Underwater hearing sensitivity of harbour seals for tonal signals and noise bands

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Contents

This report consists of 2 underwater hearing studies with 2 female harbor seals:

Underwater detection of narrow-band FM tonal signals between 0.125 and 100 kHz by harbor seals (*Phoca vitulina*)

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Summary

The underwater hearing sensitivities of two one-year-old female harbor seals were quantified in a pool built for acoustic research, using a behavioral psychoacoustic technique. The animals were trained to respond when they detected an acoustic signal and not to respond when they did not (go/no-go response). Pure tones (0.125-0.25 kHz) and narrow-band FM (tonal) signals (center frequencies 0.5-100 kHz) of 900 ms duration were tested. Detection thresholds at each frequency were quantified using the up-down staircase method. The underwater audiograms (50 % detection thresholds) of the two seals did not differ statistically: both plots showed the typical mammalian U-shape, but with a wide and flat bottom. Maximum sensitivity (54 dB *re* 1 μPa, rms) occurred at 1 kHz. The range of best hearing (10 dB from the maximum sensitivity) was from 0.5 to 40 kHz (6 □ octaves). Higher hearing thresholds (indicating poorer sensitivity) were observed below 1 kHz and above 40 kHz. Thresholds below 4 kHz were lower than those previously described for harbor seals, which demonstrates the importance of using quiet facilities, built specifically for acoustic research, for hearing studies in marine mammals. The results suggest that many anthropogenic noise sources are audible to harbor seals at greater ranges than formerly believed.

1 Introduction

The harbor seal (*Phoca vitulina*) has the most extensive geographic distribution of any seal species. It inhabits the eastern Baltic Sea as well as both eastern and western coasts of the Atlantic (30° to 80° north) and Pacific (28° to 62° north) Oceans. It leads an amphibious life, resting on land, while migration, foraging and courtship occur underwater (Burns, 2002). During the breeding season, male harbor seals produce underwater vocalizations described as growls and short broadband pulsed calls (Schusterman *et al.*, 1970; Van Parijs and Kovacs, 2002).

To determine the importance of sound for harbor seals during activities such as communication, reproduction, predator avoidance, and navigation, and the potential for disturbance by anthropogenic noise, information is needed on the species' underwater hearing sensitivity. This has been tested for pure tones (Møhl, 1968; Terhune, 1988, 1989; Turnbull and Terhune, 1993; Kastak and Schusterman, 1998; Southall *et al.*, 2005) and frequency swept tones (Turnbull and Terhune, 1994). However, in each of the seven studies, only the sensitivity of a single harbor seal over a part of the frequency range of hearing was investigated. Moreover, in each study different equipment, methodology, and signal parameters were used and the animals were of different ages (but all were males). In addition, some of the hearing thresholds may have been influenced (masked) by background noise in the research pool.

Harbor seals are found in coastal waters in which many human activities occur. To assess potential disturbance by anthropomorphic noises, it is important to obtain robust underwater hearing threshold curves for this pinniped species. For this, a quiet testing environment and multiple representative study animals are needed. Therefore, a pool and filtration system with special acoustic features designed for hearing studies was built at a quiet location in the Netherlands. Two young healthy female harbor seals were obtained specifically for this hearing study. Our aim was to determine underwater hearing thresholds for both seals over their entire hearing range.

2 Materials and Methods

A. Study animals

The study animals were two female harbor seals (codes SM.Pv.01 and SM.Pv.02), which were born at Ecomare, Texel, the Netherlands. The animals became available for the present study soon after they had been weaned. Throughout the study, the animals were healthy. They were not exposed to ototoxic medication prior to or during the study period. During the study they aged from 14 months to 18 months old and their body weight increased from around 34 kg to around 42 kg. The seals consumed between 1.4 and 1.8 kg of thawed fish (herring, *Clupea harengus*, mackerel, *Scomber scombrus*, and sprat, *Sprattus Sprattus*) divided into four meals per day. In general, the seals were fed during research sessions.

B. Study area and staff

The study was conducted at SEAMARCO's research institute, the Netherlands, which is in a remote area that was specifically selected for acoustic research. The measurements were conducted in an outdoor pool (8 m (l) x 7 m (w), 2 m deep), with an adjacent haul-out platform (**Fig. 1**). The pool walls and floor were made of plywood covered with polyester. The pool floor was 1 m below ground level. To reduce sound reverberation in the pool, the inner walls were covered with 3-cm-thick mats of coconut fiber embedded in 4-mm-thick rubber. The coconut mats extended 10 cm above the water level to reduce splashing noises caused by waves. The bottom was covered with approximately 20 cm of sand. Skimmers kept the water level constant. Seawater was pumped in directly from the nearby Oosterschelde, a lagoon of the North Sea. Most of the water (80 %) was re-circulated daily through a biological filter system to ensure year-round water clarity, so that the animals' behavior could be observed via underwater cameras during the test sessions. The remaining 20% of the water was replaced from the sea every day.

To prevent a temporary hearing threshold shift (TTS) in the seals before the hearing tests, the water circulation system and aeration system for the adjacent bio-filter were designed to be as quiet as possible. This was done by choosing 'whisper flow' pumps, mounting the pumps on rubber blocks, and connecting the pumps to the circulation pipes with very flexible rubber hoses. There was no current in the pool during the experiments, as the water circulation pump and the air pump of the bio-filter were switched off for 10 minutes before and during test sessions. This also prevented flow noise from the skimmers.

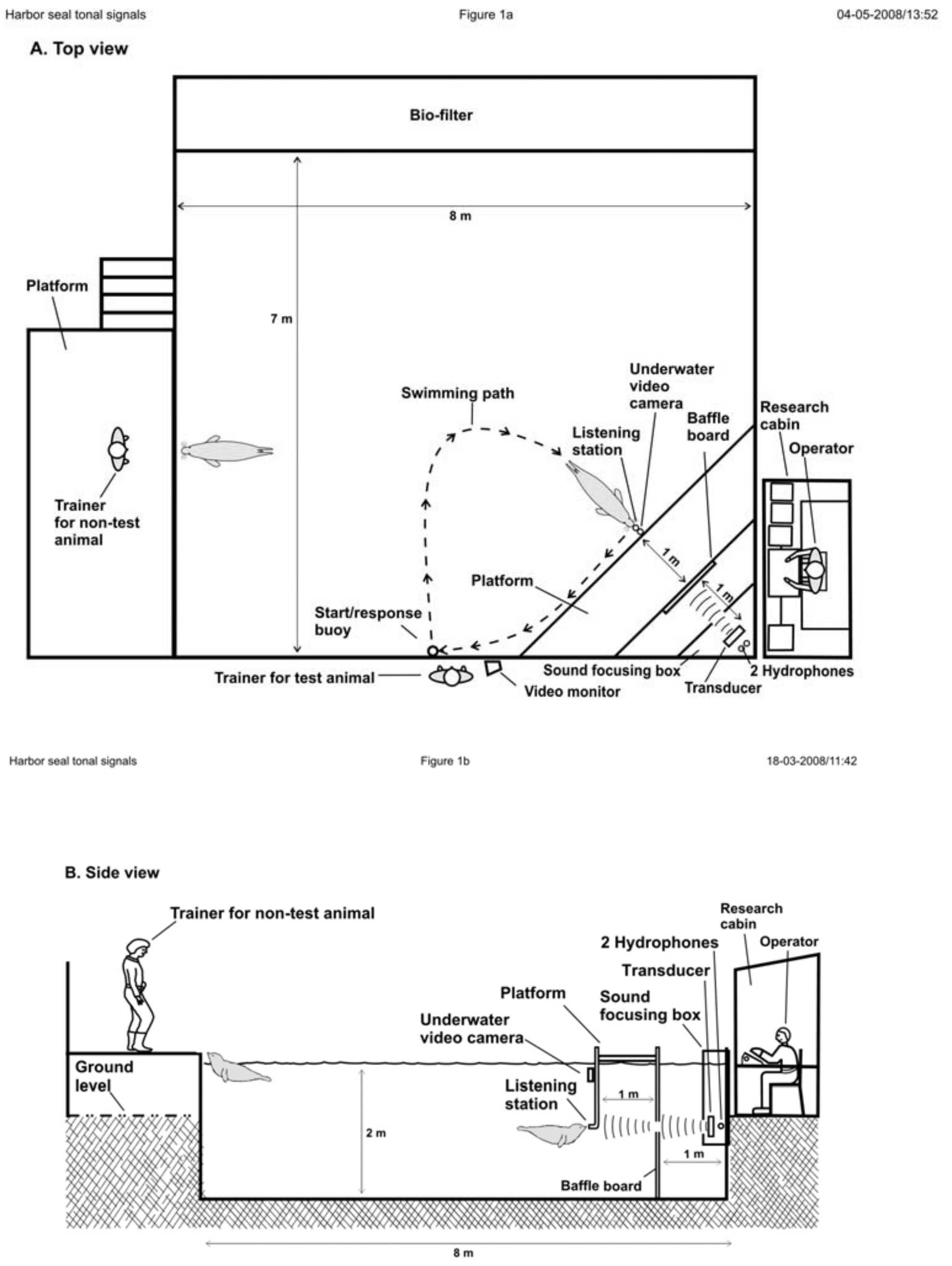

FIG. 1. The study area, showing the test harbor seal in position at the underwater listening station, and the non-test animal with the other trainer; (A) top view and (B) side view, both to scale.

The water temperature varied between 20 °C in August and 12 °C in November, and the salinity was around 34 ‰.

During test sessions, the two seals were tested in succession. The animal not being tested was trained to keep very still and quiet for half of the 30-minute session in the water next to the haul out area (this was quieter than staying on land, where a scratch of a flipper nail could trigger a false alarm in the animal being tested). The signal operator and the equipment used to produce the stimuli and listen to underwater sounds were in a research cabin next to the pool, out of sight of the animals (**Fig. 1**).

C. Test stimuli

All stimuli were produced by a waveform generator (Hewlett Packard, model 33120A). Two types of tonal signals were used. Between 125 and 250 Hz, pure tones were used. Between 500 Hz and 100 kHz, narrow-band sinusoidal frequency-modulated (FM) tonal signals (with center frequencies of 0.5, 1, 2, 4, 8, 16, 25, 31.5, 40, 50, 63, 80, and 100 kHz) were used. The modulation range of the signals was ± 1% of the center frequency (the frequency around which the signal fluctuated symmetrically), and the modulation frequency was 100 Hz (for example, if the center frequency was 10 kHz, the frequency fluctuated 100 times per second between 9.9 and 10.1 kHz). **Table I** shows the frequency ranges of the stimuli. Above 250 Hz, narrow-band FM signals were used because such signals produce fewer constructive and destructive interference effects (standing waves) in a reverberant pool than pure tones (Kastelein *et al.*, 2002, 2005; Finneran and Schlund, 2007). Similar FM signals cannot be produced at low frequencies without causing interference patterns.

A modified audiometer for testing human aerial hearing (Midimate, model 602) was used to control the duration and amplitude of signals (**Fig. 2**). The stationary portion of all signals was 900 ms in duration; the rise and fall times were 50 ms to prevent transients. The sound pressure level (SPL) at the seal's head while it was at the listening station could be varied in 5 dB increments (this step size was determined by the audiometer: 5 dB steps are generally used in human audiometry). The 125 – 500 Hz signals were amplified by means of an audio amplifier (Sony TA-F335 R; **Fig. 2**).

A directional transducer (Ocean Engineering Enterprise, model DRS-12; 30 cm diameter) was used to project the signals into the water (an impedance matching transducer was not used, in order to eliminate harmonics). Multi-path arrivals and standing waves can introduce both temporal and spatial variations in the observed SPL at the listening station. Therefore the transducer was placed in a corner of the pool in a protective wooden box lined with sound-absorbing rubber. The transducer was hung with 4 nylon cords from the cover of the box and made no contact with the box. A stainless steel weight was fixed to the lower part of the transducer to compensate for its buoyancy. The transducer was 1.85 m from the tip of the L-shaped listening station (**Fig. 1**), and was positioned so that the acoustic axis of the projected sound beam pointed at the center of the listening station (i.e. the center of the study animal's head while it was at the listening station). To reduce reflections from the bottom of the pool and water surface reaching the listening station, a baffle board was placed exactly half way between the transducer and the animal. The board consisted of 2.4 m high, 1.2 m wide 4 cm thick plywood, covered with a 2 cm thick closed cell rubber mat on the side facing the transducer. A 30 cm-diameter hole was made in the board with its center at the same level as the seal's head and the transducer (1 m below the water surface). As an indicator of the condition of the transducer, its capacitance was checked once a week with a capacity meter (SkyTronic 600.103). During the study period the capacity remained constant.

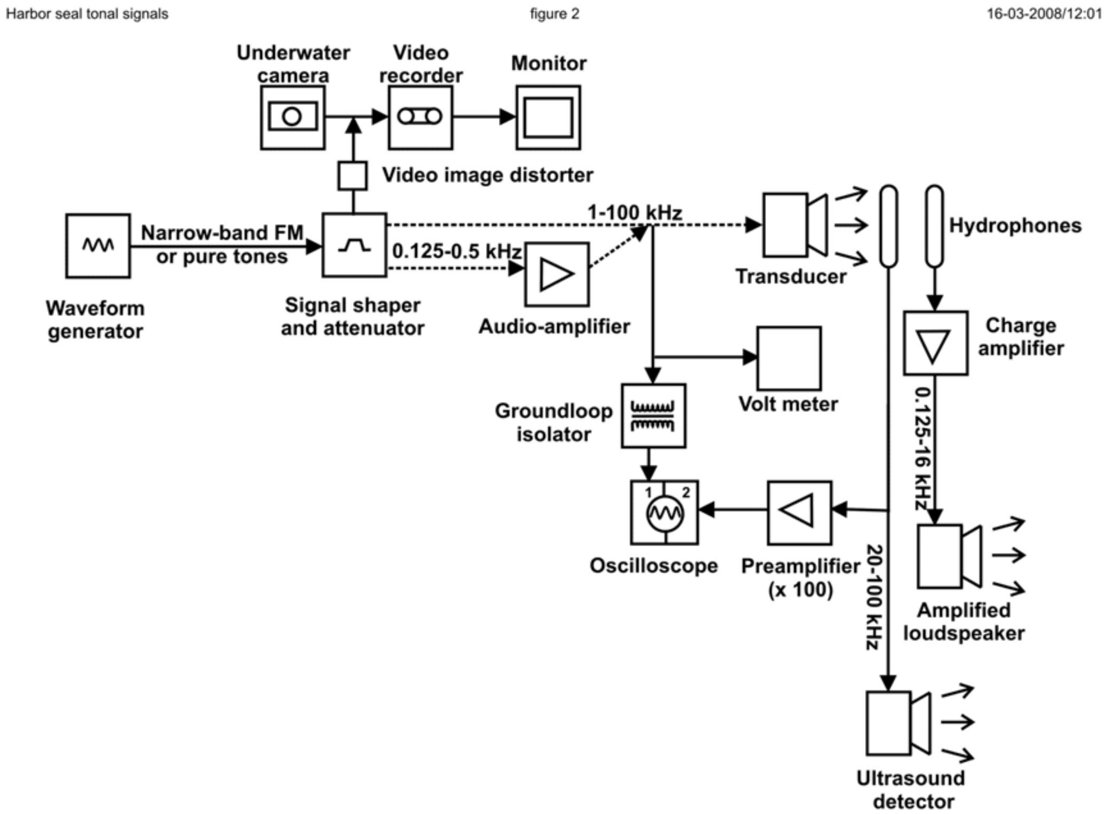

FIG. 2. Block diagram of the transmitting and listening systems.

D. Stimuli level calibration and background noise measurement

Audiograms are easily influenced by background noise in the test area. Therefore great care was taken to make the seal's listening environment as quiet as possible. Nobody was allowed to move within 15 m of the pool during sessions. Underwater background noise levels were measured monthly during the study period, under the same conditions as during the test sessions (i.e. in various weather conditions but without rain and with wind speed below Beaufort 3).

The equipment used to measure the background noise in the pool consisted of a hydrophone (Bruel & Kjær (B&K) 8101), a voltage amplifier system (TNO TPD, 0-300 kHz) and a dual spectrum analyzer system (25 Hz – 160 kHz). The system was calibrated with a pistonphone (B&K 4223) and a white noise signal (25 Hz – 40 kHz) which was inserted into the hydrophone pre-amplifier. Measurement results were corrected for the frequency sensitivity of the hydrophone and the frequency response of the measurement equipment. The customized analyzer consisted of an A/D-converter (Avisoft UltraSoundGate 116, 0 – 250 kHz) coupled to a notebook computer (sampling rate: 500 kHz). The digitized recordings were analyzed by two parallel analysis systems: 1) a Fast Fourier Transform (FFT) narrow-band analyzer (25 Hz – 160 kHz), and 2) a 1/3-octave band analyzer (25 Hz – 160 kHz).

1/3-Octave band background noise levels were determined in the range 25 Hz - 100 kHz and converted to 'equivalent sound pressure spectrum levels' (L_{eq}-method, Hassall and Zaveri, 1988), expressed in dB re 1 μPa/√Hz. **Fig. 3a** shows the power averaged **(**n = 5) background noise in the pool, alongside the self-noise of the measuring system.

The received SPL (dB *re* 1 µPa, rms) of each stimulus was measured approximately once each month at the seals' head position (**Fig. 1**). During trials, the seals' head positions (while at the listening station) were carefully monitored, and were consistent to within a few cm. The received SPL variation between calibration sessions was frequency-dependent. The deviation from the mean was generally around 2 dB for all frequencies, except 31.5 kHz, where for unknown reasons the deviation from the mean was around 5.5 dB. No harmonic distortions were present in the test frequencies at the SPLs used in the hearing tests. The linear averaged received SPL per test frequency was calculated from all five calibration sessions. The means were used to determine the session thresholds.

The received SPLs were calibrated at a level of 14 – 65 dB (depending on frequency) above the threshold levels found in the present study. The linearity of the transmitter system was checked during the study by measuring levels around 15 dB above the thresholds found in this study, and it was consistent within a few dB. At one frequency (0.125 kHz) the stimulus tone levels could not be amplified sufficiently above background noise to ensure that the measurements were not influenced by the background noise.

E. Experimental procedure

The seals were trained to respond ('go') in the presence of a signal and to withhold the response ('no-go') in the absence of a signal. A trial began when one of the animals was positioned with its head at the start/response buoy at the edge of the pool next to the trainer (**Fig.1 a)**. When the trainer gave the animal a vocal command accompanied by a gesture (pointing downwards), the animal descended to the listening station (an L-shaped, 32 mm-diameter, water-filled polyvinylchloride (PVC) tube with an end cap), so that its external auditory meatus was 200 cm from the sound source and 100 cm below the water surface (*i.e.* mid-water; **Fig. 1 b)**. Each animal was trained to position its nose against the listening station so that its head axis was in line with the projected beam axis of the transducer. The listening station was not connected to the sound box, and the transducer was suspended within the box by 4 thin ropes, so the animals were not able to use vibration via contact conduction to the nose to detect the signals. The animals' positions could be viewed from above by means of an underwater camera (Mariscope, Micro), which was attached to the listening station. The images were visible to the trainer near the start/response buoy (but out of the study animal's view when it was at the listening station) and to the operator in the research cabin.

Two trial types were conducted during each experimental session: signal-present trials and signal-absent trials. In signal-present trials, the stimulus was presented unpredictably between 4 and 10 s after the animal was positioned correctly at the listening station. A minimum waiting time of 4 s was chosen because it took about 4 s for the waves, created by the animal's descent, to dissipate. If the animal detected the sound, it responded by leaving the listening station ('go' response) at any time during the signal's duration and returning to the start/response buoy (**Fig. 1 a**). The signal operator then signaled to the trainer that the response was correct (a hit), after which the trainer gave a vocal signal and the seal received a fish reward. If the animal did not respond to the signal, the signal operator signaled to the trainer that the animal had failed to detect the signal (a miss). The trainer then signaled to the animal (by tapping softly on the side of the pool) that the trial had ended, thus calling the animal back to the start/response buoy. No reward was given following a miss. If the animal moved away from the listening station to the start/response buoy before a signal was produced (a pre-stimulus response or false alarm), the signal operator signaled to the trainer to end the trial without rewarding the animal. After a false alarm, the animal was ignored for 8-10 s by the trainer.

In signal-absent, or catch, trials the signal operator hand-signaled to the trainer to end the trial after a random interval of 4-10 s from when the seal had stationed (determined by a random number generator). The trial was terminated when the trainer blew very softly on a whistle. If the animal responded correctly by remaining at the listening station until the whistle was blown (a correct rejection), it then returned to the start/response buoy and received a fish reward. If the seal left the listening station before the whistle was blown (a pre-stimulus response or false alarm), the signal operator signaled to the trainer to end the trial without rewarding the animal. The same amount of fish was given as a reward for correct 'go' and 'no-go' responses. In both signal-present and signal-absent trials, the trainer was unaware of the trial type when she sent the animal to the listening station. After sending the animal to the listening station, the trainer stepped out of the seal's view.

A session generally consisted of 30 trials per animal and lasted for about 15 minutes per animal. The seals were always tested in the same order. Sessions consisted of 70% signal-present and 30% signal-absent trials presented in random order, and only one signal frequency was presented each day. For each session, one of four data collection sheets with different random number series was used. Each seal had its own set of four data collection sheets. In each session, the signal amplitude was varied according to the simple up-down staircase procedure, a conventional psychometric technique (Robinson and Watson, 1973). This is a variant of the method of limits, which results in a 50% correct detection threshold (Levitt, 1971).

Prior to testing a given frequency, an estimated threshold was determined during preliminary sessions, in which the rough hearing threshold per test frequency was determined using the up-down staircase procedure. During subsequent experimental sessions, the starting SPL of the signal was 10-15 dB above the estimated threshold. Following each hit, the signal amplitude on the next signal-present trial was reduced by 5 dB. Following each miss, the signal level was increased on the next signal-present trial by 5 dB. Pre-stimulus responses (false alarms) did not lead to a change in signal amplitude for the next trial. A switch in the seal's response from a detected signal (a hit) to an undetected signal (a miss), or *vice versa*, is called a reversal.

Thresholds were determined for 16 tonal signals (3 pure tones and 13 narrow-band FM signals). To prevent the animals' learning process from affecting the threshold levels, the test frequency was varied from day to day and adjacent frequencies were usually tested on successive days (going from low to high and from high to low frequencies, and so forth). This way the difference in frequency between days was limited, reducing the potential need for the study animals to adapt to a frequency. During the study we learned that the thresholds obtained for higher frequencies (> 40 kHz) were not influenced by the wind force. Therefore those frequencies were tested under relatively high wind force conditions, whereas the 0.125-0.5 kHz signals were only tested under wind force conditions below 2 Beaufort, because they required a quieter environment. Usually four experimental sessions were conducted on 5 days per week (at 0900, 1100, 1400 and 1600 h). Data were collected between August and November 2007.

Before each session, the acoustic equipment producing the stimuli was checked to ensure that it was functional and the stimuli were produced accurately (**Fig. 2**). Also the background noise level was checked to make sure it was not too high for testing. This was done in the following ways:

1) To test the sound generating and amplifying equipment, the voltage output towards the underwater transducer was measured with an oscilloscope (Dynatek 8120, 20 MHz; Channel I) and a voltmeter (Hewlett Packard 3478A). This was done with the stimulus to be used in that session, at the amplitude at which the stimuli were calibrated.

2) To test the sound level produced by the underwater transducer, the voltage output of a hydrophone (Labforce 1 BV), which was always placed in a fixed position 20 cm from the transducer and connected to a pre-amplifier (100 x), was checked with the same oscilloscope (Channel II) and voltmeter when the stimulus for that session was produced.

3) Audio stimuli (at sufficient SPLs) were checked aurally by the signal operator via another hydrophone (Labforce 1 BV), a charge amplifier (Bruel & Kjær, 2635) and an amplified loudspeaker. The operator also used this setup to monitor the background noise aurally before and during each session.

4) Ultrasonic stimuli (> 16 kHz; at sufficient SPLs) were checked for via the hydrophone (Labforce 1 BV). The signals were made audible to the signal operator by means of a modified ultrasound detector (Stag Electronics, Batbox III).

F. Analysis

The data included in the analysis were from sessions carried out after the mean session threshold had leveled off. This usually occurred within four sessions (depending on the frequency and the animal). Because no warm-up trials were used, it sometimes took several reversals before a stable threshold was reached. In these cases, the first 1-4 reversals were not included in the analysis. Sessions with more than 20 % pre-stimulus responses (i.e., more than six of the usual 30 trials per session) were not included in the analysis. These sessions occurred only four times per animal during the entire study, and usually coincided with obvious transient background noises.

Thresholds for each animal were calculated using approximately 110 pairs of reversals per frequency obtained in about 11 sessions. The hearing thresholds of the seals (per frequency) were compared by using a paired t-test.

3 Results

After the initial 1-4 sessions which were not included in the analysis, the seals' sensitivity for each test frequency was stable over the four-month study period. The mean pre-stimulus response rate (for both signal-present and signal-absent trials) varied between 3 % and 13 %, depending on the frequency (**Table I**). Most pre-stimulus responses occurred during tests with low-frequency signals.

The thresholds of the two seals were similar (t = 0.73, *d.f.* = 15, P = 0.48). The underwater audiograms (50 % detection thresholds) for the two seals showed the typical mammalian U-shape. However, the bottom part of the U was very flat and wide, the low frequency sensitivity decreased gradually, and the high frequency cut-off was steep (**Fig. 3b and Table I**). The range of best hearing (10 dB from the maximum sensitivity) was very wide: from 0.5 to 40 kHz (6 □ octaves), and sensitivity fell below 0.5 kHz and above 40 kHz.

TABLE I. The mean 50 % detection thresholds, standard deviation (SD), and total no. of reversal pairs of 14-18-month-old female harbor seals 01 and 02 for three pure tones (0.125-0.25 kHz) and 13 narrow-band FM (0.5-100 kHz) signals, and their pre-stimulus response rate based on the number of pre-stimulus responses in all trials (signal-present and signal-absent trials). Also shown are the critical ratios used to calculate the theoretical detection threshold in **figure 3b** (based on a smooth line through the data of Turnbull and Terhune, 1990, Southall *et al.*, 2000).

Center frequency (kHz)	Frequency modulation range 1% (kHz)	Critical ratio (dB)	Harbor seal 01			Harbor seal 02		
			Total no. of reversal pairs	Mean 50% detection threshold (SPL in dB re 1 μPa, rms) ± SD	Pre-stimulus response rate (%)	Total no. of reversal pairs	Mean 50% detection threshold (SPL in dB re 1 μPa, rms) ± SD	Pre-stimulus response rate (%)
0.125	Pure tone	14.6	126	77±4	9	124	74±4	9
0.200	Pure tone	14.6	112	72±4	6	90	73±4	10
0.25	Pure tone	14.7	116	65±4	11	96	69±5	7
0.5	0.495-0.505	14.8	93	61±4	11	90	64±5	12
1	0.99-1.01	15.2	128	54±4	6	103	56±4	7
2	1.98-2.02	16.3	100	57±4	5	98	57±5	9
4	3.96-4.04	19.0	126	56±5	5	113	55±4	7
8	7.92-8.08	22.0	120	61±4	10	105	58±4	3
16	15.84-16.16	25.0	118	61±4	9	109	63±4	7
25	25.75-25.25	27.0	109	57±4	8	109	58±4	3
31.5	31.19-31.82	28.0	108	64±4	8	124	63±4	5
40	39.60-40.40	-	102	61±4	13	103	60±4	8
50	49.50-50.50	-	120	73±3	5	117	70±4	6
63	62.37-63.63	-	112	109±3	8	100	106±5	5
80	79.20-80.80	-	106	119±4	5	106	119±4	3
100	99.00-101.00	-	114	127±4	5	120	125±4	4

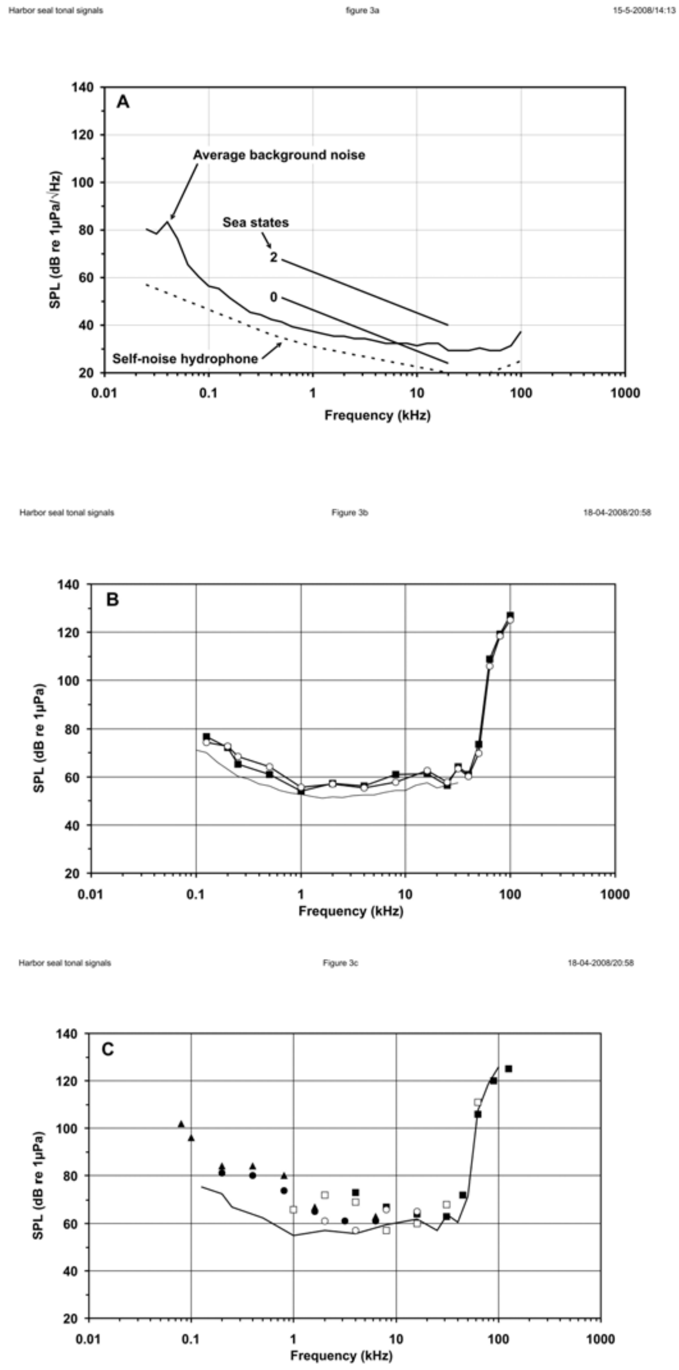

FIG 3
A) Power averaged background noise level in the pool in dB *re* 1µPa/√Hz (derived from 1/3-octave band levels; n = 5) and the self-noise of the B&K 8101 hydrophone (amplifier). Also shown are the noise levels measured at sea states 0 and 2 (Knudsen *et al.*, 1948).

B) The mean 50% detection thresholds (dB *re* 1 µPa, rms, line level) for pure tone and narrow-band FM signals obtained for female harbor seals 01 (■) and 02 (○) in the present study (for details see **Table I**). The thin line shows the calculated noise-limited theoretical detection threshold (dB *re* 1µPa) based on the background noise levels of Fig. 3A and critical ratios of harbor seal hearing (Turnbull and Terhune, 1990; Southall *et al.*, 2000).

C) The average underwater hearing threshold (in dB *re* 1µPa, rms) of the two study animals in the present study, shown as a line, and the underwater hearing thresholds found for harbor seals in previous studies [Møhl, 1968 a (± 500 ms ■); Terhune, 1988 (500 ms □); Turnbull and Terhune, 1993 (repeated signals, 50 ms, 10/s ○); Kastak and Schusterman, 1998 (500 ms ▲); Southall *et al.*, 2005 (500 ms ●)].

4 Discussions and Conclusions

A. Evaluation of the data

The biggest challenge in hearing studies is to maintain a low background noise level; we took great care to do this in the present study. The main factor influencing the LF part of the background noise spectrum in the pool was the wind (which, when increased, caused airborne wind noise and increased soil vibrations). During the four-month study period the wind speed was relatively low compared to in other years, which meant that background noise levels in the pool were very low (even partly below sea state 0, see **Fig. 3a**).

It is important to know whether the audiograms of the present study are absolute audiograms or if the signals were influenced by the background noise in the pool. **Fig. 3b** (mean audiogram levels) shows theoretical masked detection thresholds (MDT) based on the background noise levels shown in **Fig. 3a**, and the harbor seal's critical ratio (from a smooth line through the data points of Turnbull and Terhune, 1990 and Southall *et al.*, 2000; **Table I**). The noise-limited theoretical masked detection threshold is calculated as: MDT = background noise (spectrum level) + critical ratio (CR). The theoretical masked detection thresholds lie below the hearing thresholds found in the present study, suggesting that the thresholds were not masked by the ambient noise.

The 0.125-0.5 kHz signals were only tested under wind force conditions below 2 Beaufort, because false alarms occurred at higher wind speeds (probably because the animals reacted to elements of background noise which resembled the test signals). Still, the false alarm rate was generally highest for the lower frequencies (< 1 kHz in this study). Most transient background noise signals, which may well trigger false responses, are in this part of the spectrum. Because both seals were tested within the same sessions, any differences between the thresholds obtained for the two animals must have been due to differences in their hearing sensitivity and/or individual differences in their response criteria, motivational state, or behavior. Differences could not have been caused by differences in equipment, equipment settings, methodology, personnel or background noise.

In most previous studies of pinniped hearing, except in two experiments, pure tones were used as stimuli. Only the hearing of a Pacific walrus (*Odobenus rosmarus divergens*) and two Steller sea lions (*Eumetopias jubatus*) have been tested with narrow-band FM tonal signals (Kastelein *et al.*, 2002, 2005). In humans, FM signals tend to have a slightly higher arousal effect than pure tones, and therefore slightly lower hearing thresholds (< 5 dB depending on center frequency and modulation frequency; Morgan *et al.*, 1979). However, the use of FM signals instead of pure tones probably had little effect on the thresholds found in the present study. This assumption is based on a hearing test with 250 Hz signals on a Pacific walrus, in which no difference was found in thresholds between narrow-band FM signals like those used in the present study (frequency modulation only 1 % of the center frequency) and pure tone signals (Kastelein *et al.*, 2002).

Hearing thresholds depend on signal duration, and integration time is also frequency-dependent, decreasing with increasing frequencies. However, the 900 ms signal duration used in the present study was probably more than the integration time of the harbor seal's hearing system (Terhune, 1988).

B. Comparison with previous hearing studies in harbor seals

Comparing the hearing of the study seals with that of the other four harbor seals the underwater hearing sensitivities of which have been studied is not straightforward. In the various studies there are differences in the calibration methodology and threshold calculation, and variation in the threshold data between sessions. Also the background noise measurements are often limited, and lower frequency thresholds are not always free from masking influences. Researchers have used various methods, stimulus parameters such as signal type (pure tone versus FM signal) and signal duration (50-500 ms versus 900 ms), and the SPL calculation method is not specified for all the studies (peak-to-peak or RMS, causing a 9 dB difference). Despite these complications, general comparisons can be made between the underwater audiograms of the harbor seals in the present study and those in previous studies (Møhl, 1968; Terhune, 1988, 1989; Turnbull and Terhune, 1993, 1994; Terhune and Turnbull, 1995; Kastak and Schusterman, 1998; Southall *et al.*, 2005). Above 4 kHz, the thresholds found in the previous hearing studies and those found in the present study are similar. However, below 4 kHz the thresholds found in the present study were up to 20 dB lower than those found in the previous studies. Differences between the hearing sensitivity of the animals in the present studies and those in previous studies below 4 kHz may occur because:
Low frequency signals were masked by background noise in previous studies.
Animals in previous studies may have had TTS due to the high background noise levels from pumps before the hearing tests were conducted.
The signal duration in most previous studies was shorter than the one used in the present study, possibly causing an increase of the hearing threshold (not because of the integration time, but because it is difficult for the animals to distinguish between transient signals in the background noise and the test signals).
There may have been individual, gender, health condition, or age-related differences in hearing sensitivity between the test animals.
Based on the small minimum audible angles for low frequencies, Bodson *et al.* (2007) concluded that harbor seals are low frequency hearing specialists. The present study shows that harbor seals have a very wide frequency range of best hearing, and are able to hear lower frequencies better in quiet conditions than thought so far, based on previous studies.

C. Ecological significance

The most important finding of this study is that harbor seal hearing is more sensitive below 4 kHz than found in previous studies **(Fig. 3c)**. The hearing range of harbor seals overlaps in frequency with the loudest and most common anthropogenic noise sources. The effect of anthropogenic noise on marine mammals is highly variable in type and magnitude (Severinsen, 1990; Cosens and Dueck, 1993; Richardson *et al.*, 1995), and harbor seals show avoidance behavior to certain sounds in certain contexts (Kastelein *et al.*, 2006 a and b). Anthropogenic noise might reduce the time harbor seals forage in particular areas, thus reducing their physiological condition and their reproductive success. In addition to the hearing sensitivity of the harbor seal, the radii of avoidance and disturbance zones around sound sources depend on several other factors such as the general background noise level, water depth, ocean floor sediment properties, and the spectrum, source level and duration of the anthropogenic noise. In general, based on the findings of the present study, many anthropogenic noise sources are audible at greater ranges than formerly believed.

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Underwater hearing sensitivity of harbor seals (*Phoca vitulina*) for 1/3-octave noise bands between 0.2 and 80 kHz

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Summary

The underwater hearing sensitivities of two 1.5-year-old female harbor seals were measured in a quiet pool built for acoustic research, using a behavioral psychoacoustic technique. The animals were trained to respond when they detected an acoustic signal and not to respond when they did not (go/no-go response). Fourteen 1/3-octave noise bands (center frequencies 0.2-80 kHz) of 900 ms duration were tested. The underwater audiograms (50 % detection thresholds, up-down staircase method) were 61 dB re 1 µPa (± 2.5 dB) between 0.5 and 40 kHz. At lower frequencies the thresholds increased to 66 dB re 1 µPa and at higher frequencies the thresholds rose to 114 dB re 1 µPa at 80 kHz. The 1/3-octave noise band audiograms of the two seal did not differ from each other or the narrow-band FM tone thresholds at the same frequencies obtained only a few months before in the same animals. These hearing threshold values will be useful when calculating detection ranges of underwater calls and anthropogenic noises.

I. Introduction

The harbor seal (Phoca vitulina) has an extensive geographic distribution in coastal regions of temperate areas of the Northern Hemisphere. It leads an amphibious life, resting on land, while migration, foraging and courtship occur underwater (Burns, 2002). During the breeding season, male harbor seals vocalize, presumably to attract females (van Parijs and Kovacs, 2002). Many human activities create significant underwater noise levels which may interfere with their abilities to hear ecologically important sounds.

To determine the importance of sound for harbor seals during activities such as communication, reproduction, predator avoidance, and navigation, and the potential for disturbance by anthropogenic noise, information is needed on the species' underwater hearing sensitivity. The underwater hearing sensitivity of harbor seals has been tested for tonal signals (Møhl, 1968a; Terhune, 1988; Turnbull and Terhune, 1993; Kastak and Schusterman, 1998; Southall et al., 2005; Kastelein et al., 2008) and frequency swept tones (Turnbull and Terhune, 1994). However, the vocalizations of harbor seals have been described as growls and short broadband pulsed calls (Schusterman et al., 1970; Van Parijs and Kovacs, 2002). Most anthropogenic underwater sounds are not tonal, but consist of noise of various bandwidths (Richardson, 1995). Noise, in this context, refers to unwanted sound that varies over time. In nature, noise can both be a biological signal and a masker that reduces an animal's detection ability of biological signals. It is not clear how sensitive the hearing of harbor seals is for noise bands or how their sensitivity for noise bands compares to that for tonal signals. Determining the audibility of noise bands will enable the estimation of the detection range, and auditory masking effect, of a variety of biological and anthropogenic sound sources. Coupling source levels of band noises with sound transmission losses in the environment and detection threshold levels, allows modeling of the detection ranges of various broadband sounds. This is an important step in understanding at what distance harbor seals can detect, and possibly respond to, anthropogenic sounds.

The aim of the present study was to determine the hearing sensitivity of two harbor seals for 1/3-octave noise bands and compare the detection thresholds with those obtained only a few months before for tonal signals in the same animals (Kastelein et al., 2008).

II Materials and methods

A. Study animals

The study animals were two female harbor seals (codes SM.Pv.01 and SM.Pv.02). During the study they aged from 18 to 21 months old and their body weight was around 40 kg. More information about the study animals can be found in Kastelein et al. (2008).

B. Study area and staff

The study was conducted at SEAMARCO's research institute, The Netherlands. This location is in a remote area and was specifically selected for acoustic research. The measurements were conducted in an outdoor pool (8 m (l) x 7 m (w), 2 m deep), with an adjacent haul-out space (Fig. 1). Several measures were taken to make the pool as quiet as possible. More detailed information about the study area can be found in Kastelein et al. (2008).

During test sessions, the seals were tested in succession. The animal not being tested was trained to keep very still and quiet for 15 minutes in the water next to the haul out area (this was quieter than staying on land, where a scratch of a flipper nail could trigger a false alarm in the animal being tested). The signal operator and the equipment used to produce the stimuli, were in a research cabin next to the pool, out of sight of both animals (Fig. 1).

C. Test stimuli

The seals' hearing sensitivity was tested for 1/3-octave noise bands. White noise was produced by a waveform generator (Hewlett Packard 33120A) and filtered by a brick-wall band-pass filter (Krohn-Hite 3901) in 1/3-octave bands according to the standards of the American National Standards Institute (ANSI), but the band limits were rounded off by the filter. Center frequencies of the noise bands were 0.2, 0.25, 0.5, 1, 2, 4, 8, 16, 25, 31.5, 40, 50, 63, and 80 kHz (**Table I**).

A modified audiometer for testing human aerial hearing (Midimate, model 602) was used to control the duration and amplitude of signals (**Fig. 2**). The stationary portion of all signals was 900 ms in duration, and the rise and fall times of the signals were 50 ms to prevent transients. The signal duration was expected to exceed the integration time of the harbor seal's hearing system (Terhune, 1988). The free field sound pressure level (SPL) at the seal's head while it was at the listening station could be varied in 5 dB increments. This step size was determined by the audiometer and 5 dB steps are generally used in human audiometry. The 0.2 - 0.5 kHz signals were amplified by an audio amplifier (Sony TA-F335 R; **Fig. 2**).

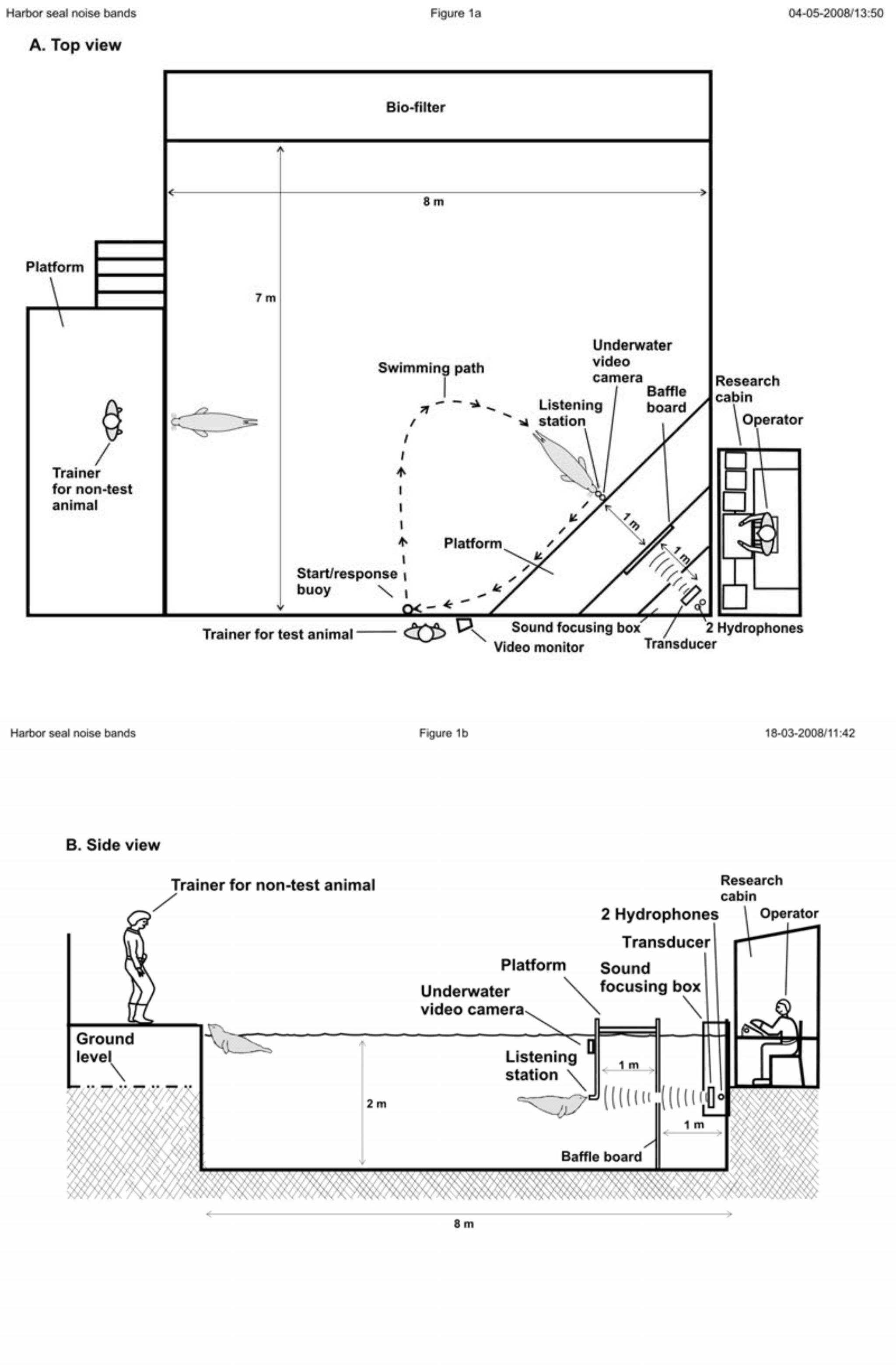

FIG. 1. The study area, showing the test harbor seal in position at the underwater listening station, and the non-test animal with the other trainer; A) top view and B) side view, both to scale.

TABLE I. The mean calibration SPLs of the 1/3-octave noise bands centered at fourteen frequencies at the location of the seals' head, and the power sum of the three 1/3-octave noise bands used to calculate the 50 % detection hearing thresholds.

Center frequency (kHz)	1/3-octave frequency range (kHz)	Mean (n = 4) received level ± SD (dB re 1 µPa, rms)			Power sum all three 1/3-octave bands (dB re 1 µPa, rms)
		1/3-octave lower	1/3-octave center	1/3-octave higher	
0.200	0.18-0.22	73±3	79±1	74±3	81
0.250	0.22-0.28	80±3	81±4	73±3	84
0.5	0.45-0.56	88±2	98±2	90±5	99
1	0.89-1.1	72±0	81±0	81±0	84
2	1.8-2.2	79±1	87±1	80±1	88
4	3.5-4.5	91±2	100±1	98±1	102
8	7.1-8.9	100±1	104±1	97±1	106
16	14-18	107±1	108±1	101±2	111
25	23-28	106±1	110±1	103±2	112
31.5	28-36	107±2	113±3	108±3	115
40	36-45	111±3	115±3	104±1	116
50	45-56	109±2	115±1	108±3	116
63	56-71	115±1	123±1	121±1	125
80	71-89	124±1	129±1	122±2	131

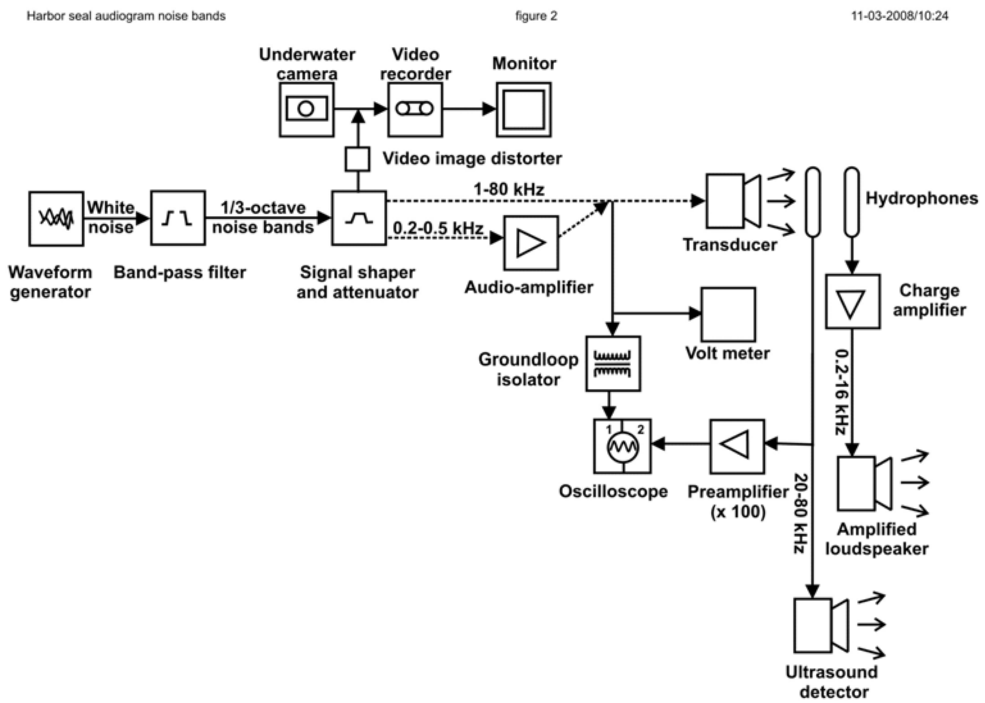

FIG. 2. Block diagram of the transmitting and listening systems.

A directional transducer (Ocean Engineering Enterprise DRS-12; 30 cm diameter) was used to project the signals into the water. An impedance matching transducer was not used in order to eliminate harmonics. Multi-path arrivals and standing waves can introduce both temporal and spatial variations in the observed SPL at the listening station. Therefore the transducer was placed in a corner of the pool in a protective wooden box lined with sound-absorbing rubber. The transducer was hung with four nylon cords from the cover of the box and made no contact with the box. A stainless steel weight was fixed to the lower part of the transducer to compensate for its buoyancy. The transducer was 1.85 m from the tip of the L-shaped listening station (**Fig. 1**), and was positioned so that the acoustic axis of the projected sound beam was pointed at the center of the listening station (i.e., the center of the study animal's head while at the listening station). To reduce reflections from the bottom of the tank and water surface reaching the listening station, a baffle board was placed exactly half way between the transducer and the animal. The board consisted of 2.4 m high, 1.2 m wide 4 cm thick plywood, covered with a 2 cm thick closed cell rubber mat on the side facing the transducer. A 30 cm-diameter hole was made in the board with its center at the same level as the seal's head and the transducer (1 m below the water surface). As an indicator of the condition of the transducer, its capacity was checked once a week with a capacity meter (SkyTronic 600.103). Throughout the study period the capacity remained constant.

D. Stimuli level calibration and background noise measurement

Great care was taken to make the seal's listening environment as quiet as possible. Nobody was allowed to move within 15 m of the pool during sessions. Underwater background noise levels were measured five times during the four-month study period, under the same conditions as during the test sessions (at various weather conditions with wind speed below Beaufort 3).

The equipment used to measure the background noise in the pool consisted of a Bruel & Kjær (B&K) 8101 hydrophone, a voltage amplifier system (TNO TPD, 0-300 kHz) and a dual spectrum analyzer system (25 Hz - 160 kHz). The system was calibrated with a pistonphone (B&K 4223) and a white noise signal (25 Hz - 40 kHz) which was inserted into the hydrophone pre-amplifier. Measurement results were corrected for the frequency sensitivity of the hydrophone and the frequency response of the measurement equipment. The customized analyzer consisted of an A/D-converter (Avisoft UltraSoundGate 116, 0 - 250 kHz) coupled to a notebook computer (sampling rate 500 kHz). The digitized recordings were analyzed by two parallel analysis systems: 1) a Fast Fourier Transform (FFT) narrow-band analyzer (25 Hz - 160 kHz), and 2) a 1/3-octave band analyzer (25 Hz - 160 kHz).

1/3-Octave band background noise levels were determined in the range 25 Hz - 100 kHz and converted to 'equivalent sound pressure spectrum levels' (L_{eq}-method, Hassall and Zaveri, 1988), expressed in dB re 1 μPa/√Hz. The mean (n = 5) background noise in the pool was very low (for the low frequency range it was below sea state 0, **Fig. 3 a).**

The received SPL (dB *re* 1 μPa, rms) of each noise band was measured approximately once each month at the seals' head position (**Fig. 1**). During trials, the seal's head position (while at the listening station) was carefully monitored, and was consistent to within a few cm. The received SPL was measured at three 1/3-octaves: the 1/3-octave test band and the two adjacent 1/3-octave bands (so the analysis bandwidth was 1 octave). The SPL of the adjacent 1/3-octave noise bands were also measured, because the slopes produced by the electronic filter were more than 90 degrees (attenuation was 115 dB/octave). Because the adjacent 1/3-octaves contained energy that may have influenced the thresholds, the power sum of the three 1/3-octave bands (1 octave bandwidth) was used to determine the session threshold. This summation resulted in an additional 1 - 3 dB being added to the sound levels of the central 1/3-octave noise bands (**Table I**) and thus the threshold levels may be slightly lower than calculated here. The arithmetic mean received SPL per frequency band was calculated based on all four calibration sessions. The variation in SPL between calibration sessions was small because noise bands produce little interference with their surroundings (*e.g.*, standing waves), and the bandwidth of the noise was wide enough to create a uniform field (Dillon and Walker, 1982).

The received SPLs were calibrated at a level of 17 - 54 dB (depending on frequency) above the threshold levels found in the present study. The attenuation linearity of the audiometer was checked during the study and was within 2 dB.

E. Experimental procedure

The seals were trained to respond ('go') in the presence of a signal and to withhold the response ('no-go') in the absence of a signal. A trial began when one of the animals was positioned with its head at the start/response buoy at the edge of the pool next to the trainer (**Fig.1 a)**. When the trainer gave the animal a vocal command accompanied by a gesture (pointing downwards), the animal descended to the listening station (an L-shaped, 32 mm-diameter, water-filled polyvinylchloride (PVC) tube with an end cap), so that its external auditory meatus was 2.0 m from the sound source and 1.0 m below the water surface (*i.e.,* mid-water; **Fig. 1 b)**. More details about the experimental procedure are described by Kastelein *et al.* (2008?).

Thresholds were determined for fourteen 1/3-octave noise bands. To prevent the animals' learning process from affecting the threshold levels for the tested center frequencies, the center frequency was varied from day to day; adjacent frequencies were tested on successive days (going from low to high and from high to low frequencies, and so forth). This way the difference in frequency between days was limited, reducing the animals' potential need to adapt to a frequency. During the course of the study it was learned that the thresholds obtained for higher frequencies (> 40 kHz) were not influenced by the wind force. Therefore those frequencies were especially tested under relatively high wind force conditions whereas, the 0.2-0.5 kHz signals were only tested under wind force condition below 2 Beaufort, because they required a quieter environment. Usually four experimental sessions were conducted 5 days per week (at 0900, 1100, 1400 and 1600 h). Data were collected between December 2007 and March 2008.

Before each session, the acoustic equipment producing the stimuli was checked to ensure that it was functional and the stimuli were produced accurately (**Fig. 2**). Also the background noise level was checked to make sure it wasn't too high for testing. This was done as described by Kastelein *et al.* (2008?).

F. Analysis

The seals had participated in a similar hearing study just before the present study (Kastelein *et al.*, 2008), and therefore the mean session thresholds were stable from the beginning. Because no warm-up trials were used, it sometimes took several reversals before a stable threshold was reached within a session. In these cases the first 1-4 reversals were not included in the analysis. Sessions with more than 20 % pre-stimulus responses (*i.e.*, six out of the usual 30 trials per session), which would have been omitted from the analysis, did not occur during the entire study period.

Thresholds for each animal were calculated using on average 115 reversal pairs per frequency, obtained in 10 sessions (**Table II**). The thresholds of each of the seals for the 1/3-octave noise bands and the average of the previously obtained tonal thresholds of these animals were compared using a paired t-test.

III. Results

The seals' sensitivity for each test frequency was stable over the four-month study period. The mean pre-stimulus response rate (for both signal-present and signal-absent trials) varied between 3 % and 10 %, depending on the animal and frequency (**Table II**).

The underwater audiograms (50 % detection thresholds) for the two seals showed the general mammalian U-shape. However, the bottom part of the U was very flat and wide, and the low frequency sensitivity decreased gradually while the high frequency cut-off was steep (**Fig. 3b and Table II**). The range of best hearing (10 dB from the maximum sensitivity) was 61 dB re 1 μPa (± 2.5 dB) from 0.5 to 40 kHz (seven 2/3 octaves). The thresholds increased to 114 dB re 1 μPa at 80 kHz. The noise band thresholds of the two seals were similar to each other (t = 1.16, *d.f.* = 13, P = 0.26). The mean thresholds of the 1/3-octave noise bands were similar to those recently obtained from the same seals to narrowband FM tonal signals (Kastelein *et* al., 2008 in prep.; Fig. 3c; t = 1.28, *d.f.* = 13, P = 0.22).

TABLE II. The mean 50 % detection thresholds, standard deviation (SD), and total no. of reversal pairs of 18-21 month-old female harbor seals 01 and 02 for fourteen 1/3-octave noise band signals, and their pre-stimulus response rate based on the number of pre-stimulus responses in all trials (signal-present and signal-absent trials).

Center frequency (kHz)	1/3-octave center frequency range (kHz)	Harbor seal 01			Harbor seal 02		
		Total no. of reversal pairs	Mean 50% detection threshold (SPL in dB re 1 μPa, rms) ± SD	Pre-stimulus response rate (%)	Total no. of reversal pairs	Mean 50% detection threshold (SPL in dB re 1 μPa, rms) ± SD	Pre-stimulus response rate (%)
0.2	0.18-0.22	135	63±3	5	131	62±4	9
0.25	0.22-0.28	123	66±3	7	131	66±3	8
0.5	0.45-0.56	93	62±4	9	92	63±4	9
1	0.89-1.1	105	54±4	10	100	54±4	7
2	1.8-2.2	119	57±4	8	114	58±4	6
4	3.5-4.5	108	59±4	6	120	59±4	5
8	7.1-8.9	128	62±3	8	112	61±4	6
16	14-18	112	61±4	8	113	59±4	7
25	23-28	131	59±3	5	111	58±4	6
31.5	28-36	108	64±4	8	111	64±4	8
40	36-45	120	62±4	7	107	63±3	8
50	45-56	118	68±4	7	107	69±4	5
63	56-71	116	90±4	7	120	84±4	7
80	71-89	103	114±4	8	134	113±3	3

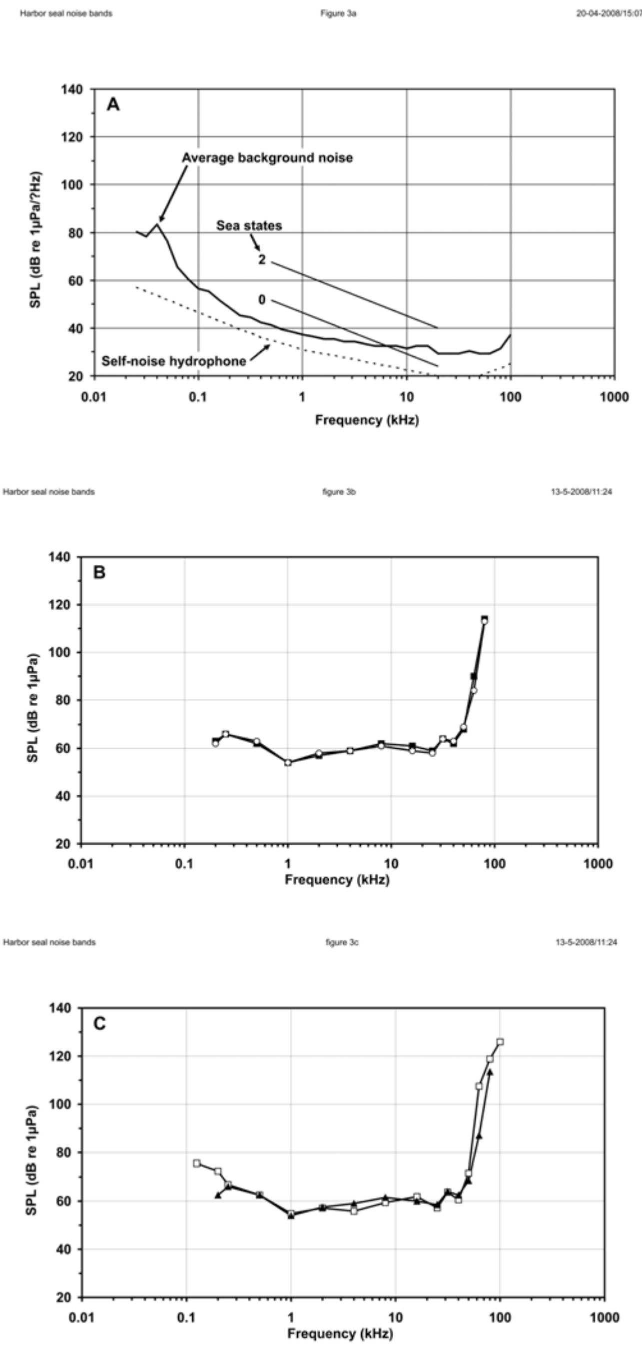

FIG 3

A) Power averaged background noise level in the pool in dB *re* 1μPa/√Hz (derived from 1/3-octave band levels; n = 5) and the self-noise of the B&K 8101 hydrophone (and amplifier). Also shown are the sea noise levels related to sea state 0 and 2 (Knudsen *et al.*, 1948).

B) The mean 50% detection thresholds (dB *re* 1 μPa, rms) for 1/3-octave noise bands obtained for female harbor seals 01 (■) and 02 (○) in the present study (for details see **Table II**).

C) The mean underwater hearing threshold (dB *re* 1μPa, rms) of the two study animals in the present study for 1/3-octave noise bands (▲), and the mean underwater hearing thresholds for tonal signals (□) of the same animals, with the same equipment, in the same environment 4 months earlier (Kastelein *et al.*, 2008).

IV. Discussion and conclusions

Because both seals were tested within the same session, any differences between the thresholds obtained for the two animals were only due to differences in the seals' hearing sensitivity or differences in motivation and were not caused by differences in equipment, equipment settings, methodology, personnel, or background noise.

The slight threshold decrease at 0.2 kHz is unexplained. The tonal thresholds were almost 10 dB higher at this frequency and the background noise did not dip here. The lower thresholds found for the HF (63 and 80 kHz) noise bands compared to the HF (63 and 80 kHz) tonal thresholds are probably because the bands were broader and contained energy at lower frequencies where the ear is more sensitive (*i.e.*, below the center frequency of the noise band). It is likely that the sound energy in the 1/3 octave bands adjacent to the test frequency had a slight impact (up to 3 dB) on the detection threshold. The relatively flat sensitivity throughout most of the seals' hearing range would enable the integration of the sound energy over a 1 octave wide band. The close similarity between the noise band and the FM tonal thresholds (Kastelein *et al.*, 2008 in prep) suggests that the seals are responding to the total sound power that is being presented.

Results from human audiometry support the validity of the 1/3-octave noise bands as a measure of hearing sensitivity. For human adults with normal hearing, narrow-band noise thresholds (1/3-octave) are essentially identical to pure-tone thresholds (Simon and Northern, 1966; Cox and McDaniel, 1986). These investigators found no significant differences in mean thresholds for the two stimuli. Orchik and Rintelmann (1978), however, did find small yet significant differences investigating the hearing sensitivity of normal-hearing young children for pure tone, warble tone and noise bands. As a result of the smaller bandwidth of the noise bands (approximately 1/6-octave), the mean thresholds for this signal type were generally higher than the mean thresholds for the other two stimulus types (by 7 dB or less).

Narrow-band noise has been credited with having attention-getting and ease-of-listening properties (Sanders and Josey, 1970) and is sometimes preferred in pediatric testing because of the greater interest value for young children. The perception of noise, a complex, more broadband stimulus, is assumed to be more directly comparable with the perception of speech. When using noise bands the sensitivity of wider areas of the basilar membrane are stimulated than when pure tone stimuli are used. Depending on the application, this can be either a strength (increased attention) or a limitation (reduced frequency-specificity).

Harbor seals produce underwater roars that are narrowband, pulsed calls (Schusterman *et al.*, 1970; van Parijs and Kovacs, 2002). The roars of harbor seals in Eastern Canada have most of their energy near 1.2 kHz (van Parijs and Kovacs, 2002). This frequency is well within the optimal detection range of the seals. Once the source levels of such vocalizations can be determined, and if the sound transmission characteristics in the area are known, it will be possible to calculate the call detection/communication range of male harbor seals.

Some anthropogenic noise sources, such as wind farms, produce sounds on an almost continuous basis, while others, such as large ships, produce more variable sounds. Noises from stationary wind farms vary slowly over time as wind speed and tidal depths vary. Noises from ships vary on a minute-by-minute basis because the transmission losses vary with water depth changes as a vessel progresses along a shipping lane.

Sea state (causing underwater noise) is mainly determined by rain and wind at mid to high frequencies and vessel traffic at lower frequencies (see Wenz curves in Urick, 1983). In nature, except for particularly quiet days with no nearby shipping or other anthropogenic noise sources, the hearing thresholds for the 1/3-octave noise bands found in the present study will often be masked by ambient noise. Given the similarity between the tonal and the 1/3-octave noise thresholds, until data on the detectability of narrow band noises in the presence of broadband masking noises are obtained, it should be appropriate to calculate likely narrow band noise detection thresholds based on the level of the background noise and the critical ratios (derived with tonal signals in noise) of the seals at the appropriate frequencies.

The sound detection thresholds in very quiet surroundings are limited by the sensitivity of the listener. At a sea state 0, in an area with little nearby vessel traffic, a broadband noise source from a ship or pile driver may be audible at great distances. It will be possible to determine the audibility of anthropogenic noises or the calls of the seals themselves once source levels and transmission losses in the area have been determined. This will be useful for estimating the potential impact of anthropogenic noises on the behaviors of seals.

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