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Auditory Sensitivity in Sea Otters (*Enhydra lutris*)

Final Report

U.S. Department of the Interior
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Authors

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Colleen Reichmuth
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1.0 INTRODUCTION

The constant pressure of human activity in coastal and pelagic marine environments has led to concern regarding the effects of anthropogenic noise on marine mammals. Recent studies dealing with acoustic communication and behavioral responses to sound, along with investigations of auditory anatomy, hearing sensitivity, and noise impacts, have established a knowledge base for some cetaceans and pinnipeds that has proven vital to regulators charged with determining safe sound exposure limits for marine mammals (Richardson et al. 1995; Southall et al. 2007). Comparable data are currently unavailable for sea otters, which have been largely ignored in the context of this issue. There have been no formal studies of sound reception in these animals and their sensory biology with respect to audition is essentially unknown. Consequently, adequate assessment of the susceptibility of sea otters to various types of anthropogenic noise is profoundly limited by the lack of basic information about their auditory capabilities.

The objective of the present study was to capitalize on a unique opportunity to obtain aerial and underwater hearing threshold measurements for sea otters in order to determine their sensitivity and susceptibility to tonal and industrial sounds. This study leveraged the availability of expertise and resources from ongoing auditory research with other marine carnivores at the University of California Santa Cruz, Long Marine Laboratory. The study was designed to fill critical data gaps about sea otters and sound that can be used to support environmental assessment of industrial and recreational activities in the coastal nearshore waters of the west coast of the United States including Alaska, Washington, Oregon, and California. In particular, the results of the study are required by the Bureau of Ocean Energy Management for adequate assessment of energy development activities, including renewable energy projects on the Pacific Outer Continental Shelf (OCS).

Specifically, the auditory sense of sea otters was investigated during this project using a behavioral approach. Captive, adult southern sea otters (*Enhydra lutris nereis*) were trained to participate in a cooperative hearing test using operant conditioning and positive reinforcement methods. This hearing test paradigm allowed auditory thresholds to be measured across a wide range of frequencies, from subjects trained to perform both in air and while diving below the water's surface. This report contains the resulting hearing curves (audiograms) and presents them in a comparative context.

The original study called for a single sea otter subject because of practical constraints. However, due to some surprising results obtained for the first subject, a second sea otter was opportunistically trained and tested under similar conditions to ensure that species-typical hearing data were obtained and reported. At the end of the allocated contract period, research for the first subject was complete, while testing of the second subject was ongoing. Therefore, final aerial and underwater audiometric measurements are presented for the first sea otter subject in this report, while final aerial results and partial underwater results are presented for the second subject.

2.0 METHODS

2.1 Study Site

All research activities were conducted at the University of California Santa Cruz at Long Marine Laboratory, in Santa Cruz, CA. Long Marine Laboratory is the marine field station of the Institute of Marine Sciences at the University and includes specialized, USDA-approved facilities for marine mammal research.

2.2 Subjects

Two southern sea otters were trained to participate in the hearing assessment (see Figure 1). Subject 1 was a 6-year-old adult male (identified as "Odin," USGS #3857-03R) that was removed from the wild in August of 2008 and deemed non-releasable by the United States Fish and Wildlife Service because of his apparent habituation to humans. Shortly thereafter he was transported to Long Marine Laboratory from the Sea Otter Research and Conservation program at the Monterey Bay Aquarium, Monterey, CA for participation in this study. Subject 1 had no previous experience with operant conditioning training when he entered the study; therefore, all training for research and husbandry was established during the course of the research program. Subject 2 was a 14-year-old adult male (identified as "Charlie," USGS #2788-97R) that was obtained on a research loan from the Aquarium of the Pacific in Long Beach, CA. From his prior captive history in a public display facility, this subject had experience with operant conditioning training for animal care and husbandry; therefore, only his training for research needed to be established during the course of the project. Each of the sea otter subjects was housed in a complex of free-flow natural seawater tanks surrounded by adjacent haul out spaces, and were fed approximately 4 kg of freshly thawed seafood daily. Both sea otters were maintained at a healthy body weight of 27 to 29 kg during the study period.

Figure 1. The adult male southern sea otters tested in the present study. (Left panel) Subject 1, identified as "Odin," USGS #3857-03R. (Right panel) Subject 2, identified as "Charlie," USGS #2788-97R.

2.3 Permissions

The research described in this report was conducted at Long Marine Laboratory at the University of California in Santa Cruz, California between July 2009 and September 2012 under the authorization of the US Fish and Wildlife permit MA186914. The animal protocols used for this research were reviewed and approved by the Institutional Animal Care and Use Committees at the University of California Santa Cruz and the Monterey Bay Aquarium in Monterey, CA. The animal facilities at Long Marine Laboratory where the research was conducted were operated under USDA certificate number 93-R-0439.

2.4 General Method

The sea otter subjects were trained for participation in behavioral audiometry using operant conditioning techniques and positive reinforcement training methods. The otters were conditioned to position themselves at a listening station and to produce a behavioral response (a nose touch to a response target)

when an auditory stimulus was presented. Correct responses (a nose touch to the response target in the presence of the stimulus or remaining in position in the absence of the stimulus) were rewarded with food. Incorrect responses (touching the response target in the absence of the stimulus or remaining in position in the presence of the stimulus) were not reinforced. Once the task (called a go/no-go procedure) was established with easily detectable sounds, the amplitude of the stimuli was progressively altered across trials. Hearing thresholds for each stimulus were then determined over multiple sessions using a psychophysical method called a "method of limits" (or modified "up-down staircase") procedure. This method involves slowly lowering the stimulus level until the subject fails to detect it, then raising the level until the subject successfully detects it. These up-down steps are repeated until a hearing threshold, defined as the level of 50% detection, can be statistically determined. The general method is the same as that used in behavioral hearing tests given to school-aged children, and the training and testing procedures involved have been successfully used to estimate the hearing sensitivity of a wide assortment of animals, including many marine mammals such as seals and sea lions.

A trainer and an experimenter conducted each experimental session in a testing environment specifically configured for the task and the sound frequencies to be used (see sections 2.5.1 and 2.6.1). To avoid inadvertent cueing of subjects and to ensure the reliability of the results obtained, a stringent control procedure was used. The experimenter operated the stimulus-generating equipment, and recorded behavioral responses from a remote location, out of view of the trainer and the test subject. The experimenter observed the animal's performance in real time on closed-circuit video that was filmed from the test apparatus (see sections 2.5.2 and 2.6.2). The trainer wore headphones that masked the experimental sounds, and was not informed of the trial condition or outcome until the trial was completed.

2.5 Aerial Audiometry

2.5.1 Testing Environment

Both sea otters were initially trained to perform the hearing test outdoors, and then were tested in environments that were selected for each subject individually. This was done to provide background acoustic conditions that were sufficient to obtain hearing thresholds that were not influenced, or constrained by, the presence of noise.

Subject 1 was tested in an outdoor enclosure. The outdoor testing environment consisted of a portion of the dry haul-out deck in the subject's living enclosure. Sessions were conducted in the quietest possible outdoor conditions, in the absence of flowing seawater and extraneous activity.

Subject 2 was tested in a custom-built hemi-anechoic chamber. This chamber comprised a 3.3 m × 2.3 m × 2.2 m double-walled, stainless steel enclosure that was lined with sound insulating material and sound absorbing wedges that delimited acoustic reflections (Eckel Industries). It included a separate, sound-isolated control room that provided space for the experimenter and sound-generating equipment. The chamber was located near the subject's living enclosure and provided acoustic conditions that approximated a quiet, free-field environment that was highly controlled (Figure 2; for details see Southall et al. 2003).

The ambient noise in the outdoor testing environment was measured prior to each testing session at the position corresponding to the center of the subject's head during the experiment. These noise measurements were recorded with a Brüel and Kjær 4189 free-field microphone and an associated self-powered Brüel and Kjær 2250 sound level meter. Noise spectral density levels were calculated from 1/3-octave band levels sampled over a 1 min interval.

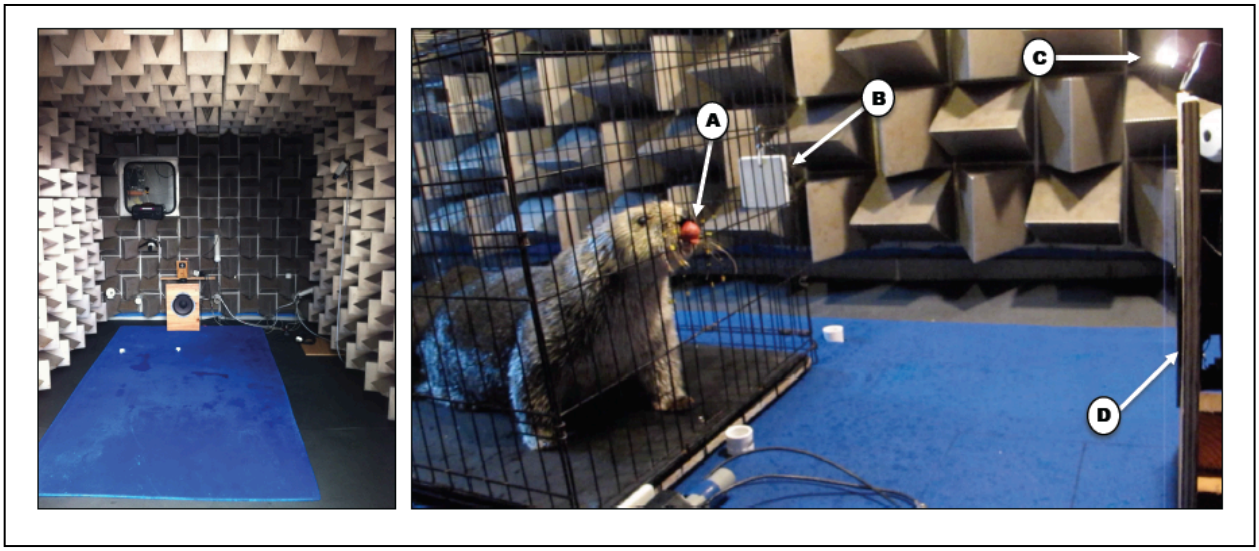

Figure 2. The aerial testing environment used for Subject 2. (Left panel) the interior of the hemi-anechoic acoustic chamber. (Right panel) Subject 2 positioned at the hearing test apparatus, with the listening station (A), the response target (B), the trial light (C), and the speaker used to project the auditory signal (D).

2.5.2 Experimental Apparatus

Both subjects were tested in the same experimental apparatus (Figure 2) which consisted of a 106 cm × 70 cm × 78 cm wire crate, inside of which were mounted the listening station and the response target. The station was in front of the subject, at eye-level and the response target was on the subject's left, 36 cm from the station. The speaker producing the test signal, and a small light that served as a trial interval indicator, were mounted directly in front of the subject, from 0.5 to 1.5 m from the station, depending on the test frequency. A second speaker was placed near the apparatus, which emitted a conditioned reinforcer that was used to mark correct responses. This sound—which was a "bell" sound during testing with Subject 1, and a "buzz" sound during testing with Subject 2—was immediately followed by the presentation of a primary reinforcer (a food reward such as a piece of freshly thawed shrimp). During testing with Subject 1, the food was passed through a PVC pipe from behind a visual barrier so that the trainer could remain out of the animal's view. The testing configuration for Subject 2 did not allow for this, so the food was passed directly to the otter from the trainer who was seated to the side of the apparatus. In both cases, the trainer wore headphones so that she would be blind to the experimental conditions until instructed by the experimenter to deliver the food reward.

A camera was mounted near the testing apparatus so that the subjects' behavior could be viewed in real time by the experimenter and digitally recorded. The video of each testing session was recorded and archived at the Cognition and Sensory Systems Lab at Long Marine Laboratory.

2.5.3 Acoustic Stimuli and Calibration

Both subjects were tested with narrow-band signals that allowed assessment of hearing sensitivity at specific frequencies. The signal duration was selected to exceed the time constant necessary for complete temporal summation in mammals, as is necessary for appropriate audiometric testing (Gelfand, 2001).

There were slight differences in signal generation for the two subjects. The acoustic stimuli used during testing with Subject 1 were pure-tone signals of 500 ms with a rise/fall time of 20 ms. Nine frequencies were tested with this subject: 0.0625, 0.125, 0.25, 0.5, 1, 2, 4, 8, and 16 kHz. The test stimuli were generated using a custom National Instruments (NI) LABVIEW virtual instrument operated from a PC

computer. The signals were sent through a NI PXI-6229 data acquisition (DAQ) card to a NI BNC-2120 connector block. The signals were then band-pass filtered with a Krohn-Hite 3550 filter and attenuated with a Tucker-Davis PA5 programmable attenuator. The outgoing test tones were presented through a JBL 2245H speaker (for test frequencies of 0.0625 and 0.125 kHz), a JBL 2123H speaker (for test frequencies from 0.5 kHz to 4 kHz), or a Morel MDT37 speaker (for test frequencies of 8 and 16 kHz).

The acoustic stimuli used during testing with Subject 2 were frequency-modulated (FM) sweeps of 500 ms with a rise/fall time of 20 ms. These signals had frequency bandwidth of 10%, centered on the following twelve frequencies: 0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 22.6, 32, 38.1 and 40 kHz. Functionally, these narrow-band signals were the same as the pure-tones used with Subject 1, but they afforded some additional benefits in the testing environment. These test stimuli were generated using a custom National Instruments (NI) LABVIEW virtual instrument (HTP © James Finneran) operated from a PC computer. The signals were sent through a NI PXI-6259 data acquisition (DAQ) card to a NI BNC-2120 connector block. The signals were then band-pass filtered with a Krohn-Hite 3364 filter and attenuated with a Tucker-Davis PA5 programmable attenuator. The outgoing test signals were presented through a JBL 2123H speaker (for test frequencies from 0.125 kHz to 8 kHz) or a Fostex FT96H speaker (for test frequencies from 16 to 40 kHz).

The temporal, spectral, and amplitude characteristics of the signals used during testing were measured and monitored in each session. Prior to each session, supra-threshold signal levels were produced and calibrated at the test frequency using a calibrated Josephson C550H microphone (0.02 to 20 kHz ± 2 dB), which was placed in a position corresponding to the center of the animal's head at the listening station. The outgoing calibration signal was sent through a Krohn-Hite 3550 filter, where it was band-passed and then amplified by 20 dB. The same NI hardware and custom software used to generate the test stimuli was used to analyze the calibration tones. An averaged fast Fourier transform (FFT) was used to measure the sound pressure level (SPL) of the calibration signal in dBrms re: 20 µPa and to ensure that no stimulus artifacts were present. The linearity of the system used to attenuate the signal during the session was also confirmed.

To verify that the calibration procedure provided a reasonable measure of the sound field surrounding the subjects' head, the 20 cm^3 area surrounding the calibration position was re-measured in 10 cm increments, across 10 cm transects located above, in the same plane as, and below, the calibration position. This area included the subjects' entire head during testing. This sound field mapping procedure was conducted prior to testing at each frequency to ensure that the received levels were within 3 dB of those measured at the listening station during session-to-session calibration.

2.5.4 Psychoacoustic Procedure

A similar psychoacoustic testing procedure was used for both subjects. Two trial types—signal-*present* trials and signal-*absent* trials—were presented within each session in a pseudo-random sequence. Each trial was 4 sec in duration. This listening interval was indicated by a light, which turned on when the subject was positioned quietly at the station, stayed on for the duration of the trial, and extinguished at the end. The subject was trained to remain in a stationary position with his nose touching the listening station until he detected a signal. When he detected the signal, he was trained move from the station to touch the response target with his nose. When he did not detect a signal he was trained to remain in position at the listening station until the trial interval was over. Each of these correct responses was marked by the presentation of the conditioned reinforcer followed by the delivery of one shrimp. On trials when he either failed to touch the response target during a signal-present trial (a "miss") or touched the response target during a signal-absent trial (a "false-alarm"), no reinforcement was provided and he was allowed to proceed to the subsequent trial after repositioning at the listening station.

Once a subject was fully trained to perform the task with supra-threshold signals at a variety of different stimulus frequencies, testing was initiated and completed for one signal frequency at a time. The experimental design required that the frequencies were tested in a shuffled order. To maintain a stable response bias during testing, the proportion of trials on which a signal was presented during each session was varied between 50% and 70%.

A test session typically comprised 30 to 45 trials and lasted 12 to 15 min. Each session began with the presentation of a supra-threshold tone. This stimulus level was approximately 20 dB above the anticipated threshold, which was deduced from prior training sessions. The stimulus level was raised and lowered during the session according to the psychophysical method of limits. For Subject 1, the signal level was lowered by a 4 dB step after each correct detection, until his first miss. From that point, the signal level was raised by 6 dB following each miss, and lowered by 2 dB following each detection, until at least five descending trial series ending in a miss were obtained. The signal level was then raised to the starting level, and another 5 to 6 trials were conducted to ensure that the session ended with a string of correct responses. Subject 2 used a similar procedure, but his step size following each detection and miss was set to 4 dB.

At each frequency, testing continued until performance across at least three sessions showed no further improvement.

2.6 Underwater Audiometry

2.6.1 Testing Environment

Two underwater testing environments were used, identified as pool A and pool B. Pool A comprised a circular, above-ground fiberglass tank that was positioned on a concrete foundation. This pool was 4 m in diameter and 0.9 m deep. The pool included a large window against which the experimental apparatus was mounted. Pool B comprised a concrete, epoxy-lined, partially in-ground tank that was 7.6 m in diameter and 1.8 m deep (Figure 3). Both pools were filled with natural seawater that was between 10 and 14°C. Ambient conditions were kept as quiet as possible during testing. There was no flowing water within 20 m of the test pool and there was no extraneous activity in adjacent areas of the facility.

The ambient noise in the underwater testing environment was measured prior to every test session at the position of the subject's head during the experiment. The noise measurements were recorded with a Reson TC4032 low-noise hydrophone (nominal sensitivity -170 dB re 1µPa/V) and a self-powered Brüel and Kjær 2250 sound level meter. Noise spectral density levels were calculated from 1/3-octave band levels sampled over 1 min. During the experiment, it was noted that the noise in the pool was substantially higher when the subject was present. Therefore, additional noise measurements were made in the same manner with the subject positioned at the underwater listening station and the hydrophone 15 cm from the position of the subject's head.

2.6.2 Experimental Apparatus

The experimental apparatus used for underwater testing was functionally similar to the one used for aerial testing but modified to be suitable for sea otters diving to a submerged listening station. The underwater apparatus was constructed of a water-filled, PVC pipe frame that was firmly secured to the wall of the underwater enclosure. The frame included a listening station, similar to the one used during aerial testing, as well as a PVC "handle-bar" which the sea otter subject gripped onto with his front paws, allowing him to stay submerged and maintain his position on the listening station during each trial (Figure 3). A response target, an underwater trial light, and an underwater camera were also mounted to the apparatus. A small buzzer, which served as the conditioned reinforcer during underwater testing, was positioned

nearby. The depth of the listening station was established so that the position of the subject's head was 0.5 m in pool A, and 1 m in pool B.

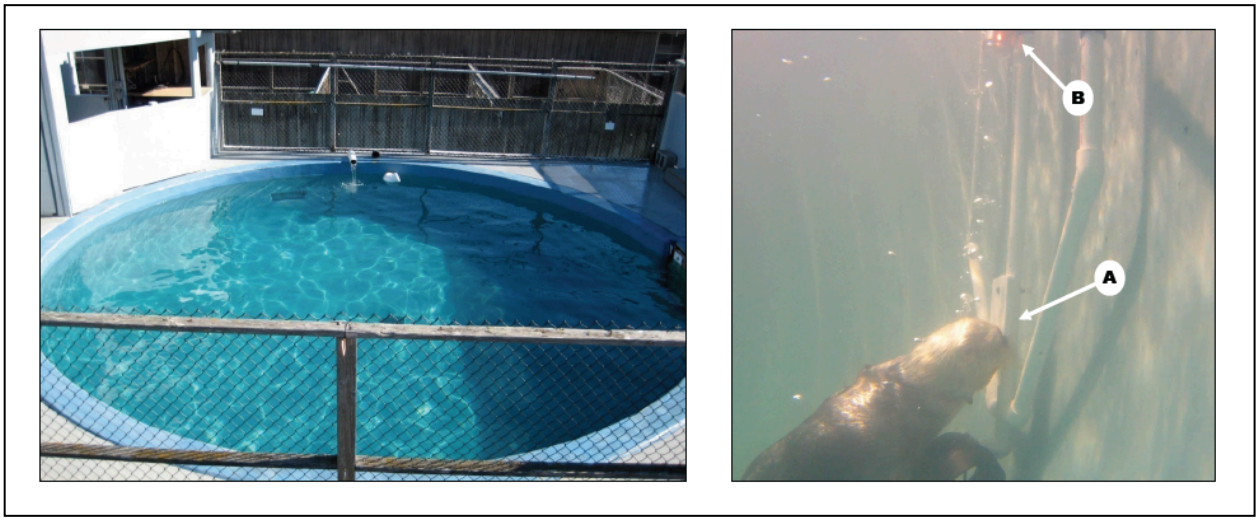

Figure 3. One of the underwater testing environments used for Subjects 1 and 2. (Left panel) The seawater-filled enclosure identified as Pool B. (Right panel) Subject 2 positioned at the underwater apparatus, with the listening station (A) and the trial light (B) shown. The response target is positioned out of view, closer to the surface, and the transducer is located behind the subject, on the opposite side of the pool.

2.6.3 Acoustic Stimuli and Calibration

The acoustic stimuli used during underwater testing with both subjects were the same FM sweeps used during aerial testing for Subject 2. These narrow-band signals provided less interaction effects in the underwater environments than pure-tone stimuli and were therefore less variable during stimulus production, calibration, and sound field mapping. The stimuli were generated using a custom National Instruments (NI) LABVIEW virtual instrument (HTP © James Finneran) operated from a PC computer. The signals were sent through a NI PXI-6259 data acquisition (DAQ) card to a NI BNC-2120 connector block. The signals were then band-pass filtered with a Krohn-Hite 3364 filter and attenuated with a Tucker-Davis PA5 programmable attenuator. The outgoing test signals were broadcast through one of several underwater transducers.

For Subject 1, test signals centered at 1, 2, 4, and 8 kHz were projected into pool A from a Lubell 1424HP transducer. The transducer was located on the same horizontal plane as the listening station (0.5 m depth) at a distance of 3 m from the listening station. Subject 1 was also tested at a frequency of 0.5 kHz in pool B. For this frequency, the same Lubell 1424HP transducer was used. It was positioned on the same horizontal plane as the listening station (1 m depth) at a distance of 6 m from the listening station.

For Subject 2, test signals centered at 4, 8, 16, 32, and 38.1 kHz were projected into pool B from a calibrated ITC 1042 hydrophone. The transducer was located on the same horizontal plane as the listening station (0.5 m depth) at a minimum distance of 3 m from the listening station. Subject 2 was also tested at frequencies of 0.125, 0.25, and 0.5 kHz in pool B. These stimuli were projected from a J11 transducer provided by the Naval Undersea Warfare Center (Newport, RI) that was located on the same horizontal plane as the listening station (1 m depth) at a minimum distance of 6 m from the listening station.

The precise configuration of the transducers relative to the position of the listening station at each frequency was determined through sound field mapping of the area filled by the subject's head during the

experiment. Sound field mapping was accomplished by measuring the received level of a calibration signal, projected from the transducer, at the center of the subjects head, and then re-measuring this calibration signal in the 20 cm^3 area surrounding that position in 10 cm increments. The final position of the transducer was selected to ensure that the level of the signal in the surrounding area was within 3 dB of the level of the signal at the calibration position.

Supra-threshold signal levels were produced and calibrated at the test frequency before every session with the Reson 4032 hydrophone, which was placed in the position corresponding to the center of the animal's head at the listening station. The same NI hardware and custom software used to generate the test stimuli was used to view and measure the incoming calibration signals.

2.6.4 Psychoacoustic Procedure

For underwater testing, the subjects were trained to perform the same acoustic signal detection task that they had performed in air, at the underwater listening station. This involved training the subjects to dive to the submerged station, hold quietly at the station until the trial light was turned on, and then touch the response target to report a signal detection or else remain in position until the light was extinguished. As during aerial testing, correct responses were marked by a conditioned reinforcer that was immediately followed by a shrimp reward given by the trainer who was positioned on the adjacent deck. Following an incorrect response, the subject was recalled to the surface without reinforcement. In either case, the trainer redirected the subject back to the underwater listening station to begin the next trial.

For Subject 1, the psychoacoustic procedure used to determine a hearing threshold at each test frequency was the same underwater as it was in air.

For Subject 2, the psychoacoustic procedure used to determine a hearing threshold at each test frequency was similar to that used in air. However, during testing in pool A, the signal level was raised by 4 dB following each miss and lowered by 2 dB following each detection. During testing in pool B, the signal level was raised and lowered in 4 dB steps as it was during aerial testing. Underwater sessions in Pool B typically contained only 20 to 30 trials due the increased difficulty of the task in the deeper pool. Therefore, a minimum of three descending trial series ending in a miss were obtained in each session, and testing was continued at each frequency until five sessions without further improvement were obtained.

2.7 Data Analysis

Auditory thresholds were calculated for each subject at each frequency in the same manner for both media. To ensure stable performance that represented the subjects' best sensitivity, the sessions from which final thresholds were determined needed to show a plateau in performance over the last 3 or 5 descending trial series and false alarm rates above 0 and less than 30%. These sessions also needed to show individual thresholds within 3 dB of one another. Fifteen descending trial series were pooled from the 3 or 5 sessions meeting these criteria at each test frequency. To determine the final hearing threshold, the mid-point of the stimulus level of the lowest detected signal and the first missed signal on each series was averaged and reported with the corresponding standard deviation. False alarm rates were also pooled and reported from these 15 trial series.

In order to assess potential masking effects, the auditory thresholds obtained for each subject were compared to the average noise spectral density levels in the test environment. The difference between the hearing threshold and the background noise in the same 1/3-octave band was considered with respect to critical ratio data available for terrestrial carnivores to determine if the conditions were sufficiently quiet to enable absolute, unmasked thresholds to be measured.

Finally, aerial and underwater audiograms were established for each subject as the absolute hearing threshold plotted with respect to signal frequency. The aerial audiograms were then compared to published audiometric data from several terrestrial carnivores, and the underwater audiograms were compared to published audiometric data from several semi-aquatic carnivores.

3.0 RESULTS

3.1 Aerial Audiometry

Aerial audiograms were completed for the two sea otter subjects. Table 1 provides the testing sequence, the threshold data with corresponding standard deviations and false alarm rates, and associated background noise levels. Graphical depictions of the aerial audiograms for the two sea otter subjects are shown in Figure 4.

Table 1

Psychoacoustic hearing data obtained for both sea otter subjects in air shown with corresponding ambient noise in the 1/3-octave band centered on the test frequency.

Subject	Frequency (kHz)	Testing Order	Threshold (dB re 20μPa)	False Alarm Rate	Ambient Noise (dB re 20μPa/√Hz)
1	0.0625	9	-	-	44.8
	0.125	5	76.4 ± 1.8	25%	39.2
	0.25	1	62.6 ± 1.7	22%	28.6
	0.5	7	43.7 ± 1.6	25%	24.4
	1.0	6	52.6 ± 1.7	25%	12.1
	2.0	2	49.3 ± 1.3	11%	6.3
	4.0	3	62.9 ± 2.2	27%	1.5
	8.0	4	74.5 ± 2.1	15%	-8.1
	16.0	8	-	-	-20.5
2	0.125	6	74.4 ± 2.0	16%	23.1
	0.25	2	56.0 ± 0.0	7%	-4.0
	0.5	3	41.5 ± 2.1	25%	-15.1
	1.0	5	23.5 ± 1.4	6%	-17.2
	2.0	7	4.0 ± 0.0	13%	< -21.6
	4.0	1	9.7 ± 1.0	23%	< -23.1
	8.0	4	-1.7 ± 1.0	7%	< -25.2
	16.0	9	5.5 ± 2.1	18%	< -28.9
	22.6	11	7.7 ± 2.4	5%	-
	32.0	8	30.4 ± 2.0	7%	-
	38.1	12	56.7 ± 2.0	21%	-
	40.0	10	70.5 ± 1.4	13%	-

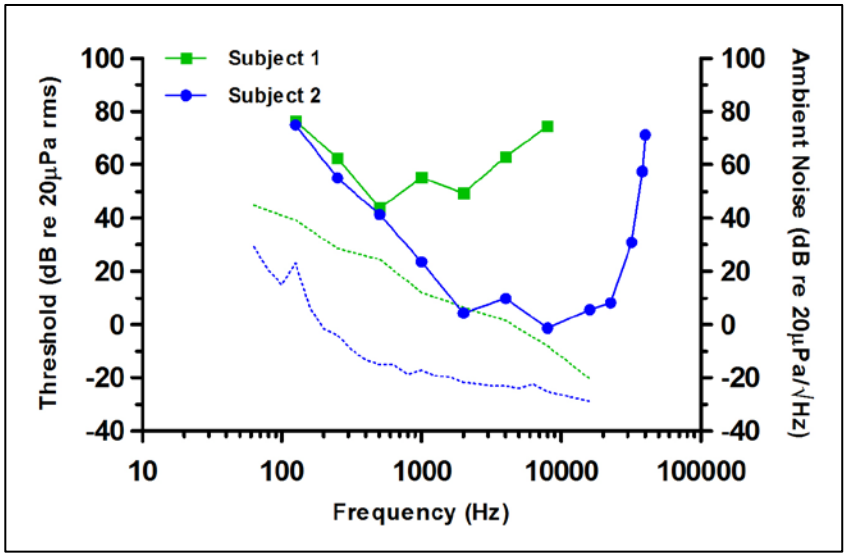

Figure 4. Aerial audiograms for two southern sea otters shown with corresponding spectrum levels of ambient noise in their testing enclosures. For Subject 1, hearing thresholds are shown by green squares; the ambient noise levels in the outdoor environment where this subject was tested are shown by the green dotted line. For Subject 2, hearing thresholds are shown by blue circles; the ambient noise levels in the acoustic chamber where this subject was tested are shown by the blue dotted line. Note that noise levels below -20 dB re 20 µPa/√Hz are below the measurement limits of the instrumentation.

The comparison of the hearing thresholds to ambient noise spectrum levels in each testing environment show that the performance of the subjects was not likely to be constrained, or masked, by the acoustic conditions in which the data were collected. In all but one case, the ambient noise was sufficiently low to confidently rule out possible masking effects, as the spectrum level of the noise was well below the measured hearing thresholds in the 1/3-octave bands surrounding the test frequencies. The observed threshold-to-noise ratios generously exceed the critical ratios that have been reported for terrestrial carnivores (see Fay, 1988). Therefore, it is reasonable to conclude that the hearing data obtained for each subject represent unmasked, or absolute, thresholds. The threshold measured for Subject 1 at 0.5 kHz was closest to the noise floor (within 20 dB), but still exceeded the theoretical noise-limited detection threshold predicted by critical ratio obtained from a domestic cat (Watson, 1963; Costalupes, 1983; Pickles, 1975).

When these data are compared between the two subjects, it is apparent that the auditory sensitivity of both sea otters is essentially the same at frequencies of 0.125, 0.25, and 0.5 kHz. However, at frequencies above 0.5 kHz, Subject 1 shows an unexpected reduction in sensitivity up to 8 kHz. Subject 1 received extensive training to confirm whether his frequency range of hearing extended beyond the narrow range from 0.125 to 8 kHz. He was unresponsive to test signals presented at 0.0625 and 16 kHz, even when stimulus levels exceeded 80 dB re 20 µPa. Within the measured range of his sensitivity, Subject 1 showed best sensitivity of 44 dB at 0.5 kHz. Repeated behavioral testing at frequencies from 0.125 to 8 kHz did not result in further improvement in his ability to detect the test signals.

Subject 2 learned the task relatively quickly and responded to test stimuli extending from 0.125 to 40 kHz without difficulty. His sensitivity continued to improve beyond 0.5 kHz to a maximum hearing sensitivity of -1.7 dB at 8 kHz. His range of best sensitivity, defined as +10 dB of the lowest hearing threshold, extended from about 1.6 to 22 kHz. His functional range of hearing, defined as +60 dB of the lowest

hearing threshold, extended from about 0.2 to 38 kHz. Subject 2 showed a significantly extended range of hearing and much higher overall sensitivity than Subject 1.

Figure 5 compares the audiogram of Subject 2 to published audiograms for two terrestrial mustelids and two other terrestrial carnivores. The least weasel, *Mustela nivalis* (Heffner and Heffner, 1985a), the domestic ferret, *Mustela putorius furo* (Kelly *et al*., 1986), the domestic dog, *Canis familiaris* (Heffner, 1983), and the domestic cat, *Felis catus* (Heffner and Heffner, 1985b) exhibit features that are considered typical of carnivore hearing, including a broad frequency range of hearing, wide range of best sensitivity, and maximum sensitivity near 0 dB. This sea otter shows a comparable frequency range of best sensitivity as well as comparable sensitivity within this range. His best sensitivity of -1.7 dB at 8 kHz is equal to that of the highly acute domestic cat and slightly better than the least weasel, the domestic ferret, and the domestic dog. His high-frequency hearing extending up to 40 kHz is similar to that of the ferret and shows a comparable—if slightly lower roll-off—to that displayed by the other carnivores. However, the sea otter's low-frequency hearing does show a pronounced divergence from all of the other carnivores. At frequencies below 2 kHz, his sensitivity declines substantially—20 to 30 dB—in comparison to his terrestrial relatives.

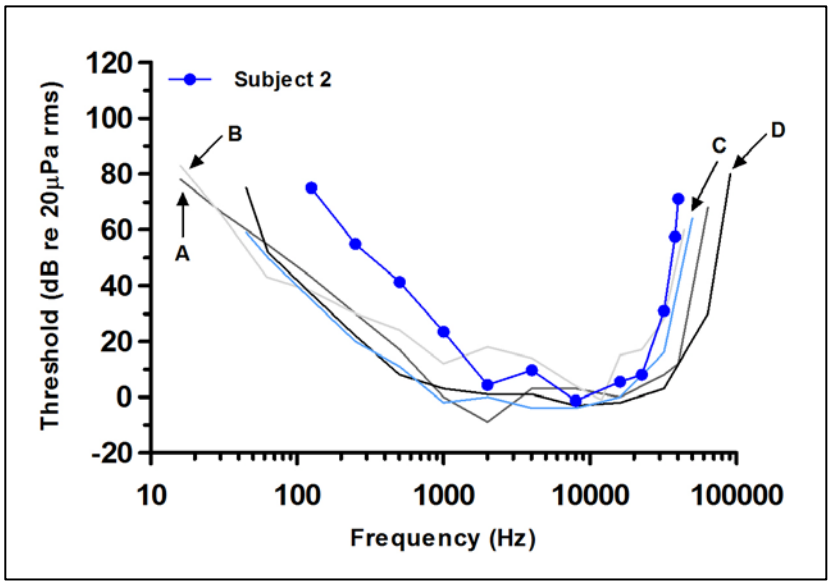

Figure 5. Aerial audiogram for Subject 2 (blue circles) shown with audiograms measured for terrestrial mustelids in similarly quiet testing environments: (A) least weasel, *Mustela nivalis* (Heffner and Heffner, 1985a) and (B) domestic ferret, *Mustela putorius furo* (Kelly *et al*., 1986), and two other terrestrial carnivores: (C) domestic dog, *Canis familiaris* (Heffner, 1983) and (D) domestic cat, *Felis catus* (Heffner and Heffner, 1985b).

3.2 Underwater Audiometry

Underwater hearing measurements were obtained for the two sea otter subjects. Table 2 provides the testing sequence, the threshold data with corresponding standard deviations and false alarm rates, and relevant background noise levels. Please note that final underwater audiometric measurements are presented for the first sea otter subject, while partial underwater results are presented for the second subject. The corresponding audiograms are depicted in Figure 6.

Table 2

Psychoacoustic hearing data obtained for both sea otter subjects under water, shown with corresponding self (bubble) noise in the 1/3-octave band centered on the test frequency.

Subject	Frequency (kHz)	Testing Order	Threshold (dB re 1μPa)	False Alarm Rate	Bubble Noise (dB re 1μPa/√Hz)
1	0.5	5	125 ± 2.3	24%	73.8
	1.0	4	134.9 ± 1.8	7%	60.0
	2.0	2	144.5 ± 1.2	8%	57.4
	4.0	1	144.9 ± 1.9	13%	46.3
	8.0	3	157.5 ± 1.4	5%	34.7
2	0.125	6	120.8 ± 1.7	23%	87.4
	0.25	7	116.0 ± 1.5	12%	78.9
	0.5	8	112.5 ± 3.0	15%	74.7
	4.0	5	87.2 ± 1.7	20%	76.5
	8.0	3	77.0 ± 1.2	20%	68.6
	16.0	1	76.3 ± 1.2	18%	61.6
	32.0	2	91.6 ± 1.5	18%	-
	38.1	4	129.3 ± 1.4	20%	-

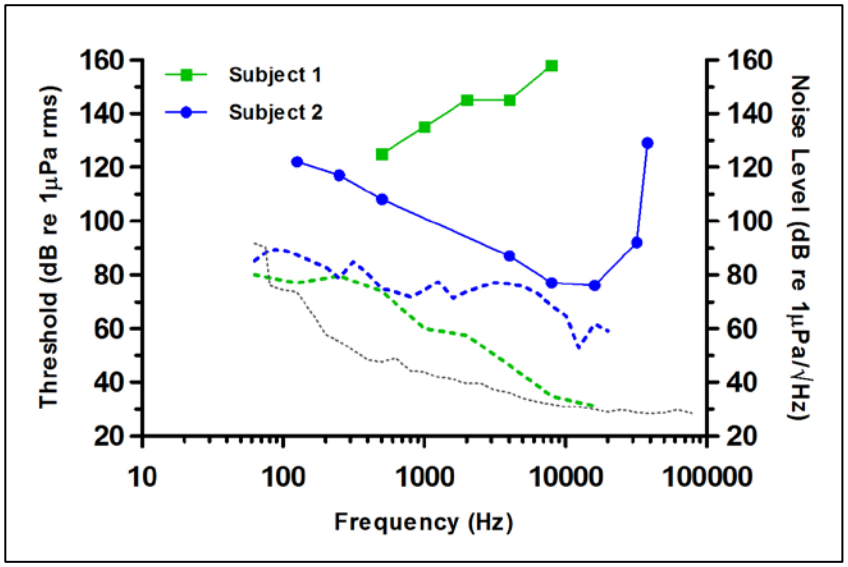

Figure 6. Underwater audiograms for two southern sea otters, shown with corresponding spectrum levels of ambient noise in their testing enclosures. For Subject 1, hearing thresholds are shown by green squares; for Subject 2, hearing thresholds are shown by blue circles. Note that thresholds shown for Subject 2 represent a preliminary data set, as underwater testing has not yet been completed at 1 or 2 kHz. Ambient noise in the testing enclosure in the absence of the subjects is shown by the grey dotted line referenced to the right axis. Both subjects produced substantial bubble noise by venting the air layer in their coats while remaining submerged at the listening station. The level of this noise is shown for Subject 1 by the green dotted line and for Subject 2 by the blue dotted line.

In the underwater testing environments, the determination of whether the background acoustic conditions constrained the threshold measurement was more problematic than in air. The test pools were sufficiently quiet in the absence of the subjects to allow absolute threshold measurements to be obtained, as shown by the comparison between the hearing thresholds and the underwater ambient noise floor in Figure 6. However, it became apparent during testing that the subjects were generating unexpectedly high levels of self-noise in the environment by the continuous venting of air from their coats while submerged at the listening station. This bubble noise was broadband and time varying, both in terms of frequency content and amplitude, and it elevated the spectrum level of ambient noise in the testing enclosure by as much as 40 dB.

Figure 6 and Table 2 allow comparison of the bubble noise produced by each subject with their measured hearing thresholds. For Subject 1, it is clear that the background noise, even with bubbles present, did not constrain the measurements of hearing thresholds at any of the frequencies tested. The thresholds for this subject exceed the noise spectrum levels in the 1/3-octave bands surrounding each test frequency by at least 50 dB. Further, the shape of the audiogram followed an opposite trend than the noise, confirming that the hearing data determined for this subject represent unmasked thresholds. However, the situation was different for the second subject.

For Subject 2, the measured thresholds for the lowest frequencies tested (0.125, 0.250, and 0.5 kHz) exceed his bubble noise by more than 30 dB. Comparison with critical ratios available for pinnipeds (Southall *et al.,* 2000) and terrestrial carnivores (Fay, 1988) suggests that these thresholds are not masked and therefore represent absolute hearing sensitivity. The situation is similar at the highest frequencies tested thus far (32 and 38.1 kHz). Therefore, the lower and upper frequency hearing limits are unmasked by self-noise. The bubble venting by Subject 2 does, however, interfere with his hearing across the range of his best sensitivity. Frequencies from 4 to 16 kHz have threshold-to-noise ratios of less than 15 dB, indicating that they are likely constrained by the second subject's self-noise. Due to the fact that underwater testing with Subject 2 is currently ongoing, and hearing thresholds at 1 kHz and 2 kHz have not yet been measured, questions concerning this sea otter's sensitivity, or the effect of bubble noise on thresholds at these frequencies cannot be addressed.

With these points in mind, the auditory performance of Subject 2 shows a range of functional hearing and best sensitivity that is similar underwater to that determined in air. This individual's most sensitive frequency underwater was 8 kHz, but the threshold value of 77 dB re 1µPa was limited by bubble noise. When the underwater audiogram is compared to that of two other amphibious carnivores, the California sea lion, *Zalophus californianus* (Reichmuth and Southall, 2011) and the harbor seal, *Phoca vitulina vitulina* (Kastelein *et al*., 2009), a few trends are apparent (See Figure 7). The sea otter, like the California sea lion and other otariid pinnipeds, has high frequency hearing that is similar in both media and shows a steep roll-off above 30 kHz. The range of best sensitivity also appears similar, although the threshold values of the sea otter are elevated by self-generated noise. The sea otter shows a narrower range of functional hearing and decreased overall sensitivity relative to the harbor seal (which, like several other phocid pinnipeds, has acute underwater hearing encompassing a nine-octave frequency span). The most striking feature evident from the comparison of the sea otter's underwater hearing relative to that of the two pinnipeds shown, is the difference in low-frequency sensitivity. The sea otter is about 25 dB less sensitive than the sea lion and more than 40 dB less sensitive than the harbor seal in the frequency range of 0.25 to 0.5 kHz.

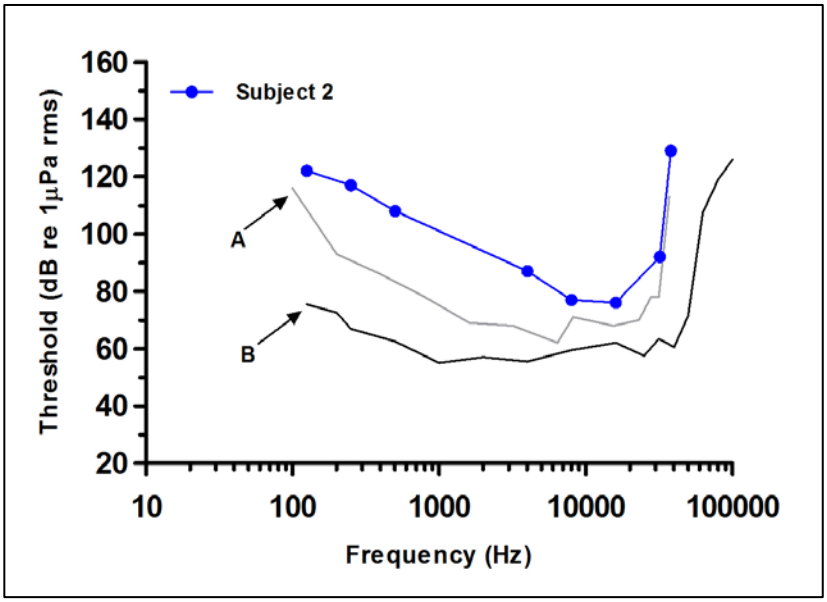

Figure 7. Underwater audiogram for Subject 2 (blue circles) shown with audiograms measured for semi-aquatic carnivores: (A) California sea lion, *Zalophus californianus* (Reichmuth and Southall, 2011) and (B) harbor seal, *Phoca vitulina vitulina* (Kastelein *et al*., 2009). Auditory thresholds shown here for Subject 2 represent a preliminary data set, as underwater testing has not yet been completed at 1 kHz or 2 kHz. Also note that the acoustic environments in which these audiograms were obtained was quite different, due to the sea otter's self-generated bubble noise which masked hearing thresholds across the range of best sensitivity (4, 8, and 16 kHz).

4.0 DISCUSSION

Auditory thresholds were successfully obtained from the two captive southern sea otters that were trained for participation in the present study. Both subjects initially learned to perform the hearing test in air and later transferred the behavior to a submerged apparatus so that underwater threshold measurements could be obtained. While the otters were trained and tested under quite similar conditions, very different performance measures of hearing sensitivity were obtained from the two individuals.

The first subject tested was brought into captivity from the wild as an adult and required significant time for acclimation and training. Since no auditory data was available for sea otters at the time the study began, it was difficult to interpret the initial aerial hearing thresholds that were obtained. While his functional hearing was narrow in frequency range and elevated in sensitivity relative to terrestrial mustelids and other carnivores, it was impossible to know whether this unexpected result was due to species-typical features of the sea otter auditory system, individual differences in this sea otter, or some other factor. To rule out possible factors related to behavior or experimental conditions, repeated testing under rigorous experimental controls were conducted. Thresholds obtained using these additional measures confirmed this subject's poor aerial hearing abilities.

At the same time this subject began training for underwater audiometry, an independent assessment of the frequency range of hearing for this animal and three other captive adult sea otters was initiated using passive testing methods. This approach involved a controlled exposure experiment (CEE) in which loud tonal signals, as well as blank "control" signals, were intermittently presented to resting otters over a period of multiple sessions. In this way, the upper and lower limits of hearing could be rapidly assessed by evaluation of behavioral responses. The summary results of this CEE study were reported by Ghoul

and Reichmuth (2010). They confirmed that the sea otter identified as Subject 1 in the present study had a narrow range of hearing extending from 0.125 to 8 kHz. They also demonstrated that other sea otters could detect auditory signals over a much broader frequency range extending to at least 32 kHz. This finding provided evidence that the hearing capabilities of the first sea otter subject were not likely to be representative of the species and that the audiometric testing of additional subjects was necessary.

Despite the problematic results from Subject 1, underwater testing of this subject was continued while additional funding and a new sea otter subject were sought. The results obtained for Subject 1 under water showed similar trends to those obtained in air. These results, along with comparison to aerial and underwater hearing data for other carnivores, indicated deafness in this subject at low and high frequencies, as well as a significant reduction in sensitivity across his limited frequency range of hearing.

The second sea otter subject to enter the study showed a different pattern of hearing sensitivity. His aerial audiogram revealed a fairly broad range of functional hearing from 0.2 to 38 kHz, with best sensitivity comparable to that of terrestrial carnivores known to have excellent hearing (eg. felids, canids, and mustelids). However, this sea otter also showed relatively poor low-frequency sensitivity that was virtually identical to that of the first subject.

The underwater audiogram of Subject 2 revealed a range of hearing sensitivity that was comparable to that observed in air. However, underwater thresholds measured within his range of best sensitivity were noise-limited by bubbles released while diving, from the layer of air contained in his fur coat. Significantly, his hearing at low frequencies was unaffected by this masking noise. His auditory thresholds at 0.125, 0.25, and 0.5 kHz were elevated well above the noise, indicating poor sensitivity at these frequencies. While underwater testing of this subject is ongoing, the results thus far provide a fairly complete picture of the hearing capabilities of this individual.

The primary results of this study can be summarized as follows for Subjects 1 and 2:

The hearing of the first subject cannot be considered representative for sea otters and it would be inappropriate to use these data for regulatory decision-making or environmental assessment of potential acoustic impacts on sea otters. The cause of the hearing loss documented for Subject 1 is unknown, since this sea otter lived in the wild until adulthood.

The audiograms reported for the second individual are limited by sample size (n=1); however, the results are consistent with available data for terrestrial carnivores as well as with a recent assessment of hearing range in sea otters conducted using alternative methods (Ghoul and Reichmuth 2010). Specifically, the results from the second subject indicate that:

(1) Although sea otters are adapted for a semi-aquatic lifestyle and spend most of their lives at sea, they have retained acute aerial hearing sensitivity that rivals that of the best terrestrial carnivores.

(2) At low frequencies, the hearing capabilities of sea otters are not as sensitive as expected. This result is supported by several factors. First, the low-frequency thresholds that were measured for Subject 2 were rigorously obtained under highly controlled conditions and were not masked by noise. Second, these low-frequency thresholds were entirely consistent for this subject when his aerial and underwater measurements, obtained months apart, were compared. Finally, the low-frequency thresholds obtained from Subject 2 in air were the same as those obtained for Subject 1 in air, despite different testing environments and equipment used for the two individuals. While Subject 1 has apparent hearing loss at 1 kHz and above, it appears that his low-frequency hearing is the same as Subject 2 and is not impaired at the tested frequencies of 0.125, 0.25, and 0.5 kHz.

Therefore, it is reasonable to conclude that the threshold values reported here for these frequencies are reliable at the level of the species as well as the individual.

(3) Sea otters have a broad range of hearing sensitivity that extends well into ultrasonic frequencies. This is perhaps not surprising given that many other carnivores have good high frequency hearing, and that the calls of sea otters have broadband spectral components that exceed 30 kHz (Ghoul and Reichmuth, 2010).

(4) The range of functional hearing is similar in air and under water, but bubble noise created by venting of air from the coat limits hearing sensitivity across much of that range. The significance of the self-noise created by diving sea otters is as yet unresolved. Whether this bubble noise restricts the ability of wild sea otters to detect sounds while diving and foraging, or perhaps even draws attention to submerged sea otters from swimming predators, cannot be addressed until more information is available from the field. The captive otters in this study vented air continuously for dives up to 40 seconds; however, these dives were quite shallow (≤1 m) relative to those of foraging otters. If the air within the coat is compressed and retained during dives exceeding a few meters rather than released into the water column, wild otters may be significantly more sensitive to frequencies in the range of 4 to 16 kHz than reported here.

If the aerial and underwater audiograms provided here for the second sea otter subject are considered fairly typical for southern sea otters, it is likely that these data—with the caveats discussed above—can be applied to northern sea otters as well (*Enhydra lutris lutris*). While auditory data sometimes varies by species or family group, it rarely diverges at the level of subspecies. However, this has been known to occur in species or breeds that have experienced inbreeding, as have southern sea otters (Larson *et al.,* 2002).

With respect to the broader issues of management and conservation, the present data can be applied to environmental assessment problems in a manner similar to that conducted with pinnipeds and other marine mammals (*e.g.,* National Research Council, 1994, 2000, 2003, 2005; Richardson *et al.,* 1995). These efforts also rely, in large part, on hearing data obtained from small sample sizes of trained subjects. At the grossest level, the hearing ranges reported here can be used to establish weighting functions that are appropriate for sea otters (see Southall *et al.,* 2007). Such weighting functions can be used to determine sound frequencies that can be eliminated from concern because they are inaudible (below or above the frequency bandwidth of hearing). For sea otters, it appears that these weighting functions would conservatively fit within those proposed for pinnipeds in air and under water (see Southall *et al*., 2007). Further, the unexpectedly elevated low-frequency hearing roll-off documented for both sea otter subjects in this study is significant and worthy of further investigation, as most anthropogenic noise in marine environments, including that related to transportation and oil and gas production, is generated at frequencies below 1 kHz.

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