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Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals

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The underwater hearing sensitivity of a two-year-old harbor porpoise was measured in a pool using standard psycho-acoustic techniques. The go/no-go response paradigm and up–down staircase psychometric method were used. Auditory sensitivity was measured by using narrow-band frequency-modulated signals having center frequencies between 250 Hz and 180 kHz. The resulting audiogram was U-shaped with the range of best hearing (defined as 10 dB within maximum sensitivity) from 16 to 140 kHz, with a reduced sensitivity around 64 kHz. Maximum sensitivity (about 33 dB *re* 1 μPa) occurred between 100 and 140 kHz. This maximum sensitivity range corresponds with the peak frequency of echolocation pulses produced by harbor porpoises (120–130 kHz). Sensitivity falls about 10 dB per octave below 16 kHz and falls off sharply above 140 kHz (260 dB per octave). Compared to a previous audiogram of this species (Andersen, 1970), the present audiogram shows less sensitive hearing between 2 and 8 kHz and more sensitive hearing between 16 and 180 kHz. This harbor porpoise has the highest upper-frequency limit of all odontocetes investigated. The time it took for the porpoise to move its head 22 cm after the signal onset (movement time) was also measured. It increased from about 1 s at 10 dB above threshold, to about 1.5 s at threshold. © *2002 Acoustical Society of America.* [DOI: 10.1121/1.1480835]

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I. INTRODUCTION

The harbor porpoise (*Phocoena phocoena*) is one of the smallest cetacean species and has a relatively wide distribution (Gaskin, 1992). All over its distribution area it is accidentally caught in fisheries (Northridge, 1991). Attempts are being made to reduce this bycatch of harbor porpoises by deterring them with underwater acoustic alarms (pingers). In some cases this technique seems promising (Lien *et al.*, 1995; Kraus *et al.*, 1997; Laake *et al.*, 1998; Trippel *et al.*, 1999; Gearin *et al.*, 2000; Culik *et al.*, 2000). However, much research is still needed to refine this technique, and to determine if habituation occurs, and if so, how it can be avoided (Kastelein *et al.*, 1997, 2000, 2001). Some current questions are: how many alarms are needed to deter harbor porpoises from a net? Is the best approach one alarm with a high source level (SL) in the center of the net, or several alarms with lower SLs distributed over the length of the net? What is the minimal distance at which a porpoise should be deterred, and what should the SLs be under various ambient noise levels? Parameters to consider in relation to SL and number of alarms are: acoustic pollution of the oceans, costs, energy demand of the pingers, efficiency in reducing bycatch, availability, and ease of use.

The first step to answer these questions is to acquire fundamental information about the underwater hearing sensitivity of harbor porpoises. The underwater hearing of the harbor porpoise has been previously studied behaviorally by Andersen (1970) and by means of electrophysiological tests (Bibikov, 1992; Popov *et al.*, 1986). Andersen (1970) used one animal, but did not report the ambient noise level, and did not explain how the thresholds were determined. The hearing of the harbor porpoise tested by Andersen, for frequencies above 8 kHz, was poor compared to that of other odontocetes (Thomas *et al.*, 1988), whereas anecdotal information at sea and in captivity suggests that harbor porpoise hearing is more sensitive. Also, the mismatch between the porpoise's own phonation and area of best hearing caused doubt about the validity of the audiogram reported by Andersen. Electrophysiological measures using auditory brain stem evoked potential responses (ABR) and click signals provide only a rough estimate of hearing thresholds because ABR is an onset phenomenon (Supin *et al.*, 1993). It is difficult to determine the appropriate sound pressure level values for a given response. Hearing thresholds are usually described in terms of the root mean square (rms) value of the sound pressure level (SPL) at the subject's threshold of hearing and for sounds of longer duration than the integration time. The onset feature of ABR makes it difficult to properly estimate the rms SPL associated with an ABR threshold. In addition, the ABR studies on underwater hearing in marine mammals are usually carried out in very small reverberating tanks, which make it difficult to control the actual SPL at the location of the animal's head.

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Hence, the underwater hearing abilities of a harbor porpoise needed reassessment as this could prove to be essential in developing a strategy to protect this marine mammal species. Fortunately, the opportunity arose to conduct hearing experiments after a stranded juvenile harbor porpoise had been raised at the Harderwijk Marine Mammal Park, The Netherlands. While investigation of the hearing sensitivity of the harbor porpoise could increase the fundamental knowledge of hearing abilities in cetaceans, this study also contributes to the ultimate goal of determining the optimal characteristics (e.g., frequency, SL, their number, distribution) of acoustic alarms devices mounted on gillnets that significantly reduce the bycatch of harbor porpoises.

II. MATERIALS AND METHODS

A. Subject

The study animal was a stranded male harbor porpoise (code PpSH047) which had been raised at the Netherlands Cetacean Research and Rehabilitation Center at the Harderwijk Marine Mammal Park from the age of approximately 8 months. During the experiment, the animal aged from 1.5 to 3 years, his body weight increased from 28 to 29 kg, his body length from 122 to 132 cm, and his girth anterior to the pectoral fins (at the auditory meatus) from 65 to 66 cm. Veterinary records showed that the animal had not been exposed to oto-toxic medication.

The animal received 1.2–2 kg of thawed fish (sprat, *Sprattus sprattus*, and herring, *Clupea harengus*) per day divided over 6 meals. The meal size during a hearing test session (first meal of the day) was disproportionally large (0.45 kg). The diet was supplemented by vitamins specially developed for marine mammals (Akwavit, Twilmij B. V., Stroe, The Netherlands). The animal had no previous experience with psychophysical testing.

B. Facility

The animal was kept in an indoor concrete oval pool [8.6 m (l)×6.3 m (w), 1.2 m deep; Fig. 1] at the Research and Rehabilitation Center at the Harderwijk Marine Mammal Park, The Netherlands. Attention was paid to ensure a constant water level. Average water temperature was 19.5 °C, and average salinity was 2.2% NaCl. There was no current in the pool during the experiments, as the circulation pump (and the pump of the other pool in the building) was shut off 10 min before and during sessions. During the study period the study animal shared the pool with a 6-year-old female striped dolphin (*Stenella coeruleoalba*), a 1-year-old male harbor porpoise, or a 2-year-old female harbor porpoise. Nonstudy animals were kept quiet and fed at the opposite end of the pool during the experimental sessions in order to eliminate any distractions and interferences during a session. An adjacent room served as the observation and data collection laboratory, where all the controlling electronics were housed and where the equipment operator was seated during the experiments (Fig. 1). The operation of the equipment was not visible to the porpoise.

C. Signals and signal generation

A diagram of the signal generation system is shown in Fig. 2. Signals were produced by a wave form generator (Hewlett Packard, model 33120A). Each acoustic stimulus consisted of a narrow-band sinusoidally frequency-modulated (FM) signal (wobble) of 2.0 s duration. The signals had 150 ms rise and fall times to prevent abrupt signal onset and offset transients. The steady state portion of the signal thus was 1.7 s. The frequency modulation range of each stimulus signal was $\pm 1\%$ of the center frequency (i.e., the frequency around which the signal fluctuated symmetrically; see Table I), and the modulation frequency was 100 Hz. For example: if the signal's center frequency was 100 kHz, the frequency fluctuated 100 times per second (100 Hz) between 99 and 101 kHz ($\pm 1\%$). The study had started with pure tones, but this resulted in thresholds that varied by up to 15 dB between sessions. Repeated measurements of the SPL at the location of the porpoise's head indicated a difference in SPL of up to about 15 dB. These were suspected to have been caused by reflections of a long pure tone causing constructive and destructive interference of the signal. Therefore it was decided to use narrow-band FM signals. The advantage of using narrow-band FM signals is the reduction of propagation effects (multipath interferences) on the signals reaching the animal. However, narrow-band FM signals probably have a slightly higher arousal effect than pure tones, causing probably slightly lower thresholds. The use of narrow-band FM signals is therefore a trade-off: it provides a relatively stable SPL at the animal's head, but reduces comparability with previous studies on odontocete hearing.

A custom-built signal shaper and attenuator was used to control the amplitude of the signals. The sound pressure level at the porpoise's head while it was at the underwater listening station could be varied in 1dB steps. Before each session, the voltage output level of the system at the input of the transducer was verified with calibration levels (while the attenuator was at the same setting as during the calibrations) by using an oscilloscope (Dynatek, model 8120).

The lower frequency signals (250 Hz–32 kHz) were projected by an underwater low frequency piezoelectric transducer (Ocean Engineering Enterprise, USA, model DRS-8; 25 cm diameter) with an impedance matching transformer (Ocean Engineering Enterprise, USA). The 0.25, 0.5, and 1 kHz signals were amplified with a wide-band amplifier (Toellner, type TOE 7607). The 2–32 kHz signals needed no additional amplification. The higher frequency signals (32–180 kHz) were projected by a custom-built transducer consisting of a circular disk of 1–3 composite piezoelectric material (Material Systems Inc., Littleton, MA, U.S.A.), and an effective radiating aperture diameter of 4.5 cm. The thickness of the piezoelectric material was 0.64 cm. The piezoelectric element was a 6.4-cm-diam disk that was encapsulated in degassed polyurethane epoxy. The 32–180 kHz signals did not need amplification. The porpoise's hearing threshold for the 32 kHz signal was tested with both transducers. The sound propagation beam of each transducer was always aligned with the animal's body axis while it was at the station.

The porpoise's hearing sensitivity was measured at cen-

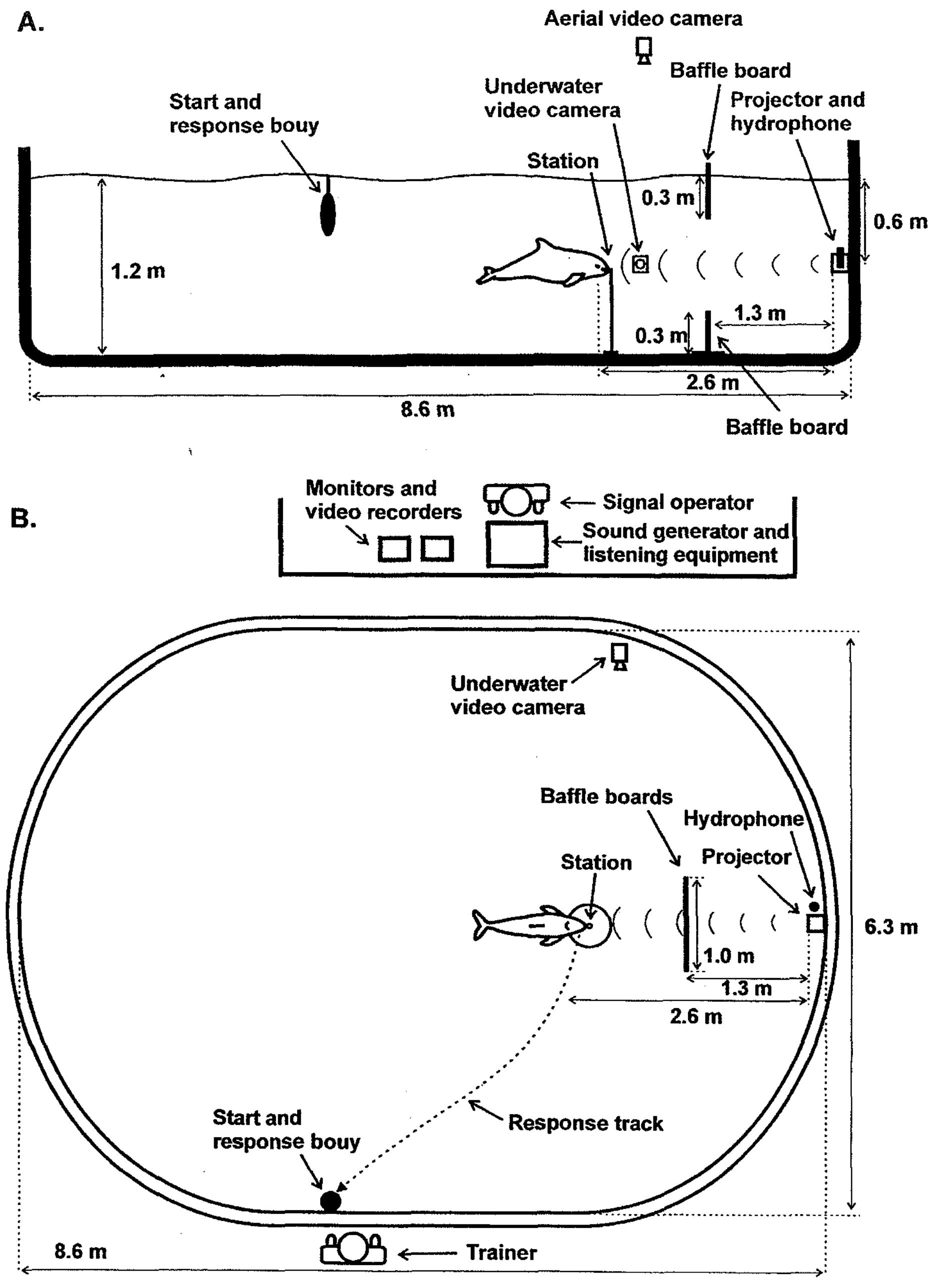

FIG. 1. The study area, showing the harbor porpoise in the correct position at the listening station: (a) sideview and (b) topview.

ter frequencies of 0.25, 0.5, 1, 2, 4, 8, 16, 32, 50, 64, 80, 100, 120, 130, 140, 150, 160, and 180 kHz. The low frequency cutoff of 250 Hz was determined by the limits of the sound production system, and was the lowest frequency the low frequency transducer could produce without distortions. Because the sonar signals of porpoises consist of narrow-band signals around 120 kHz (Møhl and Andersen, 1973; Verboom and Kastelein, 1995, 1997), the possibility of an acoustic fovea around 120 kHz was considered by using frequencies of 100, 130, 140, and 150 kHz. Originally, a one-octave frequency spacing for frequencies below 64 kHz was planned. However, the animal's sensitivity at 64 kHz was found to be lower than expected so that two additional frequencies (50 and 80 kHz) around 64 kHz were introduced. The high frequency cutoff of 180 kHz was determined by the limitations of the calibrating equipment to calibrate higher frequencies. The -3 dB beam width of the transducer at 130 kHz was approximately 15.6°. Since for a specific circular piston transducer the beam width is inversely proportional to frequency, the -3 dB beam width at 180 kHz should be approximately 11.3°. At a distance of 2 m, the -3 dB beam width will cover a circle having a diameter of 39 cm, which is larger than the head of the porpoise. The advantage of the transducers used in this study is that, at high frequencies, they are directional sound transmitters, causing less reflection from the sides of the pool. To reduce reflections from the water surface and the pool floor affecting the signal SPL at the animal's head, two baffle boards (6 mm thick, 30 cm $\times$ 100 cm aluminum plates covered with closed-cell neoprene) were placed perpendicular to the animal's axis, one breaking the water surface, and one at the pool floor (Fig. 1). The two boards were connected with nylon rope so they could be removed from the pool between sessions.

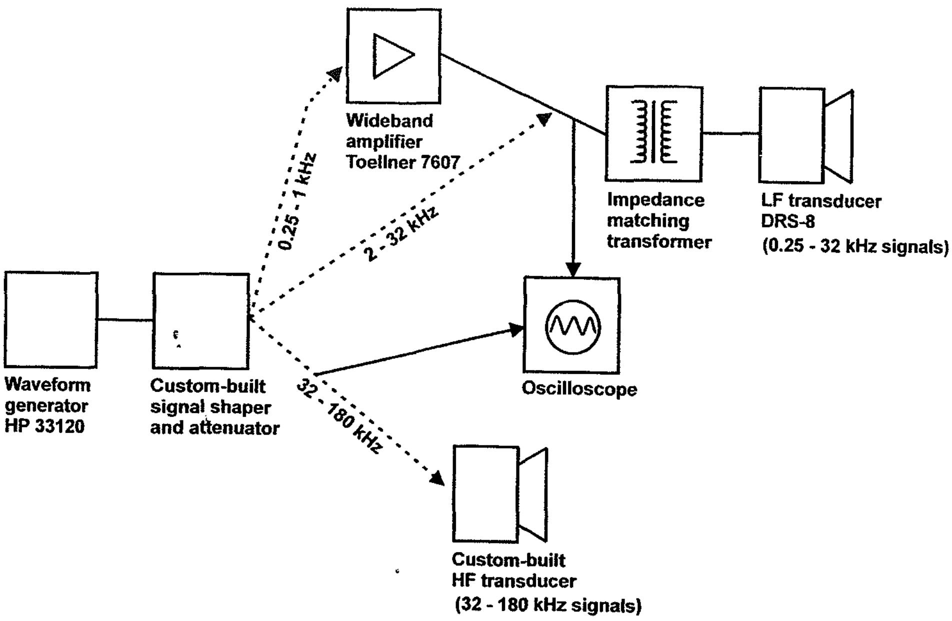

FIG. 2. Block diagram of the signal generation system used in the porpoise hearing study.

D. Signal calibration and monitoring

The signal SPLs (dB *re* 1 μPa, rms) for each test frequency were calibrated each month at the position of the porpoise's head when it was at the listening station during test sessions (2.6 m from the transducer). The porpoise was not at the station during the calibrations. The location of the porpoise's head while at the station relative to the transducer was always within a few cm in all six directions (he thus stayed within the 3 dB beamwidth of the transducer), and the animal did not adjust its position to a spot with a potentially higher signal SPL. The calibration equipment used for all signals consisted of a hydrophone (Brüel & Kjaer 8101; the calibration curve of this particular hydrophone showed that its frequency response was flat up to 100 kHz), a conditioning amplifier (Brüel & Kjaer, Nexus 2690), connected via a coaxial module (National Instruments, model BNC-2090) to a computer with an analog input/output card (National Instruments, PCI-MIO-16E-1, 12 bit resolution). The system was calibrated with a pistonphone (Brüel & Kjaer, 4223). For the calibration of signals above 100 kHz the frequency response of the measurement system was taken into account. To confirm this approach, a second hydrophone (B&K 8103) with a flat response (+1 dB/−2 dB) up to about 120 kHz was used with the frequency response of the measurement

TABLE I. The underwater 50% detection thresholds of a male harbor porpoise for 18 narrow-band FM signals, session threshold range, number of sessions, total number of reversals, and false alarm rate over all (signal present and signal absent) trials.

Center frequency (kHz)	FM range 1% of center frequency (kHz)	Mean 50% detection threshold (dB *re* 1 μPa)	Session threshold range (dB *re* 1 μPa)	Number of sessions (n)	Total No. of reversals	False alarm rate (%)
0.25	0.2475–0.2525	115	112–118	12	88	5
0.5	0.495–0.505	92	89–96	12	90	6
1	0.99–1.01	80	76–86	14	92	7
2	1.98–2.02	72	66–78	12	90	10
4	3.96–4.04	67	64–72	12	70	6
8	7.92–8.08	59	56–62	12	91	5
16	15.84–16.16	44	39–49	12	73	9
32	31.68–32.32	37[a]	28–42	15	103	9
50	49.5–50.5	36	33–39	12	99	8
64	63.36–64.64	46	40–51	12	75	3
80	79.2–80.8	37	36–40	12	90	5
100	99–101	32	29–35	12	80	9
120	118.8–121.2	33	31–37	12	75	9
130	128.7–131.3	35	28–40	12	73	5
140	138.6–141.4	36	32–41	12	83	5
150	148.5–151.5	60	57–63	12	83	4
160	158.4–161.6	91	87–97	12	91	10
180	178.2–181.8	106	97–111	12	84	7

[a]Based on the mean of 7 session thresholds measured with the LF transducer and 8 session thresholds determined with the HF transducer.

system taken into account. The values obtained with the B&K 8103 matched the results obtained with the B&K 8101.

The signals were digitized at a sample rate of 512 kHz in blocks of 0.2 s and fast Fourier transformed (FFT) into the frequency domain using a Hanning window. The highest peak in the spectrum was selected to determine the SPL and five consecutive 0.2 s time blocks were used to calculate the average SPL. Each month, the average SPL of each signal frequency was measured with the attenuator at the calibration setting (usually about 12 dB above the 50% detection threshold SPL). The analysis of the signals in the frequency domain was compared to rms analysis in the time domain, and the results matched. The linearity of the attenuator was also checked frequently.

Signals were analyzed with special attention to potential harmonics, especially with the low frequency, high amplitude signals (0.25, 0.5, and 1 kHz). These low frequency signals produced harmonics with energy well below the hearing thresholds obtained for those frequencies. The monthly SPL calibrations varied within 4 dB. The SPLs from the calibration nearest in time of the sessions were used to determine the session thresholds. Checks were often made for potential transients caused by pressing the signal button, both with and without the sound generator attached to the signal shaper/attenuator, or with the sound generator attached, but with the amplitude setting at 0. When the equipment was in the above-mentioned situations, the animal did not respond to the action of pressing the signal button. This was done at low and high amplitude settings of the sound generating system.

Before each session, the system was further verified by aurally monitoring the stimulus (usually at a higher amplitude than used during the session) via a hydrophone (LabForce 1BV) positioned directly adjacent to the transmitting transducer. The output of the monitoring hydrophone was connected to either an amplifier and loudspeaker for the frequencies up to 16 kHz, or to a bat-detector (Batbox III; Stag Electronics, Steyning, UK) for the signals with frequencies 32 kHz and above (maximum frequency possible was 120 kHz).

E. Background noise

Man-made noises in the vicinity were directly coupled into the pool. Therefore all indoor activities were stopped during sessions (nobody was allowed to move in the building). The water pumps in a nearby engine room were switched off 10 min before each session. The underwater background noise level was measured under the same conditions as during the study. Background noise in the pool was measured up to 8 kHz (at higher frequencies the ambient noise could not be measured, as the electronic noise of the recording system was higher than the ambient noise) by using the B&K 8101 hydrophone and the earlier described acoustic amplifier and conversion equipment. To allow comparison of the ambient levels and the hearing threshold levels, the recording and analysis methodology of the ambient levels was the same as that for the stimuli calibrations described previously. The recorded ambient signal was analyzed by FFT in ten blocks of 0.2 s. Of each block, the ambient levels of the tested frequencies were exported to a spreadsheet to calculate the average spectral level over 2 s (10 blocks). These levels are plotted in Fig. 4.

F. Experimental procedure

Training the porpoise for the hearing experiment took five months (August–December 1998). Operant conditioning using positive reinforcement was used for all training. A session began after the signal production equipment had been setup and the signal operator had set the frequency and the SPL for the first trial of the session. The amplitude in first trial of the first session of each frequency was set at about 20 dB above the threshold reported by Andersen (1970). A trial began with the animal stationed at the start and response buoy. When the trainer rang a bell, the animal swam to the listening station, which was the end of a 3-cm-diam water-filled PVC tube, and placed its head so that its auditory meatus was 2.6 m from the sound source, about 65 cm below the water surface (Fig. 1). He was trained to station with the tip of rostrum at the station and his body axis in line with the beam of the transducer. Because it was expected that the porpoise would have directional hearing (like in bottlenose dolphins; Au and Moore, 1984; Schlundt *et al.*, 2002), a maximum deviation in the porpoise's position of only 5° from the beam axis was accepted in all directions. Trials were canceled when the animal was not in the correct position. Due to the consistent behavior of the animal, no warm-up trials were conducted before the actual session began.

Signals were initiated following a random delay of 3 and 6 s after the porpoise stationed. If the animal detected the sound it left the station (go response) at any time during the 2 s signal duration and returned to the start and response buoy [Fig. 1(b)]. The signal operator told the trainer that the response was correct (a hit), after which the trainer gave a vocal signal and the porpoise received a fish. If the animal did not respond to the sound (a miss) the signal operator would tell the trainer that the animal's response was incorrect. The trainer would then signal the animal (by tapping on the side of the pool) that the trial had ended, thus calling him back to the start and response buoy. No reward was given. If the animal moved away before a signal was produced (a false alarm), the signal operator would notify the trainer to end the trial and not provide a reward to the animal.

For signal-absent trials, the signal operator told the trainer, after a random time period between 4 and 10 s after the porpoise had stationed, to end the trial by blowing a whistle. In case of a correct response (a correct rejection), the animal would return to the start buoy and receive a fish reward. If the porpoise left the station before the whistle was blown (a false alarm), the signal operator notified the trainer to end the trial and not reward the animal. The amount of fish reward for correct go and no-go trials was the same. After a correct response trial, the next trial would start as soon as the porpoise voluntarily returned to the start buoy.

A single frequency was tested during each session. A modified up/down staircase psychometric technique was used (Robinson and Watkins, 1973), a variance of the method of limits, which results in a 50% correct detection threshold (Levitt, 1971). If the animal heard a signal and responded to it (a hit), the next signal presented was 4 dB less intense. If the animal did not hear a signal and remained at the station (a miss), the following signal levels were increased in 4 dB steps until the animal detected the signal again. The starting SPL of a session was set at 12–16 dB above the threshold found during that frequency's previous session. False alarms did not result in a change in signal amplitude for the next signal trial. A session usually consisted of 29 trials and lasted for about 15 min. Harbor porpoises have problems in doing more trials per session, in contrast to bottlenose dolphins *Tursiops truncatus* (Johnson, 1967) and false killer whales, *Pseudorca crassidens* (Thomas *et al.*, 1988). The attention span of small odontocete species seems shorter than those of larger species. Each session consisted of 50% signal-present and 50% signal-absent trials based on a pseudorandom series table (Gellermann, 1933), with the modification that the first trial in a session was always a signal-absent trial. To end in a positive way, the last trial was always followed by a correct response so the animal always received a reward after the last trial. Each session, one of 12 different data collection sheets with different Gellermann series was selected. Sessions with more than 15% false alarms were eliminated, because these usually coincided with restless behavior of the animal (swimming circles in the pool between trials and/or coming late to the start buoy). To avoid unintentional cueing, the trainer did not know before or during trials whether a signal was present or absent (double blind presentation). When the porpoise left the station, the operator observed the animal's behavior on two monitors in the cabin (Fig. 1), told the trainer whether or not to reward the porpoise, and recorded the animal's responses. Sometimes other behaviors were solicited from the porpoise between trials to occupy the animal during short periods of visible or audible disturbances outside the building. The order in which the frequencies were tested was randomized so that the effects of potential learning did not covary with test frequencies.

A switch in the porpoise's response from a detected signal (a hit) to a successive nondetected signal (a miss), and *vice versa*, is called a reversal. Amplitudes at which the animal reversed its response behavior were taken as data points. The mean 50% detection threshold per session was defined as the mean amplitude of the reversals in that session (usually 7 reversals per session; range 4–12). The overall mean threshold was determined by taking the mean of 12–15 session thresholds. Sessions were only used after the session threshold leveled off, which usually occurred after about 2–4 sessions with a particular frequency.

Data were collected between March 1999 and October 2000. Generally, one session was conducted daily (5 days/week) between 0830 and 0915 h (first feed of the day), so that the porpoise had not been fed for 15 h before a session, and when the park was still closed to visitors. When the park was closed between October 1999 and March 2000, two sessions were conducted on each of 5 mornings per week (between 0830–0915 and 1115–1200 h). No differences in average hearing thresholds were found between the 0830 and 1115 h sessions. In total 6300 trials (18 frequencies×12 sessions/frequency×29 trials/session) were analyzed.

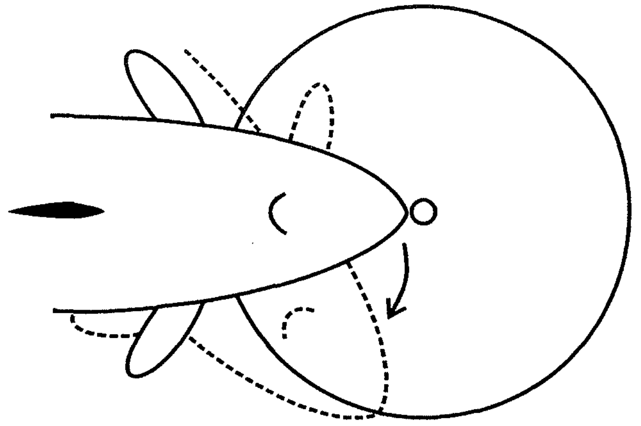

FIG. 3. The track of the porpoise's rostrum between the onset of the sound signal and the tip of the rostrum at the edge of the circle (a distance of 22 cm). The time this required is defined as the movement time.

G. Visual monitoring and image recording

To check the animal's position at the station and to gather data on his reactions and movement times to a stimulus, the animal's behavior was recorded by two video cameras. The images were visible in the signal operator's room. The porpoise was filmed from its left side by an underwater video camera (Mariscope, Micro, Kiel, Germany; Fig. 1). An aerial camera (Hapé, model CA 28) was hung from the ceiling just above the water surface and provided a top view of the animal. An infrared LED just in front of the lens, that was screened off so that it could not be seen by the animal, was filmed by the camera and showed when a sound was produced. Tests in which the LED was switched off showed that it was not a cue for the animal, as similar thresholds were reached as when the LED was operating (activated when the acoustic stimulus was presented). In addition, tests were done with only the LED being activated without the transducer being connected: the animal did not react to the LED's on switch. The images were recorded on videotape for later analysis.

H. Video analysis for movement time

From the images recorded by the aerial video camera, the movement time was measured to the nearest 40 ms (duration of one frame). The movement time was defined as the time between the onset of the signal (onset of LED) and the time the tip of the animal's rostrum was at the perimeter of a white 44-cm-diam white disk on the pool floor below the station (Fig. 3). The movement time was calculated for each signal trial of the following frequencies: 0.25, 0.50, 1, 2, 4, 8, 16, 32, 64, 100, 120, and 140 kHz. Per frequency a graph was made showing signal amplitude versus movement time and a trend line was drawn through all available data points (a minimum of ten movement time measurements per signal level was set as a minimum for a level to be included into the graph). Thereafter amplitudes were normalized to the 50% detection threshold of each particular frequency.

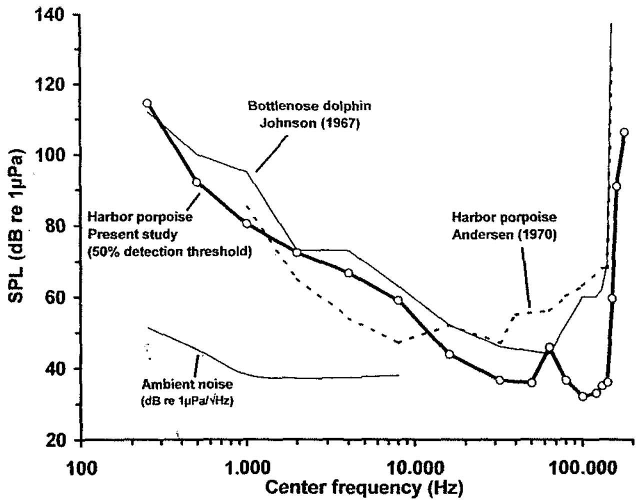

FIG. 4. The mean 50% detection thresholds in dB *re* 1 μPa (rms) for the tested narrow-band FM signals in the present study ($n = 12-15$ mean session threshold per frequency, for details see Table I). Also shown is the audiogram determined by Andersen (1970) for one harbor porpoise (sample size per frequency threshold unknown, and definition of the threshold unknown), and the audiogram of an Atlantic bottlenose dolphin (Johnson, 1967). The spectral level (dB *re* 1 μPa/$\sqrt{\text{Hz}}$; note that this is a different unit than the one along the *Y* axis) of the ambient noise in the pool is shown up to 8 kHz.

III. RESULTS

A. Hearing sensitivity

The 50% detection thresholds for the 18 narrow-band FM signals of the harbor porpoise are listed in Table I. The resulting audiogram for this porpoise was U-shaped (Fig. 4), with hearing capabilities from 0.25 to 180 kHz (9.5 octaves). Maximum sensitivity (about 33 dB *re* 1 μPa) occurred between 100 and 140 kHz (for details see Table I). The range of most sensitive hearing (defined as 10 dB within maximum sensitivity) was from 16 to 140 kHz (3.1 octaves), with a reduced sensitivity around 64 kHz. The less sensitive hearing for this frequency was not a narrow-band phenomenon, as was shown by the slightly decreased sensitivity for the 50 and 80 kHz signals. The animal's hearing became less sensitive below 16 kHz and above 140 kHz. Sensitivity decreased by about 10 dB per octave below 16 kHz and fell sharply at a rate of 260 dB per octave above 140 kHz. The average false alarm response rate per frequency varied between 4% and 10% of all trials, and was on average over all frequencies 7% (Table I).

The 32 kHz average (over 7 sessions) threshold measured with the LF transducer was 36.4±5.3 dB (*re* 1 μPa), while the average (over 8 sessions) threshold for the same frequency determined with the HF transducer was 36.8 ±4.1 dB. No significant difference was found between the mean thresholds (two-sample *T*-Test; $T = 0.13$, degrees of freedom$= 11$, $P = 0.899$). Therefore all 15 session thresholds were used in the calculation of average 50% detection threshold for the 32 kHz signal. The match between the 32 kHz thresholds obtained with the two transducers suggests that the shape of the audiogram is not influenced by differences in transducer characteristics. The animal's sensitivity for each test frequency was stable over the two-year study period.

B. Movement times in relation to SPL

A negative relationship occurred between signal amplitude and movement time for all frequencies tested. When the SPL of a signal came closer to the animal's hearing threshold for that frequency, the animal would move more slowly than after louder signals (Fig. 5). The slope of the movement time was about −50 ms per dB above threshold. It usually took about 80 ms (=reaction time) between the onset of the signal and the beginning of the animal's head movement. In all cases, the animal reached the parameter of the circle with its rostrum during the signal presentation (2000 ms including the 150 ms rise and fall times). The variation of the 50% detection threshold between sessions varied per frequency. In some cases (1, 16, 32, and 64 kHz) the sample size for signals with SPLs below the 50% detection threshold was too low (<10) to be included into the graph. In general a session began about three 4-dB steps above the 50% detection threshold.

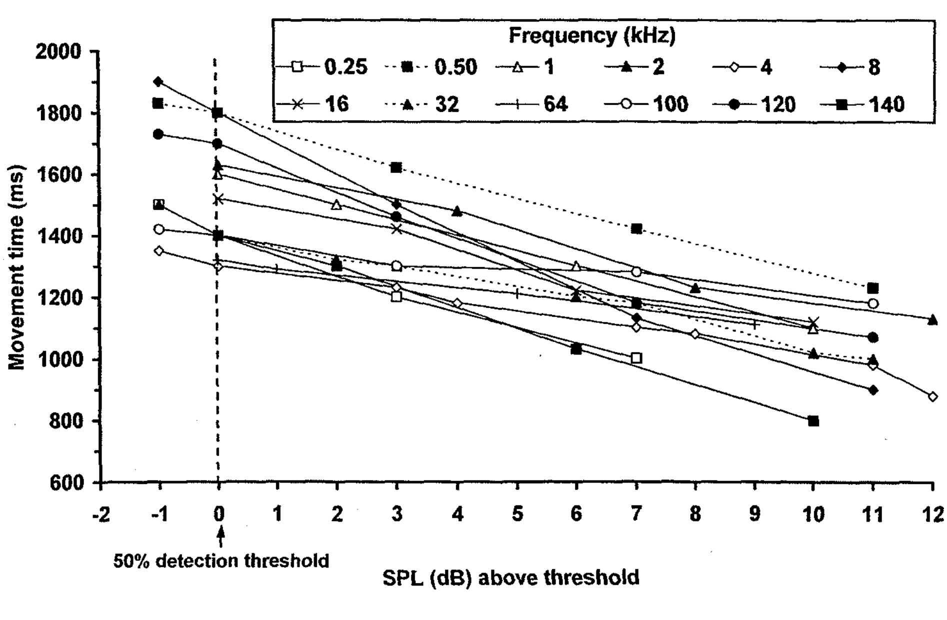

FIG. 5. The relationship between SPL relative to the 50% detection threshold and the average movement time of the porpoise for 12 narrow-band FM signals. The movement time decreases as the SPL increases. The sample size per data point increases as the SPL gets closer to the threshold, as a result of the up/down staircase method. In some cases (1, 16, 32, and 64 kHz) the sample size for signals with levels below the 50% detection threshold was too low (<10) to be included into the graph. In general a session began about three 4 dB steps above the 50% detection threshold.

IV. DISCUSSION AND CONCLUSIONS

A. Evaluation of the data

The comparatively low false alarm rate of the study animal is typical for marine mammals (Schusterman, 1974, 1976; Sauerland and Dehnhardt, 1998), but is also influenced by the way the animal was trained, and by the signal present/signal absent ratio. The porpoise probably only indicated the presence of a signal when it was confident of perceiving one. The present data, therefore, might represent a relatively conservative estimate of the auditory abilities of the harbor porpoise.

Two features of the method used influenced the 50% detection threshold: the pseudorandom Gellermann order in which the two trial types were presented, and the random time period between when the porpoise stationed and when the signal from the transducer or the whistle of the trainer were presented. Both these criteria reduced the possible anticipation by the animal, which may have influenced his response.

B. Comparison with previous harbor porpoise hearing studies

The audiogram of the present study deviates somewhat from the one made by Andersen (1970; Fig. 4). Between 2 and 8 kHz the hearing of the animal in the present study was less sensitive than that of the animal tested by Andersen. The thresholds in this frequency range found in the present study resemble more those found in other odontocetes (Johnson, 1967; Hall and Johnson, 1971; Jacobs and Hall, 1972; White *et al.*, 1978; Awbrey *et al.*, 1988; Thomas *et al.*, 1988; Wang *et al.*, 1992; Sauerland and Dehnhardt, 1998; Nachtigall *et al.*, 1995). However, above 8 kHz, the hearing of the animal in the present study was much more acute than that of the porpoise tested by Andersen. Age, sex, prior environment, individual differences, all could be factors contributing to the differences between the hearing sensitivity of the animal in the present study and that reported by Andersen (1970), as was shown to occur in bottlenose dolphins by Ridgway and Carder (1997). Differences in equipment and methodology could also have played a role. The results of the present study might be more representative of the hearing sensitivity of a young harbor porpoise with good hearing since the range of greatest hearing sensitivity found corresponds to the peak frequency of echolocation pulses of this species (120–130 kHz; Møhl and Andersen, 1973). A match between the frequency of sonar signals and area of best hearing is also found in the greater horseshoe bat (*Rhinolophus ferrumequinum*; Long, 1977). However, this match between the sonar signal frequency of peak energy and frequency range of highest hearing sensitivity is not found in the bottlenose dolphin (Johnson, 1967) and the false killer whale (Thomas *et al.*, 1988). In these species, the peak frequency of echolocation signals is dependent on the amplitude of the signal, and the bandwidth of the signals is wider than in the harbor porpoise and greater horseshoe bat. In general the frequency range of best hearing is around the average frequency of the echolocation signals.

Bibikov (1992) used auditory brainstem responses to test the hearing of a harbor porpoise that was contained in a very small tank (probably causing standing waves). He also found the lowest response threshold around 130 kHz. Popov *et al.* (1986) measured evoked potentials of the auditory cortex of a harbor porpoise also in a very small tank, and found the lowest evoked potential threshold curves within 120–130 kHz, but also found an additional sensitivity peak between 20 and 30 kHz. The latter peak was not found in the present psychophysical study, although the porpoise's hearing was fairly sensitive between 16 and 50 kHz. However, the auditory brainstem response method involves the use of short broadband signals so that the results are not very frequency-specific. In most cases, it is not clear to what frequency the auditory system is responding when it is given a short broadband acoustic stimulus.

Popov and Supin (1990) also found a decreased hearing sensitivity in the middle of audiograms; between 40 and 100 kHz in a harbor porpoise and between 30 and 60 kHz in an Amazon river dolphin (*Inia geoffrensis*). This supports the idea that the insensitivity phenomenon around 64 kHz found in the present study is a species, instead of an individual, characteristic.

The anatomical data of Ketten and Warzok (2000) suggest that the harbor porpoise should have a higher frequency of best hearing than was indicated by Andersen (1970). The high sensitivity region at 100 kHz observed in the present study is consistent with the measurement of ganglion cell density by Ketten. Ketten's preliminary data suggest an area of high ganglion cell density (over 10 000 cells/mm) located in the mid basal turn segment of the cochlea of the harbor porpoise, which would coincide with the 95–110 kHz region of the basilar membrane, and is in general agreement with data of the present study.

C. Comparison with hearing studies on other odontocetes

Underwater hearing thresholds have been determined in psychophysical tests for nine other odontocete species: The Atlantic bottlenose dolphin (Johnson, 1967; Fig. 4), killer whale, *Orcinus orca* (Hall and Johnson, 1971; Szymanski *et al.*, 1999), Amazon river dolphin, *Inia geoffrensis* (Jacobs and Hall, 1972), beluga whale, *Delphinapterus leucas* (White *et al.*, 1978; Awbrey *et al.*, 1988; Johnson, 1992; Klishin *et al.*, 2000), false killer whale (Thomas *et al.*, 1988), baji (Chinese river dolphin), *Lipotes vexillifer* (Wang *et al.*, 1992), tucuxi, *Sotalia fluviatilis guianensis* (Sauerland and Dehnhardt, 1998), Risso's dolphin, *Grampus griseus* (Nachtigall *et al.*, 1995), and Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (Tremel *et al.*, 1998). In most of these studies the shape of the audiograms and the maximum sensitivities were fairly similar (maximum sensitivities were within about 10–15 dB). The upper frequency of hearing varied from about 90 to 150 kHz, except for the killer whale in the study of Hall and Johnson (1971).

The hearing sensitivity of the harbor porpoise in the present study is within the range of those of the other odontocetes up to around 32 kHz. However, above 32 kHz the study animal's hearing is more acute and the upper frequency limit of hearing is higher than those of the other odontocetes.

D. Movement time

The movement time measured in the present study consists only for a very small percentage of the time difference between the LEDs on switch and the sound arriving at the animal. The time delay caused by the travel time of sound through the water (2.6 m distance/1500 m/s speed of sound) is 1.7 ms. This transmission time is negligible in relation to the movement times found in this study (850–1900 ms). These movement times are longer than the acoustic response times (145–448 ms) in bottlenose dolphins (Ridgway *et al.*, 1991), but this may be because the bottlenose dolphins only had to activate their vocalization system, whereas the porpoise in the present study had to put its entire body into action and move its rostrum 22 cm to the side (coping with the drag in water).

The closer the SPL of the signal to the 50% detection threshold, the slower the porpoise moved away from the station. In bottlenose dolphins, measuring acoustic responses to acoustic stimuli, Ridgway *et al.* (1991) also found that response times varied with stimulus amplitude, but also that it varied with stimulus duration, an aspect that was not tested in the present study. The increase in movement speed with increasing signal amplitude is fairly similar for the 12 analyzed frequencies. The slower movements with decreased SPL suggests that the animal uses some sort of likelihood criterion. It will continue to collect information about the signal, until it reaches a point where the likelihood that a signal was either present or absent exceeds some threshold value. In other words, the animal continues to listen until it is, say, 90% certain that it will make a correct decision. The higher movement times at lower SPLs suggest that the levels were reaching the hearing thresholds.

The reaction time (defined as the time between the onset of the signal and the start of the animal's movement) was fairly constant (around 80 ms) although the resolution of the analysis technique was low (one video frame is 40 ms). In humans, reaction time depends on the individual, the required behavior, and the stimulus (Henry, 1961; Carlson and Jensen, 1982). Comparison between studies is often difficult, because reaction time is influenced by the distance between the brain and the body parts that have to be activated (Davis, 1984).

E. Ecological significance and suggestions for future research

The frequency band of harbor porpoise echolocation signals lies within the frequency band of best hearing found in the present study. Thus, the hearing and echolocation signals of harbor porpoises are adapted for navigation and foraging in conditions where vision is limited or absent. Harbor porpoises are high latitude animals, living in an environment where biological noise is not high and broadband. The small size of harbor porpoise probably plays a major role in the use of higher frequencies for echolocation. For any frequency, the bigger the sound production organ, the narrower the beam. The harbor porpoise, being one of the smallest odontocetes, has a broad transmission beam (Au *et al.*, 1999), but the use of high frequency echolocation signals compensates for this as higher frequencies provide better directivity.

Relative to, for instance, the bottlenose dolphin, the sonar signals of the harbor porpoise have a lower SL (Au *et al.*, 1999), but the porpoise compensates for this to some degree by having lower hearing threshold levels around the frequency of peak energy. Despite its good hearing, the harbor porpoise's echolocation target detection abilities are poor (Kastelein *et al.*, 1999). Yet this is not surprising since the source level of the harbor porpoise is between 50 and 60 dB lower than that of the bottlenose dolphin (Au *et al.*, 1999) so that its better hearing sensitivity cannot compensate for such large differences in source levels.

The present study suggests that an acoustic alarm should have most energy between 100 and 140 kHz, the frequency range of best hearing of the harbor porpoise. Besides saving energy (such signals need to be less loud to be heard by porpoises than lower and higher frequency signals), such signals will be inaudible to most other marine organisms.

To be able to estimate the distance at which harbor porpoises can hear each other, acoustic alarms on fishing nets, or vessels under varying ambient noise conditions, additional information is needed. To understand fully how the harbor porpoise is adapted acoustically to its environment, information needs to be obtained on how it hears in the presence of masking noise (critical ratios, critical bands), how it hears sounds of different duration, and how well it spatially resolves sounds coming from different directions (directivity index).

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Andersen, S. (1970). "Auditory sensitivity of the harbour porpoise, *Phocoena phocoena*," in *Investigations on Cetacea*, edited by G. Pilleri (Institute for Brain Research, Bern), Vol. 2, pp. 255–259.

Au, W. W. L., Kastelein, R. A., Rippe, T., and Schooneman, N. M. (1999). "Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*)," J. Acoust. Soc. Am. 196, 3699–3705.

Au, W. W. L., and Moore, P. W. B. (1984). "Receiving beam patterns and directivity indices of the Atlantic bottlenose dolphin *Tursiops truncatus*," J. Acoust. Soc. Am. 75, 255–262.

Awbrey, F. T., Thomas, J. A., and Kastelein, R. A. (1988). "Low-frequency underwater hearing sensitivity in belugas, *Delphinapterus leucas*," J. Acoust. Soc. Am. 84, 2273–2275.

Bibikov, N. G. (1992). "Auditory brainstem responses in the Harbor porpoise (*Phocoena phocoena*)," in *Marine Mammal Sensory Systems*, edited by J. A. Thomas, R. A. Kastelein, and A. Ya Supin (Plenum, New York), pp. 197–211.

Carlson, J. S., and Jensen, C. M. (1982). "Reaction time, movement time, and intelligence: A replication and extension," Intelligence 6, 265–274.

Culik, B. M., Koschinski, S., Tregenza, N., and Ellis, G. (2000). "Reactions of harbour porpoises (*Phocoena phocoena*) and herring (*Clupea harengus*) to acoustic alarms," Mar. Ecol.: Prog. Ser. 211, 255–260.

Davis, M. (1984). "The mammalian startle response," in *Neural Mechanisms of Startle Behavior*, edited by R. C. Eaton (Plenum, New York), pp. 287–351.

Gaskin, D. E. (1992). "Status of the Harbour Porpoise, *Phocoena phocoena*, in Canada," Can. Field Naturalist 106, 36–54.

Gearin, P. J., Gosho, M. E., Laake, J. L., Cooke, L., DeLong, R. L., and Hughes, K. M. (2000). "Experimental testing of acoustic alarms (pingers) to reduce bycatch of harbour porpoise, *Phocoena phocoena*, in the state of Washington," J. Cetacean Research and Management 2, 1–9.

Gellermann, L. W. (1933). "Chance orders of alternating stimuli in visual discrimination experiments," J. Gen. Psychol. 42, 206–208.

Hall, J. D., and Johnson, C. S. (1971). "Auditory thresholds of a killer whale," J. Acoust. Soc. Am. 51, 515–517.

Henry, F. M. (1961). "Reaction time-movement time correlations," Percept. Mot. Skills 12, 63–66.

Jacobs, D. W., and Hall, J. D. (1972). "Auditory thresholds of a fresh water dolphin, *Inia geoffrensis* Blainville," J. Acoust. Soc. Am. 51, 530–533.

Johnson, S. C. (1967). "Sound detection thresholds in marine mammals," in *Marine Bioacoustics*, edited by W. N. Tavolga (Pergamon, New York), Vol. 2, pp. 247–260.

Johnson, S. C. (1971). "Auditory masking of one pure tone by another in the bottlenose porpoise," J. Acoust. Soc. Am. 49, 1317–1318.

Johnson, S. C. (1992). "Detection of tone glides by the beluga whale," in *Marine Mammal Sensory Systems*, edited by J. A. Thomas, R. A. Kastelein, and A. Ya. Supin (Plenum, New York), pp. 241–247.

Kastelein, R. A., Au, W. W. L., Rippe, H. T., and Schooneman, N. M. (1999). "Target detection by an echolocating harbor porpoise (*Phocoena phocoena*)," J. Acoust. Soc. Am. 105, 2493–2498.

Kastelein, R. A., de Haan, D., Staal, C., Schooneman, N. M., and Vaughan, N. (2001). "The influence of three acoustic alarms on the behaviour of harbour porpoises (*Phocoena phocoena*) in a floating pen," Marine Environ. Res. 52, 351–371.

Kastelein, R. A., Goodson, A. D., Lien, J., and de Haan, D. (1995). "The effects of acoustic alarms on Harbour porpoise (*Phocoena phocoena*) behaviour," in *Harbour Porpoises, Laboratory Studies to Reduce Bycatch*, edited by P. E. Nachtigall, J. Lien, W. W. L. Au, and A. J. Read (De Spil, Woerden, The Netherlands), pp. 157–167.

Kastelein, R. A., de Haan, D., Goodson, A. D., Staal, C., and Vaughan, N. (1997). "The effects of various sounds on a harbour porpoise (*Phocoena phocoena*)," in *The Biology of the Harbour Porpoise*, edited by P. E. Nachtigall, J. Lien, W. W. L. Au, and A. J. Read (De Spil, Woerden, The Netherlands), pp. 367–383.

Kastelein, R. A., Rippe, H. T., Vaughan, N., Schooneman, N. M., Verboom, W. C., and de Haan, D. (2000). "The effect of acoustic alarms on the behavior of harbor porpoises (*Phocoena phocoena*) in a floating pen," Marine Mammal Sci. 16, 46–64.

Ketten, D. R. (private communication).

Ketten, D. R., and Wartzok, D. (2000). "Three-dimensional reconstructions of the dolphin ear," in *Sensory Abilities of Cetaceans*, edited by J. Thomas and R. Kastelein (Plenum, New York), pp. 81–105.

Klishin, V. O., Popov, V. V., and Supin, A. Ya. (2000). "Hearing capabilities of a beluga whale, *Delphinapterus leucas*," Aquat. Mammals 26, 212–228.

Kraus, S., Read, A. J., Solow, A., Baldwin, K., Spradlin, T., Williamson, J., and Anderson, E. (1997). "Acoustic alarms reduce porpoise mortality," Nature (London) 388, 525.

Laake, J., Rugh, D., and Baraff, L. (1998). "Observations of harbor porpoise in the vicinity of acoustic alarms on a set gill net," NOAA Technical Memorandum NMFS-AFSC-84, U.S. Dept. of Commerce. 40 pp.

Levitt, H. (1971). "Transformed up-down methods in psychoacoustics," J. Acoust. Soc. Am. 49, 467–477.

Lien, J., Hood, C., Pittman, D., Ruel, P., Borggaard, D., Chisholm, C., Wiesner, L., Mahon, T., and Mitchell, D. (1995). "Field tests of acoustic devices on groundfish gillnets: Assessment of effectiveness in reducing harbour porpoise by-catch," in *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil, Woerden, The Netherlands), pp. 349–364.

Long, G. R. (1977). "Masked auditory thresholds from the bat, *Rhinolophus ferrumequinum*," J. Comp. Physiol. 116, 247–255.

Møhl, B., and Andersen, S. (1973). "Echolocation: High-frequency component in the click of the harbour porpoise (*Phocoena ph.* L.)," J. Acoust. Soc. Am. 53, 1368–1372.

Nachtigall, P. E., Au, W. W. L., Pawloski, J. L., and Moore, P. W. B. (1995). "Risso's dolphin (*Grampus griseus*) hearing thresholds in Kaneohe Bay, Hawaii," in *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil, Woerden), pp. 49–53.

Northridge, S. P. (1991). "An updated world review of interactions between marine mammals and fisheries," FAO Fish. Tech. Paper 251 (Suppl. 1), 58 pp.

Popov, V. V., Ladygina, T. F., and Supin, A. Ya. (1986). "Evoked potentials of the auditory cortex of the porpoise, *Phocoena phocoena*," J. Comp. Physiol., A 158, 705–711.

Popov, V. V., and Supin, A. Ya. (1990). "Electrophysiological studies of hearing in some cetaceans and a manatee," in *Sensory Abilities of Cetaceans*, edited by J. Thomas and R. Kastelein (Plenum, New York), pp. 405–415.

Ridgway, S. H., and Carder, D. A. (1997). "Hearing deficits measured in some *Tursiops truncatus*, and discovery of a deaf/mute dolphin," J. Acoust. Soc. Am. 101, 590–594.

Ridgway, S. H., Carder, D. A., Kamolnick, P. L., Skaar, D. J., and Root, W. A. (1991). "Acoustic response times (RTs) for *Tursiops truncatus*," J. Acoust. Soc. Am. 89, 1967–1968.

Robinson, D. E., and Watkins, C. S. (1973). "Psychophysical methods in modern psychoacoustics," in *Foundations of Modern Auditory Theory*, edited by J. V. Tobias (Academic, New York), Vol. 2, pp. 99–131.

Sauerland, M., and Dehnhardt, D. (1998). "Underwater audiogram of a *Tucuxi* (*Sotalia fluviatilis guianensis*)," J. Acoust. Soc. Am. 103, 1199–1204.

Schlundt, C. E., Carder, D. A., and Ridgway, S. H. (2002). "The effect of projector position on the hearing thresholds of dolphins (*Tursiops truncatus*) at 2, 8 and 12 kHz." in *Echolocation in Bats and Dolphins*, edited by J. Thomas, C. Moss, and M. Vater (The University of Chicago Press, Chicago).

Schusterman, R. J. (1974). "Low false-alarm rates in signal detection by marine mammals," J. Acoust. Soc. Am. 55, 845–848.

Schusterman, R. J. (1976). "California sea lion underwater auditory detection and variation of reinforcement schedules," J. Acoust. Soc. Am. 59, 997–1000.

Supin, A. Ya., Popov, V. V., and Klishin, V. O. (1993). "ABR frequency tuning curves in dolphins," J. Comp. Physiol., A 173, 649–656.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., and Henry, K. R. (1999). "Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms," J. Acoust. Soc. Am. 84, 936–940.

Thomas, J. A., Chun, N., Au, W. W. L., and Pugh, K. (1988). "Underwater audiogram of a false killer whale (*Pseudorca crassidens*)," J. Acoust. Soc. Am. 84, 936–940.

Tremel, D. P., Thomas, J. A., Ramirez, K. T., Dye, G. S., Bachman, W. A., Orban, A. N., and Grimm, K. K. (1998). "Underwater hearing sensitivity of a Pacific white-sided dolphin, *Lagenorhynchus obliquidens*," Aquatic Mammals **24**, 63–69.

Trippel, E. A., Strong, M. B., Terhune, J. M., and Conway, J. D. (**1999**). "Mitigation of harbour porpoise (*Phocoena phocoena*) by-catch in the gillnet fishery in the lower Bay of Fundy," Can. J. Fish. Aquat. Sci. **56**, 113–123.

Verboom, W. C., and Kastelein, R. A. (**1995**). "Acoustic signals by Harbour porpoises (*Phocoena phocoena*)," in *Harbour Porpoises, Laboratory Studies to Reduce Bycatch*, edited by P. E. Nachtigall, J. Lien, W. W. L. Au, and A. J. Read (De Spil, Woerden, The Netherlands), pp. 1–39.

Verboom, W. C., and Kastelein, R. A. (**1997**). "Structure of click train signals of harbour porpoises (*Phocoena phocoena*)," in *The Biology of the Harbour Porpoise*, edited by A. J. Read, P. R. Wiepkema, and P. E. Nachtigall (De Spil, Woerden, The Netherlands), pp. 343–362.

Wang, D., Wang, K., Xiao, Y., and Sheng, G. (**1992**). "Auditory sensitivity of a Chinese river dolphin, *Lipotes vexillifer*," in *Marine Mammal Sensory Systems*, edited by J. A. Thomas, R. A. Kastelein, and A. Ya. Supin (Plenum, New York), pp. 213–221.

White, M. J. Jr., Norris, J., Ljungblad, D. K., Baron K., and di Sciara, G. (**1978**). "Auditory thresholds of two beluga whales (*Delphinapterus leucas*)," HSWRI Technical Report No. 78–109, Hubbs Marine Research Institute, San Diego, California.