

Auditory masking in odobenid and otariid carnivores^{a)}

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ABSTRACT:

As the only living species within the odobenid lineage of carnivores, walrus (*Odobenus rosmarus*) have no close relatives from which auditory information can be extrapolated. Sea lions and fur seals in the otariid lineage are the nearest evolutionary outgroup. To advance understanding of odobenid and otariid hearing, we conducted behavioral testing with two walrus and one California sea lion (*Zalophus californianus*). Detection thresholds for airborne sounds were measured from 0.08 to at least 16 kHz in ambient noise conditions and then re-measured in the presence of octave-band white masking noise. Walrus were more sensitive than the sea lion at lower frequencies and less sensitive at higher frequencies. Critical ratios for the walrus ranged from 20 dB at 0.2 kHz to 32 dB at 10 kHz, while critical ratios for the sea lion ranged from 16 dB at 0.2 kHz to 35 dB at 32 kHz. The masking values for these species are comparable to one another and to those of terrestrial carnivores, increasing by about 3 dB per octave with increasing frequency. Despite apparent differences in hearing range and sensitivity, odobenids and otariids have a similar ability to hear signals in noisy conditions. © 2023 Acoustical Society of America.

<https://doi.org/10.1121/10.0020911>

(Received 10 May 2023; revised 15 August 2023; accepted 23 August 2023; published online 15 September 2023)

[Editor: Brian Branstetter]

Pages: 1746–1756

I. INTRODUCTION

Concern for rising levels of noise in ocean ecosystems has prompted many recent studies of marine mammal hearing. Several comprehensive reviews reveal significant knowledge gains as well as important data gaps (e.g., Erbe *et al.*, 2016; Mooney *et al.*, 2012; Nummela, 2008; Southall *et al.*, 2019). Among amphibious marine mammals, the best studied with respect to hearing are the phocid carnivores. These “true seals” are linked within a common phylogenetic lineage that exhibits a broad frequency range of sensitive hearing and notable auditory adaptations to support marine living (see Hanke and Reichmuth, 2022). By comparison, the auditory biology of the otariid (sea lions and fur seals) and odobenid (walrus) carnivore lineages is lesser known and would benefit from further investigation.

The otariid carnivores, or “eared seals,” include 14 living species. Their auditory anatomy is similar to that of terrestrial carnivores but with reduced and rolled pinnae, notable changes in bony structure related to sound conduction in water, and soft tissue adaptations including the presence of cavernous tissue and the thickening of cartilaginous structures to protect the ear during diving (see Nummela, 2008; Repenning, 1972). Otariids rely on sound for orientation, social communication, and threat assessment both in

air and in water (see Charrier, 2021). Most sound production is airborne and occurs on terrestrial haul-outs, but males in particular are known to emit barks and clicks under water (Schusterman and Balliet, 1969).

Terrestrial and aquatic hearing have been studied in three otariid species (see Hanke *et al.*, 2021). Behavioral audiometric data are available for northern fur seals *Callorhinus ursinus* (Babushina *et al.*, 1991; Moore and Schusterman, 1987), California sea lions *Zalophus californianus* (Cunningham *et al.*, 2014a; Kastak and Schusterman, 1998, 2002; Moore and Schusterman, 1987; Mulsow *et al.*, 2011; Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013; Reichmuth and Southall, 2012; Schusterman, 1974; Schusterman *et al.*, 1972; Reichmuth *et al.*, 2017), and Steller sea lions *Eumetopias jubatus* (Kastelein *et al.*, 2005; Mulsow and Reichmuth, 2010). While these species span the extremes of size and phylogenetic distance among otariids, they have similar auditory profiles, suggesting the available measurements are representative of otariids as a group (Mulsow and Reichmuth, 2010). The functional frequency range of hearing (measured at the 60 dB re 20 μ Pa level) is about 0.2–38 kHz in air, with hearing capabilities extending slightly higher in water. The range of best hearing (measured at 20 dB re minimum threshold) occurs from 1 to 23 kHz in air and over an even wider range of 0.35–37 kHz in water. Auditory masking has been evaluated in California sea lions and northern fur seals at frequencies between 0.5 and 32 kHz (Moore and Schusterman, 1987; Southall *et al.*, 2000, 2003). However,

^{a)}Portions of this work were presented at the Effects of Sound in the Ocean on Marine Mammals (ESOMM) Conference in 2022.

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there are inconsistencies between the limited available data and expected frequency-dependent masking patterns for mammalian carnivores.

Odobenid carnivores are represented by only one extant species of walrus, *Odobenus rosmarus*, which has no close living relatives. This species last shared a common ancestor with otariids more than 24×10^6 years ago and is even further removed from the phocid lineage and all other carnivores (Berta *et al.*, 2018; Boessenecker and Churchill, 2018). Compared to otariids—which are found in most temperate oceans in areas of high productivity—walruses have a restricted geographic range limited to the shallow continental shelf areas of Arctic and sub-Arctic seas (Fay, 1982; MacCracken *et al.*, 2017). Walruses lack external pinnae and have small ear openings, as well as significantly enlarged ear drums, middle ear cavities, and ossicles (Kastelein *et al.*, 1996b; Repenning, 1972). While they share some morphological adaptations with phocids, their auditory structures are also similar to those of otariids, leading to a somewhat “intermediate” ear type (see Nummela, 2008; Repenning, 1972). Walruses are among the most vocal of the pinnipeds (the suborder comprising phocid, otariid, and odobenid carnivores). In contrast to other species, they produce a wide range of social sounds in air and under water year round (see Miller and Kochnev, 2021; Mouy and Hannay, 2012), and observations from passive acoustic monitoring suggest they also use underwater sounds in non-social contexts (Mouy and Hannay, 2012).

Understanding of hearing ability in the walrus is limited, with measures of auditory sensitivity available from one adult male Pacific walrus (*Odobenus rosmarus divergens*) tested both under water and in air. This male had a demonstrated hearing range from 0.125 to just 15 kHz in water (Kastelein *et al.*, 2002), with worse sensitivity than both phocids and otariids. The same individual tested with airborne sounds in outdoor conditions exhibited poor sensitivity (>60 dB re 20 μ Pa) from 0.125 to 8 kHz; however, higher frequencies were not tested due to equipment limitations, and the authors report that measurements were likely constrained by environmental noise (Kastelein *et al.*, 1996a). Playback studies with wild Atlantic walruses (*Odobenus rosmarus rosmarus*) on terrestrial haul-outs confirmed responses to tonal stimuli within the same frequency range (Kastelein *et al.*, 1993). More recently, Reichmuth *et al.* (2020) determined that the audible range of terrestrial hearing in walruses extends from at least 0.06 to 23 kHz—broader than previously tested but still narrow in comparison to other carnivores. While a coarse understanding of their auditory biology is emerging, there are no available measures of auditory masking for walruses.

For regulatory and management purposes related to anthropogenic acoustic exposures, odobenids are typically grouped into the same category with otariid carnivores (Finneran, 2015; Southall *et al.*, 2019), along with one mustelid (sea otter, *Enhydra lutris*) and one ursid carnivore (polar bear, *Ursus maritimus*). The separation of these “other marine carnivores” from phocid carnivores is based

mostly upon aspects of auditory biology that set the phocids apart. Exploring finer scale similarities and differences in hearing ability among marine carnivores will address outstanding questions concerning species- and taxa-specific auditory adaptations. Some applied information such as onset thresholds for temporary or permanent hearing loss will be difficult or impossible to gather from multiple species. Other relevant aspects of hearing, such as metrics of auditory masking, can be more readily studied within a comparative framework.

Auditory masking—which occurs when one sound interferes with the detection of another—can be studied in relatively simple conditions (i.e., *without* the need for specialized testing rooms or pools) where a controlled noise background can be generated. Several quantitative studies of masking in marine mammals have addressed the challenges of receiving biologically relevant cues within noisy backgrounds (see Branstetter and Sills, 2022; Erbe *et al.*, 2016). The most fundamental metric of masking, the critical ratio, describes the difference in decibels between the sound pressure level (SPL) of a tonal signal at detection threshold and the power spectral density level of spectrally flat masking noise centered on the tone frequency (Fletcher, 1940; Moore, 1993). These frequency-dependent signal-to-noise ratios describe the level by which a given signal must exceed surrounding noise to be detected by a listener. Critical ratios vary across species with different hearing profiles (Fay, 1988). Significantly, they are independent of the hearing pathway and medium (air or fluid) in which sound is received (see Reichmuth, 2012), allowing for empirically determined critical ratio values to be applied to both environments utilized by amphibious pinnipeds.

Here, we provide measures of hearing and masking for otariid and odobenid subjects trained to listen for airborne tones both in ambient outdoor conditions and within a background of spectrally flat masking noise. Detection thresholds and critical ratios are compared between sea lions and walruses and to data currently available for related species.

II. METHODS

A. Subjects

Audiometric testing was conducted at SeaWorld San Diego (San Diego, CA) and Long Marine Laboratory at the University of California Santa Cruz (Santa Cruz, CA). Subjects were in good health with no known otological problems or prior exposure to ototoxic medications. Odobenid subjects were an adult female and a sub-adult male Pacific walrus identified as *Chou Chou* (11–12 years) and *Mitik* (9 years). Neither had prior experience with audiometry. The otariid subject was an adult female California sea lion identified as *Ronan* (NOA0006602; 13–14 years). This sea lion had participated in several audiometric studies, including measures of in-air and underwater sensitivity as a function of frequency (Reichmuth *et al.*, 2013; Reichmuth *et al.*, 2017), ultrasonic hearing and masking trials (Cunningham and Reichmuth, 2016), and auditory

assessments using complex stimuli (Cunningham *et al.*, 2014a; Cunningham *et al.*, 2014b). Testing for all subjects occurred between May 2021 and December 2022 during three rounds of data collection following intermittent training over the preceding 18 months.

Cooperative behavior for husbandry and research tasks was established using operant conditioning methods and positive reinforcement (fish, clam, or squid). Individual diets were predetermined by veterinary and animal care staff to maintain optimal health and weight. Animal diets were not constrained for research purposes, and subjects were offered their scheduled diet daily regardless of performance during auditory tasks.

In addition to the primary animal subjects, the hearing of one adult male human (21 years) was tested using the same equipment and environment as the sea lion to validate the experimental procedure through comparison to published hearing and masking thresholds (see SuppPub1 in the supplementary material).¹

B. Environment and apparatus

Auditory testing with walrus was conducted outdoors in the Wild Arctic facility at SeaWorld San Diego in a 7 m × 4 m pen adjacent to the primary living enclosure. The floor and two side walls were cement, while the front and back walls were enclosed by metal bars spaced 50 cm apart. The top of the pen was open to the environment but shaded by tarpaulin. The testing apparatus comprised a station marker and response target that were positioned at the bars facing a walkway. The white 15 cm × 15 cm square station was firmly affixed to a metal bar at the height of the center of the subject's head while in a relaxed sitting posture—0.84 m elevation for the female, 1.0 m elevation for the male. A black 15 cm × 15 cm square response target was mounted to another bar 0.5 m to the subject's left side at the same height. The speaker used to project auditory stimuli was affixed on a tripod in the walkway, 1.0 m directly in front of the station and 1.2 m from the center position of the subject's head during testing. The station, response target, and speaker were in the same horizontal plane for each walrus.

The sea lion and human subject were tested in a similar setup at Long Marine Laboratory. Trials were conducted in an outdoor 5 m × 3.5 m holding pen, with two walls of vinyl-coated chain link fencing to the front and left side of the subject and two rigid walls of synthetic high-density polyethylene (HDPE) at the subject's right and rear. The top of the enclosure was covered with shade cloth. Similar to the walrus configuration, a white station and black response target were attached to the fence at the height of the subject's head (0.84 m) in a relaxed position, 50 cm apart. The speaker was positioned in the adjacent walkway 1.0 m in front of the station and 1.2 m from the center position of the subject's head during testing.

In both facilities, the trainer and experimenter were concealed from the subject's view during audiometric

testing. The experimenter was positioned behind a visual barrier, while the trainer stepped behind a nearby blind at the start of each trial. The instrumentation used to generate acoustic stimuli (Sec. II C) was configured within a waterproof case placed behind a barrier and linked to the speaker via a cable. A Hero8 video camera (GoPro, San Mateo, CA) was securely placed in the walkway to record each session.

Ambient noise was measured daily in test-ready conditions with a calibrated, self-powered 2250 sound level meter (sampling rate 48 kHz; Brüel & Kjaer A/S, Naerum, Denmark) with a free-field 1/2-in. type 4966 microphone. The microphone was placed at the center position of the subject's head during testing. Noise power spectral density levels [PSDs; dB re (20 μPa)²/Hz] for frequencies from 0.0125 and 20 kHz were calculated from the median of 1-min, unweighted 1/3-octave band 50th percentile measurements (L50) obtained throughout testing. Noise above 20 kHz was less than 0 dB re 20 μPa, as measured with an MK301 microphone capsule (0.005–100 kHz, ±2 dB; Microtech Gefell GmbH, Gefell, Germany) with a C617 body (Josephson Engineering, Santa Cruz, CA) and BPS-1 power supply (Stewart Electronics, Rancho Cordova, CA) linked to a battery-powered Fostex FR-2 Field Memory Recorder (Fostex Company, Tokyo, Japan).

C. Stimulus generation and calibration

Test frequencies were 0.08, 0.1, 0.2, 0.5, 1, 2, 4, 10, and 16 kHz for the walrus; this range was extended to include 32 kHz for the sea lion based on expected differences in high-frequency hearing limits (Reichmuth *et al.*, 2020; Reichmuth *et al.*, 2017). The human subject was tested at a subset of these frequencies as well as 8 kHz to align with available critical ratio data (e.g., Hawkins and Stevens, 1950). Signals were 1-s pure tones with 50-ms linear ramps generated (1 MHz update rate) from a laptop personal computer (PC) in LabVIEW (NI, Austin, TX) using Hearing Test Program (HTP) software (Finneran, 2003). Signals passed through an NI USB-6251 data acquisition board, a 0.1–250 kHz bandpass active filter module (Krohn-Hite, Brockton, MA), and a two-channel Mix 2:1 passive mixer (Radial Engineering, Vancouver, Canada) before being projected through a KH 80 DSP powered studio monitor with internal amplifier (0.057–21 kHz, ±3 dB; Neumann, Berlin, Germany). The filter module was bypassed to enable testing at low frequencies (0.08 and 0.1 kHz). For testing at 32 kHz, filtered signals were mixed using a TDT signal ladder (Tucker-Davis Technologies, Alachua, FL) before passing through an NX1000 two-channel power amplifier (Behringer, Illich, Germany) and were projected through a Vifa ultrasonic dynamic speaker (Avisoft Bioacoustics, Glienicke/Nordbahn, Germany).

To confirm a stable received sound field, audiometric signals at each test frequency were spatially mapped within a 3 cm × 3 cm × 3 cm area surrounding (and including) the position of each ear. Maximum variability in received SPL (dB re 20 μPa) relative to ear position was ±2 dB.

Test signals were calibrated before each session at the right or left ear position, whichever was associated with the greater received level during sound field mapping. Signals were inspected as waveforms and spectrograms at a range of amplitudes to confirm the absence of artifacts. Spectra of the signals used for audiometry are provided in SuppPub2.¹ During mapping and calibration between 0.08 and 16 kHz, signals were received by the 2250 sound level meter and 4966 microphone and passed through the same NI USB data acquisition board used for signal generation before being measured in HTP software. At 32 kHz, signals were received by the Microtech Gefell MK301 microphone capsule with the Josephson C617 body and Stewart BPS-1 power supply and passed through the same data acquisition hardware and software used for the lower frequencies.

Masking stimuli were continuous, octave-wide bands of Gaussian (white) noise centered at each test frequency from 0.1 to 10 kHz for walrus and from 0.2 to 32 kHz for the sea lion. Masking noise was generated and spectrally flattened in the testing environment prior to each session using a custom LabVIEW virtual instrument, which compensated for the frequency response of the outgoing equipment chain and environment. During testing, masking noise was sent from the computer sound card using Audacity® software (version 3.0.0), mixed with the signal at the passive mixer, and projected through the same Neumann KH 80 speaker. For testing at 32 kHz, masking noise and filtered signals were mixed using the TDT signal ladder before passing through the NX1000 two-channel power amplifier and being projected through the ultrasonic Vifa speaker.

Masks were spatially mapped across the same grid described previously, with maximum variability in octave-band SPL relative to ear position of ± 2 dB. Masking noise was calibrated before each session to ensure that the noise was spectrally flat, with the SPL of each 1/3-octave band within 1 dB of the center band and center band SPL within 1 dB of target level. Spectra of maskers used for audiometry are provided in SuppPub2.¹ To ensure appropriate masking conditions at each frequency, the target PSD of the masking noise was set either equal to or 5 dB above the SPL of the corresponding ambient threshold value. This masker level always exceeded the ambient noise in the surrounding 1/3-octave band. The same incoming equipment chain was used for mapping and calibration of masking stimuli as for the pure-tone signals, along with the LabVIEW virtual instrument used for generating masking noise.

D. Audiometry

Audiometric protocols were the same for all subjects. The auditory task consisted of both signal-present and signal-absent trials in a go/no-go signal detection paradigm (Stebbins, 1970) similar to that used in previous behavioral studies of walrus hearing (Kastelein *et al.*, 2002; Kastelein *et al.*, 1996a; Reichmuth *et al.*, 2020). For each trial, correct responses (remaining still at the station when no signal was presented or touching the response target when a signal was

presented) were marked with a conditioned acoustic reinforcer (a verbal “OK” or whistle bridge) followed by a food reward delivered near the station. Correct responses to signal-present and signal-absent trials were reinforced equally. Incorrect responses (misses on signal-present trials and false detections on signal-absent trials) were not reinforced, and the subject was re-prompted to the station before moving on to the next trial.

During each session, signal frequency was held constant while signal amplitude was varied based on subject performance using an adaptive staircase method (Stebbins, 1970). The first signal-present trial in a session contained an easily detectable signal, after which amplitude was decreased by 2–4 dB following each correct detection until the first miss. Signal amplitude was then increased by 6 dB after each miss and decreased by 2 dB after each correct detection until 3–8 descending (hit-to-miss) transitions were obtained. The larger ascending step size minimized consecutive errors, while the smaller descending step size enabled precise determination of hit-to-miss transitions. The session ended with several easily detectable signals following the last miss to maintain stimulus control on the task.

Within a session, signal-present and signal-absent trials were presented in a predetermined, pseudorandom order at a ratio of 70:30. The interval of each trial was 6 s, during which signal onset could be varied. Approximately 40 trials were conducted per session, depending on the subject’s motivation. Subjects participated in 1–2 sessions per day with the duration of each session kept within the optimal attention span of each subject and without exceeding 15 min. False alarm rates were determined for each session as the proportion of false detections on signal-absent trials.

E. Ambient hearing thresholds

Data collection at each frequency began by measuring hearing thresholds in the ambient conditions of the testing environment, with frequencies tested to completion in a shuffled order. Ambient hearing thresholds were collected over 2–3 sessions and calculated from 9–15 consecutive, stable (standard deviation < 3 dB) hit-to-miss transitions. Thresholds were estimated as the average of these hit-to-miss transitions.

F. Masked hearing thresholds and critical ratios

Masked hearing thresholds were measured at each frequency following threshold measurements in ambient conditions. Masking noise was played throughout the session to establish a uniform, artificial noise floor; auditory fatigue during a session was not expected due to the relatively low masking noise levels used (Yost, 2000). Testing was conducted using the same method described for ambient thresholds. Masked thresholds were determined from 15 stable (standard deviation < 2 dB) hit-to-miss transitions obtained over 2–4 consecutive sessions. Critical ratios for each frequency were calculated as the difference (in dB) between

the SPL of the masked hearing threshold and the mean PSD level of the octave-band masker.

After data collection was completed, critical ratios were added to corresponding noise spectral density levels measured during ambient threshold testing. This provided an estimate of the lowest threshold that could be measured at each frequency in this testing environment (Kastelein *et al.*, 2005). These theoretical lowest thresholds were compared to ambient threshold measurements to evaluate whether the measured hearing thresholds were constrained by environmental noise.

III. RESULTS

A. Ambient noise conditions

Ambient noise levels in both outdoor testing environments were highest at low frequencies and declined with increasing frequency, as expected (Table I and Fig. 1). At SeaWorld San Diego, ambient noise spectral density levels ranged from 47 dB re $(20 \mu\text{Pa})^2/\text{Hz}$ at 0.08 kHz to $-10 \text{ dB re } (20 \mu\text{Pa})^2/\text{Hz}$ at 16 kHz. At Long Marine Laboratory, outdoor noise levels ranged from 33 dB re $(20 \mu\text{Pa})^2/\text{Hz}$ at 0.08 kHz to $-24 \text{ dB re } (20 \mu\text{Pa})^2/\text{Hz}$ or less at and above 16 kHz. Ambient noise conditions were, on average, 15 dB

lower at Long Marine Laboratory compared to SeaWorld San Diego.

B. Ambient hearing thresholds

Ambient hearing thresholds for walruses were collected at nine frequencies from 0.08 to 16 kHz (Table I and Fig. 1, upper panel). These were similar (within 4 dB) for both individuals at the five common test frequencies. Best sensitivity (lowest threshold) was 35 dB re $20 \mu\text{Pa}$ at 10 kHz. Below 10 kHz, ambient thresholds increased gradually to 74 dB re $20 \mu\text{Pa}$ at 0.08 kHz. The high-frequency roll-off was effectively captured for both subjects above 10 kHz, where sensitivity declined by approximately 15 dB within a half-octave. Hearing thresholds were 57 and 53 dB re $20 \mu\text{Pa}$ for the two subjects at 16 kHz, just below the nominal high-frequency hearing limit of 60 dB [as defined by Heffner and Heffner (2008)]. False alarm rates were similar across subjects and frequencies: 0.16 (range: 0.06–0.24) for female *Chou Chou* and 0.20 (range: 0.18–0.27) for male *Mitik*. Threshold-to-noise offsets—measured as the difference between hearing threshold and ambient noise at each frequency—varied between 16 and 34 dB, except at 16 kHz, where the offset was 63 dB. Walrus ambient thresholds were consistent with previously reported detection thresholds for the species

TABLE I. Ambient hearing thresholds for airborne tones for two Pacific walruses (*Chou Chou* and *Mitik*) and one California sea lion (*Ronan*), along with corresponding false alarm rates and noise levels in the outdoor testing environment. Detection thresholds at each frequency were calculated as the average of the hit-to-miss transitions. (Note: Initial ambient threshold measurements at 4 kHz were unexpectedly high for both walrus subjects. Testing at this frequency was repeated for both subjects after the completion of primary data collection.) False alarm rates were calculated as the proportion of responses on signal-absent trials (>25 trials per frequency). Ambient noise levels in the 1/3-octave band surrounding the test frequency were measured prior to each session and are presented as median (50th percentile) spectral density levels.

Species	Subject	Tone frequency (kHz)	Test order	Ambient noise [dB re $(20 \mu\text{Pa})^2/\text{Hz}$]	Outdoor ambient threshold (dB re $20 \mu\text{Pa}$)	Standard deviation	Hit-to-miss transitions (n)	False alarm rate	Threshold-to-noise offset (dB)
Pacific walrus	<i>Chou Chou</i>	0.08	9	48	74	1.7	15	0.21	26
		0.1	8	41	65	2.0	15	0.22	24
		0.2	3	40	62	3.0	10	0.24	22
		0.5	5	31	47	1.5	10	0.18	16
		1	2	26	48	1.4	9	0.22	22
		2	7	20	47	1.0	12	0.06	27
		4	4	14	43	1.5	10	0.19	29
	<i>Mitik</i>	10	1	3	37	1.2	9	0.06	34
		16	6	-6	57	1.3	10	0.10	63
		0.5	2	31	51	1.2	13	0.27	20
		2	4	20	48	1.0	10	0.15	28
		4	1	14	45	1.3	12	0.18	31
		10	5	3	35	1.3	10	0.21	32
		16	3	-6	53	1.2	15	0.23	59
California sea lion	<i>Ronan</i>	0.08	10	33	83	1.3	15	0.19	50
		0.1	7	32	79	2.1	15	0.25	47
		0.2	3	27	62	2.7	15	0.13	35
		0.5	6	17	46	0.9	15	0.07	29
		1	2	12	38	2.5	15	0.08	26
		2	8	8	32	1.8	15	0.12	24
		4	4	1	24	1.2	15	0.22	23
		10	1	-15	9	2.0	15	0.13	24
		16	5	-24	4	1.3	15	0.13	28
		32	9	<0	47	1.3	15	0.11	>47

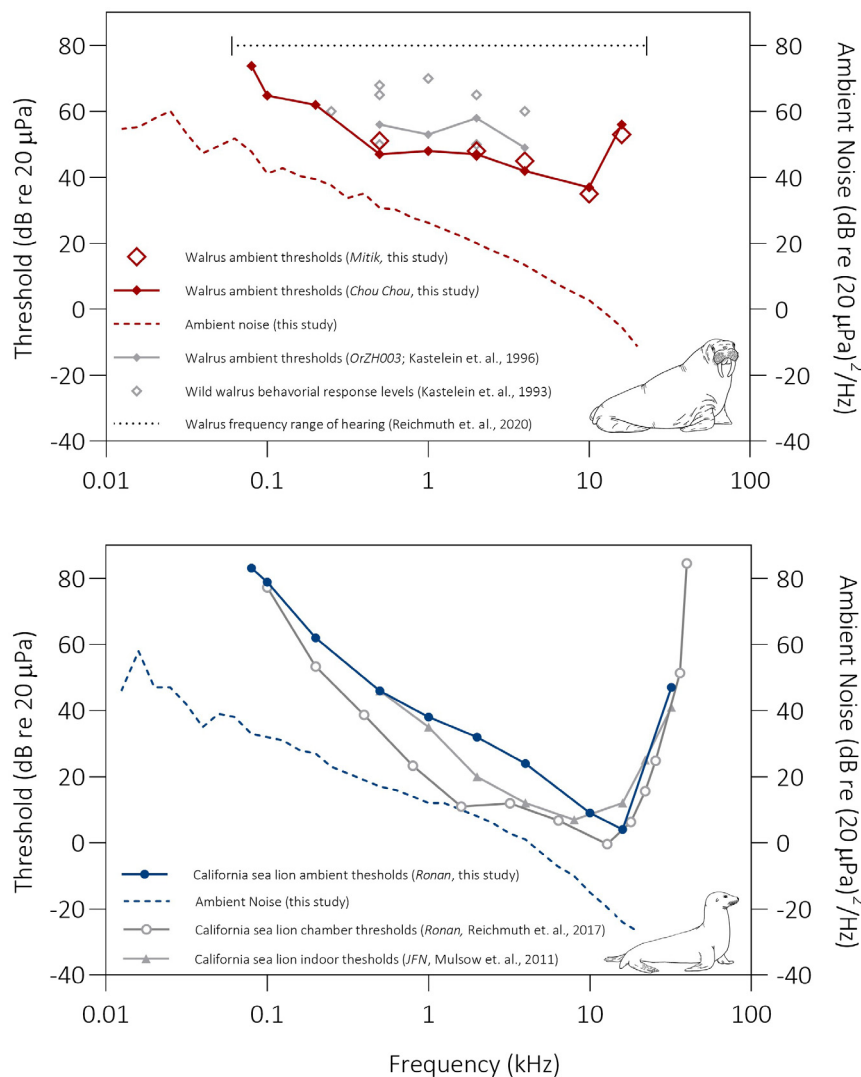


FIG. 1. (Color online) Ambient hearing thresholds are shown for two Pacific walrus (*Chou Chou* and *Mitik*, upper panel) and one California sea lion (*Ronan*, lower panel) for frequencies between 0.08 and 16 kHz or 32 kHz, respectively. Associated median noise levels (L50) are plotted as dashed lines corresponding to the right-hand y-axes. For comparison to the walrus data, ambient thresholds collected previously with a single adult male walrus (Kastelein *et al.*, 1996a), behavioral response measurements with wild walruses (Kastelein *et al.*, 1993; $n = 5$), and the frequency range of hearing for two adult female walruses at 80 dB (Reichmuth *et al.*, 2020; $n = 2$) are provided. For comparison to the sea lion data, absolute (unmasked) thresholds measured in a hemi-anechoic chamber are shown for the same sea lion subject (Reichmuth *et al.*, 2017), along with data collected with another individual in a controlled environment (Mulsow *et al.*, 2011).

(Kastelein *et al.*, 1996a); the low- and high-frequency roll-offs also aligned with a prior estimate of hearing range (Reichmuth *et al.*, 2020).

Ambient hearing thresholds for the California sea lion were collected at ten frequencies from 0.08 to 32 kHz (Table I and Fig. 1, lower panel). Consistent with a prior evaluation of this subject’s absolute hearing (Reichmuth *et al.*, 2017), the sea lion showed best sensitivity at 16 kHz, with a lowest measured threshold of 4 dB re 20 µPa. Low-frequency sensitivity rolled off to 83 dB re 20 µPa at 0.08 kHz, while high-frequency sensitivity declined by 43 dB over one octave, to 47 dB re 20 µPa at 32 kHz. Offsets between measured thresholds and associated ambient noise ranged from 23 to 50 dB and were greatest at the lowest and highest frequencies tested. The sea lion’s mean false alarm rate across all frequencies was 0.12 (range: 0.07–0.25), similar to that of the two walrus subjects.

C. Masked thresholds and critical ratios

Walrus critical ratios were calculated from masked thresholds at frequencies from 0.2 to 10 kHz (Table II and Fig. 2). Masked thresholds were not measured at 0.08, 0.1, or

16 kHz, as the required stimulus levels (based on ambient thresholds) exceeded the capabilities of the equipment. Critical ratios generally increased with increasing frequency from 17 dB at 0.5 kHz to 32 dB at 10 kHz. There was a slight upward inflection at 0.2 kHz with a critical ratio of 20 dB. At the four frequencies where both individuals were tested, critical ratios were within 2 dB of one another. False alarm rates were again similar: 0.23 (range: 0.20–0.29) for the female *Chou Chou* and 0.21 (range: 0.17–0.24) for the male *Mitik*.

Critical ratios for the sea lion were evaluated at frequencies from 0.2 to 32 kHz. Masked thresholds at 0.08 and 0.1 kHz could not be measured. The critical ratios ranged from 18 at 0.2 kHz to 34 dB at 32 kHz (Table II and Fig. 2). The linearity of the observed trend (i.e., in dB with the logarithm of frequency) is notable. The mean false alarm rate for the sea lion was 0.14 (range: 0.06–0.23).

Critical ratios for both species were similar and showed a predictable increase in about 3 dB per octave with increasing frequency (Fig. 2). While there are no comparable data available for odobenid carnivores, these values are consistent with those previously reported for otariids at frequencies below 2 kHz (Southall *et al.*, 2003, 2000).

TABLE II. Masked in-air hearing thresholds and critical ratios for two Pacific walrus (*Chou Chou* and *Mitik*) and one California sea lion (*Ronan*), shown with false alarm rates and spectral density levels for flat-spectrum, octave-band masking noise. Masker spectral density level for each frequency was set at or +5 dB above the corresponding ambient threshold for each subject. [Note: The masking noise target spectral density level at 4 kHz was set based on initial (unexpectedly high) ambient threshold measurements for walrus *Chou Chou* and was, therefore, 14 dB higher than the reported ambient threshold. This masker level should not influence the corresponding critical ratio value.] Masked thresholds were calculated as the average of the hit-to-miss transitions. False alarm rates were calculated as the proportion of responses on signal-absent trials (>37 trials per frequency).

Species	Subject	Tone frequency (kHz)	Test order	Masker level [dB re (20 μPa) ² /Hz]	Masked threshold (dB re 20 μPa)	Standard deviation	Hit-to-miss transitions (n)	False alarm rate	Critical ratio (dB)
Pacific walrus	<i>Chou Chou</i>	0.2	3	62	82	1.5	15	0.26	20
		0.5	5	52	69	1.5	15	0.20	17
		1	2	48	66	1.7	15	0.21	19
		2	6	47	71	1.5	15	0.21	25
		4	4	57	87	1.4	15	0.29	30
	<i>Mitik</i>	10	1	37	69	2.0	15	0.24	32
		0.5	2	56	73	1.4	15	0.17	17
		2	3	48	74	1.0	15	0.22	26
		4	1	45	86	1.5	15	0.22	29
		10	4	35	65	1.5	15	0.24	30
California sea lion	<i>Ronan</i>	0.2	3	62	80	0.9	15	0.14	18
		0.5	6	52	72	1.8	15	0.13	20
		1	2	38	60	1.6	15	0.19	23
		2	7	38	66	1.7	15	0.09	28
		4	4	24	53	1.8	15	0.18	28
		10	1	9	37	1.3	15	0.23	28
		16	5	9	42	1.3	15	0.14	33
32	8	46	80	1.0	15	0.06	34		

Critical ratios were higher than existing data for otariids at frequencies above 2 kHz (Moore and Schusterman, 1987; Southall et al., 2003). Validation data obtained for the human subject in the same test conditions generated frequency-dependent critical ratios (SuppPub1)¹ that were within a few dB of most previously published values (Hawkins and Stevens, 1950; Hienz and Sachs, 1987; Houtsma, 2005). Therefore, the results obtained in this masking study can be considered comparable to those obtained in traditional auditory testing conditions.

D. Theoretical lowest threshold values

Ambient thresholds that were likely constrained by environmental noise were revealed through *post hoc*

comparison to theoretical lowest threshold values (Fig. 3). For walrus, ambient thresholds at frequencies from 0.08 to 10 kHz were similar to the corresponding theoretical values, suggesting that measured thresholds in this range were masked by background noise. At 16 kHz, ambient thresholds for both walrus subjects were well above theoretical lowest values, indicating that these were valid measurements of absolute hearing sensitivity. For the sea lion, ambient hearing thresholds from 1 to 16 kHz were similar to theoretical lowest values. At lower and higher frequencies, ambient thresholds exceeded theoretical lowest thresholds and were not influenced by ambient noise. For the human subject, measured thresholds <8 kHz were masked in outdoor ambient conditions based on comparison to theoretical lowest threshold values.

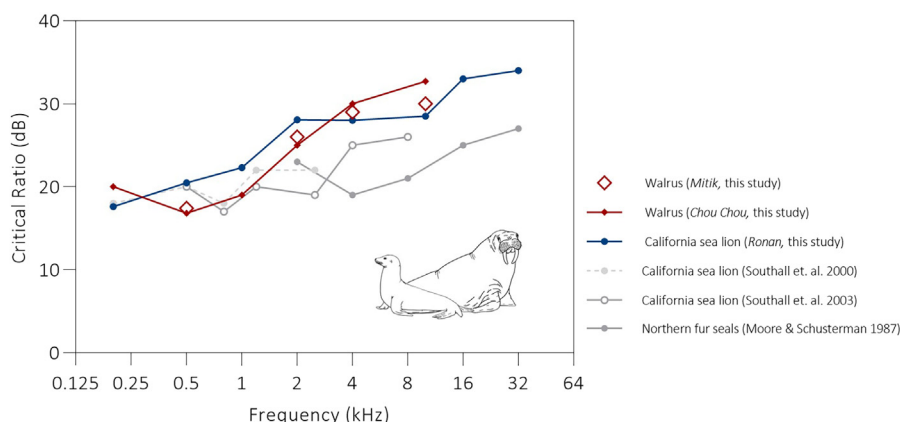


FIG. 2. (Color online) Auditory critical ratios measured in air for two Pacific walrus (*Chou Chou* and *Mitik*) and one California sea lion (*Ronan*) for frequencies between 0.2 and 10 kHz or 32 kHz, respectively. Also shown are critical ratios reported previously for otariids: California sea lions [Southall et al. (2000), n = 1; Southall et al. (2003), n = 1] and northern fur seals [Moore and Schusterman (1987), n = 2].

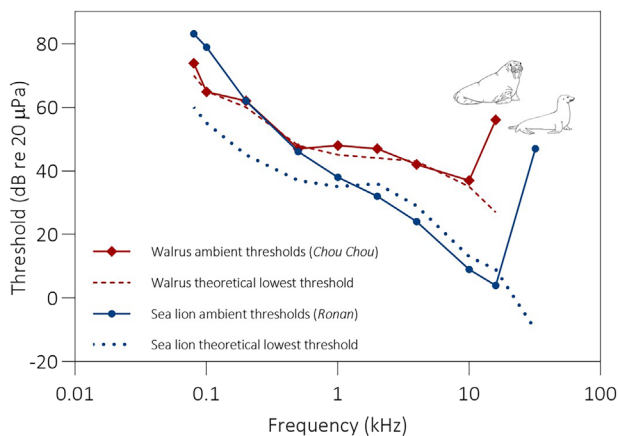


FIG. 3. (Color online) Ambient hearing thresholds are shown for Pacific walrus *Chou Chou* and California sea lion *Ronan* for frequencies between 0.08 and 16 kHz or 32 kHz, respectively. Theoretical lowest thresholds calculated by adding the ambient noise spectral density level to the critical ratio measured at each test frequency are shown as dotted or dashed lines. Theoretical lowest thresholds at 0.1 and 0.08 were estimated by extrapolation from critical ratio data collected at higher frequencies. Thresholds that fall above their corresponding dashed lines are more likely to reflect absolute hearing sensitivity; those that fall near or below the dotted line are likely constrained by background noise.

IV. DISCUSSION

A. Hearing in ambient conditions

Auditory thresholds were measured with a California sea lion in ambient outdoor conditions to provide information for subsequent masking experiments. These ambient thresholds followed expected trends in sensitivity across the frequency range of hearing. Thresholds were elevated at some frequencies relative to those previously measured for the same subject in the quiet conditions of a hemi-anechoic chamber (Reichmuth *et al.*, 2017) and those obtained for another sea lion tested using headphones in semi-controlled conditions (Mulsow *et al.*, 2011). Comparison of these datasets indicates that background noise in the outdoor testing environment predictably constrained hearing thresholds in this study from 0.5 to 10 kHz. There was near-perfect correspondence between the thresholds reported here and those measured for the same individual in quiet conditions at 0.1 kHz (the lowest frequency previously tested), 16 kHz (in the range of best hearing), and 32 kHz (the highest frequency tested). Hearing at 32 kHz was also similar to that measured by Mulsow *et al.* (2011). While no comparative auditory data were available below 0.1 kHz, the measured threshold of 83 dB re 20 μ Pa at 0.08 kHz follows this subject's previously reported low-frequency roll-off (Reichmuth *et al.*, 2017).

Post hoc evaluation of theoretical lowest thresholds derived from ambient noise and critical ratios confirmed that hearing thresholds for the sea lion from 0.5 to 10 kHz were masked, while hearing thresholds at 0.08, 0.1, 0.2, and 32 kHz were absolute (unmasked) measures of hearing. The lowest ambient threshold of 4 dB re 20 μ Pa at 16 kHz was near the theoretical limit but is assumed to be an absolute

measure of hearing given the direct agreement with data for the same subject in quiet conditions (Reichmuth *et al.*, 2017). These absolute and masked auditory thresholds conform to available and predicted data for this individual and for this better-studied species, validating the behavioral audiometric approach taken here. Thus, findings for the California sea lion increase confidence in the interpretation of hearing and masking data collected using the same methods for the walruses in this study.

Ambient threshold data for walruses collected in outdoor conditions are consistent with the few available auditory data reported for trained (Kastelein *et al.*, 1996a) and free-ranging walruses (Kastelein *et al.*, 1993). The better sensitivity values measured for the individuals in this study may be attributable to methodological differences or lower background noise levels. Even so, based on comparison to theoretical lowest thresholds, ambient thresholds for the walruses in the present study were constrained by background noise at all frequencies except 16 kHz. Thus, walrus absolute hearing thresholds at and below 10 kHz are expected to be lower than the values reported here. Thresholds at 16 kHz are well above the noise and are unmasked, capturing the high-frequency roll-off in auditory sensitivity for these individuals. The apparently poor high-frequency hearing ability of these walruses is consistent with findings from Reichmuth *et al.* (2020) and Kastelein *et al.* (2002) that suggest an upper-frequency limit of hearing near 20 kHz in air and water for this species. This corresponds well with their bandwidth of aerial sound production (from 0.2 to at least 20 kHz) (Charrier *et al.*, 2010; Miller, 1985). The upper-frequency limit for walruses is lower than for phocid and otariid pinnipeds, as well as terrestrial carnivores that hear up to at least 30 kHz (Fay, 1988; Heffner and Heffner, 2008; Reichmuth *et al.*, 2013). Anatomical studies confirm adaptations, such as hypertrophy of the ossicular bones and a large interaural distance (Kastelein *et al.*, 1996b; Nummela, 2008), that may constrain high-frequency hearing ability and potentially improve hearing at lower frequencies in odobenids. In fact, despite background noise being higher in the walrus testing environment, walrus ambient thresholds were 9 dB lower than the sea lion's absolute threshold at 0.08 kHz and 14 dB lower at 0.1 kHz. Given that walrus hearing thresholds were noise limited below 16 kHz, it is possible that their true low-frequency hearing ability is even better than described here.

For all three subjects, elevated ambient thresholds at most frequencies highlight the necessity of using specialized, sound-attenuating facilities to fully characterize absolute hearing sensitivity. Such quiet conditions, however, are not required to effectively evaluate auditory masking.

B. Hearing in noise

Reliable masked hearing measurements were obtained in ambient outdoor conditions by artificially elevating and flattening the noise floor over which audiometric signals were presented. This made it possible to evaluate walrus

hearing in a zoological facility without a specialized environment for audiometric testing. This approach was validated with critical ratios collected for a person under the same conditions that were consistent with data previously reported for human subjects (as shown in SuppPub1).¹

The ability to detect signals in noise was similar for the sea lion and walrus subjects despite demonstrated differences in hearing sensitivity. Critical ratio values for both species were comparable to or higher than available data for otariids (Moore and Schusterman, 1987; Southall *et al.*, 2003, 2000). Several factors may help to reconcile these observed differences (highlighted in Fig. 2). In the current study, critical ratios were obtained using equalized, spectrally flattened white noise floors that exceeded environmental noise, which minimized variability within the octave band surrounding the test frequency. The equalization procedure precisely controlled the spectral “flatness” of the masker, likely to a greater degree than in previous studies. While the present study used continuous rather than intermittent masking noise, there was no evidence of auditory fatigue or loudness adaptation based on within-session performance. The masking stimuli were set equal to or just above ambient threshold values, allowing signals to be presented at lower levels than in many other studies. Often, critical ratios are measured in the presence of noise that exceeds the subject’s ambient or unmasked detection threshold by 10–20 dB (e.g., Holt and Schusterman, 2007; Reichmuth *et al.*, 2013; Southall *et al.*, 2003). The relatively quieter masker levels used in the present study ensured that audiometric signals were also of lower amplitude and minimized potential amplitude-related artifacts, such as transient harmonics or spectral splatter, that could result in artificially low masked thresholds. Finally, the present datasets extended across a wider frequency range than previously available, including lower frequencies (<0.5 kHz), which more definitively revealed trends for critical ratios as a function of frequency.

Sea lion and walrus critical ratios were generally comparable to those of terrestrial carnivores (Fay, 1988). Good agreement across mammalian carnivores of differing sizes and evolutionary relatedness suggests that many have evolved similarly in terms of their ability to extract signals from noise—despite species differences in absolute hearing sensitivity. One exception may be the phocid seals, which typically have lower critical ratios than other pinnipeds (Branstetter and Sills, 2022; Erbe *et al.*, 2016; Reichmuth, 2012), indicating that they may be better adapted to hearing in noisy environments.

C. Applications to predicting noise effects

Psychoacoustic measures of auditory masking are often based on detection of pure-tone stimuli in the presence of band limited white noise, which is not necessarily representative of *in situ* listening scenarios. While this caveat remains true in the present study, theoretical lowest threshold calculations approximated ambient detection thresholds

for all three subjects listening in the complex noise conditions of their respective outdoor testing environments. In practice, critical ratios paired with ambient noise measurements likely provide a more accurate representation of hearing than absolute threshold measurements, because noise in most natural environments is usually high enough to influence hearing (Dooling and Blumenrath, 2013). Thus, masking parameters are particularly useful for understanding hearing in the real world. If ambient noise levels exceed absolute detection thresholds in a given environment—as they did at most frequencies in both test facilities used in this study—hearing thresholds can be determined based on noise measurements and critical ratios alone. In such sufficiently noisy environments, the observed agreement between walrus and sea lion critical ratio values results in similar predicted thresholds for both species—despite differences in their unmasked hearing abilities. Further, as auditory masking is a cochlear phenomenon (at least in terms of the energetic masking tested here), it is independent of hearing pathway and medium (see Reichmuth, 2012; Erbe *et al.*, 2016; Branstetter and Sills, 2022). As a result, critical ratios of amphibious marine mammals are the same in air and water, despite individual differences in absolute sensitivity between the two media (Renouf, 1980; Reichmuth *et al.*, 2017; Southall *et al.*, 2003; Turnbull and Terhune, 1990). The masking data provided in this study can therefore be applied to estimate listening space, communication ranges, and zones of influence around human-generated noise sources in both aerial and underwater environments.

Using critical ratios paired with ambient noise measurements to predict what an individual can hear in a particular environment is effective when applied to relatively stable noise backgrounds. However, this approach may overestimate the extent of masking when noise is spectrally complex, temporally structured, or highly variable (e.g., Branstetter and Sills, 2022; Erbe *et al.*, 2016; Langemann *et al.*, 1998). Empirical masking studies using complex signals in the presence of non-Gaussian noise can be used to better predict detection thresholds for animals operating in time-varying natural environments (see Branstetter *et al.*, 2013; Cunningham *et al.*, 2014b). Masking predictions can be further enhanced through the measurement of the critical bandwidth (Fletcher, 1940) at which masking occurs and an improved understanding of the effects of noise level on auditory masking.

D. Conclusions

Among marine mammals, walruses have been understudied from the standpoint of hearing and noise. The present study includes confirmation of enhanced low-frequency hearing and constrained/limited high-frequency hearing in air and provides critical ratio measurements applicable in air or water across most of the hearing range. It is apparent that an absolute (completely unmasked) in-air audiogram for walruses would require testing in an acoustically controlled, artificially quiet environment. However, the present method

of estimating critical ratios in outdoor conditions—validated through testing of human and sea lion subjects—can be applied to obtain masking data from species such as the walrus that cannot easily be tested in ideal conditions. As marine mammal hearing is often limited by ambient noise in nature, both in air and under water, a robust understanding of auditory masking is a conservation priority.

Despite apparent differences in hearing ability, odobenid and otariid carnivores are similarly able to detect signals within sufficiently noisy conditions. Overall, placing these taxa within the same functional hearing group is a pragmatic, conservative management approach. However, additional protection may be warranted for walruses at low frequencies, where most anthropogenic noise occurs.

ACKNOWLEDGMENTS

Funding was provided by the U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), and U.S. Navy’s Living Marine Resources Program. We are grateful to Dr. Joel Garlich-Miller (USFWS), Dr. Chadwick Jay and Dr. Anthony Fischbach (USGS Alaska Science Center Walrus Research Program), and Dr. Anu Kumar and Mandy Shoemaker [Living Marine Resources (LMR)] for their support. Access to walrus subjects was made possible through in-kind support from SeaWorld San Diego and through initial coordination by the Walrus Conservation Consortium. This work would not have been possible without the involvement of the dedicated animal care and training teams at Sea World San Diego and Long Marine Laboratory. We particularly thank John Stewart, Bill Hoffman, Keleigh Owens, Denise Higginbotham, Jeni Smith, Nick Northcraft, Cathy Stull, and Dr. Todd Schmitt from SeaWorld and Jenna Sullivan, Dr. Caroline Casey, Sarah Santich, Madilyn Pardini, Noah Packard, Sebastian Caamaño, and Shannon Stoll from Long Marine Laboratory. Software used to carry out hearing tests and to generate masking noise was provided by Dr. James Finneran (U.S. Navy Marine Mammal Program). We thank Dr. Brian Branstetter and two reviewers for helpful comments on this manuscript. This is SeaWorld Parks and Entertainment technical contribution number 2023-2. The authors have no conflicts of interest to disclose. Federal permission for access to the walruses was granted under public display authorization to SeaWorld San Diego by the USFWS. Auditory trials were conducted with the approval of the Animal Welfare Committee at SeaWorld San Diego. Federal authorization for sea lion research was granted by the U.S. National Marine Fisheries Service under marine mammal research permits 18902 and 23554. Animal research at both facilities was conducted with approval and oversight by the Institutional Animal Care and Use Committee at the University of California Santa Cruz. The participation of the undergraduate student volunteer in auditory trials met the ethical criteria specified in the Belmont Report (1978). The data that support the findings of this study are available from the corresponding author upon reasonable request.

¹See supplementary material at <https://doi.org/10.1121/10.0020911> for validation masking data with a human subject (SuppPub1) and spectra of the signals and maskers used for audiometry (SuppPub2).

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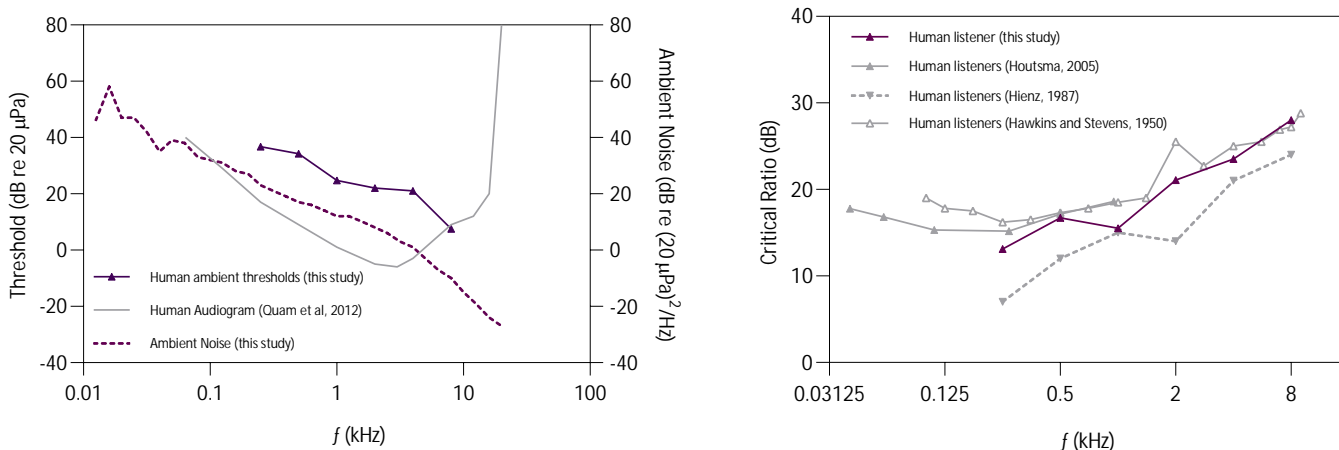
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Supplement 1. Comparative ambient hearing thresholds and critical ratio data for a human subject



The hearing capabilities of one adult male human subject were measured to validate the audiometric procedure used in this study. The undergraduate student volunteer was tested with the same equipment and psychophysical methods as those applied with the walrus and California sea lion subjects, and in the same outdoor testing environment that was used for the sea lion at Long Marine Laboratory in Santa Cruz, California. The subject was 21 years old with apparently normal hearing. His participation met the ethical criteria specified in the Belmont Report.

Panel A. Ambient hearing thresholds are provided for the human subject, along with a composite human audiogram measured in an acoustic chamber. Auditory data are shown on the left y-axis and corresponding background noise levels from the present study are shown on the right y-axis. The subject's ambient hearing thresholds were largely constrained by environmental noise in the outdoor testing facility. The threshold measured at 8 kHz was consistent with published data collected in a quiet environment and likely reflects absolute hearing sensitivity. Thresholds at 0.25, 0.5, 1, and 4 kHz were approximately one critical ratio above the ambient noise, and thus are assumed to be masked.

Panel B. Auditory critical ratios for the human subject. Masked thresholds were measured outdoors at 0.25, 0.5, 1, 2, 4, and 8 kHz in the presence of octave-band, spectrally flat noise set 5 dB above the corresponding ambient hearing threshold. Critical ratios were calculated as the difference between the SPL of the masked threshold and the PSD of the masking noise. Critical ratio values were 13, 17, 15, 21, 23, and 28 dB at the ascending target frequencies. Critical ratios increased predictably with frequency and were consistent with data published for other human subjects. The consistency between the critical ratio data collected here and critical ratio values published previously for human subjects validate the experimental approach taken in this study. These findings confirm that accurate measures of auditory masking in outdoor facilities are possible with calibrated and spectrally-flattened masking stimuli that exceed the ambient noise background.

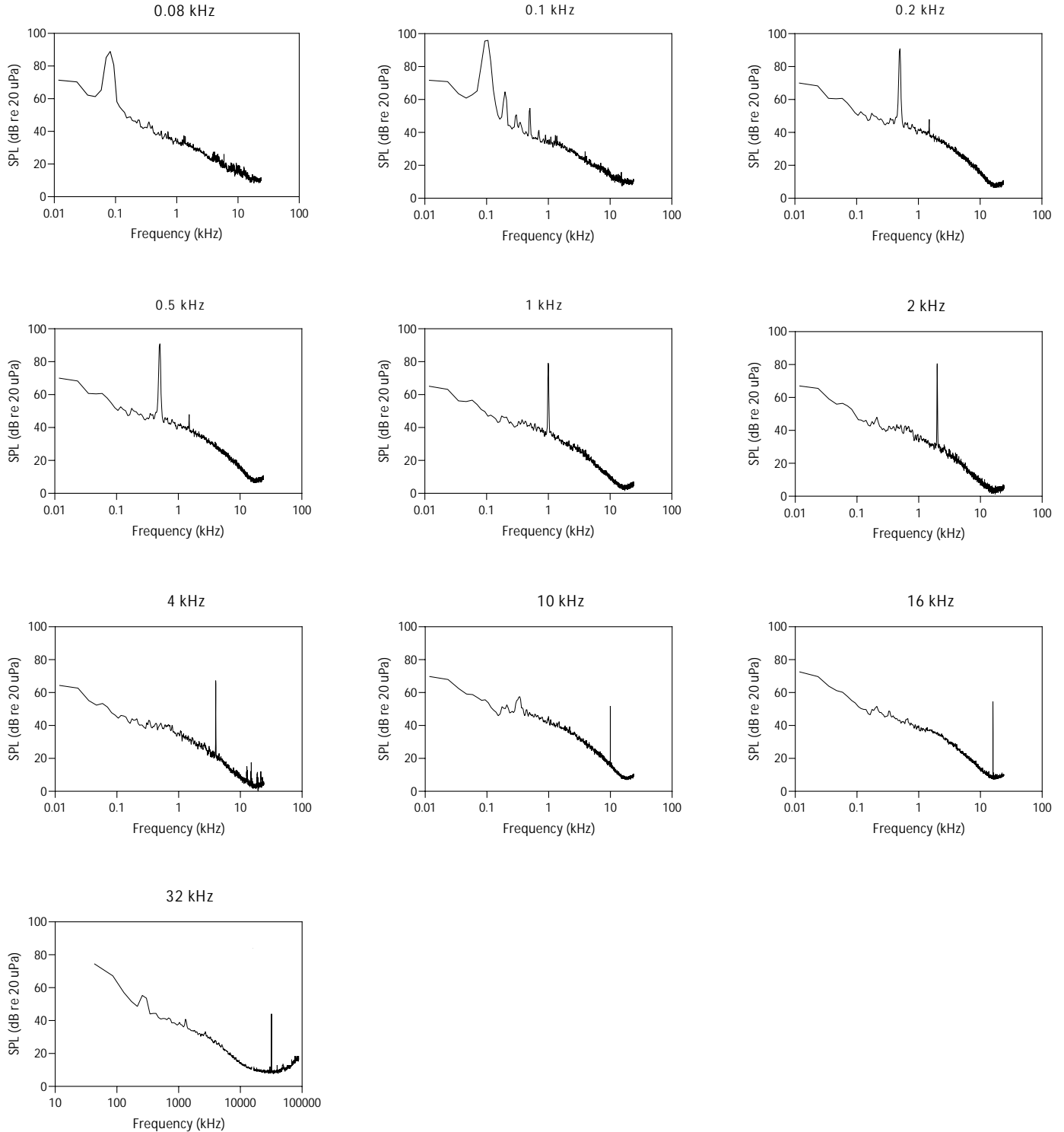
¹Quam, R., Ramsier, M., Fay, R., and Popper, A. (2017). Primate Hearing and Communication, Vol. 63, 141–174 pages. doi: 10.1007/978-3-319-59478-1

²Hawkins, T. E., and Stevens, S. S. (1950). "The Masking of Pure Tones and of Speech by White Noise," *J. Acoust. Soc. Am.*, 22, 6–13. doi:10.1121/1.1906581

³Hienz, R. D., and Sachs, M. B. (1987). "Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*)," *J. Comp. Psychol.*, 101, 16–24. doi:10.1037/0735-7036.101.1.16

⁴Houtsma, A. J. M. (2005). "A note on pure-tone masking by broadband noise under free-field and insert-phone conditions (L)," *J. Acoust. Soc. Am.*, 117, 490–491. doi:10.1121/1.1841611

Supplement 2a. Representative spectra of tonal signals used in audiometry. Signals were recorded at the calibration position in the absence of the subject at a sampling rate of 48 kHz (signals ≤ 16 kHz) or 96 kHz (32 kHz) as described in the methods. Calibration levels exceeded ambient thresholds by about 20 dB at each test frequency. These plots illustrate a ‘worst case’ scenario for signal quality for lower amplitude signals (near threshold). Spectra are plotted from .wav recordings encompassing the complete 1-s signal using a hamming window and an FFT size of 4096. Signals are shown within the ambient noise background of the testing environment at Long Marine Laboratory.



Supplement 2b. Representative masker spectra used in audiometry. Spectrally flattened octave-band masking noise centered at the test frequency was recorded at the calibration position in the absence of the subject. Maskers were recorded at representative levels used for the California sea lion. Spectra are plotted from .wav recordings using a hamming window and an FFT size of 4096. Maskers are shown within the actual ambient noise background of the testing environment at Long Marine Laboratory.

