar, noise, pinnipeds, Phocid, harbor seal, *Phoca vitulina*

Introduction

Sound is important for marine animals as a means of orientation and communication, and to locate prey, conspecifics, and predators (Richardson, 1995; Nowacek et al., 2007; Wright et al., 2007). Therefore, marine mammals are likely to be disturbed by noise in their environment. In addition to natural noises, human activities increasingly add noise to the environment. Anthropogenic noise has increased during the last century (McDonald et al., 2006, 2008) and may have negative physiological, auditory, and behavioral effects on marine fauna (Richardson, 1995; National Research Council [NRC], 2003).

Navies worldwide contribute to the background noise by employing shipping, explosions during exercises and removal of ammunition, and various types of sonar systems. Active sonars, which are used to detect submarines, produce intermittent underwater sounds. Many navies use mid-frequency active sonar systems (MFAS; with sweeps in the 5 to 10 kHz range), and, more recently, low-frequency active sonar systems (LFAS; with sounds in the 0.1 to 2 kHz range). The duration of the sweeps and of the intervals between them can be altered depending on the expected distance of target submarines (Funnell, 2009).

Compared to the larger oceans, the Baltic Sea is relatively shallow (average depth 52 m, leading to increased occurrence of reverberations) and has low salinity (leading to reduced sound absorption). Consequently, anti-submarine warfare active sonar systems tailored to the Baltic Sea typically operate at higher frequencies than those of most North Atlantic Treaty Organization (NATO) navies (Pihl & Ivansson, 2009): sonar signals peak at, or above, 25 kHz and are similar to some of those used worldwide in fisheries sonar (Simrad, 2015a, 2015b).

The harbor seal (*Phoca vitulina*), a marine mammal species distributed widely in the shallow coastal waters of the Northern Hemisphere, including in the Baltic, may be influenced by sonar signals. A 25-kHz sonar signal falls within the most sensitive hearing frequency range of the harbor seal (Kastelein et al., 2009a, 2009b, 2010b), so the sensation level (i.e., the level of a signal above the basic tonal 50% hearing threshold) of the harbor seal for sonar signals at this frequency is expected to be relatively high.

Harbor seals are known to be deterred by anthropogenic underwater noises produced during seismic surveys (Harris et al., 2001), by acoustic alarms to prevent unwanted predation on aquaculture farms (Taylor et al., 1997; Yurk & Trites,

Top view

2000), and by underwater data communication signals (Kastelein et al., 2006b). Behavioral response threshold levels of harbor seals have been determined for noise bands around 12 kHz (Kastelein et al., 2006b) and for tonal signals between 8 and 45 kHz (Kastelein et al., 2006a). The received levels, spectra, and familiarity of underwater sounds play important roles in determining the effect they have on the behavior of harbor seals (Jacobs & Terhune, 2002). In addition, the local availability of food may affect behavioral responses (Götz & Janik, 2010), and the ecological meaning of the sounds if, for example, they resemble the vocalizations of predators (Deecke et al., 2002).

The goal of the present study was to determine the behavioral response threshold sound pressure levels (SPLs) of harbor seals for ultrasonic sonar



Figure 1. Top and side scale views of the study facility, showing the study animals, the location of the aerial cameras, the underwater transducer emitting the sonar signals, the listening hydrophone, and the three haul-out platforms. Also shown is the research cabin which housed the equipment and the operator.



Figure 2. The background noise in the pool represented in ½-octave bands (SPL averaged over 10 s). Above 3.5 kHz, the noise was dominated by the self-noise of the recording system.



Figure 3. The waveforms of the three sonar signals of around 25 kHz used in the present study: (a) the 50-ms FM sound type, (b) the 600-ms CW sound type, and (c) the Combo sound type (300-ms FM followed by 600-ms CW); the duty cycles and inter-pulse intervals of the sequences that the harbor seals (*Phoca vitulina*) were exposed to in the study differed between the three sound types (see Table 1).

	Sonar sound type					
	FM	CW	Combo			
Description	Hyperbolic down-sweep	Amplitude modulation, bell curve	Combination of the FM & CW			
Frequency band (kHz)	25.5-24.5	25	25.5-24.5			
Signal duration (ms)	50	600	300 + 600 = 900			
Inter-pulse interval (s)	2	10	10			
Duty cycle (%)	2.4	5.6	8.3			
Calculation of weighted equivalent						
SPL (Leg):						
Correction for duty cycle	-16.2 dB	-12.5 dB	-10.8 dB			
Weighting correction	-5.0 dB	-5.0 dB	-5.0 dB			

Table 1. Details of the three sonar sound types (frequency modulated = FM, continuous wave = CW, and combination = Combo) that were tested on the harbor seals (*Phoca vitulina*)

signals presented as three sound types. With this information, combined with information on the source level, the background noise, and local propagation conditions, the extent of the area around a sonar source in which harbor seal behavior is likely to be influenced can be estimated.

Methods

Study Animals and Study Area

The study animals were two female harbor seals (01 and 02). During the study, they were both 5.5 y old, and their body weights were approximately 60 kg. The two seals had very similar hearing, probably representative for harbor seals of

their age (Kastelein et al., 2009a, 2009b, 2010b). The harbor seals' hearing was tested after the present study and had not changed since the study of Kastelein et al. (2010b).

The study was conducted at the SEAMARCO Research Institute, The Netherlands, which is in a remote area specifically selected for acoustic research. The research was conducted in an outdoor pool (8 m \times 7 m, 2 m deep) with haul-out platforms (see Figure 1). The pool was designed and constructed to be as quiet as possible and to reduce reflections of sounds above 25 kHz (see Kastelein et al., 2009b). A research cabin next to the pool housed the audio and video equipment as well as the operator, who was out of sight of the harbor seals.



Figure 4. The $\frac{1}{2}$ -octave spectra of the FM, CW, and Combo signals recorded in the pool (all three signals had similar spectra with peak frequencies at 25 kHz). The signals were recorded up to 50 kHz as this is the upper limit of the harbor seal's hearing frequency range (Kastelein et al., 2009a, 2009b).

Underwater Background Noise and Test Stimuli The background noise in the pool between 25 Hz and 160 kHz was measured twice during the study, under conditions that were typical of the tests (no rain and wind force Beaufort 4 or below). The background noise level was low (see Figure 2). Above 3.5 kHz, the level was mainly determined by the self-noise of the recording equipment.

Three sonar sound types were tested: (1) hyperbolic frequency-modulated signals (FM sound type), (2) amplitude-modulated continuous waves (CW sound type), and (3) a combination of the FM and CW signals (Combo sound type). The sonar sound types were chosen to resemble signals used operationally by the Swedish Navy. All signals had center frequencies of 25 kHz and were presented at the same source levels $(\pm 1 \text{ dB})$, measured in units of dB re 1 µPa root mean square. However, the durations of the signals and the duty cycles of the three sound types were different, resulting in different weighted equivalent SPLs (Leq) (Hassall & Zaveri, 1988), though all were appropriate for operational naval use (Figure 3; Table 1). Due to the difference in duty cycles, a CW signal presented at the same source level as an FM signal had a 3.7 dB higher weighted Leq. A Combo signal had a 5.4 dB higher Leq than an FM signal at the same source level (Table 1).

Audio and Video Equipment

The digitized sequences (WAV files; sample frequency 96 kHz, 16-bit) were played back by laptop computer 1 (Acer Aspire - 5750) with a program written in LabVIEW, Version 2010, to an external data acquisition card (NI - USB6259), the output of which was digitally controlled in 1 dB steps with the LabVIEW program. Via an isolation transformer (Lubell - AC1424HP), the sounds were projected under water by a directional-piezoelectric transducer (Ocean Engineering Enterprise - DRS-12; 30 cm diameter). The transducer was suspended 1 m below the water surface on the northeastern side of the pool (Figure 1). The output of the sound system to the transducer was monitored via an oscilloscope (Dynatec - 8120), a voltmeter (Hewlett Packard – 3478A), and a spectrum analyzer (Velleman - PCSU1000). The spectra of the three sound types were similar (Figure 4). The attenuation system was linear over the SPL range used in the study.

The harbor seals' behavior was filmed from above by two aerial cameras (Conrad – 750940) with wide-angle lenses. Camera 1 was placed on a pole 6 m above the water surface in the southern corner of the pool (Figure 1). The entire surface of the pool was captured on the video image except the area behind the baffle board. Camera 2 filmed the area behind the baffle board. The output of camera 1 was digitized with an analog-to-digital converter (Smart Group – Zolid) and stored on laptop computer 2 (Medion – MD98110).

The audio part of the background noise and the test sounds were recorded via a custom-built hydrophone and a pre-amplifier (Brüel & Kjær [B&K] - 2635). The output of the pre-amplifier was digitized via the analog-to-digital converter and recorded to laptop computer 2 in synchrony with the video images. The output was fed to an amplified loudspeaker so that the operator in the research cabin could monitor the background noise during sessions. The signals from the hydrophone were also fed to an ultrasound detector (Batbox II) so that the sonar signals were audible to the operator. Via a microphone, the operator added the date, time of day, session number, and sonar sound type being tested to the video recording at the start of each session.

Acoustic Measurements

The sound distribution in the pool was quantified while the three sound types were being produced and the animals were not in the pool. The recording and analysis equipment consisted of three hydrophones (B&K – 8106) with a multichannel high-frequency analyzer (B&K PULSE - 3560 D), and a laptop computer with *Labshop*, Version 12.1 (B&K PULSE). The system was calibrated with a pistonphone (B&K – 4223). The signals were low-pass filtered (3rd order Butterworth filter, cut-off frequency: 50 kHz), and the sample rate was set at 500 kHz.

Acoustic Characterization of the Sequences

The sound sequences were characterized in terms of their SPL. The SPL (dB re 1 μ Pa) was averaged over the duration of each signal. The analysis was done in the time domain. The duration (t90) was determined as the time interval between the points when the cumulative sound exposure (the integrated broadband sound pressure squared) reached 5 and 95% of the total sound exposure (i.e., the duration contained 90% of the total energy in the signal; Madsen, 2005). The SPL (dB re 1 μ Pa) was determined from the power sum of ½-octave bands from 1 to 50 kHz.

Sound Distribution

To determine the sound distribution in the pool, the SPL for each sonar sound type was measured at 36 locations (on a horizontal grid of 1×1.15 m). The SPL was measured by a hydrophone at each of three depths per location on the grid (0.5, 1.0, and 1.5 m below the water surface). Thus, the SPL was measured at 108 locations in the pool for each sonar sound type. The reported SPLs were based on one recording per location. The distribution of



Figure 5. The broadband SPL (the SPL determined from the power sum of $\frac{1}{2}$ -octave bands from 1 to 50 kHz) distribution in the pool as a function of the distance to the transducer (which was at a depth of 1 m) for the three sonar sound types —(a) FM, (b) CW, and (c) Combo—measured at three depths (0.5 m: O, 1 m: \Box and 1.5 m: \blacktriangle ; n = 36 measurements per depth; some data points overlap); all three sound types were transmitted at an SPL_{avree} of 128 dB re 1 μ Pa (a level used only during the pilot study).

the SPL, as measured at 108 positions in the pool, is shown for each sonar signal in Figure 5. The SPL in the pool varied little over distance at 0.5 and 1.5 m depth, but the SPLs at 1 m depth (the depth of the transducer) showed a gradient up to about 3 m. The harbor seals used most of the pool and swam at all depths during the baseline and test sessions, so the average SPL in the pool is used to describe the average received SPL (SPL_{avrec}) by the harbor seals in this study.

Determination of the SPLs of the Playback Sequence

The following three levels were determined during a pilot study in which the source level of each sonar sound type was gradually increased:

- 1. For the FM sound type, a SPL_{av.rec} which fell just below the threshold of behavioral change; for the CW and Combo sound types, this was approximated at 20 dB below the maximum producible level.
- 2. The maximum SPL_{avrec}, that could be produced by the transducer without changing the sonar signals' spectrum
- 3. An intermediate SPLav.rec.

These three SPLs_{avrec} for each sonar sound type were then tested in the sessions (Table 2).

Experimental Procedures

The transducer used to produce the sonar signals was placed in the pool at the beginning of the day, at least 1 h before the first sessions started (Figure 1). Each session consisted of a 30-min baseline period (no sound emission), followed immediately by a 30-min test period (sound emission). Usually two sessions were conducted per day, 5 d/wk, beginning between 0900 and 1500 h.

In each session, one sonar sound type was tested at one of the three SPLs, and each of the nine sonar sound type/level combinations was tested in six sessions (18 sessions per sonar sound type; 54 sessions in all). The sonar sound type/level combinations were tested in random order. With the exception of the operator in the research cabin, people were not allowed within 15 m of the pool during tests. Tests were not carried out during rainfall or when wind speed was above Beaufort 4 (5.5 to 7.9 m/s) as under these conditions the sonar sounds may have been partly masked by ambient noise. The study was conducted between February and May 2012.

Behavioral Data Recording, Response Parameters, and Analysis

The spot sampling method was used to record the behavior of the two harbor seals objectively: every 10 s, the operator recorded whether each seal's head was under water or in the air; and if it was in the air, the location of the seal was recorded (grid location in the water or on one of the three platforms). Thus, per animal, the behavior was scored 180 times per 30-min test or baseline period. In the video images, the seals could not always be distinguished from each other (particularly while they were under water or when only one head was visible). The seals could be seen clearly under water only under certain light levels, light angles, and water clarity conditions (occurring in about 20% of sessions). Therefore, the behavioral scores of both seals were pooled. When they were hauled out, the seals could be identified, but this information was not used in the analysis.

Table 2. The three average received SPLs \pm standard deviations (SDs; dB re 1 µPa; n = all 108 measurement locations in the pool) at which the sonar sound types (FM, CW, and Combo) were presented in the sessions (determined during a pilot study). The SPLs of the CW and Combo varied more (larger SDs) than that of the FM, probably because standing waves were created by the CW and Combo sound types (see Figure 5). The duty cycles and inter-pulse intervals of the sequences that the harbor seals were exposed to in the study differed between the three sound types (see Table 1).

Level descriptions	Average received SPL ± SD (dB re 1 μPa)			
	FM	CW	Combo	
For the FM sound type, SPL which fell just below the threshold of behavioral change. For the CW and Combo, <i>ca</i> . 20 dB below the maximum producible level	125 ± 3.7	135 ± 4.7	135 ± 4.2	
Intermediate level	137 ± 3.6	146 ± 4.5	147 ± 4.1	
Maximum level that was producible without changing the sonar signal's spectrum	158 ± 3.4	156 ± 4.9	156 ± 4.3	

The harbor seals' locations were quantified to determine whether they responded to the sounds by swimming away from the transducer (although they were not expected to because the sound distribution in the pool was fairly homogenous; Figure 5). This was done as follows: from the video camera images, the locations of the seals at scoring moments when the seals' heads were visible during the baseline and test periods were marked on a grid superimposed (via a transparent sheet) on the screen of laptop computer 2. The grid was formed by lines between markers on the pool's sides. All the video recordings were analyzed by one person to ensure consistency.

Five behavioral parameters were used to quantify the harbor seals' responses to the sonar sounds: (1) the distance between their locations and the transducer at scoring moments when the seals' heads were visible during baseline and test periods, (2) the number of scores for which they were in the water but with their heads above the water surface, (3) the number of scores for which they were hauled out on one of the three platforms (i.e., entirely out of the water), (4) the number of times the animals jumped during baseline and test periods, and (5) the seals' swimming speed during test periods relative to their speed recorded during corresponding baseline periods (recorded as faster, similar, or slower).

Two-tailed paired *t*-tests were used where appropriate to compare the parameters in baselines with those in the associated test periods. Bonferroni corrections for multiple comparisons were applied, resulting in a level of significance of 0.017 (Zar, 1999). In response to sounds at levels that had an effect, harbor seals were predicted to spend more time with their heads above water or hauled out, jump more, and swim fasterthan during baseline periods.

Results

Baseline Behavior

During baseline periods (and most of the test periods), the harbor seals usually swam vertical ovals in the pool, generally diagonal relative to the pool. The mean distance between the seals and the transducer $(4.2 \pm 0.5 \text{ m} - \text{mean} \pm \text{standard devia$ $tion})$ was similar in all 54 baseline periods.

In baseline periods, on average, the harbor seals spent most of their time (80% of 360 scores in 54 sessions of 30 min) under water, 20% of scores with their heads above water, and only a small number of hauled outs were observed (< 1% of scores). The harbor seals did not jump at all during the baseline periods.

Behavior During Test Periods

In all test periods, the mean distance between the harbor seals and the transducer was very similar to that during baseline periods $(4.2 \pm 0.4 \text{ m})$. The lack of movement away from the transducer was as expected from the minimal SPL gradient in the pool (a gradient existed only at 1 m depth and only up to about 3 m from the transducer; Figure 5). The distance was not considered in further analysis because it was not affected by the sounds.

FM Sound Type

At the lowest SPL_{av.rec} (125 dB re 1 μ Pa; calculated from all 108 measurement locations), the harbor seals did not respond to the FM sound type.

At the SPL_{avrec} of 137 dB re 1 μ Pa, they swam significantly more frequently with their heads out of the water than in the baseline periods (22% of scores compared to 18% in associated baseline periods). They also hauled out more frequently (1% of scores compared to 0% in baseline periods) and jumped 15 times. They swam faster in five out of six test sessions than during the baseline periods.

At the highest SPL_{av,rec.} (158 dB re 1 μ Pa), the harbor seals spent more time with their heads out of the water (25% of scores compared to 23% in associated baseline periods), hauled out more frequently (2% of scores compared to 0% in baseline periods), and jumped 37 times (see Table 3). They also swam faster in four out of six test sessions than during the baseline periods.

CW and Combo Sound Types

The harbor seals did not respond to the CW and Combo sound types (they did not swim significantly more frequently with their heads out of the water and did not haul out more frequently than in the baseline periods; they did not jump in the test periods and did not swim faster in test sessions than during the baseline periods), even at the highest SPLavree. (156 dB 1 μ Pa) (Table 3).

Discussion

Evaluation

The study was conducted with only two animals. Their hearing was probably representative for harbor seals of their age; for tonal signals and ¹/₃-octave noise bands, the hearing sensitivity of the two animals was similar (Kastelein et al., 2009a, 2009b, 2010b).

Other playback experiments with marine mammals have revealed individual differences in responses to sounds—for instance, in belugas (*Delphinapterus leucas*) in a pool subjected to playbacks of offshore oil drilling noise (Thomas

Table 3. Results of paired *t*-tests to compare the harbor seals' scores with only their heads out of the water, scores entirely on land (hauled out), and numbers of jumps in baseline and associated test periods at three SPL_{Swzec}. (dB re 1 µPa; calculated from all 108 measurement locations) for each sonar sound type (FM, CW, and Combo). The sample size for each test is six sessions (180 observations). Exact *p* values are shown when significant ($\alpha = 0.017$ following Bonferroni correction); NS = not significant. In all cases where the test was significant, the value for the test period was as predicted (i.e., harbor seals spent more time with their heads above water, hauled out, or jumped more than during baseline periods).

	FM	ſ				CW			С	ombo	
SPL _{av.rec.}	Head above water	Hauled out	Jumps	SPL _{w.re} .	Head above	Hauled out	Jumps	SPL _{w.re} .	Head above water	Hauled out	Jumps
125	NS	NS	NS	135	5 NS	NS	NS	135	NS	NS	NS
137	0.008	NS	NS	146	5 NS	NS	NS	147	NS	NS	NS
158	0.006	NS	0.007	156	5 NS	NS	NS	156	NS	NS	NS

et al., 1990), and in harbor seals responding to underwater data communication signals (Kastelein et al., 2006b). The behavioral response data of the present study, though scientifically robust, should be used with caution. Behavior depends not only on hearing sensitivity but also on many individual properties of animals (e.g., age, sex, experience, genetics, nature, or disposition) and on the context (e.g., season, water depth, distance to shore, being alone or in a group, proximity to a feeding area, etc.). Thus, the behavioral response threshold levels are approximate and will remain approximate even after many more studies, though testing the same sounds on a larger number of individuals would provide a better understanding of the range of received levels which cause the behavioral responses seen in the present study.

Due to the characteristics of the pool, a slight SPL gradient up to around 3 m occurred only at the depth of 1 m. The relatively homogeneous SPL distribution probably explains why the harbor seals generally did not move away from the sound source; there was no quiet zone in the pool. Due to their swimming speed and pattern they could be exposed to several different SPLs per s. During test periods with the FM sound, the harbor seals spent more time at the water surface than during the baseline periods. Near the surface, relatively low SPLs and no SPL gradient occurred (Figure 5). The SPL measurements and behavioral observations suggest that the received levels reported in the present study (based on the mean of all SPLs measured in the pool) may be, at most, around 2 dB higher than the actual SPLs experienced by the harbor seals during their exposure to the FM sound.

Behavioral Response Threshold SPL

The Combo sound type was expected to elicit a similar behavioral response as the FM sound type because the Combo signal contained the FM signal. However, although the duty cycle of the Combo sound type (8.3%) was higher than that of the FM sound type (2.5%), the inter-pulse interval of the FM sound type was much shorter (2 s) than that of the Combo sound type (10 s). It is not clear which combination of sound parameters caused the responses observed in the harbor seals in the present study.

For the FM signal, the behavioral response threshold SPL was between 125 and 137 dB re 1 µPa, so ~131 dB re 1 µPa. Previous behavioral research on harbor seals has provided behavioral response threshold levels. Underwater data transmission signals in the 8 to 18 kHz range produce behavioral response thresholds SPLs (Leq of signal series) of ~107 dB re 1 µPa (Kastelein et al., 2006b), 8 kHz tonal signals of 128 dB re 1 µPa, 16 kHz tonal signals of 120 dB re 1 µPa, a 32 kHz signal of 122 dB re 1 µPa, and 45 kHz signals of 128 dB re 1 µPa (Kastelein et al., 2006a). However, the stimuli used in these studies differed considerably in frequency. To incorporate the differences in duty cycle and frequency, the weighted Leg (Hassall & Zaveri, 1988) for a series of signals was used for direct comparison (Table 4).

Other studies in pools have shown deterring effects of anthropogenic sounds on harbor seals, but, in most cases, behavioral response threshold values were not derived. Bowles & Andersen (2012) showed that harbor seals touched objects in water with acoustic pingers less frequently than objects without pingers. Harbor seals also react to underwater sounds at sea. Fjälling et al. (2006) showed that catch damage was less in salmon-trap nets in the Baltic Sea with acoustic deterrent devices (ADDs) than in nets without them. Anderson & Hawkins (1978) recorded the responses of both captive and wild harbor seals to tones and played back killer whale (*Orcinus orca*) vocalizations. They found that one sound caused a captive harbor seal to respond, but it habituated quickly to the sounds. No responses were seen in

the wild harbor seals. No source or received levels were reported, so possibly the received level was below the behavioral response threshold level.

Götz & Janik (2010) compared behavioral responses of harbor seals to playbacks of sounds based on a model of sensory unpleasantness for humans, using sounds from ADDs and sounds with assumed neutral properties in different contexts of food motivation. In a captive experiment with food presentation, seals habituated quickly to all sound types presented at normalized received SPLs of 146 dB re 1 µPa (root mean square); however, the fast habituation of avoidance behavior was accompanied by a weak sensitization process affecting dive times and place preference in the pool. Experiments in the wild in which animals were tested without food presentation revealed differential responses of seals to different sound types. Avoidance behavior was observed at received levels of 135 to 144 dB re 1 µPa (sensation levels of 59 to 79 dB). Sounds maximized for "roughness" and perceived as unpleasant by humans also caused the strongest avoidance responses in harbor seals, suggesting that sensory pleasantness may be the result of auditory processing that is not restricted to humans.

The behavioral response threshold for the FM signal in the present study is within the range of behavioral response thresholds found for sweeps in previous studies. Behavioral response thresholds

for CW tend to be higher than those for sweeps. Whether this is due to differences in frequency (pure tones vs sweeps) or in temporal pattern (continuous vs intermittent), or both, is not clear.

Comparison with the Responses of a Harbor Porpoise

Because of the great overlap in distribution areas of the harbor seal and harbor porpoise (*Phocoena phocoena*), both species live in coastal waters in which high-frequency sonar systems are used, a study similar to the present one (same sounds and duty cycles) was conducted with a harbor porpoise (Kastelein et al., 2015). The harbor porpoise responded to lower SPL_{Savrec} of the FM sound type than the CW sound type (his response threshold SPL was between 76 and 125 dB re 1 μ Pa). The Combo sound type had the greatest effect on the harbor porpoise. In contrast, the harbor seals in the present study mainly responded to the FM sound type, indicating that the behavioral response to these sonar signals is species-specific.

The difference in the magnitude of the two species' responses could be partly because the harbor seals could only hear the fundamental frequency of the sonar signals (25 kHz) as their hearing is sensitive only up to \sim 50 kHz (Kastelein et al., 2009a, 2009b). The harbor porpoise could also hear the side bands (71 and 121 kHz; Kastelein et al., 2010a) as harbor porpoise hearing is

Table 4. Comparison of the harbor seals' behavioral response threshold SPL found in the present study with those reported by Kastelein et al. (2006a, 2006b); signal levels are corrected for duty cycle differences (by calculating L_{eq}) and weighted based on the seal audiogram by Kastelein et al. (2009b), which was from the harbor seals used in the present study (resulting in weighted L_{eq}).

Study	Signal	Mean received behavioral response threshold SPL (dB re 1 µPa)	Duty cycle & dB correction to calculate L _{eq} of signal series (dB re 1 µPa)	Signal center frequency & type	Weighting correction	Weighted L _{eq} of signal series (dB re 1 µPa)
Present study	FM	131	2.4% -16.2 dB	25 kHz sweep	-5.0 dB	110
Kastelein et al., 2006b	Signal S1	108	80% -1.0 dB	12.5 kHz sweep	-1.3 dB	106
Kastelein et al., 2006b	Signal S2	107	60% -2.2 dB	12.5 kHz varying tones	-1.3 dB	104
Kastelein et al., 2006b	Signal S3	107	80% -1.0 dB	12.5 kHz sweep	-1.3 dB	105
Kastelein et al., 2006b	Signal S4	107	100% 0 dB	12.5 kHz noise	-1.3 dB	106
Kastelein et al., 2006a	8 kHz	141	5% -13.0 dB	8 kHz CW tone	-0.3 dB	128
Kastelein et al., 2006a	16 kHz	133	5% -13.0 dB	16 kHz CW tone	-2.0 dB	118
Kastelein et al., 2006a	32 kHz	135	5% -13.0 dB	32 kHz CW tone	-7.5 dB	115
Kastelein et al., 2006a	45 kHz	141	5% -13.0 dB	45 kHz CW tone	-14.5 dB	114

sensitive up to \sim 150 kHz. Results of the present study and of research on the effects of underwater data transmission signals (Kastelein et al., 2005, 2006b) suggest that, in the frequency ranges tested, harbor porpoises generally react to lower levels of the same sounds than harbor seals.

Implications for Sonar Use

The present study showed that, at the duty cycles and SPLs used, only the FM sound type caused significant behavioral effects in harbor seals at SPLs_{avrec} above 125 dB re 1 μ Pa. The possible effects of signals with different parameters (e.g., duty cycles, signal durations, frequencies, waveforms) are unknown, but the results suggest that, for harbor seals, during peace time exercises and in fisheries, the use of CW and Combo signals is preferred to the use of FM signals (at the signal duration and duty cycles used in the present study).

As well as the source level, operational characteristics and the use of sonar signals influence their effect on marine mammals. Harbor seals are unlikely to habituate to, and thus ignore, sonar sounds that occur only rarely. Kastelein et al. (2006a) noted that harbor seals did not habituate to daily 45-min presentations of high-amplitude tone pulses over a period of 40 d. Jacobs & Terhune (2002) observed that wild harbor seals exposed to ADD sounds for weeks or months did not react when an ADD was activated at a lower amplitude than usual; they were habituated to the sounds. Götz & Janik (2010) showed that captive harbor seals habituated quickly to aversive sounds when food was available during the exposure periods, showing that responses are context-dependent.

When sonar signals are used at sea, variation in environmental parameters leads to high levels of variability in the response distances of marine mammals. For this reason, distance ranges, rather than exact distances, at which the sonar sounds elicit responses should be considered when assessing effects and planning mitigation measures.

Recommendations for Future Research

In the present study, the effects of sound type and duty cycle cannot be separated as the duty cycle was different for each of the three sonar sound types. It would be of interest to test the sounds used in the present study at the same duty cycle in order to clarify the effect of sound type on the behavioral responses of harbor seals to sounds (i.e., to determine if it is the spectrum that determines the effect, the received energy, or both).

A related question is whether harbor seals, when receiving a series of signals, respond to the equivalent SPL (L_{eq}) of the entire series or to the SPL in the individual signals. A study with various

SPLs, signal durations, and inter-pulse intervals may provide data to answer this question.

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