Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) fornarrow-band sweeps (0.125-150 kHz)

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Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) for narrow-band sweeps (0.125-150 kHz)

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The underwater hearing sensitivity of a two-year-old harbor porpoise was measured using a standard psycho-acoustic technique under very low ambient noise conditions. Auditory sensitivity was measured for narrow-band sweeps with center frequencies between 0.125 and 150 kHz. The audiogram was U-shaped; range of best hearing (within 10 dB of maximum sensitivity) was from 13 to ~140 kHz. Maximum sensitivity (threshold ~39 dB re 1 μPa) occurred at 125 kHz, at the peak frequency of echolocation pulses produced by harbor porpoises. Reduced sensitivity occurred at 32 and 63 kHz. Sensitivity fell by ~10 dB per octave below 16 kHz, and declined sharply above 125 kHz. Apart from this individual's *ca.* 10 dB higher sensitivity at 0.250 kHz, *ca.* 10 dB lower sensitivity at 32 kHz, and *ca.* 59 dB lower sensitivity at 150 kHz, his audiogram is very similar to that of porpoise ID no. 02 (Kastelein *et al.*, 2010), the subject of many hearing and behavioral response studies. Both animals and porpoise ID no. PpSH047 (Kastelein *et al.*, 2002) have similar hearing sensitivity that is likely to be representative for harbor porpoises in general. Decisions based on information from previous harbor porpoise studies by Kastelein *et al.* do not need to be modified.

I. INTRODUCTION

The harbor porpoise (*Phocoena phocoena*) is one of the smallest cetacean species and has a relatively wide distribution in coastal waters of the northern hemisphere (Gaskin, 1992). Human activities producing underwater sound, such as shipping, oil and gas exploration (seismic surveys) and piling construction of wind farms are common nowadays in coastal waters. The harbor porpoise is protected in many waters, so it is important to know how anthropogenic sounds may affect its ecology. A first step in evaluating the impact of sound is understanding the hearing range and hearing sensitivity of this species.

Underwater hearing of the harbor porpoise has been studied behaviorally (Andersen 1970) and by means of electrophysiological tests (Popov *et al.*, 1986; Bibikov, 1992). Andersen (1970) used one animal, but did not report the ambient noise level, and did not explain how the thresholds were determined, making it unclear whether the reported hearing thresholds were masked or not. The hearing of the harbor porpoise tested by Andersen, for frequencies above 8 kHz, was poor compared to that of other odontocetes, whereas anecdotal information from animals at sea and in captivity suggests that harbor porpoise's hearing is sensitive above 8 kHz. In addition, the mismatch between the porpoise's own phonation and its frequency range of best hearing caused doubt about the validity of the audiogram reported by Andersen (1970).

Electrophysiological measurements using auditory brain stem evoked potential responses (ABR) and click signals provide relative hearing thresholds (Supin *et al.*, 1993), but these need to be validated by behavioral hearing thresholds. It is difficult to determine the appropriate sound pressure level values for a given response (often zero to peak levels are used). Hearing thresholds are usually described in terms of the level of the root-mean-square sound pressure (i.e., sound pressure level, abbreviated as SPL) at the subject's threshold of hearing, for sounds of longer duration than the integration time. The onset feature of ABR makes it difficult to estimate the SPL associated with an ABR threshold. In addition, ABR studies on underwater hearing in marine mammals are usually carried out in very small reverberating tanks, which makes it difficult to control the actual SPL at the location of the animal's head. Audiograms of the same individuals derived with the AEP technique can differ much from those derived with a psychophysical technique (Finneran and Houser, 2006).

In order to gain insight into the effects of anthropogenic noise on the harbor porpoise, a behavioral underwater audiogram was needed. The hearing of a young male porpoise (ID no. PpSH047) was tested psychophysically under unmasked conditions by Kastelein *et al.* (2002). The animal was used in another hearing study, to determine the critical ratio for a 4 kHz signal (Kastelein and Wensveen, 2008). A second young male porpoise (ID no. 02) was tested with the same method under quiet conditions by Kastelein *et al.* (2010). The audiograms of both animals were very similar. Porpoise ID no. 02 was used in many other hearing studies:

- Critical ratio (Kastelein *et al.*, 2009),
- Integration time (Kastelein *et al.*, 2010),
- Hearing threshold for 1-2 kHz and 6-7 kHz sweeps (Kastelein *et al.*, 2011a),
- hearing thresholds for 1.4 kHz helicopter dipping sonar signals (Kastelein *et al.*, 2011b), hearing thresholds for impulsive sounds (Kastelein *et al.*, 2012a),
- Thresholds for single 1-2 kHz and 6-7 kHz up-sweeps and down-sweeps causing startle responses (Kastelein *et al.*, 2012c),
- TTS (temporary hearing threshold shift) due to continuous octave-band noise centered around 4 kHz (Kastelein *et al.*, 2012b),
- TTS due to a continuous 1.5 kHz pure tone (Kastelein *et al.*, 2013a),
- hearing thresholds for pile driving sound (Kastelein et al., 2013b),
- equal latency contours and auditory weighting functions (Wensveen *et al.*, 2014),
- TTS due to 1-2 kHz sonar signals (Kastelein *et al.*, 2014a),
- TTS due to 6-7 kHz sonar signals (Kastelein *et al.*, 2014b),
- TTS due to pile driving sounds (Kastelein *et al.*, 2015a), and
- TTS due to intermittent and continuous 6-7 kHz sonar sweeps (Kastelein *et al.*, 2015b).

In human and terrestrial mammal hearing studies, a large number of subjects are often used to determine average audiograms and threshold ranges. However, such numbers are not available for marine mammal hearing studies; in fact most marine mammal species' audiograms are based on only one individual (David, 2011; Mooney *et al.*, 2012). So far, valid behavioral audiograms exist for only two individual harbor porpoises (ID nos. PpSH047 and 02; Kastelein *et al.*, 2002; 2010). Those animals had similar hearing. Regulatory agencies world-wide have based underwater sound criteria on the acoustic studies conducted with these two harbor porpoises, so it is very important to determine whether their hearing is representative of the species. Deriving audiograms from several individuals per marine mammal species was recommended by Southall *et al.* (2007). Therefore, when a young male harbor porpoise became available for a psychophysical hearing study in an appropriate hearing test facility, the opportunity was taken to test its hearing.

II. MATERIALS AND METHODS

A. Study animal and study area

The male harbor porpoise in this study (ID no. 04) was two years old, his body weight was around 30 kg, his body length was 130 cm, and his girth at the axilla was approximately 73 cm. The animal received between 1.6 and 2.4 kg of thawed fish per day (depending on the season), divided over four meals. Variation in the animal's performance was minimized by making weekly adjustments (usually in the order of 100 g) to his daily food ration, based on his weight and performance during the previous week, and the expected change in water and air temperatures in the following week.

The study was conducted at the SEAMARCO Research Institute, the Netherlands. Its location is remote and quiet, and was specifically selected for acoustic research. The animal was kept in a pool complex designed and built for acoustic research, consisting of an outdoor pool (12 m x 8 m; 2 m deep) connected via a channel (4 m x 3 m; 1.4 m deep) to an indoor pool (8 m x 7 m; 2 m deep) in which the hearing tests were conducted. All pumps were switched off 10 min. before each hearing test and left off during tests. By the time a test started, no water flowed over the skimmers, so there was no flow noise during testing. Details of the study area are presented by Kastelein *et al*. (2012 b).

Great care was taken to make the harbor porpoise's listening environment as quiet as possible. Only researchers involved in the hearing tests were allowed within 15 m of the pool during hearing test sessions, and they were required to stand still. Under test conditions the background noise in the pool was very low (see Kastelein et al., 2012 b).

B. Acoustics

SPL measurements

The background noise and hearing test signals were measured monthly during the study period. The sound measurement equipment consisted of two hydrophones [Brüel & Kjaer (B&K) – 8106] with a multichannel high-frequency analyzer (B&K PULSE - 3560 D), and a laptop computer with B&K PULSE software (Labshop, version 12.1). The system was calibrated with a pistonphone (B&K - 4223). The SPLrms (dB re 1 µPa) of each hearing test signal was derived from the received 90% energy flux density divided by the corresponding 90% time duration (Madsen, 2005).

The received SPL of each hearing test signal was measured at the position of the harbor porpoise's head during the hearing tests. The calibration measurements were conducted with two hydrophones, one at the location of each auditory meatus of the harbor porpoise when it was positioned at the listening station. The SPL at the two locations differed by 0 to 2 dB, depending on the test frequency. The average SPL measured via the two hydrophones was used to calculate the stimulus level during hearing threshold tests. The received SPLs were calibrated at levels of approximately 15 dB above the threshold levels found in the present study (depending on the frequency). The linearity of the transmitter system was checked during each calibration and was found to deviate by less than 1 dB within a 20 dB range.

Hearing test signals

Narrow band up-sweeps (linear frequency-modulated tones) were used as hearing test signals instead of pure tones, because sweeps lead to very stable and precise thresholds (Finneran and Schlundt, 2007). The hearing test signals were generated digitally (Adobe Audition, version 3.0; sample rate 768 kHz). The linear up-sweeps started and ended at ± 2.5% of the center frequency (**Table I**), and had durations of 1 s, including a linear rise and fall in amplitude of 50 ms. The WAV files used as hearing test signals were played on a laptop computer (Micro-Star International - M5168A) with a program written in LabVIEW, to an external data acquisition card (NI - USB6251), the output of which could be controlled in 1 dB steps with the LabVIEW program. The output of the card went through a ground loop isolator, a custom-built buffer, a custom-made variable passive low-pass filter, a custom-built buffer and (only for 0.125, 0.250 and 0.500 kHz) a variable active low-pass filter (Krohn-Hite - 3362), and drove several transducers to test the porpoise's wide hearing frequency range (0.125-150 kHz). The following four transducers were used, each performing optimally in a specific frequency band:

- 0.125, 0.25 and 0.500 kHz sounds were projected with a directional inductive moving coil transducer [Underwater Sound Reference Division (USRD) J-11], via a power amplifier (Samson HQ VPA2450 MB).
- 1, 2, 4, 6.5, 8, 9.2, and 13 kHz sounds were projected by a balanced tonpilz piezoelectric acoustic transducer (Lubell - LL916; 1.5- 8 kHz) through an isolation transformer (Lubell – AC202).
- 16, 32 and 63 kHz sounds were projected by a piezoelectric acoustic transducer (International Transmission Company- 6084).
- 125 and 150 kHz sounds were projected by a custom-built directional transducer (WAU-q7b) consisting of a disc of 1-3 composite piezoelectric materials (Material Systems Inc., Littleton, MA, U.S.A.), with an effective radiating aperture diameter of 4.5 cm. The thickness of the piezoelectric materials was 0.64 cm. The piezoelectric element was a 6.4 cm diameter disk that was encapsulated in degassed polyurethane epoxy.

C. Hearing test procedures

Each hearing test trial began with the animal at the start/response buoy. The level of the hearing test sweep used in the first trial of the session was approximately 6 dB above the hearing threshold determined during the previous sessions. When the trainer gave a hand signal, the harbor porpoise was trained to swim to the listening station. The methodology was as described by Kastelein *et al.* (2012b). The signal level was varied according to the one-up one-down adaptive staircase method (Cornsweet, 1962). This conventional psychometric technique (Robinson and Watson, 1973) leads to a 50% correct detection threshold (Levitt, 1971). The SPL at the harbor porpoise's head while it was at the listening station was varied by the operator in 2 dB increments. A switch from a test signal level that the harbor porpoise responded to (a hit), to a level that he did not respond to (a miss), and *vice versa*, was called a reversal.

Each complete hearing session consisted of ~30 trials and lasted for up to 12 min. Sessions consisted of 2/3 signal-present and 1/3 signal-absent trials offered in quasi-random order. There were never more than three consecutive signal-present or signal-absent trials. Per frequency, the mean 50% detection threshold was based on at least 60 reversals obtained in at least 6 sessions (the sample sizes for 6.5 and 9.2 kHz were much greater because they were part of other simultaneous hearing studies). Usually three hearing test sessions were conducted per day. Data were collected between August 2013 and June 2014.

III. RESULTS

Pre-stimulus responses occurred in between 7% and 15% of all trials, depending on the test frequency; the average pre-stimulus response rate was 11% (**Table I**).

The harbor porpoise's 50% detection thresholds for the 15 narrow-band sweeps are listed in **Table I**. The resulting audiogram for this porpoise was U-shaped (**Fig. 1**), and demonstrated hearing ability from 0.125 to 150 kHz. Maximum sensitivity (around 39 dB re 1 μPa) occurred at 125 kHz (**Table I; Fig. 1**). The range of most sensitive hearing (defined as within 10 dB of maximum sensitivity) was from 13 to ~140 kHz (estimated by interpolation between 125 and 150 kHz). Reduced sensitivity occurred at 32 and 64 kHz. The animal's hearing was less sensitive below 16 kHz and above 125 kHz. Sensitivity decreased by about 10 dB per octave below 16 kHz and fell sharply above 125 kHz.

Table I. The underwater 50% detection thresholds of young male harbor porpoise ID no. 04 for 15 narrow-band sweeps, total number of reversals (the sample size for the mean), and overall pre-stimulus response rate (pooled for signal-present and signal-absent trials). A pre-stimulus response during signal absent trials is defined as the animal swimming away from the listening station before the whistle was blown signaling the end of the trial.

Center frequency (kHz)	Sweep range (± 2.5 % of center frequency) (kHz)	Mean 50% hearing threshold (dB re 1 μPa)	SD (dB)	Total no. of reversals	Pre-stimulus response rate (%)
0.125	0.122-0.128	119	1.6	60	15
0.25	0.244-0.256	105	2.2	70	7
0.5	0.488-0.513	92	1.6	60	13
1	0.975-1.025	85	1.9	66	7
2	1.95-2.05	74	3.4	60	10
4	3.9-4.1	63	1.7	60	15
6.5	6.35-6.65	63	2.2	148	14
8	7.8-8.2	58	2.0	64	12
9.2	8.97-9.43	54	2.4	106	8
13	12.675-13.325	47	2.2	60	12
16	15.6-16.4	44	2.1	60	11
32	31.2-32.8	59	2.1	68	10
63	61.425-64.575	52	1.6	60	7
125	121.875-128.125	39	1.8	60	9
150	146.250-153.750	114	2.4	70	11

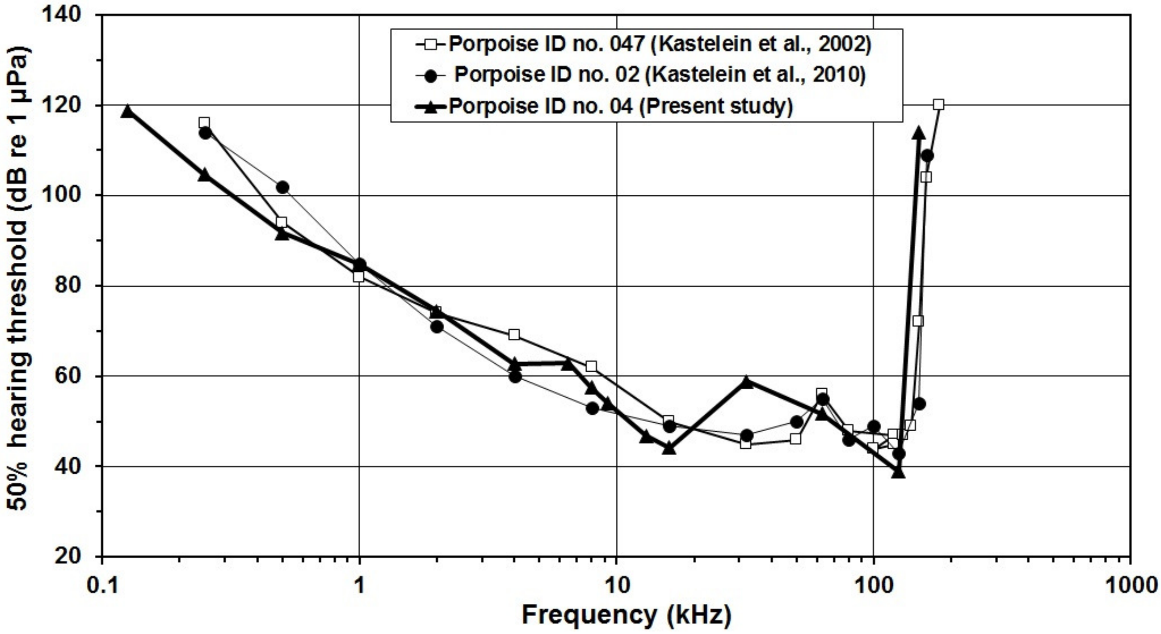

FIG. 1. The mean 50% hearing thresholds of the young male harbor porpoise (ID no. 04) for narrow-band linear up-sweeps (900 ms) in the present study (n ≥ 60 reversals per frequency, see **Table I**). Also shown are the audiograms of two other young male harbor porpoises [ID no. PpSh047; Kastelein *et al*. 2002; 1700 ms frequency-modulated signals (warbles), corrected for modulation, and ID no. 02; Kastelein *et al*. 2010; 900 ms frequency-modulated signals (warbles)]. For standard deviations, see **Table I**.

IV. DISCUSSION AND CONCLUSIONS

In comparing the audiogram of the present study animal with those of the two previously tested male harbor porpoises (summarized in Kastelein *et al*., 2010; **Fig. 1**), it should be remembered that different signals were used in the three studies: narrow-band sweeps in the present study and narrow-band sinusoidal frequency-modulated tones (warbles) in the previous studies. The modulation range (frequency around which the signal fluctuated symmetrically) was ± 1% of the center frequency, 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; Kastelein *et al*., 2002; 2010). In the present study, sweep modulation was ± 2.5% of center frequency. Despite these differences, all the signals were narrow-band, so no effects of signal type on the measured hearing threshold are expected. The basic audiogram of the young male harbor porpoise in the present study was very similar to those of the two previously tested young male harbor porpoises (**Fig. 1**). In all three animals, maximum sensitivity occurred at 125 kHz, at the peak frequency of echolocation pulses produced by harbor porpoises (120-130 kHz). The main differences between the animals' hearing sensitivity are:

1) The hearing of the animal in the present study is around 10 dB more sensitive for signals of 0.250 kHz than that of the two previously tested animals. This is unlikely to be due to differences in background noise or methodology: porpoise ID no. 02 was tested again for this frequency during the present study (using the same narrow-band sweeps), and his threshold was still the same as reported by Kastelein *et al*. (2010).

2) Within their range of most sensitive hearing, the two previously tested porpoises had a slight dip in hearing sensitivity at 63 kHz, whereas the animal in the present study had slightly reduced hearing sensitivity at both 32 kHz and 63 kHz. This reduced hearing may function as a low-pass filter for less relevant sounds below ~80 kHz, thus improving the focus on echolocation signals at 125 kHz (Møhl and Andersen, 1973; Kamminga and Wiersma, 1981). Why the exact frequency range of the sensitivity dip differs slightly between the three porpoises is unknown, but differences could be due to variation in the anatomy of the cochlea (Ketten, 2000).
3) The hearing of the animal in the present study was less acute at 150 kHz than that of porpoises ID nos. PpSH047 and 02. However, another harbor porpoise (ID no. 01), which only participated in a critical ratio study, could not hear 150 kHz signals at all, though his critical ratios for the other frequencies were very similar to those of porpoise ID no. 02 (Kastelein *et al.*, 2009).

It can be concluded that, apart from these minor differences, the three healthy young male harbor porpoises showed similar hearing ranges and hearing sensitivity under very low ambient noise conditions. Thus, the hearing of harbor porpoise ID no. 02, on which many acoustic studies have been based, seems to be representative of that of young male harbor porpoises in general. The present study therefore indicates that there is no need to amend or question research in which information from hearing studies of harbor porpoise ID no. 02 was used, or to modify underwater sound criteria based on data from this animal. It should be noted that even though animals have similar hearing, their behavioural responses to sound may differ between individuals.

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LITERATURE CITED

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, 255-259.

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 Press, New York), pp.197-211.

Cornsweet, T.N. (**1962**). "The staircase method in psychophysics," J. Acoust. Soc. Am. **75**, 485-491.

David, A. (**2011**). "Underwater environmental assessment on marine mammals and fish by high power anthropogenic radiated sound," Acoustics **27**, 1-8.

Finneran, J.J. , Houser, D.S. (**2006**). "Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (Tursiops truncatus)," J. Acoust. Soc. Am. **119**,3181-3192. _DOI: 10.1121/1.2180208.

Finneran, J. J., and Schlundt, C. E. (**2007**). "Underwater sound pressure variation and bottlenose dolphin (*Tursiops truncatus*) hearing thresholds in a small pool," J. Acoust. Soc. Am., **122**, 606-614.

Gaskin, D. E. (**1992**). Status of the harbour porpoise, *Phocoena phocoena*, in Canada, *Canadian Field-Naturalist,* **106**, 36-54.

Kamminga, C. and Wiersma, H. (**1981**). "Investigations of Cetacean Sonar II. Acoustical Similarities and Differences in Odontocete Sonar Signals," Aquatic Mamm. **8**, 41-62.

Kastelein, R. A., Bunskoek, P., Hagedoorn, M., Au, W. W. L. and de Haan, D. (**2002**). "Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals," J. Acoust. Soc. Am. **112**, 334-344.

Kastelein, R. A., and Wensveen, P. J., (**2008**). "Effect of two levels of masking noise on hearing threshold of a harbor porpoise (*Phocoena phocoena*) for a 4.0 kHz signal," Aquatic Mammals **34**, 420-425.

Kastelein, R. A., Wensveen, P. J., Hoek, L., Au, W. W. L., Terhune, J. M., de Jong, C. A. F. (**2009**). "Critical ratios in harbor porpoises (*Phocoena phocoena*) for tonal signals between 0.315 and 150 kHz in random Gaussian white noise", J. Acoust. Soc. Am. **126**, 1588-1597.

Kastelein, R. A., Hoek, L., de Jong, C. A. F., and Wensveen, P. J. (**2010**). "The effect of signal duration on the underwater detection thresholds of a harbor porpoise (*Phocoena phocoena*) for single frequency-modulated tonal signals between 0.25 and 160 kHz," J. Acoust. Soc. Am. **128**, 3211-3222.

Kastelein, R. A., Hoek, L., and de Jong, C. A. F. (**2011a**). "Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) for sweeps (1-2 kHz and 6-7 kHz bands) mimicking naval sonar signals," J. Acoust. Soc. Am. **129**, 3393-3399.

Kastelein, R. A., Hoek, L., and de Jong, C. A. F. (**2011b**). "Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) for helicopter dipping sonar signals (1.43-1.33 kHz) (L)," J. Acoust. Soc. Am. **130**, 679-682.

Kastelein, R. A., Gransier, R., Hoek, L., and de Jong, C. A. F. (**2012a**). "The hearing threshold of a harbor porpoise (*Phocoena phocoena*) for impulsive sounds (L)", J. Acoust. Soc. Am. **132**, 607-610.

Kastelein, R.A., Gransier, R., Hoek, L. and Olthuis, J. (**2012b**). "Temporary threshold shifts and recovery in a harbor porpoise (*Phocoena phocoena*) after octave-band noise at 4 kHz," J. Acoust. Soc. Am. **132**, 3525-3537.

Kastelein, R. A., Steen, N., Gransier, R., Wensveen, P. J., and de Jong, C. A. F. (**2012c**). "Threshold received SPLs of single 1-2 kHz and 6-7 kHz up-sweeps and down-sweeps causing startle responses in a harbor porpoise (*Phocoena phocoena*)," J. Acoust. Soc. Am. **131**, 2325–2333.

Kastelein, R. A., Gransier, R., Hoek, L. and Rambags, M. (**2013a**). "Hearing frequency thresholds of a harbor porpoise (*Phocoena phocoena*) temporarily affected by a continuous 1.5 kHz tone," J. Acoust. Soc. Am. **134**, 2286-2292. DOI: http://dx.doi.org/10.1121/1.4816405.

Kastelein, R.A., Hoek, L., Gransier, R., and de Jong, C.A.F. (**2013b**). "Hearing thresholds of a harbor porpoise (*Phocoena phocoena*) for playbacks of multiple pile driving strike sounds" J. Acoust. Soc. Am. **134**, 2302-2306. DOI: http://dx.doi.org/10.1121/1.4817842.

Kastelein, R. A., Hoek, L., Gransier, R., Rambags, M., and Claeys, N. (**2014a**). "Effect of level, duration, and inter-pulse interval of 1-2 kHz sonar signal exposures on harbor porpoise hearing," J. Acoust. Soc. Am. **136**, 412-422. DOI: http://dx.doi.org/10.1121/1.4883596.

Kastelein, R. A., Schop, J., Gransier, R., and Hoek, L. (**2014b**). "Frequency of greatest Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) depends on the noise level," J. Acoust. Soc. Am. **136**, 1410-1418, DOI: 10.1121/1.4892794

Kastelein, R. A., Gransier, R., Marijt, M. A. T., and Hoek, L. (**2015a**). "Hearing frequencies of a harbor porpoise (*Phocoena phocoena*) temporarily affected by played back offshore pile driving sounds," J. Acoust. Soc. Am. **137**, 556–564, DOI: 10.1121/1.4906261.

Kastelein, R. A., Gransier, R., Schop, J., and Hoek, L. (**2015b**). "Effect of intermittent and continuous 6-7 kHz sonar sweep exposures on harbor porpoise (*Phocoena phocoena*) hearing," J. Acoust. Soc. Am. **137**, 1623-1633.

Ketten, D. R. (**2000**). "Cetacean Ears," in *Hearing by Whales and Dolphins*, edited by W. W. L. Au, A. N. Popper, and R. R. Fay (Springer, New York), pp. 43-108.

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

Madsen, P. T. (**2005**). "Marine mammals and noise: Problems with root mean square sound pressure levels for transients," J. Acoust. Soc. Am. **117**, 3952-3957.

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

Mooney, T. A., Yamato, M., and Branstetter, B. K. (**2012**). Hearing in Cetaceans: From Natural History To Experimental Biology". in *Advances in Marine Biology* (Editor Michael Lesser), Elsevier. **63**, 197-246. doi: 10.1016/B978-0-12-394282-1.00004-1.

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.

Robinson, D. E., and Watson, 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.

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R. Jr., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., and Tyack, P. L. (**2007**). "Marine Mammal Noise Exposure Criteria: Initial Scientific Recommendations," Aquat. Mamm. **33**, 411-521.

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

Wensveen, P. J., Huijser, L. A. E., Hoek, L. and Kastelein, R.A. (**2014**). "Equal latency contours and auditory weighting functions for the harbour porpoise (*Phocoena phocoena*)," J. Exp. Biol. **217**, 1-11 DOI:10.1242/jeb.091983.