*Aquatic Mammals* 2014, *40*(3), 243-251, DOI 10.1578/AM.40.3.2014.243

# Hearing in Sea Otters (*Enhydra lutris*): Audible Frequencies Determined from a Controlled Exposure Approach

Asila Ghoul and Colleen Reichmuth

*Institute of Marine Sciences, Long Marine Laboratory, University of California Santa Cruz, Santa Cruz, CA 95060, USA*
*E-mail: asila@ucsc.edu*

## Abstract

The sea otter (*Enhydra lutris*) is an amphibious marine mammal that is vulnerable to coastal anthropogenic disturbance. Effective management of noise-generating activities within sea otter habitats requires information about hearing that is presently unavailable for this species. As an initial step toward describing the auditory capabilities of sea otters, we used a controlled exposure approach to conservatively estimate the aerial frequency range of hearing in four captive individuals. The study was designed to determine which frequencies were audible to each animal rather than to quantify auditory sensitivity. To this end, the sea otters were intermittently exposed to relatively high-amplitude tones between 0.063 and 45.3 kHz—and to blank "control" events—during periods of sustained rest. Positive responses to both the sound exposure trials and the control trials were scored by experimentally blind observers and used to determine statistically reliable detections at each frequency. The widest confirmed hearing range measured for the sea otters was 0.125 to 32 kHz. Our results indicate that sea otters can detect a broad range of airborne sounds, similar to many terrestrial carnivores that have been studied. These are the first hearing measurements obtained for this species, and the results are relevant to improving understanding of sea otter acoustic communication, evolutionary biology, and behavioral ecology, as well as in supporting ongoing conservation efforts. This method can be adapted to examine the acoustic detection capabilities of species for which little data are available and for which conventional audiometry may prove challenging.

**Key Words:** sea otter, *Enhydra lutris*, hearing, controlled exposure experiment

## Introduction

The sea otter (*Enhydra lutris*) is an amphibious marine mammal that was hunted to near extinction during the late 18th and early 19th century fur trade. Due to slow population growth in California and declining populations in southwest Alaska and parts of Russia, sea otters are presently classified as Endangered by the International Union for Conservation of Nature (IUCN) (2013). Sea otters are particularly sensitive to anthropogenic pollution and disturbance (U.S. Fish and Wildlife Service [USFWS], 2003), in part because they inhabit small home ranges restricted to nearshore coastal environments (Riedman & Estes, 1990). Human-generated noise sources, including marine construction and transportation, recreational activities, seismic surveys, energy extraction, and military operations, are also commonly concentrated in nearshore areas. However, due to the absence of information concerning the auditory biology of sea otters (Ghoul & Reichmuth, 2012), these noise sources cannot be appropriately considered in regional management plans (Southall et al., 2009).

Auditory profiles characterizing the sensitivity of individuals across sound frequencies are necessary to describe the hearing capabilities of any species. Research efforts to obtain such detailed aerial and underwater audiograms from a trained sea otter using psychophysical methods are ongoing in our laboratory. However, to provide auditory information on multiple individuals, we developed a controlled exposure method to test captive, untrained sea otters. Our aim was to rapidly estimate the hearing range of several sea otters using airborne sounds so that this information could be used by resource managers to broadly identify noise sources of potential relevance vs those of lesser concern.

Controlled exposure experiments have become important tools for investigating the behavioral reactions of free-ranging marine mammals to sound (Tyack et al., 2003; Deecke, 2006; Nowacek et al., 2007; Southall et al., 2012). These field experiments are commonly used to describe the effects of particular sounds on focal individuals in order to answer applied research questions directed at wildlife management and conservation (e.g., Frankel & Clark, 2000; Madsen et al., 2006). Controlled exposure experiments to study marine mammal hearing, though not as common, have been successfully conducted in both captive (e.g., Kellogg & Kohler, 1952; Kastelein et al., 2012) and wild (e.g., Dahlheim & Ljungblad, 1990; Kastelein et al., 1993) settings. In the present study, we adapted and improved available controlled exposure methods to passively estimate the frequency range of hearing in captive sea otters.

Our experimental design called for testing four sea otter subjects across a wide range of frequencies using relatively high-amplitude sounds. The goal was to determine which frequencies were audible to each individual rather than to provide direct measures of auditory sensitivity. An important component of this method was the use of negative (blank) controls to establish comparative measures of arousal and/or vigilance within and between exposure sessions. We compared positive behavioral responses to the presentation of tones to those scored for the same subject during corresponding control events. This comparison occurred within each frequency for each subject to statistically identify the detected sound frequencies. Given the conservative nature of the CEE approach—that is, lack of an observable behavioral response does not necessarily indicate lack of detection—our design called for more replicates at frequencies showing fewer positive responses and allowed for greater sampling at the upper and lower frequency limits of hearing. We predicted that due to their vigilant nature (Scammon, 1968), sea otters would be well-suited to this passive behavioral approach.

## Methods

### *Subjects*

Four adult male sea otters were evaluated. The sea otters were identified as "Wick," 10 y (USGS 3317-00); "Morgan," 13 y (USGS 0992-98); "Taylor," 16 y (USGS 0958-93); and "Odin," 7 y (USGS 3857-03). Wick, Morgan, and Taylor were individually housed in free-flow, natural seawater pools with adjacent haul-out areas at the Marine Wildlife Veterinary Care and Research Center in Santa Cruz, California. Odin was housed in a similar enclosure at the Long Marine Laboratory, in Santa Cruz. Although all subjects were captive individuals, none were trained to actively participate in this study. Prior to the current experiment, Odin had been trained for psychoacoustic testing of aerial hearing (Ghoul, 2010).

### *Testing Enclosures and Experimental Configuration*

Test sessions were conducted in four different outdoor environments. Wick, Morgan, and Taylor were tested in their primary living enclosures. These three enclosures were similar in terms of the shape and size of the pool (circular; 4 to 6 m in diameter) and adjacent dry haul-out space (at least 16 m$^2$), and were enclosed with nylon mesh fencing. Odin was tested in an enclosed portion of his primary living space. This area included a 4.5 × 2 m rectangular pool with 10 m$^2$ of haul-out space enclosed with wooden walls and vinyl-coated chain-link fencing.

Experimental set-ups were similar for each sea otter. The experimenter and the sound-generating equipment were located indoors at least 10 m from the testing enclosures—outside of visual or acoustic contact with subjects. A high-definition digital video camera was used to record each experimental session. This camera was positioned above the subject's enclosure and was connected to a closed-circuit TV monitor in the building, allowing the experimenter to monitor the subject and conduct the experiment remotely. This camera was strategically placed to provide a high-resolution image of the specific area that the subject was most likely to use during periods of sustained rest. Additional security cameras located throughout the enclosure were also used to ensure that the subject could be monitored in real time by the experimenter in all possible locations and from several angles.

Seawater inflow valves were turned off prior to experimental sessions to minimize background noise during testing. Aerial ambient noise in each enclosure was measured at the end of every session with a Brüel & Kjær 2250 Sound Analyzer coupled to a Brüel and Kjær 4189 diffuse-field microphone (nominal sensitivity -26 dB ± 1.5 dB re 1V/Pa, 0.006 to 20 kHz). Unweighted, 1-min equivalent continuous noise levels ($L_{eq}$) were measured in ⅓-octave bands with center frequencies ranging from 0.04 to 20 kHz.

### *Acoustic Stimuli and Calibration*

The stimuli used during controlled sound exposures were 1 s pure tones. The tones had 40 msec rise/fall times to prevent transients generated at the level of the speaker. Twelve frequencies were tested: 0.063, 0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 22.6, 32, and 45.3 kHz. The stimuli were generated by a *LabVIEW* virtual instrument operated from a laptop computer. Signals were sent through a National Instruments (NI) USB-6251 DAQ device and then low-pass filtered at 250 kHz with a Krohn-Hite filter module. Low-frequency test signals (0.063 to 2 kHz) were amplified using a Radio Shack 40-Watt PA amplifier and projected from a JBL 2245H speaker. Mid-frequency signals (4 to 32 kHz) were amplified in the same manner and projected from two Fostex FT96-H speakers. The signal at 45.3 kHz was sent through a Reson VP-1000 for amplification and projected from two Tucker-Davis (TD) ES1 electrostatic speakers, which were driven by a TD ED1 electrostatic speaker driver.

Source levels were measured for each frequency prior to testing to ensure signals that were as loud as possible (at least 80 $dB_{RMS}$ re 20 $\mu$Pa sound pressure level, hereafter dB SPL) without harmonic distortion. To accomplish this, an ACO-Pacific 7016 microphone (0.005 to 120 kHz ± 2 dB) was positioned 1 m from the center of each speaker. The incoming signals were low-pass filtered at 200 kHz by a Krohn-Hite filter module and sent through the NI USB-6251 DAQ device. Following this procedure, the signal output voltages were fixed at each frequency and remained constant throughout subsequent calibration and testing. In addition to measuring source level SPL at 1 m, the signal levels were also measured for each speaker at distances of 2, 3, 4, and 5 m in an outdoor, relatively free-field environment that was comparable to the test enclosures. The 0 V (control) signal output was also measured to ensure that there were no transients or artifacts present when triggering test stimuli.

### *Procedure*

The speakers and video camera were set up in the test enclosure at least 1 h prior to the start of each experimental session to allow the subject to acclimate to the testing equipment. The position of the speaker(s) was determined by the preferred resting location of each subject. The primary speaker was placed on axis with, and at the same height as, the subject's anticipated location, as close to 1 m as the fencing would allow. To account for the directionality of high-frequency tonal signals, two speakers were used to simultaneously project the stimulus frequencies at and above 4 kHz to provide better coverage of the area. In these cases, the second speaker was placed on the adjacent or opposite side of the enclosure, either 90° or 180° relative to the primary speaker.

Each session consisted of 24 experimental trials: 12 sound exposures and 12 blank controls. The 12 control trials were identical to sound exposure trials except that the output voltage was set to zero. The 12 sound exposure trials included four presentations of each of three predetermined test frequencies. These trials were intermixed into four consecutive blocks that contained one exposure at each frequency as well as three control trials in a shuffled order.

Sessions were conducted during the late afternoon or early evening as this was the time of day that the sea otters tended to rest and exhibit calm behavior that was optimal for testing. Prior to each session, the subject was offered his last meal of the day and then left alone in the testing enclosure. The experimenter remotely monitored the subject by video and waited for specific behavioral criteria to be met. Testing was initiated when the animal was (1) within 1 to 5 m of a speaker and (2) in a relaxed behavioral state (e.g., calmly grooming or resting) with his head above the water's surface. Once these criteria were continuously maintained for 2 min, the experimenter triggered one of the two exposure types according to the predetermined testing sequence. Subsequent trials were initiated after a minimum interval of 2 min. The experimenter and an assistant recorded information from the trials in real time, including the time of each exposure, the subject's location during an exposure, and a preliminary description of each response.

Subjects were tested in blocks of similar frequencies to minimize the number of speakers needed within one session. For all subjects, high frequencies (22.6 to 45.3 kHz) were tested first, followed by low frequencies (0.063 to 2 kHz), then mid frequencies (4 to 16 kHz). Subjects were required to complete testing at each set of frequencies before moving on to the next set. Each of the four subjects completed testing in seven to nine sessions, each lasting 1 to 3 h. Some sessions were terminated before the predetermined sequence could be completed due to heightened subject activity level or lighting conditions that were insufficient for monitoring responses. In these cases, the trials were completed in a separate session on a different day. The entire experiment was conducted over a period of 4 mo, from March to June 2010.

Precautions were included in the experimental design to minimize the potential effects of auditory habituation. Within a single session, sound exposures of up to four frequencies were mixed and separated by control trials so that there was at least a 10-min interval separating exposures of the same frequency. Further, there was a minimum separation of 2 d between test sessions for each sea otter subject, and during the majority of the study, each animal was not tested more frequently than once per week.

### *Data Analysis*

The stimulus levels (dB SPL) received by the sea otter subjects were estimated for each sound exposure event from the frequency-specific source levels measured at each speaker, the subject's location within the testing enclosure during each trial, and the estimated transmission loss, assuming spherical spreading of the sound source. This was accomplished using the equation

$$RL = SL - 20 \log (r)$$

where RL is the received level, SL is the measured source level, and $r$ is the distance between the subject and the nearest projecting speaker. The assumption of spherical spreading was validated using the calibration levels measured for each test frequency at distances of 1 to 5 m. These data showed actual transmission losses from 15 to 25 log ($r$) within the 5 m range used during testing. Signal-to-noise levels were determined as the difference between the estimated received signal level on each exposure trial and the measured noise level for each session within the ⅓-octave band containing the test frequency.

The video recordings obtained during each session were processed with video editing software and referenced to the digital clock used to record the exact time of each exposure event. A red square was inserted as an encoded visual marker to indicate the 3-s time interval that bracketed each sound exposure or control trial, and the audio was stripped from the recording.[1]

Two independent observers who were unaware of the exposure conditions on each trial scored the prepared video data. Each observer was instructed to carefully monitor the subject using the red square as a visual marker for each trial interval and to compare the subject's baseline behavior (i.e., behavior during the 2 min preceding each trial) to behavior within the trial interval to determine whether a positive response had occurred. A positive response was defined as any deviation from baseline behavior that occurred during the 3-s trial interval. A negative response was defined simply as no change. Each observer was allowed to watch the trial an additional two times if a decision could not be made after the first viewing, at which time they had to make a decision. If the scores of the two observers did not agree on a given trial, the experimenter independently scored the trial after viewing the isolated trial under the same conditions as the observers. In addition to recording the outcome of each trial, the observers were asked to briefly describe each positive response. Following the experiment, a measure of Cohen's Kappa was calculated to assess inter-observer agreement on the 643 independent trials scored in the experiment.

The video scores were used to determine audible frequencies for each sea otter. To determine whether a statistically significant detection had occurred at a given frequency, positive responses on sound exposure trials were compared to the positive responses on control trials from the same session using a one-tailed Fisher's Exact Test with a 0.05 alpha level. A minimum of 4 sound exposure trials and 12 control trials were used for this analysis. If the comparison between the number of positive responses on the 4 exposures vs the 12 controls for a given frequency failed to show a significant difference, the trials were repeated in a subsequent session to double the sample size to 8 exposures and 24 controls. Increasing the sample size at frequencies that elicited fewer responses (and were likely to be less salient) allowed for more rigorous testing at the upper and lower frequency limits of each subject's hearing range.

A given test frequency was characterized as audible and assigned a PASS status when the Fisher's Exact Test yielded a significant difference between exposure and control trials. This could be achieved with either the minimum sample size ($n$ = 4 sound exposures vs $n$ = 12 controls) or the doubled sample size ($n$ = 8 vs $n$ = 24) if the minimum sample size did not result in a pass. A FAIL status was assigned to a test frequency when detection significance could not be reached after repeated sampling ($n$ = 8 vs $n$ = 24). Statistically reliable differences in exposure vs control conditions were used in this way to conservatively determine audible frequencies between 0.063 and 45.3 kHz for each of the four sea otter subjects.

To consider the effect of habituation on subject behavior during test sessions, we pooled the responses for each subject and divided these data into two categories on the basis of trial position. We compared positive and negative responses scored during the first half of sessions (sound exposure trials 1 through 6) to positive and negative responses scored during the last half of sessions (sound exposure trials 7 through 12) using a one-tailed Fisher's Exact Test. As the trials within each session were evenly distributed, this analysis allowed us to determine whether subject responsivity decreased with successive exposures in a session.

---

[1] A video link has been placed on the *Aquatic Mammals* website (see www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=694&catid=48&Itemid=101), which shows two trials clipped from a test session with a captive, adult male sea otter. The first is a *control trial* during which no signal was presented, and the second is a *sound exposure trial,* during which an 8 kHz test tone was presented. The red square delineated each trial interval for the observers, who reviewed and scored the video data while remaining blind to the experimental conditions.

**Table 1.** The aerial frequency range of hearing determined for four sea otters (*Enhydra lutris*); positive behavioral responses scored for exposure (tonal signals) and control (no sound) conditions are shown out of the total number of trials presented at each test frequency for each subject. Statistically significant detections were determined by comparing the within-frequency response rates observed under both conditions. A test frequency was characterized as audible (**PASS**) when the statistical test yielded a one-tailed $p$-value less than 0.05. Conservative estimates of each sea otter's audible hearing range (far right) were defined by the lowest and highest audible frequencies.

| | | Frequency (kHz) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0.063 | 0.125 | 0.25 | 0.5 | 1 | 2 | 4 | 8 | 16 | 22.6 | 32 | 45.3 | Audible range (kHz) |
| Wick | Exposure | 2/8 | 5/8 | 3/4 | 3/4 | 3/4 | 4/4 | 4/4 | 3/4 | 4/4 | 3/4 | 3/4 | 0/8 | 0.125-32 |
| | Control | 0/24 | 2/24 | 0/12 | 0/12 | 1/12 | 1/12 | 1/12 | 1/12 | 1/12 | 1/12 | 1/12 | 2/24 | |
| | Outcome | FAIL | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | FAIL | |
| Morgan | Exposure | 0/8 | 6/8 | 3/4 | 3/4 | 4/4 | 3/4 | 3/4 | 4/4 | 4/4 | 6/8 | 6/8 | 1/8 | 0.125-32 |
| | Control | 0/24 | 0/24 | 0/12 | 0/12 | 1/12 | 1/12 | 1/12 | 1/12 | 0/12 | 3/24 | 3/24 | 3/24 | |
| | Outcome | FAIL | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | FAIL | |
| Taylor | Exposure | 1/8 | 2/8 | 2/8 | 3/8 | 2/8 | 3/4 | 3/4 | 3/4 | 4/4 | 5/8 | 1/8 | 0/8 | 0.5-22.6 |
| | Control | 0/24 | 0/24 | 0/24 | 1/24 | 2/24 | 1/12 | 0/12 | 0/12 | 3/12 | 3/24 | 3/24 | 3/24 | |
| | Outcome | FAIL | FAIL | FAIL | **PASS** | FAIL | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | FAIL | FAIL | |
| Odin | Exposure | 3/8 | 4/4 | 4/4 | 4/4 | 4/4 | 4/4 | 4/4 | 7/8 | 3/8 | 0/8 | 2/8 | 2/8 | 0.125-8 |
| | Control | 2/24 | 1/12 | 1/12 | 0/12 | 1/12 | 1/12 | 2/12 | 4/24 | 3/24 | 3/24 | 1/24 | 1/24 | |
| | Outcome | FAIL | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | **PASS** | FAIL | FAIL | FAIL | FAIL | |

## Results

The controlled exposure approach identified audible frequencies for each subject as shown in Table 1. The data obtained from both Wick and Morgan showed audible frequency ranges extending from 0.125 to 32 kHz, a span of nine octaves. These two sea otters exhibited the widest frequency range of hearing of the four individuals tested. Taylor's frequency range of hearing extended from 0.5 to 22.6 kHz; however, Taylor failed to show a significant number of positive responses at 1 kHz. Odin's estimated range of audible frequencies spanned only six octaves, from 0.125 to 8 kHz. None of the sea otters showed significant detections at 0.063 or 45.3 kHz, the lowest and highest frequencies tested. In addition, none of the subjects showed decreased responsivity to trials presented in the latter portion of testing sessions (Fisher's Exact Tests, $p > 0.05$), indicating that auditory habituation did not influence the likelihood of observing a positive response in this paradigm.

Received signal levels ranged from 71 to 110 dB SPL during testing, depending on the frequency and the subject's position relative to the speaker. When compared across subjects, the maximum variation of received levels within a particular frequency was at 32 kHz (range: 75 to 93 dB). The test frequencies with lowest variability in received levels were 0.063, 1, and 2 kHz (range: 93 to 99 dB, 90 to 98 dB, and 91 to 98 dB, respectively). Ambient noise levels measured in each testing enclosure were consistent throughout the experiment. When the noise profiles were compared across enclosures, they showed similar trends—background noise was highest at 0.125 kHz and decreased with increasing frequency. Analysis of the subjects' received signal levels relative to corresponding ambient noise data resulted in consistently high signal-to-noise levels on sound exposure trials. At test frequencies from 0.063 to 1 kHz, signal-to-noise levels ranged from 34 to 69 dB. At test frequencies from 2 to 16 kHz, signal-to-noise levels were 51 to 88 dB. The ⅓-octave band level of ambient noise was lowest (≤ 14 dB) at 20 kHz. While noise levels were not measured above 20 kHz, the typical pattern of declining noise with increasing frequency observed in the outdoor test environments suggest that the ⅓-octave band levels of noise from 22.6 to 45.3 kHz would not be higher than that measured at 20 kHz. Signal-to-noise levels at test frequencies of 22.6, 32, and 45.3 kHz are thus assumed to be a minimum of 57 dB.

The discrete (positive or negative response) scores from the blind observers showed agreement on 93% of trials (Cohen's Kappa = 0.822), with 42 of 643 trials settled by a third reviewer of the video. A variety of response types were reported. The observers recorded startle responses, usually characterized by an abrupt full-body spasm; orienting responses, in which the sea otter turned his head or performed a visual search behavior; directed movements, either toward or away from the speaker; and interruptions or pauses in baseline behavior. Response magnitude also varied, both within and between subjects. Relatively high-magnitude responses, such as exaggerated and abrupt alterations in baseline behavior, sometimes lasted up to 10 s post exposure. Responses that were relatively low in magnitude, such as pauses in baseline behavior or brief head turns, also occurred. High-quality video footage and a testing procedure that required extended resting and/or relaxed baseline behavior from the subject prior to every trial made these low-magnitude responses discernible to the observers. Similar mild responses were also occasionally recorded during control trials: 6 to 9% of control trials were scored as positive responses, across subjects. These "false positives" provided an essential measure of each sea otter's level of arousal or vigilance during a session, against which the reliable responses on sound exposure trials were statistically detected using the Fisher's Exact Test.

## Discussion

The widest confirmed range of audible frequencies for the sea otters—extending nine octaves from 0.125 to 32 kHz—is consistent with what is known about auditory capabilities in other mustelids. Preliminary hearing data for North American river otters (*Lontra canadensis*) suggest that they are also sensitive to airborne sounds up to 32 kHz (see Evans & Bastian, 1969; Gunn, 1988). Both the domestic ferret (*Mustela putorius furo*) and the least weasel (*Mustela nivalis*) have even broader ranges of hearing sensitivity, spanning over 10 octaves up to 44 and 51 kHz, respectively (Heffner & Heffner, 1985; Kelly et al., 1986). The slightly narrower hearing ranges observed for the sea otters compared to these terrestrial mustelids may reflect the constraints inherent to this testing method. At test signals approaching the high- and low-frequency limits of the hearing range, even high-amplitude sounds have relatively low sensation levels. In other words, decreased signal saliency at these frequency extremes is less likely to elicit strong behavioral responses. This issue is confounded at low frequencies where responses may also be influenced by higher background noise, which reduces signal-to-noise levels. Therefore, although Wick and Morgan did not reliably respond to sounds below 0.125 kHz or above 32 kHz in this study, it is likely that their functional hearing ranges are wider than predicted by the controlled exposure method. Based on our conservative assessment, the 0.125 to 32 kHz range measured in Wick and Morgan represents a minimum estimate of the range of aerial hearing that is likely typical of wild sea otters.

The results from the oldest sea otter tested (Taylor) showed a narrower frequency span that was not continuous. This may be explained by a combination of factors, including individual hearing differences and environmental effects. Taylor's estimated high-frequency hearing limit was not likely constrained by ambient noise (received signal-to-noise levels exceeded 57 dB). Rather, Taylor's failure to respond to tones above 22.6 kHz may be attributable to presbycusis (Gates & Mills, 2005). Taylor was 16 y at the time of testing—close to the maximum reported age of 20 y for a wild sea otter (Monson et al., 2000), and age-related hearing loss may have impaired his high-frequency hearing.

Odin did not reliably detect test signals higher than 8 kHz. It is unlikely that his lack of responsivity to higher frequency signals was influenced by environmental effects (received signal-to-noise levels exceeded 51 dB at all frequencies) or age-related effects (Odin was 7 y at the time of testing). Odin's anomalous results in the current study were compared to independent psychophysical data that were collected with him at our laboratory prior to the current study.[2] During these direct behavioral measurements of hearing sensitivity, despite rigorous training and repeated testing, Odin was unable to detect airborne pure tone signals above 8 kHz (see Ghoul, 2010, for unpublished data). The auditory data obtained from the controlled exposure approach used here show an aerial hearing range for Odin that is entirely consistent with the psychophysical results. The agreement between these two data sets obtained independently with the same subject is noteworthy: it demonstrates that our passive, controlled exposure method provided a robust and accurate measurement of aerial hearing range for this individual. Further, these results confirm that Odin's limited hearing range is not likely to be representative of species-typical hearing capability given the expanded hearing ranges determined for Wick and Morgan in the present study.

This investigation provides much needed insight into the auditory capabilities of sea otters. On a practical level, the findings will allow resource managers to make more informed decisions by incorporating species-specific information into risk assessments. For example, the frequency range of hearing estimated in the present study can be used in regulatory contexts to identify or exclude airborne sounds of potential concern. Furthermore, hearing range measurements have recently been used to develop precautionary weighting functions for marine mammals (Southall et al., 2007). In the absence of any auditory data for sea otters, Finneran & Jenkins (2012) proposed that sea otters should be classified with otariid pinnipeds (sea lions and fur seals) for this purpose. The similar aerial hearing ranges for the sea otters measured herein, as compared to available data for otariids (see Moore & Schusterman, 1987; Mulsow & Reichmuth, 2010; Mulsow et al., 2011; Reichmuth et al., 2013), provides the first experimental support for this grouping. It remains to be seen whether sea otters, like otariids, will exhibit hearing ranges under water that are similar to those measured in air.

The most pressing research need concerning sound reception in sea otters remains the measurement of species-typical hearing sensitivity (audiograms) both in air and under water. Additionally, comparative studies of auditory anatomy, neurophysiological assessment of auditory function, and detailed characterization of acoustic communication in natural settings are all required to better describe the acoustic ecology of this species. Finally, opportunistic or experimental field investigations of behavioral responses to sound are necessary to evaluate how wild sea otters respond to offshore and nearshore noise sources. Such efforts would add to the limited available knowledge of hearing and acoustic communication in sea otters (Riedman & Estes, 1990; McShane et al., 1995; Solntseva, 2007; Ghoul et al., 2009).

The controlled sound exposure method used herein demonstrates that sea otters are acoustically vigilant and exhibit measurable behavioral responses to sound. The method was statistically rigorous, non-invasive, relatively rapid, and did not require training of captive animals. We successfully avoided confounds of habituation by carefully structuring the schedule of sound exposures received by a given subject. Certain features of this method, such as incorporation of blank control trials to identify false positive rates and response scoring by observers unaware of experimental conditions, may prove useful in behavioral response studies of free-ranging animals, regardless of whether response data are obtained visually or with specialized tags (e.g., Miller et al.,

---

[2] Preliminary estimates of auditory detection thresholds were measured with Odin prior to the current study so that an aerial audiogram could be obtained for this individual. Odin's hearing was suspected to be abnormal early on in the testing phase because of elevated thresholds. This was unable to be confirmed at the time because sea otter hearing was previously unstudied.

2014). A similar passive approach could also be applied to obtain information on functional hearing ranges in species that are not typically maintained in captivity or that may be difficult to test with conventional audiometric methods.

### Acknowledgments

The protocols described herein were conducted with the approval of the Institutional Animal Care and Use Committees of the University of California Santa Cruz and the Monterey Bay Aquarium under U.S. Fish and Wildlife Service Permit MA186914-1. Support was provided in part by the Bureau of Ocean Energy Management through Award M09PC00022-004 to C. Reichmuth; the Packard Ocean Sciences Endowment at UC Santa Cruz; and the Sea Otter Research and Conservation Program at the Monterey Bay Aquarium in Monterey, California. The authors gratefully acknowledge Drew Burrier, Arial Brewer, William Hughes, and Michelle Hannenburg for assisting with experimental sessions and observational scoring; Terrie Williams and Traci Kendall for providing access to animal subjects; Brandon Southall, Lilian Carswell, Peter Cook, and Andrew Rouse for commenting on earlier versions of this paper; as well as the entire team at the Cognition and Sensory Systems Laboratory at UC Santa Cruz for enabling this study. Portions of this research were presented at the 2nd International Conference on the Effects of Noise on Aquatic Life in Cork, Ireland (2010) and at the 161st meeting of the Acoustical Society of America in Seattle, Washington (2011).

### Literature Cited

Dahlheim, M. E., & Ljungblad, D. K. (1990). Preliminary hearing study on gray whales (*Eschrichtius robustus*) in the field. In J. A. Thomas & R. Kastelein (Eds.), *Sensory abilities of cetaceans: Laboratory and field evidence* (pp. 335-346). New York: Plenum Press. http://dx.doi.org/10.1007/978-1-4899-0858-2_22

Deecke, V. B. (2006). Studying marine mammal cognition in the wild: A review of four decades of playback experiments. *Aquatic Mammals*, *32*(4), 461-482. http://dx.doi.org/10.1578/AM.32.4.2006.461

Evans, W. E., & Bastian, J. (1969). Marine mammal communication: Social and ecological factors. In H. T. Anderson (Ed.), *The biology of marine mammals* (pp. 425-475). New York: Academic Press.

Finneran, J. J., & Jenkins, A. K. (2012). *Criteria and thresholds for U.S. Navy acoustic and explosive effects analysis* (Unpublished report). San Diego: Space and Naval Warfare Systems Center Pacific. 60 pp.

Frankel, A. S., & Clark, C. W. (2000). Behavioral responses of humpback whales (*Megaptera novaeangliae*) to full-scale ATOC signals. *The Journal of the Acoustical Society of America*, *108*, 1930-1937. http://dx.doi.org/10.1121/1.1289668

Gates, G. A., & Mills, J. H. (2005). Presbycusis. *The Lancet*, *366*, 1111-1120. http://dx.doi.org/10.1016/S0140-6736(05)67423-5

Ghoul, A. (2010). *Preliminary investigations of sound reception in southern sea otters (*Enhydra lutris nereis*)* (Unpublished Master's thesis). University of California Santa Cruz.

Ghoul, A., & Reichmuth, C. (2012). Sound production and reception in the southern sea otter (*Enhydra lutris nereis*). In A. N. Popper & A. Hawkins (Eds.), *The effects of noise on aquatic life* (pp. 157-159). Berlin: Springer-Verlag. http://dx.doi.org/10.1007/978-1-4419-7311-5_35

Ghoul, A., Reichmuth, C., & Mulsow, J. (2009, October). Source levels and spectral analysis of southern sea otter (*Enhydra lutris nereis*) scream vocalizations. *Proceedings of the Eighteenth Biennial Conference on the Biology of Marine Mammals*, Quebec City, Canada.

Gunn, L. M. (1988). *A behavioral audiogram of the North American river otter (*Lutra canadensis*)* (Unpublished Master's thesis). San Diego State University, San Diego, CA.

Heffner, H. E., & Heffner, R. E. (1985). Hearing in mammals: The least weasel. *Journal of Mammalogy*, *66*, 745-755. http://dx.doi.org/10.2307/1380801

International Union for Conservation of Nature (IUCN). (2013). *2013 IUCN red list of threatened species*. Retrieved 10 June 2014 from www.iucnredlist.org.

Kastelein, R. A., van Ligtenberg, C. L., Gjertz, I., & Verboom, W. C. (1993). Free field hearing tests on wild Atlantic walruses (*Odobenus rosmarus rosmarus*) in air. *Aquatic Mammals*, *19*(3), 143-148.

Kastelein, R. A., Steen, N., Gransier, R., Wensveen, P. J., & de Jong, C. A. F. (2012). Threshold received sound pressure levels of single 1-2 kHz and 6-7 kHz upsweeps and downsweeps causing startle responses in a harbor porpoise (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, *131*, 2325-2333. http://dx.doi.org/10.1121/1.3682032

Kellogg, W. N., & Kohler, R. (1952). Reactions of the porpoise to ultrasonic frequencies. *Science*, *116*, 250-252. http://dx.doi.org/10.1126/science.116.3010.250

Kelly, J. B., Kavanagh, G. L., & Dalton, J. C. H. (1986). Hearing in the ferret (*Mustela putorius*): Thresholds for pure tone detection. *Hearing Research*, *24*, 269-275. http://dx.doi.org/10.1016/0378-5955(86)90025-0

Madsen, P. T., Johnson, M., Miller, P. J. O., Aguilar Soto, N., Lynch, J., & Tyack, P. L. (2006). Quantitative measures of air-gun pulses recorded on sperm whales (*Physeter macrocephalus*) using acoustic tags during controlled exposure experiments. *The Journal of the Acoustical Society of America*, *120*, 2366-2379. http://dx.doi.org/10.1121/1.2229287

McShane, L. J., Estes, J. A., & Riedman, M. L. (1995). Repertoire, structure, and individual variation of vocalizations in the sea otter. *Journal of Mammalogy*, *76*, 414-427. http://dx.doi.org/10.2307/1382352

Miller, P. J. O., Antunes, R. N., Wensveen, P. J., Samarra, F. I. P., Alves, A. C., Tyack, P. L., . . . Thomas, L. (2014). Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *The Journal of the Acoustical Society of America*, *135*, 975-993. http://dx.doi.org/10.1121/1.4861346

Monson, D., Estes, J. A., Siniff, D. B., & Bodkin, J. B. (2000). Life history plasticity and population regulation in sea otters. *Oikos*, *90*, 457-468. http://dx.doi.org/10.1034/j.1600-0706.2000.900304.x

Moore, P. W., & Schusterman, R. J. (1987). Audiometric assessment of northern fur seals (*Callorhinus ursinus*). *Marine Mammal Science, 3,* 31-53. http://dx.doi.org/10.1111/j.1748-7692.1987.tb00150.x

Mulsow, J., & Reichmuth, C. (2010). Psychophysical and electrophysiological aerial audiograms of a Steller sea lion (*Eumetopias jubatus*). *The Journal of the Acoustical Society of America*, *127*, 2692-2701. http://dx.doi.org/10.1121/1.3327662

Mulsow, J., Finneran, J. J., & Houser, D. S. (2011). California sea lion (*Zalophus californianus*) aerial hearing sensitivity measured using auditory steady-state response and psychophysical methods. *The Journal of the Acoustical Society of America*, *129*, 2298-2306. http://dx.doi.org/10.1121/1.3552882

Nowacek, D. P., Thorne, L. H., Johnston, D. W., & Tyack, P. L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, *37*, 81-115. http://dx.doi.org/10.1111/j.1365-2907.2007.00104.x

Reichmuth, C., Holt, M. M., Mulsow, J., Sills, J. M., & Southall, B. L. (2013). Comparative assessment of amphibious hearing in pinnipeds. *Journal of Comparative Physiology A*, *199*, 491-507. http://dx.doi.org/10.1007/s00359-013-0813-y

Riedman, M. L., & Estes, J. A. (1990). *The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history* (USFWS Biological Report 90[14]). Washington, DC: U.S. Fish and Wildlife Service.

Scammon, C. M. (1968). *The marine mammals of the northwestern coast of North America described and illustrated: Together with an account of the American whale fishery* [Re-issue]. New York: Dover Publications.

Solntseva, G. N. (2007). *Morphology of the auditory and vestibular organs in mammals, with emphasis on marine species*. Sofia, Bulgaria: Pensoft Publishers & Brill Academic Publishers. http://dx.doi.org/10.1163/ej.9789004162020.1-244

Southall, B. L., Moretti, D., Abraham, B., Calambokidis, J., DeRuiter, S. L., & Tyack, P. L. (2012). Marine mammal behavioral response studies in southern California: Advances in technology and experimental methods. *Journal of Marine Science and Technology*, *46*, 48-59.

Southall, B. L., Berkson, J., Bowen, D., Brake, R., Eckman, J., Field, J., . . . Winokur, R. (2009). *Addressing the effects of human-generated sound on marine life: An integrated research plan for U.S. federal agencies*. Washington, DC: Interagency Task Force on Anthropogenic Sound and the Marine Environment of the Joint Subcommittee on Ocean Science and Technology.

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R. Jr., . . . Tyack, P. L. (2007). Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquatic Mammals* (Special Issue), *33*(4), 412-522.

Tyack, P. L., Gordon, J., & Thompson, D. (2003). Controlled exposure experiments to determine the effects of noise on marine mammals. *Marine Technology Society Journal*, *37*, 41-53. http://dx.doi.org/10.4031/002533203787537087

U.S. Fish and Wildlife Service (USFWS). (2003). *Final revised recovery plan for the southern sea otter (*Enhydra lutris nereis*)*. Portland, OR: USFWS. 165 pp.