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Underwater hearing sensitivity of a Pacific white-sided dolphin, *Lagenorhynchus obliquidens*

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Summary

Using a Descending Staircase Method, we measured the underwater hearing sensitivity of a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) from 75 Hz through to 150 kHz. The dolphin, housed at the John G. Shedd Aquarium, stationed in an underwater hoop and responded to hearing a 2-second sinewave with a go/no-go response. The dolphin had a U-shaped audiometric curve, similar to other mammals, with best sensitivities from 2 kHz to 128 kHz (e.g., <90 dB re 1 μPa). The lowest measurable sensitivities were 145 dB at 100 Hz and 131 dB at 140 kHz. Below 8 kHz and above 100 kHz, this dolphin's underwater hearing was similar to other odontocetes. At 16 kHz, 32 kHz and 64 kHz the hearing was less sensitive, similar to *Inia geoffrensis*, *Lipotes vexillifer* and *Grampus griseus*.

Introduction

The ocean abounds with natural sounds from wind, waves, ice, rain, seismic events and soniferous marine life (Wenz, 1962). However, there is increasing concern about possible deleterious effects caused by human-generated noise in the ocean, such as sounds associated with oil/gas exploration and production, marine construction, commercial fishing, vessel traffic, military operations and acoustical oceanography (Richardson *et al.*, 1991; 1995). This concern prompted several studies to determine the extent of any effects on marine mammals (Reeves, 1977; Myrberg, 1978; Mansfield, 1983; Stirling & Calvert, 1983; Richardson *et al.*, 1990, 1991, 1995; Mulroy, 1991; Simmonds & Lopez-Jurado, 1991).

To evaluate the potential impact of anthropogenic noise, the underwater amplitude sensitivities of a species over a broad range of frequencies must be understood. The underwater hearing sensitivities of several odontocetes are known from audiograms based on behavioral responses: bottlenose dolphin, *Tursiops truncatus* (Johnson, 1967); beluga, *Delphinapterus leucas* (White *et al.*, 1978; Awbrey *et al.*, 1988; Johnson, 1992); killer whale, *Orcinus orca* (Hall & Johnson, 1971; Bain *et al.*, 1993); false killer whale, *Pseudorca crassidens* (Thomas *et al.*, 1988; Nachtigall *et al.*, 1995); Risso's dolphin, *Grampus griseus* (Nachtigall *et al.*, 1995); harbor porpoise, *Phocoena phocoena* (Andersen, 1970); Chinese River dolphin, *Lipotes vexillifer* (Wang *et al.*, 1992); and Amazonian River dolphin, *Inia geoffrensis* (Jacobs & Hall, 1972). Although all species showed a typical U-shaped pattern in frequency responses, few studies tested frequencies below 1 kHz (Awbrey *et al.*, 1988; Johnson, 1992; Nachtigall *et al.*, 1995). Using behavioral responses, we measured the underwater hearing capabilities for a Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, from 75 Hz to 150 kHz.

Materials and methods

Dolphin and facility

A female Pacific white-sided dolphin housed at the John G. Shedd Aquarium in Chicago Illinois, weighed 91 kg and ate about 12 kg of fish per day at either a hearing threshold session or a public presentation. The oceanarium housed five other dolphins and four belugas who were distracted during hearing tests with a special training session conducted away from the test pool. For tests, the dolphin swam into an off-exhibit medical pool (8 × 5.5 × 3 m). This pool (Fig. 1) allowed easy separation of the dolphin for tests and had minimal ambient noise and standing wave problems.

Test scenario

When given a hand cue from the trainer, the dolphin swam to an underwater hoop at a depth in line with an underwater projector. The equipment

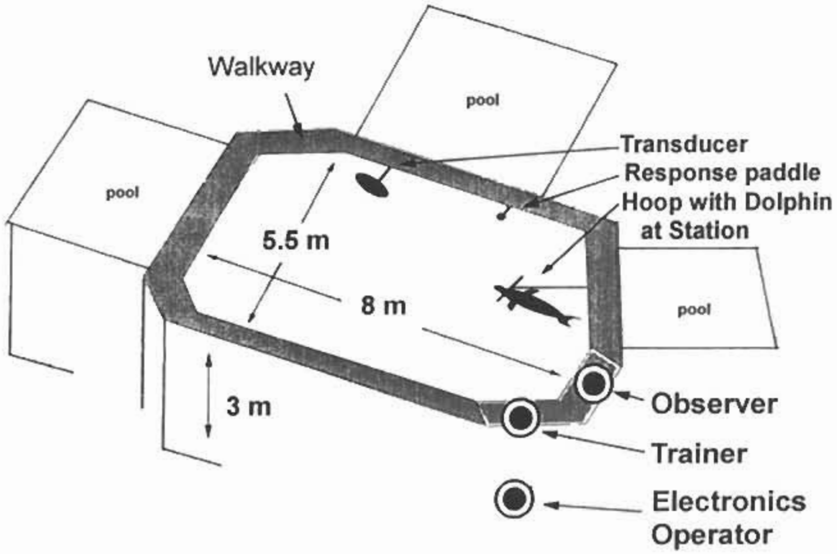

Figure 1. Dimensions of pool, position of researchers and placement of electronic equipment.

operator indicated to the trainer whether the trial had a signal or no signal. The signal started randomly between 4 and 12 s after the dolphin stationed. The animal had 15 s after the tone to back out of the hoop (go response). The dolphin swam across the pool, touched a response paddle, and returned to the trainer for a fish reward. During a no-signal trial, the dolphin remained in the hoop (no-go response) until given a release whistle at random times between 14 and 22 s after entering the hoop. After release, the dolphin left the hoop and returned to the trainer for fish reinforcement. False alarms (i.e., the dolphin left the hoop and touched the paddle even though no signal was present) and misses (i.e., the dolphin did not respond to a previously detected signal level) were not reinforced and the trainer delayed the next trial for a few seconds.

Threshold criteria

We measured underwater hearing thresholds in dB re 1 μPa in approximate octave intervals from 75 Hz to 150 kHz. Sessions were conducted in six-trial blocks, with randomized presentations of three signal and three no-signal trials per block (Gellerman, 1933). We bracketed the approximate threshold at each test frequency so the first warm up level was 25 dB above threshold. For frequencies with <25 dB above threshold, the first warm up was at 0 dB attenuation. The first block was a warm up, with signal attenuation in 5-dB steps. During the warm ups, the trainer used secondary reinforcers such as applause, rubs, or a water spray and varied the number of fish as a reward.

Within test blocks, however, secondary reinforcement was not allowed and the fish reward was fixed to alleviate differential reinforcement between signal and no-signal trials. Between each six-trial block, the trainer used fish and secondary reinforcements for performing two other trained behaviors, thus providing some variety for the dolphin.

During data collection, attenuation changed in a Descending Staircase Method (Fay, 1988). After each correct response to a signal trial, the amplitude for the next trial decreased by 3 dB until the dolphin no longer responded, e.g., a "miss". Then, the amplitude increased in 3-dB steps until the subject responded, e.g., a "hit". A reversal was the midpoint between the signal level at the first miss and the next hit. Sessions consisted of 40–60 trials, with two to eight reversals per session. At least 15 reversals spread among four or more sessions were averaged to determine the amplitude threshold for each frequency. A session was defined as unacceptable if there was more than one miss or false alarm during the warm up if the false alarm rate for the entire session exceeded 20%.

Electronic equipment

A Wavetek function generator (model 90) produced the sinusoidal test signal. A Krohn-Hite filter (model KH3901) high and lowpass filtered the signal to a gating/attenuating control box. The control box delayed the signal by 0.5 s and provided a rise-time of 190 ms. The signal remained at maximum amplitude for 1.62 s, followed by a 190 ms fall-time. The control box had a 1-dB attenuator to select the signal level and a switch to

Table 1. Underwater hearing thresholds in dB re 1 μPa for a Pacific white-sided dolphin, reported by frequency and projecting transducer

Frequency	Transducer	Number of reversals	Signal level at hoop* Mean	Maximum	Minimum	Average attenuation at threshold	Amplitude sensitivity at threshold
75 Hz	J13	0	146	–	–	no response	?
100 Hz	J13	11	146	–	–	1	145
125 Hz	J13	16	141	–	–	4	137
250 Hz	J13	6	141	–	–	14	127
250 Hz	J9	21	145	146	143	18	127
500 Hz	J9	16	138	143	138	20	118
1 kHz	J9	18	133	134	129	27	106
2 kHz	J9	15	136	140	136	49	87
4 kHz	J9	17	134	140	133	61	73
8 kHz	J9	17	125	128	121	59	66
16 kHz	F30	19	113	117	113	40	73
32 kHz	F30	16	120	121	119	54	66
64 kHz	F30	16	125	129	125	61	64
100 kHz	F30	18	126	133	126	48	78
128 kHz	F30	22	127	135	126	49	78
135 kHz	F30	14	129	134	126	34	95
140 kHz	F30	11	132	134	126	1	131
150 kHz	F30	0	130	130	130	no response	?

*Average of 5 calibrations taken throughout the study; note only 1 calibration was available for the J13 transducer.

control whether the signal was on or off during a trial.

Because of the broad range of frequencies tested, three different transducers were used (Table 1). A pipe bar clamp attached the J9 and F30 projectors to the walkway, 5 m from the hoop at a depth of 1 m (Fig. 1). A hoist suspended the J13 projector 8 m from the hoop at a depth of 1 m. A Hafler (series 9290) amplified the signal for projection from either a J9 (linear frequency response 40 Hz to 20 kHz ± 3 dB) or F30 (linear frequency response 10 kHz to 150 kHz ± 3 dB) projector. For the J13 projector (linear frequency response 10 Hz to 3 kHz ± 3 dB), a Crown (DC-300A series II) amplified the signal. We confirmed the signal levels in Vrms into the transducer before each session using a Radio Shack (model 22-181A) true rms voltmeter.

Calibration of signal level

We examined signals on an oscilloscope for standing wave problems at all test frequencies. Signal level at the hoop was measured in dB re 1 μPa for each frequency before the study using two receiving hydrophones; an H52 hydrophone (sensitivity − 180 dB re 1 μPa) and a cylindrical ARGOTEC hydrophone (sensitivity − 202 dB re 1 μPa) and two channels of a Rockland System 90, Signal Analysis Workstation. Signal levels at the hoop were measured again at the end of the study using a B & K (model 8103) hydrophone (sensitivity − 211 dB re 1 μPa), an Ithaco (model 601C) hydrophone (sensitivity − 169 dB re 1 μPa) and two channels of a LeCroy (model 9300) real time spectrum analyzer. The final signal level at the hoop was an average of five calibrations (Table 1). A threshold was calculated as the difference between the average signal level at the hoop and the average attenuation over all reversals at that frequency.

The presence of extraneous sounds could affect the dolphin's attentiveness for hearing a signal, e.g. mechanical sounds from pool filters and pumps or sounds from other dolphins or belugas. Therefore, we periodically measured the underwater sound pressure level of ambient noise in the pool using a B & K SPL meter (model 2230), filter set (model 1625), hydrophone (model 8103) and a calibrated piston phone (model 4223).

Results and discussion

We measured the underwater audiogram of the female Pacific white-sided dolphin between 100 Hz and 140 kHz (Table 1). The dolphin did not respond to 75 Hz at 146 dB re 1 μPa or to 150 kHz at 127 dB re 1 μPa. The lowest measurable sensitivities were 145 dB at 100 Hz and 131 dB at 140 kHz. The dolphin was most sensitive (<90 dB re 1 μPa) to frequencies between 2 kHz and 128 kHz (Figs 2–4). Below 1 kHz, the hearing sensitivity dropped at a gradual rate of about 43 dB

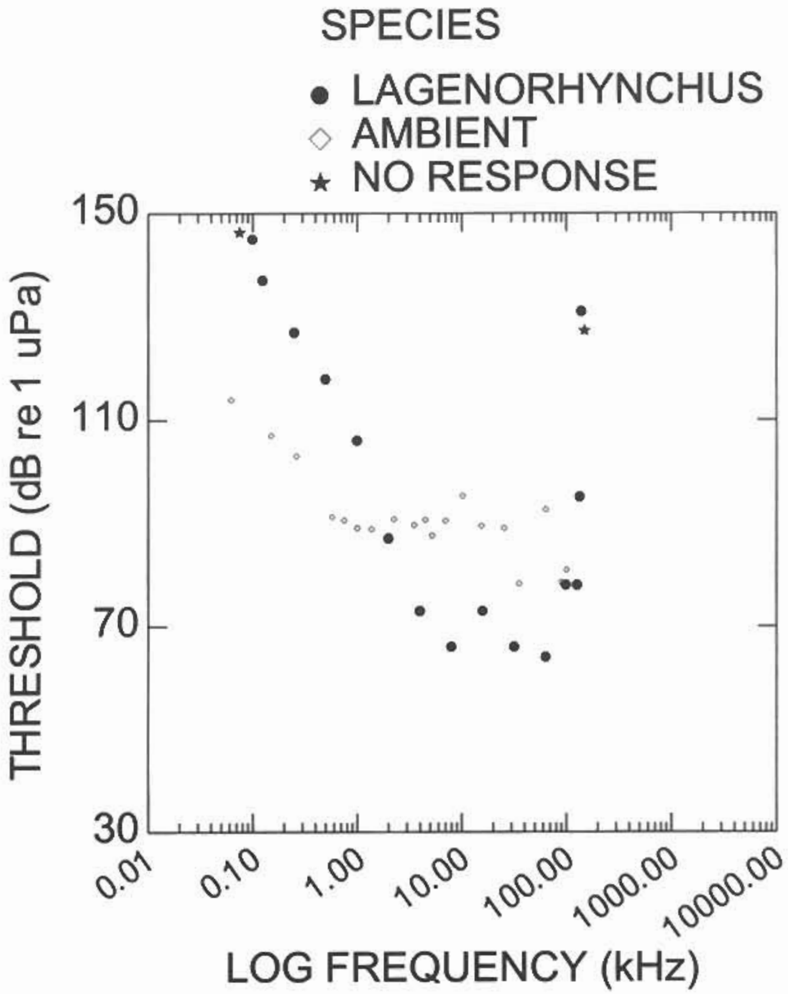

Figure 2. Underwater audiogram of a Pacific white-sided dolphin compared to pool noise; ambient noise measurements taken over a 100 kHz bandwidth.

per kHz. Similar decreases in sensitivity occur at low frequencies in *Delphinapterus* (Awbrey *et al.*, 1988; White *et al.*, 1978), in *Tursiops* (Johnson, 1967) and in *Pseudorca* (Thomas *et al.*, 1988). Above 100 kHz, the Pacific white-sided dolphin's sensitivity decreased sharply at a rate of 1.4 dB per kHz. Similar decreases in sensitivity occur above 64 kHz in *Pseudorca* (Thomas *et al.*, 1988), above 64 kHz in *Lipotes* (Wang *et al.*, 1992), above 80 kHz in *Grampus* (Nachtigall *et al.*, 1995), above 100 kHz in *Inia* (Jacobs & Hall, 1972), above 115 kHz in *Delphinapterus* (White *et al.*, 1978) and above 120 kHz in *Tursiops* (Johnson, 1967). Odontocetes fall into two groups based on hearing sensitivity at mid-frequencies. *Delphinapterus*, *Phocoena* and *Pseudorca*, have greater sensitivity in the middle frequency range (Fig. 3). *Inia*, *Lipotes*, *Grampus* and *Lagenorhynchus* have less sensitivity in the middle frequency range (Fig. 4). All these audiograms are based on single animals, so they could represent individual differences as well as species differences.

Even though the signal levels started well above the ambient, the Pacific white-sided dolphin's threshold dropped below the pool noise between 4 kHz and 64 kHz. Other audiograms conducted in pools are similarly limited by ambient noise. The audiogram on *Grampus* by Nachtigall *et al.* (1995) could have been masked by ambient noise from snapping shrimp. In fact, only a few audiometric studies on odontocetes report the ambient pool levels (Johnson, 1967; Hall & Johnson, 1971;

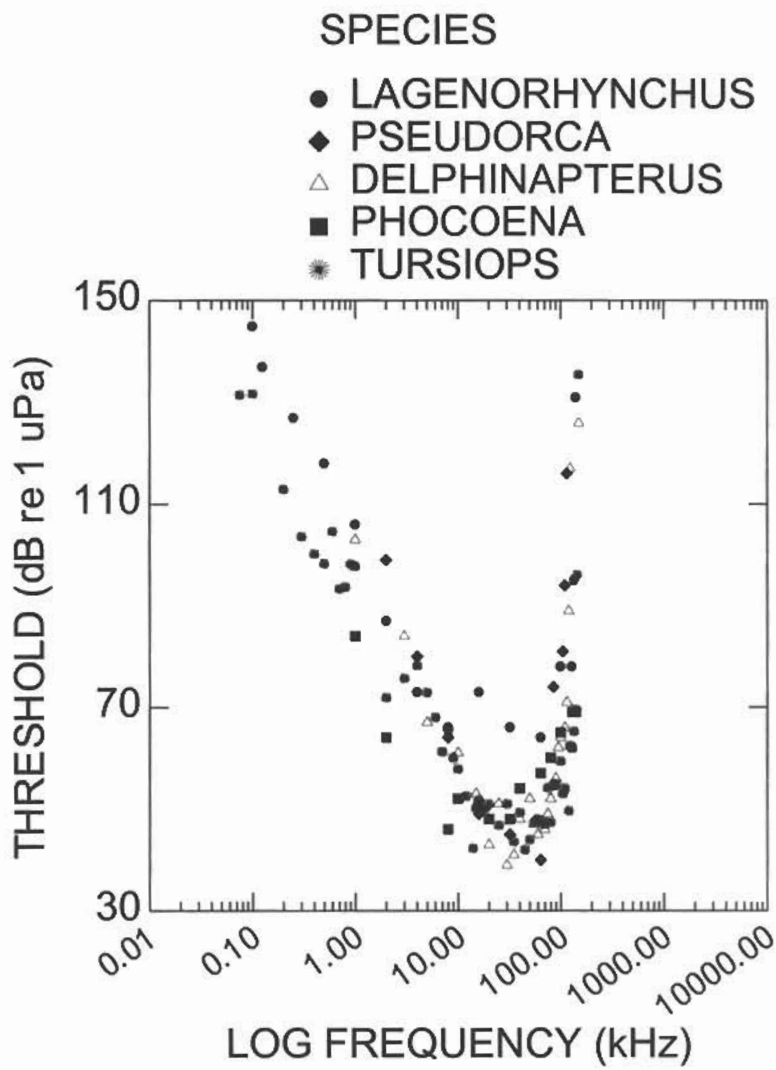

Figure 3. Underwater audiograms of odontocetes with more sensitive mid-frequency hearing.

Jacobs & Hall, 1972; Thomas *et al.*, 1988, 1990). Few aquatic environments have ambient levels as low as 40 dB re 1 μPa, which is the most sensitive hearing of any odontocete measured so far. According to Richardson *et al.* (1995), it is more appropriate to measure broadband ambient noise in a per Hz basis or as a Noise Level (NL). In this pool, NL decreased at higher frequencies; from 17.6 dB re 1 $\mu Pa/Hz^{1/2}$ at 250 Hz, 16.3 dB at 1.2 kHz, 15.1 at 3.5 kHz 14.6 dB at 5 kHz, 15.1 dB at 10 kHz, 15.2 dB at 16 kHz, 14.5 dB at 32 kHz, 14.1 dB at 64 kHz, to 14.2 dB at 100 kHz. Johnson (1967) reported NL for his bottlenose dolphin study at 16.6 dB between 100 and 316 Hz, at 10.1 dB between 316 and 1000 Hz, and at 5.1 dB between 1000 and 3200 Hz. In comparison, thresholds at the middle frequencies of the dolphin in our study could have been masked slightly by ambient pool noise, but not to the extent in the study on *Grampus*, where ambient noise from snapping shrimp produced NL between 40 and 70 dB.

Most anthropogenic noise in the ocean occurs at less than 1 kHz (Richardson *et al.*, 1995). The underwater hearing of the Pacific white-sided dolphin was not sensitive at low frequencies, e.g., ranging from 145 dB at 100 Hz to 106 dB at 1 kHz.

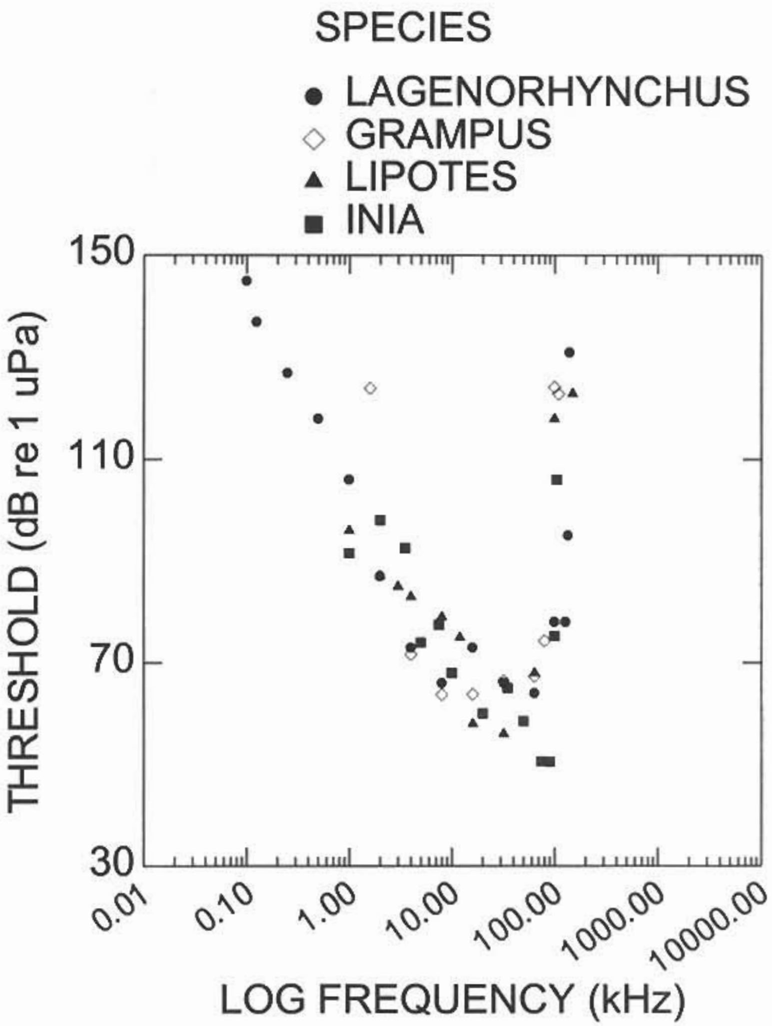

Figure 4. Underwater audiograms of odontocetes with less sensitive mid-frequency hearing.

Kryter (1985) reported that for humans listening under water a signal level of 80 dB above the threshold caused a temporary threshold shift. If we make a similar comparison with *Lagenorhynchus obliquidens*, anthropogenic noise in water would need to be 225 dB at 100 Hz or 186 dB at 1 kHz to cause a temporary threshold shift. There are anthropogenic noises at these frequencies and source levels (see Table 6.9 from Richardson *et al.*, 1995), e.g. super tankers, ship sonars and sounds used for seismic exploration. However, farfield sounds in a water environment attenuate at a rapid rate of 6 dB per doubling of distance from the source. So, anthropogenic noise is not likely a problem for this dolphin species, except at close ranges from a very high amplitude source.

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