

Hearing in the sea otter (*Enhydra lutris*): auditory profiles for an amphibious marine carnivore

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Abstract In this study we examine the auditory capabilities of the sea otter (*Enhydra lutris*), an amphibious marine mammal that remains virtually unstudied with respect to its sensory biology. We trained an adult male sea otter to perform a psychophysical task in an acoustic chamber and at an underwater apparatus. Aerial and underwater audiograms were constructed from detection thresholds for narrowband signals measured in quiet conditions at frequencies from 0.125–40 kHz. Aerial hearing thresholds were also measured in the presence of octave-band masking noise centered at eight signal frequencies (0.25–22.6 kHz) so that critical ratios could be determined. The aerial audiogram of the sea otter resembled that of sea lions and showed a reduction in low-frequency sensitivity relative to terrestrial mustelids. Best sensitivity was -1 dB *re* 20 μ Pa at 8 kHz. Under water, hearing sensitivity was significantly reduced when compared to sea lions and other pinniped species, demonstrating that sea otter hearing is primarily adapted to receive airborne sounds. Critical ratios were more than 10 dB higher than those measured for pinnipeds, suggesting that sea otters are less efficient than other marine carnivores at extracting acoustic signals from background noise, especially at frequencies below 2 kHz.

Keywords Sea otter · Hearing · Audiogram · Masking · Critical ratio

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Introduction

Sea otters (*Enhydra lutris*) are coastal-living marine mammals with a unique life history—while they forage under water on benthic invertebrates, they perform necessary biological functions relating to communication, reproduction, and thermoregulation primarily at the water's surface. Remarkably little is known about the sensory biology of sea otters. Observations suggest that they use a combination of environmental cues to perform critical behaviors (Kenyon 1969; Hines and Loughlin 1980; Kvitek et al. 1991). However, the extent to which their senses are adapted for amphibious living is poorly described.

Sea otters are one of several mustelid carnivores to adopt an aquatic lifestyle, but only one of two extant species (sea otter and marine otter, *Lontra felina*) to inhabit the marine environment. In contrast to the pinnipeds (seals, sea lions, and walrus) which diverged from terrestrial carnivores more than 25 million years ago (Berta 2012), the ancestors of modern sea otters entered the sea only 3–5 million years ago (Berta and Morgan 1985), making their land-to-sea transition a relatively recent one. It is likely that sea otters have some degree of sensory specialization relative to other mustelids that parallel the morphological, physiological, and ecological traits that have been influenced by their transition from land to sea (see Estes 1989; Bininda-Emonds et al. 2001). For example, sea otters exhibit a well-developed system for visual accommodation under water, with adaptive features that are derived from those of terrestrial mammals, without compromising the ability to see well in air (Murphy et al. 1990).

Few studies have commented on the auditory anatomy of sea otters (but see early reference in Pocock 1928). Kenyon (1969) noted that when compared to their semi-aquatic and terrestrial relatives, the sea otter's external ears are small

and curled, and while held erect when at the water's surface, they are tightly folded downwards against the head when diving. Based on these observations, Kenyon suggested that this mobile pinna might be an aquatic adaptation designed to prevent water from entering the ear canal when submerged. Further, Solntseva (2007) identified several derived features of the outer and middle ear of sea otters (e.g., pinna is reduced in size, with conical shape; thickening of the tympanic membrane; change in size and form of ossicles) that are shared with otariid pinnipeds, and apparently related to their marine lifestyle. However, it is unknown whether such anatomical modifications are related to aquatic hearing capabilities or are primary adaptations for swimming and diving.

Published research concerning the significance of sound to sea otters is limited to two studies that describe the individual variation and vocal repertoire of airborne calls (McShane et al. 1995) and vocal communication at the surface between females and their dependent pups (Sandegren et al. 1973). Sea otters have never been observed to produce vocalizations under water; however, certain calls emitted in air are loud enough to penetrate beneath the water's surface (Ghoul and Reichmuth 2012). As sea otters feed primarily on sessile, benthic invertebrates, it is unlikely that they rely on acoustic cues during foraging. However, the manner in which sea otters utilize their senses to acquire and capture prey has not been studied. Richardson (1995a) reviewed available information regarding the behavioral responses of wild sea otters to underwater sounds. These scant data, drawn from unpublished reports, suggest that sea otters at the water's surface are relatively insensitive to marine seismic operations and underwater playbacks of industrial sounds (Riedman 1983, 1984) and perhaps more sensitive to biologically relevant sounds projected in air or in water (Davis et al. 1987). More recent assessment of the behavioral responses of captive sea otters to tonal sounds indicates audibility of airborne sounds extending to at least 32 kHz (Ghoul and Reichmuth 2014). However, without direct audiometric measures available for the species, predicting the relative significance of airborne and underwater acoustic cues is problematic.

An improved understanding of the acoustic ecology of sea otters is needed to support ongoing conservation efforts. Despite federal protection throughout their range, and the implementation of long-term management programs, several sea otter populations (e.g., California and southwestern Alaska) remain designated as threatened under the Endangered Species Act (1973). Higher than expected mortality rates (Tinker et al. 2006) have been attributed to the combined effects of resource limitation, contaminant exposure, entanglement, and coastal pollution, among other factors (Estes et al. 2003; Jessup et al. 2007; US Fish and Wildlife Service 2009). Further, sea

otters are vulnerable to several sub-lethal threats because of their overall dependence on a narrow margin of usable coastal habitat and their individual confinement to small home ranges within that habitat (Tinker et al. 2013). At present, the lack of information about their auditory sense makes it difficult to anticipate whether sound-generating activities in or near areas used by sea otters may be harmful to them. Such anthropogenic activities include those related to recreation, transportation, construction, seismic imaging, and military operations. To address this knowledge gap, hearing research is needed for the species (Southall et al. 2009).

In this study, we behaviorally measured the auditory sensitivity of a trained adult male sea otter across the frequency range of hearing under water and in air. The measurements were conducted in quiet laboratory environments to provide amphibious hearing profiles for the species. Hearing was also evaluated in a masking scenario by measuring aerial auditory thresholds for the same subject under conditions of controlled noise so that critical ratios could be estimated and used to improve the efficacy of management practices.

Materials and methods

Subject and study site

Auditory measurements were obtained from a captive southern sea otter (*Enhydra lutris nereis*) over the course of a study period extending from April 2011 to March 2013. The subject was an adult male identified as *Charlie* (USGS #2788-97R) that was 14 years old at the beginning of the study. *Charlie* was obtained on a research loan from the Aquarium of the Pacific in Long Beach, California, to the University of California Santa Cruz. He had a known health history with no reported otological problems and no systemic exposure to ototoxic medication. Due to his captive history in a public display facility, this sea otter had substantial experience with operant-conditioning training for behavioral management and animal care purposes.

Charlie was housed in free-flow, natural seawater pools surrounded by adjacent haul-out areas at Long Marine Laboratory, Santa Cruz, California, USA. His diet was not constrained for experimental purposes, and he typically received one-third to one-half of his daily ration of freshly thawed seafood (shrimp, squid, and clam) during participation in experimental sessions. His body weight was 27–29 kg during the experiment, an average size for an adult male southern sea otter (Riedman and Estes 1990). His inter-aural distance was 20 cm in curvilinear length (measured dorsally) or 10 cm in linear distance between the two pinnae.

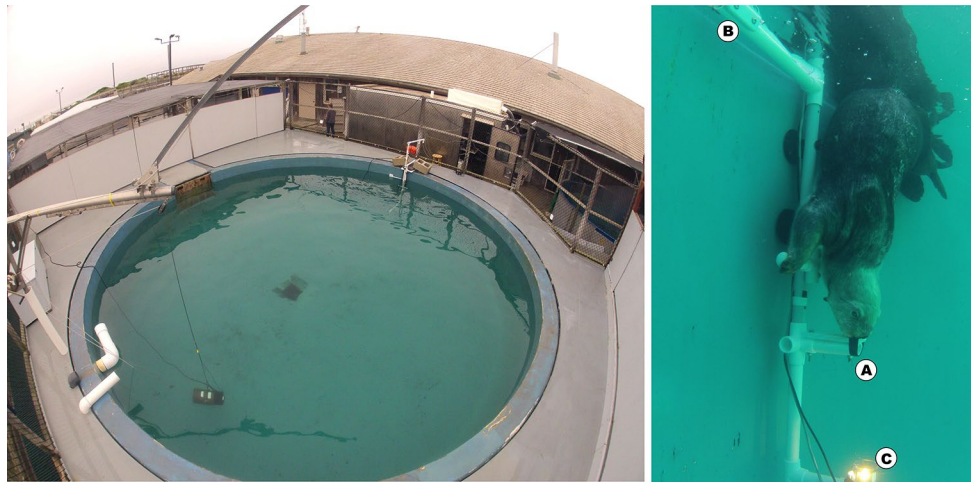


Fig. 1 (Left panel) The seawater-filled pool used to test the hearing of the sea otter under water. The J11 transducer and testing apparatus are visible on the *left* and *right* sides of the enclosure, respectively.

(Right panel) The sea otter positioned at the apparatus during the hearing test procedure; the listening station (a), the response target (b), and the trial light (c) are shown

Underwater audiometry

Testing environment

The testing pool was a concrete, epoxy-lined, partially in-ground tank that was 7.6 m in diameter and 1.8 m deep (Fig. 1, left panel). The pool was filled with natural seawater that was between 10 and 14 °C. During testing, ambient conditions were as calm as possible. There was no flowing water within 20 m of the test pool and there was no extraneous activity in adjacent areas of the facility.

Ambient noise measurement

Ambient noise in the underwater testing environment was measured prior to every test session. A Reson TC4032 low-noise hydrophone (nominal sensitivity -170 dB *re* 1 μ Pa/V, 0.01–80 kHz, ± 2.5 dB) was placed at the position of the subject's head during testing and coupled to a battery-powered Brüel and Kjær 2250 Sound Analyzer (48 kHz sampling rate). Noise spectral density levels from 0.04 to 20 kHz were calculated from 1/3-octave band levels sampled over 1 min. To cover the entire frequency bandwidth used during audiometric testing, additional noise measurements were obtained in a similar manner at the end of the experiment using the same hydrophone coupled to a battery-powered Fostex FR-2 Field Memory Recorder (192 kHz sampling rate). These measurements (0.04–78 kHz) were made in the absence of the subject, as well as with the subject positioned at the underwater listening station and the hydrophone 15 cm from the center position of the subject's head.

Experimental apparatus

The experimental apparatus used for underwater testing was constructed of a water-filled, PVC pipe frame that was firmly secured to the pool wall, in a fixed location. The apparatus included a listening station that was designed to maintain the subject's head in a stable orientation at a depth of 0.5 m during testing; a handlebar, 15 cm above the station, which the sea otter held onto with his front paws to stay submerged and motionless when listening; a response target located above the water's surface, 60 cm from the station; an underwater camera that allowed an experimenter to observe the sea otter during test sessions; and a light that was controlled by the experimenter and used to indicate the trial interval (Fig. 1, right panel). A small buzzer, used as a conditioned reinforcer, was also coupled to the apparatus frame, above the surface. The apparatus was designed so that the sea otter could comfortably maintain an inverted body position with his head and upper body submerged and oriented downward, and his hindquarters relaxed and floating at the surface (Fig. 1, right panel). This orientation was necessary to avoid a continuous release of noise-generating bubbles from the sea otter's pelage (a condition that occurred only when the animal's body was completely submerged) and to allow background noise conditions to remain sufficiently low for audiometry.

Acoustic stimuli and calibration

The sea otter was tested using narrowband signals that allowed for measurement of hearing sensitivity at specific frequencies. The signal duration (500 ms) was selected to

exceed the time constant necessary for complete temporal summation as determined for other terrestrial and marine carnivores (Costalupes 1983b; Holt et al. 2012). The acoustic signals were narrowband, frequency-modulated (FM) sweeps that were appropriate for audiometry in reverberant enclosures (Kastelein et al. 2002; Finneran and Schlundt 2007). The linear rise- and fall-times of the sweep were 5 % of the signal duration (25 ms) and the bandwidth of the sweep was 10 % of the center frequency. The signals were centered on the following eleven frequencies: 0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 22.6, 32, and 38.1 kHz. National Instruments (NI) LabVIEW software with the Hearing Test Program (HTP) virtual instrument (Finneran 2003) was used to generate the signals. Signals generated in HTP were sent through a desktop PC to a NI USB-6259 data acquisition (DAQ) module, a Krohn-Hite 3364 analog band-pass filter, a Tucker-Davis PA5 programmable attenuator, and a Hafler P1000 amplifier prior to reaching an underwater transducer. Test signals from 0.125 to 2 kHz were projected through a J11 transducer provided by the US Naval Undersea Warfare Center. Test signals from 4 to 38.1 kHz were projected through an International Transducer Corporation (ITC) 1042 hydrophone.

The precise configuration of the transducer relative to the fixed position of the testing apparatus was chosen to minimize variability in the received signal. The placement of the transducer was independently determined for each test frequency through sound field mapping (in the absence of the subject). The received sound pressure level (SPL) of each test signal was measured at 27 points within a rectangular 20 × 20 × 10 cm imaginary grid that surrounded the position of the subject's head at the listening station. The transducer position was determined for a given test frequency when received signal SPLs measured at each position in the grid varied by ≤ 3 dB from the center position.

The signal generation system was calibrated prior to every session (in the absence of the subject). Test signals were projected at various levels and received by the Reson TC4032 hydrophone, which was mounted in a fixed position corresponding to the center of the subject's head (between the ears) during testing. Signals from the receiving hydrophone passed through the same filter, DAQ module, and HTP software as previously described, and were then measured (in SPL) and inspected in both time and frequency domains to confirm stimulus integrity. Signal voltage was attenuated over a 50-dB range to ensure linearity of attenuation during audiometry.

Psychoacoustic testing

An auditory go/no-go procedure was used to measure the sea otter's underwater thresholds. Experimental sessions were conducted from a hidden control room that contained

the stimulus generation and calibration equipment. This room was equipped with a video surveillance system that allowed an experimenter to observe the session from the underwater camera. The experimenter conducted every aspect of the session except for the delivery of food reinforcement to the sea otter. This was provided by a trainer who was located in the testing enclosure, but remained unaware of the specific experimental conditions. At the beginning of the session, the sea otter was given access to the testing pool, where he waited for the trainer's cue to dive to the underwater apparatus and begin the signal detection task. Once the sea otter was correctly positioned with his nose on the listening station (Fig. 1, right panel), the experimenter activated the underwater light. This light stayed on for the duration of the trial interval (4 s). Two trial types—*signal-present* trials and *signal-absent* trials—were presented within each session. When a signal was projected, the sea otter was trained to report detection by leaving the station, swimming up to the surface, and touching his nose to the response target. During trials when the signal was absent, the sea otter was trained to remain in position at the underwater listening station for the full duration of the trial interval (until the trial light turned off). The experimenter marked each of these correct responses with the buzzer, which was immediately followed by the delivery of one shrimp from the trainer. When the sea otter failed to touch the response target during a signal-present trial (*miss*), or touched the response target during a signal-absent trial (*false alarm*), the subject was recalled to the surface without reinforcement by the trainer, and was redirected to the underwater station to begin the next trial. An example of the underwater hearing test is shown in Online Resource 1.

Each session contained 30–45 trials with a pre-determined proportion of signal-present trials that was 60–70 %. The ratio of signal-present trials was adjusted between sessions to maintain a stable response bias for the subject throughout the experiment. Each session contained the prescribed ratio of trial types shuffled in a pseudorandom manner, with the trial order constrained by a maximum run length (number of trials of the same type, presented sequentially) of four. This provided increased variability over a typical Gellermann (1933) series.

The first signal presented in a session was of a level that was easily detected by the subject (about 20 dB above threshold, based on performance during previous training sessions). Following correct detection by the subject at the highest level, the signal was lowered and raised in 4-dB steps according to an adaptive staircase procedure (Cornsweet 1962). Following each correct detection, the signal level was lowered on the next signal-present trial until the subject missed, at which point the signal level was raised until correctly detected. This step-wise adjustment of the signal based on the subject's response on the previous trial

was continued until at least five descending trial series ending in a miss were completed. The signal level was then raised to the starting level, and several more trials were conducted to ensure that the session ended with a string of correct responses. Each session lasted 15–20 min, and the sea otter usually completed one session per day. Testing at a single frequency was continued until a reliable hearing threshold could be calculated, at which point testing at the next frequency would begin. To control for practice effects, the frequency testing order was shuffled, and after testing at the last frequency was completed, additional sessions were conducted at the first test frequency to ensure that this threshold estimate remained stable over time.

Threshold determination

Preliminary thresholds were estimated for every test session that included at least five descending trial series. First, the trials within the session were divided into three phases: the *warm-up* phase, which included the first series of trials leading up to, but not including, the first miss of the first descending series; the *test* phase, which included all trials within the five descending series, including the last descending miss; and the *cool-down* phase, which included the trials containing signals at supra-threshold levels. For sessions that included more than five descending series, only the last five were included in the test phase, and all preceding trials were considered a part of the warm-up phase. A measure of the subject's response bias was also estimated for each session by calculating a *false alarm rate*, defined as the number of signal-absent trials in which the subject reported a detection, out of the total number of signal-absent trials. This metric allowed the experimenter to carefully monitor and control the subject's response bias on a session-by-session basis.

Individual session thresholds were calculated according to the method of Dixon and Mood (1948). To ensure that the hearing threshold obtained represented stable performance (free of practice effects) two criteria were applied. Only sessions with low variability (standard deviation <3 dB) and non-significant improvement in performance with session length (measured by regression analysis) were considered to be acceptable. Once three sessions meeting these criteria were obtained, two additional criteria were evaluated: if the individual session thresholds were within 3 dB of one another, and the combined false alarm rates from the test phases of these sessions were >0 % and <30 %, then testing at that frequency was completed. The final hearing threshold at each frequency was determined from the average of the thresholds obtained in the three individual sessions.

Underwater hearing thresholds (dB *re* 1 μ Pa) were plotted as a function of frequency (kHz) to construct the sea

otter's underwater audiogram. Hearing capabilities were described as in Reichmuth et al. (2013), with the frequency range of best hearing defined as falling within 20 dB of the lowest measured threshold. The sea otter's underwater audiogram was compared to those measured for several other marine carnivores, obtained using similar methods in relatively quiet testing pools.

Aerial audiometry

Testing environment

The aerial hearing assessment was conducted in a modified hemi-anechoic chamber (Eckel Industries). This testing room was a 3.3 \times 2.3 \times 2.2 m double-walled, stainless steel enclosure lined with sound insulating material and sound absorbing wedges to minimize acoustic reflections (Fig. 2, left panel). It included an adjacent, sound-isolated control room that provided space for the experimenter and equipment. The chamber was located near the subject's living enclosure and provided a quiet, direct-field acoustic environment that was highly controlled (for details see Reichmuth et al. 2013).

Ambient noise measurement

Ambient noise in the acoustic chamber was measured on a total of 21 days spanning the period of aerial testing. The measurements were obtained with the Brüel and Kjær 2250 Sound Analyzer coupled to a Brüel and Kjær 4189 diffuse-field microphone (nominal sensitivity -26 dB \pm 1.5 dB *re* 1 V/Pa, 0.006–20 kHz). Noise spectral density levels from 0.04 to 20 kHz were calculated from 1/3-octave band levels sampled over 1 min. Above 20 kHz, equipment limitations prevented ambient noise measurements below 0 dB *re* 20 μ Pa.

Experimental apparatus

The apparatus used for aerial testing was located inside of the acoustic chamber and consisted of a 106 \times 70 \times 78 cm rectangular wire crate, to which the listening station and response target were mounted (Fig. 2, right panel). The station was directly in front of the subject (at eye-level) and the response target was 36 cm to the left of the station, on the same horizontal plane. The speaker producing the test signal, and a small light used to delineate the trial interval, were mounted directly in front of the subject (outside of the crate) between 0.5 and 1.5 m from the station, depending on the test frequency. The buzzer, which served as the conditioned reinforcer, was mounted to the side of the crate. During testing, food rewards were passed directly to the subject from the trainer who was seated in the corner of

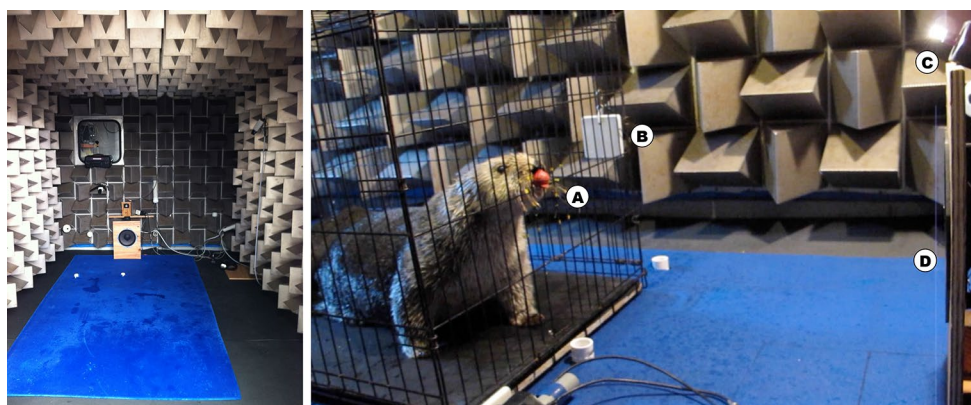


Fig. 2 (Left panel) The hemi-anechoic chamber used to test the hearing of the sea otter in air. (Right panel) The sea otter positioned in the apparatus during the hearing test procedure; the listening station (a),

the response target (b), the trial light (c), and the vertically mounted speaker (d) are shown

the test chamber. The trainer was blind to the experimental conditions until instructed by the experimenter to deliver a food reward. A camera mounted near the testing apparatus allowed the session to be viewed in real time by the experimenter.

Acoustic stimuli and calibration

The acoustic stimuli used for aerial audiometry were the same narrowband, FM sweeps used during underwater testing and were centered at the following 12 test frequencies: 0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 22.6, 32, 38.1, and 40 kHz. These signals were generated by and sent out through the same software, hardware, and signal processing equipment that were used during underwater testing. Test signals from 0.125 to 8 kHz were presented through a JBL 2123H speaker, and test signals from 16 to 40 kHz were presented through a Fostex FT96H speaker.

The sound field in the area surrounding the subject's head was mapped in the acoustic chamber prior to testing at each frequency, as previously described. The aerial calibration signals were measured at an additional eight points, which were included into the $20 \times 20 \times 10$ cm mapping grid to allow for higher-resolution data in the space surrounding the subject's two ears. As in water, the received SPLs at each position within the rectangular grid (including the additional eight points around the ears) did not vary by more than 3 dB from the daily calibration position. However, due to increased certainty in the transmission path of sound to the ear during aerial hearing, the daily calibration position was designated to be at the position of the ear that received the higher SPL during sound field mapping for each test frequency (rather than the center of the head between the ears).

Prior to every session, test signals were measured and monitored in a similar fashion as previously described. Calibration signals were received with one of two microphones placed in the calibration position determined during the mapping procedure. A Josephson C550H microphone (nominal sensitivity -40 dB *re* 1 V/Pa, 0.02–20 kHz, ± 2 dB) was used for test frequencies from 0.125 to 16 kHz. A Microtech Gefell MK301 microphone (nominal sensitivity -46 dB *re* 1 V/Pa, 0.005–100 kHz, ± 2 dB) with an ACO Pacific 4016 preamplifier and PS9200 power supply was used for test frequencies from 22.6 to 40 kHz.

Psychoacoustic testing

The sea otter subject was trained to perform the same go/no-go procedure used during underwater testing, inside of the hemi-anechoic chamber. This involved training the sea otter to enter the acoustic chamber, allow the door to be closed behind him, walk inside the experimental apparatus (wire crate), and to position his nose on the listening station. The sea otter reported detection of a signal by touching the response target located to his left. The psychophysical testing method, schedule of reinforcement, and session structure were identical to those used during underwater testing. An example of the in-air hearing test is shown in Online Resource 2.

Threshold determination

The session data were obtained and analyzed using the same procedure as described for underwater audiometry. Aerial hearing thresholds (dB *re* 20 μ Pa) were plotted as a function of frequency (kHz) to construct the sea otter's aerial audiogram, which was compared to previously

published audiometric data from several other terrestrial and marine carnivores, obtained using similar methods.

Critical ratio measurements

Following completion of the aerial audiogram, masked aerial hearing thresholds were measured in the acoustic chamber so that the subject's ability to detect sounds in the presence of noise could be evaluated. The aim was to determine critical ratios—or difference (in dB) between the SPL of the masked threshold and the spectral density level of the surrounding masking noise—for signals from 0.25 to 22.6 kHz. The testing environment and apparatus were the same as those described for aerial audiometry.

Acoustic stimuli and calibration

The test stimuli were a subset of the same narrowband, FM sweeps used to measure the aerial audiogram: 0.25, 0.5, 1, 2, 4, 8, 16, and 22.6 kHz. These signals were generated using the same software, hardware, and signal processing equipment as previously described. Sound field mapping of the test signals was not necessary for the masking experiment because the projecting transducer configuration and the position of the subject during testing were identical to the previous testing conditions. The received signal levels were calibrated prior to each testing session.

The masking noise in the acoustic chamber was projected continuously during the session from the same speaker used to project the test signal. The masking noise was calibrated prior to each testing session. The noise had a bandwidth of one octave that was centered at the test frequency. Depending on the frequency, the spectral density level of the noise was either 10 or 20 dB above the absolute threshold previously measured for the same sea otter subject. The noise was spectrally flattened through a filtering process to approximate a band of white noise, according to several criteria. The spectral density levels (measured directly) across the center 1/3-octave band were within ± 5 dB at the calibration position. The level of the center 1/3-octave band, and the levels of the adjacent 1/3-octave bands were each within ± 3 dB of the desired noise level and within ± 3 dB of one another. Prior to testing at each frequency, the received sound field was measured to confirm that the 1/3-octave band criteria were maintained across the $20 \times 20 \times 10$ cm mapping grid surrounding the subject's head.

The masking noise was created using AVS Audio Editor software (for frequencies from 0.25 to 8 kHz), or MATLAB (for frequencies of 16 and 22.6 kHz). Both software platforms were operated from a desktop computer. The outgoing masking noise was amplified using the Hafler P1000 (where it could be mixed with the test signal) before being sent to the same transducers used during aerial audiometry.

During noise calibration, the incoming masking noise was received from the appropriate microphone and passed through a Roland Quad-Capture USB 2.0 external sound card (192 kHz sampling rate) to a battery-powered laptop computer, so that it could be analyzed with SpectraPLUS-SC software.

Psychoacoustic testing

The sea otter was trained to enter the acoustic chamber and perform the go/no-go procedure while the masking noise was continuously projected from the test speaker. The psychophysical testing method, schedule of reinforcement, and session structure during the masking experiment were identical to those used during absolute audiometry.

Threshold determination

The masked hearing thresholds were collected and determined using an identical procedure as was described for absolute audiometry. Critical ratios were calculated for each test frequency as the difference between the target noise spectral density level and the masked aerial hearing threshold. These critical ratios (dB) were plotted as a function of frequency (kHz) and compared to previously published masking data from one terrestrial and two marine carnivores, obtained using similar methods.

Results

Underwater audiogram

Underwater auditory detection thresholds for narrowband signals are provided for the sea otter subject at 11 frequencies with corresponding false alarm rates and ambient noise levels (Table 1). The sea otter's underwater audiogram is depicted from these threshold data (Fig. 3a), along with ambient noise in the testing pool under two conditions: (1) with the sea otter subject present on the listening station, and (2) with the sea otter absent from the testing pool. Noise generated by the subject in the testing pool was successfully reduced through careful design of the testing configuration (i.e., the sea otter's body position during testing to minimize air venting), which is apparent by the small difference (<5 dB) in background noise conditions with and without the sea otter present on the listening station (Fig. 3a). The underwater audiogram obtained for the sea otter in this configuration shows a compressed shape, with a markedly shallow roll-off in low-frequency sensitivity, a narrow range of best hearing, and a sharp decline in sensitivity on the high-frequency end. Low-frequency (≤ 1 kHz) sounds could not be detected at levels below 100 dB *re*

Table 1 Underwater auditory detection thresholds measured for a sea otter using a psychoacoustic method. Also shown are the spectrum levels of ambient noise in the testing pool (with the sea otter present), the sea otter's average false alarm rates during the detection task, and the frequency testing order

Frequency (kHz)	Threshold (dB re 1 μ Pa)	Ambient noise (dB re 1 μ Pa/ $\sqrt{\text{Hz}}$)	False alarm (%)	Testing order
0.125	116	74	7	4
0.25	103	55	8	6
0.5	102	48	17	3
1	101	44	21	1
2	90	39	15	5
4	83	36	22	8
8	69	32	7	2
16	69	30	13	7
22.6	77	30	18	11
32	105	29	17	9
38.1	141	28	19	10

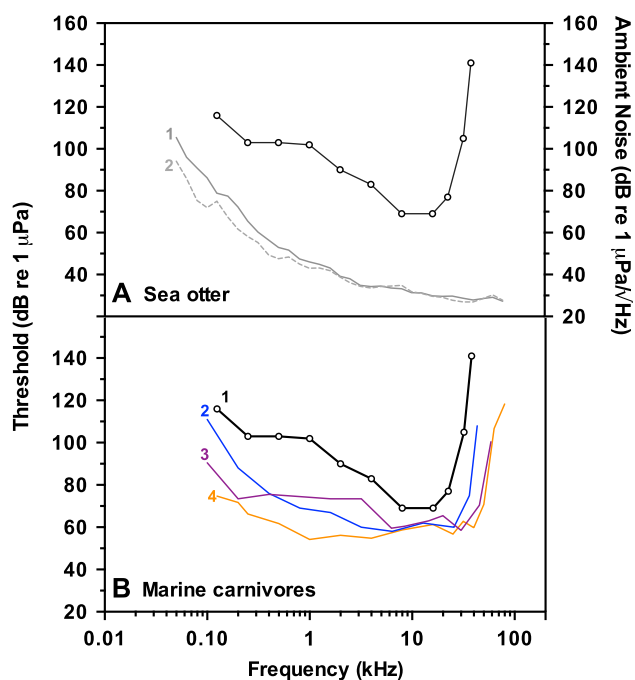


Fig. 3 Underwater auditory thresholds plotted as a function of frequency for a sea otter (this study) and three other marine carnivores. **a** Sea otter audiogram shown with corresponding spectrum levels of ambient noise in the testing pool: (1) with the sea otter present, and (2) without the sea otter present. **b** Audiograms for: (1) sea otter, (2) California sea lion, *Zalophus californianus* (Reichmuth et al. 2013), (3) northern elephant seal, *Mirounga angustirostris* (Kastak and Schusterman 1999), and (4) harbor seal, *Phoca vitulina* (Kastelein 2010)

1 μ Pa. Sensitivity improves above 1 kHz, and the 20-dB bandwidth of best hearing occurs between 2 and 26 kHz, with the lowest threshold of 69 dB re 1 μ Pa measured at 8 and 16 kHz. Hearing sensitivity is reduced above 22.6 kHz, with sensitivity declining by \sim 85 dB/octave between 22.6 and 38.1 kHz, where the highest threshold of 141 dB re 1 μ Pa was measured. The minimum difference between

measured hearing thresholds and associated ambient noise spectral density levels was 42 dB (125 Hz).

The underwater audiogram for the sea otter was compared to data for three other marine carnivores—the California sea lion (Reichmuth et al. 2013), the northern elephant seal (Kastak and Schusterman 1999), and the harbor seal (Kastelein et al. 2009)—tested under similar experimental conditions (Fig. 3b). Of the four species, the sea otter has the least sensitive underwater hearing, and has auditory capabilities most similar to the California sea lion. The sea otter's lowest underwater threshold of 69 dB re 1 μ Pa is 11 dB higher than the best threshold of 58 dB re 1 μ Pa reported for the California sea lion at 1 kHz. With a bandwidth of best hearing sensitivity spanning 3.7 octaves under water, the sea otter shows the narrowest range in comparison to the California sea lion (6.7 octaves) and the harbor seal (8.6 octaves). The sea otter also shows reduced sensitivity on the high- and low-frequency ends of the audiogram relative to the pinnipeds shown in Fig. 3b. The maximum frequency the sea otter detected was 38.1 kHz (at a level of 141 dB re 1 μ Pa), whereas the hearing ranges of the sea lion and harbor seal extend much higher in frequency at much quieter levels (to 43 kHz and 60 kHz, respectively, at 100 dB re 1 μ Pa). Although the sea otter detected underwater signals down to the lowest frequency tested (0.125 kHz), thresholds measured at and below 2 kHz were 12 to 34 dB higher than those reported for the sea lion within the same frequency range.

Aerial audiogram

Aerial auditory detection thresholds for narrowband signals were measured for the sea otter at 12 frequencies (Table 2), and the corresponding aerial audiogram is shown with the ambient noise spectral density levels in the acoustic chamber (Fig. 4a). The sea otter's aerial audiogram has a U-shape, characteristic of mammalian hearing. Beginning at 0.125 kHz, the sea otter's hearing sensitivity increases

Table 2 Aerial auditory detection thresholds measured for a sea otter using a psychoacoustic method. Also shown are spectrum levels of ambient noise in the acoustic chamber, the sea otter's average false alarm rates during the detection task, and frequency testing order

Frequency (kHz)	Threshold (dB re 20 μ Pa)	Ambient noise (dB re 20 μ Pa/ \sqrt Hz)	False alarm (%)	Testing order
0.125	75	22	16	6
0.25	55	-5	7	2
0.5	42	-16	18	3
1	23	-17	6	5
2	4	-21	13	7
4	10	-23	23	1
8	-1	-25	7	4
16	5	-29	18	9
22.6	8	<0	5	11
32	31	<0	7	8
38.1	58	<0	21	12
40	71	<0	13	10

monotonically (18 dB/octave) with increasing frequency up to 2 kHz. The 20-dB bandwidth of best sensitivity is broad, spanning 1.2–27 kHz. Within this range, the audiogram shows a notch at 4 kHz, where the hearing threshold is elevated by 6–11 dB relative to those thresholds measured at adjacent frequencies. Hearing is most sensitive at 8 kHz, where the lowest threshold of -1 dB *re* 20 μ Pa was measured. Above 22.6 kHz, high-frequency sensitivity declines rapidly (76 dB/octave) to 40 kHz, the highest frequency tested.

Ambient noise in the acoustic chamber (Fig. 4a) decreased substantially with increasing frequency, and from 2 to 20 kHz the spectral density level of the noise was below -20 dB *re* 20 μ Pa/ \sqrt Hz (the lower limit of measuring capability). Above 20 kHz, the spectral density levels from 20 to 50 kHz were likely equally low, although the testing equipment had a lower limit of 0 dB *re* 20 μ Pa/ \sqrt Hz in this frequency range. The difference between measured hearing thresholds and associated ambient noise spectral density levels (measured or estimated) was more than 40 dB at the low- and high-frequency ends of the audiogram. Within the 20-dB bandwidth of best sensitivity, these differences were smaller (24–34 dB).

The aerial audiogram obtained for the sea otter was compared to the aerial audiograms for five terrestrial carnivores (Fig. 4b) and three marine carnivores (Fig. 4c) that were tested in similar experimental conditions. The sea otter shares several features of aerial hearing with the terrestrial carnivores. The sea otter's lowest threshold is the same as that reported for the domestic dog (-1 dB *re* 20 μ Pa, measured at 8 kHz) and the ferret (-1 dB *re* 20 μ Pa, measured at 12 kHz). The sea otter and the ferret are most similar with respect to high-frequency hearing—both are sensitive to sounds that extend to a 38-kHz high-frequency hearing limit (at 60 dB *re* 20 μ Pa), which is slightly lower in frequency than that of the other terrestrial carnivores. The sea otter's 20-dB bandwidth of best sensitivity spans 4.5 octaves, and though it is comparable to that measured for

the ferret (0.7–27 kHz, spanning 5.3 octaves), it is truncated. This is especially evident on the low-frequency end of the audiogram, where the sea otter's hearing sensitivity is notably poorer than all four of the terrestrial carnivores.

The closest similarity in overall aerial hearing capability is seen between the sea otter and one of the marine carnivores, the California sea lion (Fig. 4c). A comparison between these two amphibious mammals shows remarkable agreement in bandwidth of best sensitivity, high- and low-frequency hearing abilities, as well as lowest measured thresholds and frequencies of best sensitivity.

Auditory masking

Aerial auditory detection thresholds for narrowband signals were also measured for the sea otter in the presence of continuous, octave-band masking noise, centered at each of eight test frequencies from 0.125 to 22.6 kHz. The auditory masking data, including the calibrated masking noise spectral density levels, masked thresholds, and resulting critical ratios are provided (Table 3). The critical ratios are shown alongside similar data published for three other carnivores (Fig. 5). The critical ratios show an overall increase with increasing frequency. At and above 2 kHz, the sea otter's critical ratios increase by 2.9 dB/octave up to 22.6 kHz, the highest frequency tested. Below 2 kHz, however, critical ratios are more variable with respect to frequency and higher than expected based on the comparative data.

Discussion

Assessment of auditory measures

The underwater audiogram, aerial audiogram, and critical ratio measurements reported for one southern sea otter in

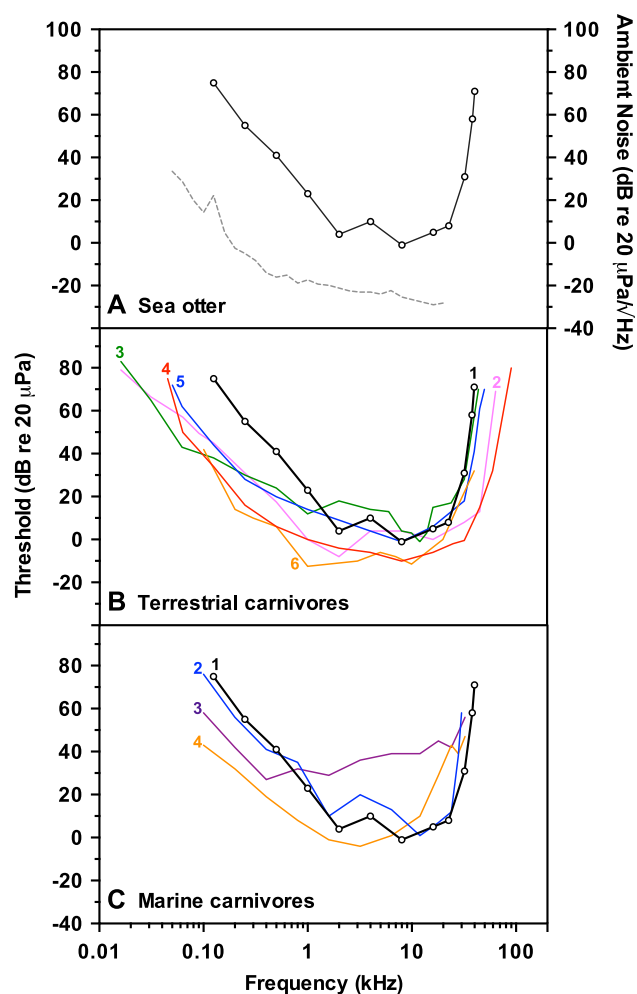


Fig. 4 Aerial auditory thresholds plotted as a function of frequency for a sea otter (this study) shown alongside similar data from five terrestrial carnivores and three marine carnivores. **a** Sea otter audiogram shown with corresponding spectrum levels of ambient noise in the acoustic chamber. **b** Audiograms for (1) the sea otter and five terrestrial carnivores: (2) least weasel, *Mustela nivalis* (Heffner and Heffner 1985a), (3) ferret, *Mustela putorius* (Kelly et al. 1986), (4) domestic cat, *Felis catus* (Heffner and Heffner 1985b; Neff and Hind 1955), (5) domestic dog, *Canis familiaris* (Heffner 1983), and (6) raccoon, *Procyon lotor* (Wollack 1965). **c** Audiograms for (1) the sea otter and three other marine carnivores: (2) California sea lion, *Zalophus californianus* (Reichmuth et al. 2013), (3) northern elephant seal, *Mirounga angustirostris* (Reichmuth et al. 2013), and (4) harbor seal, *Phoca vitulina* (Reichmuth et al. 2013)

this study are the first auditory profiles available for the species. While the data provided are for one subject, the psychoacoustic thresholds are thorough and can be considered reliable for this individual. In all three experiments, the behavioral responsiveness of the sea otter was maintained at an optimal level, and the acoustic stimuli and background noise were carefully measured to ensure adequate conditions for audiometry.

As expected, the sea otter was most liberal about responding when signal level was close to threshold, and

importantly, was equally liberal for all test conditions. The average test-phase false-alarm rates of 15, 13, and 17 % for the three experiments (range 5–25 %) confirm that the response bias of the subject during each threshold measurement was consistent, and consequently, that comparisons made within and between experiments reflect real differences in auditory capabilities. Additionally, the measured differences between hearing thresholds and ambient noise in the surrounding 1/3-octave frequency band show that the hearing measurements obtained are not limited (in most, if not all cases) by noise in the testing environment. The 42-dB minimum elevation of hearing thresholds relative to associated spectral density noise levels in the underwater enclosure—even with the subject in position in the sound field—confirm that the underwater audiogram is entirely unmasked. In the acoustic chamber, while thresholds were measured in extremely quiet conditions, the sea otter's acute hearing sensitivity at 2, 8, and 22.6 kHz brings the lower portion of the audiogram within 24–34 dB of the maximum (measurable) noise floor. This is a typical condition of aerial hearing measurements for animals obtained in acoustic chambers (Heffner and Heffner 2007) and likely did not influence the hearing thresholds measured for this sea otter. This view is supported by the critical ratio measurements later obtained for this individual. As a result, both the underwater and aerial audiograms for this sea otter are apparently unmasked and can be considered absolute measures of best hearing capabilities.

The sea otter in the present study was an adult male aged 14 years, and while male sea otters may survive to more than 20 years in captivity (Brennan and Houck 1996), they rarely survive more than 15 years in the wild (Riedman and Estes 1990). Therefore, it is important to evaluate the likelihood of hearing loss in this individual and the ability to draw inferences from these data about species-typical hearing capabilities. The aerial audiogram of this sea otter shows typical features of normal mammalian hearing and there is no evidence of conductive hearing loss. The aerial audiogram of this sea otter shows typical features of normal mammalian hearing and there is no evidence of conductive hearing loss. The notch in best aerial sensitivity at 4 kHz is characteristic of mild noise-induced hearing loss associated with aging (Wilson and McArdle 2013) and therefore may not be evident in young subjects. The most common feature of age-related hearing loss is a reduction in high-frequency hearing capabilities. However, this subject shows a high-frequency hearing limit of 38 kHz, which is consistent with that of another mustelid carnivore (the ferret), and exceeds that determined for younger sea otters using more coarse behavioral methods (Ghoul and Reichmuth 2014). It is, therefore, reasonable to conclude that the high-frequency hearing limit measured in this study is reliable, but possibly conservative for the species. The most surprising feature of the sea otter's aerial audiogram is the unusual roll-off in low-frequency hearing sensitivity. This feature is likely not unique to this individual

Table 3 Auditory critical ratios obtained for a sea otter tested in air. Masked thresholds were measured in the presence of continuous, octave-band noise (centered at each of eight test frequencies) using a psychoacoustic method. Also shown are the sea otter's average false alarm rates during the detection task, and frequency testing order

Frequency (kHz)	Masking noise (dB re 20 μ Pa/ \sqrt Hz)	Masked threshold (dB re 20 μ Pa)	Critical ratio (dB)	False alarm (%)	Testing order
0.25	65	92	27	20	5
0.5	52	81	29	25	1
1	43	71	28	13	4
2	24	50	25	15	2
4	30	59	29	13	6
8	19	48	29	18	3
16	25	56	31	11	7
22.6	28	63	34	20	8

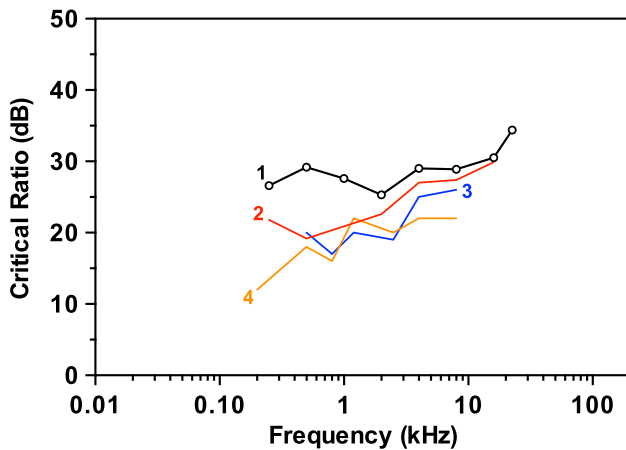


Fig. 5 Auditory critical ratios obtained in air at eight frequencies for (1) a sea otter (this study) and three other carnivores: (2) domestic cat, *Felis catus* (Costalupes 1983a), (3) California sea lion, *Zalophus californianus* (Southall et al. 2003a), and (4) harbor seal, *Phoca vitulina* (Southall et al. 2003a)

or a result of aging or experimental confounds. Hearing loss restricted to the low-frequency end of the audiogram is uncommon. Furthermore, more sensitive hearing thresholds have been measured for other species at low frequencies in the same testing enclosure (Reichmuth et al. 2013), suggesting that environmental conditions were not the limiting factor. Finally, the aerial hearing thresholds measured for this subject at 0.125–0.5 kHz are within 5 dB of those obtained with a second, younger male sea otter tested in the same laboratory (Reichmuth and Ghoual 2012). In summary, the present data reported for one adult male sea otter appear to be representative, with the caveats that thresholds near 4 kHz and above 30 kHz may slightly underrepresent best hearing abilities in younger individuals, and that testing of at least one additional subject is warranted.

Comparative aspects of amphibious hearing sensitivity

The audiograms obtained for the sea otter are most easily interpreted by comparison with other carnivore species

(both terrestrial and marine) for which similar data are available. This approach can help identify features of hearing that may have been altered through selection pressures related to amphibious living. In many ways, the sea otter's aerial audiogram resembles those of terrestrial mustelids (ferret and least weasel) as well as those of representative canids (domestic dog), felids (domestic cat), and procyonids (raccoon). Both the frequency region of best sensitivity (1.2–27 kHz) and the absolute value of best sensitivity (–1 dB re 20 μ Pa) for the sea otter overlap with those of the terrestrial species. Mid- and high-frequency hearing is most similar among the sea otter, ferret, and dog, while the cat appears to be a hearing specialist in terms of best absolute sensitivity (–10 dB re 20 μ Pa), range of best sensitivity (0.375–40 kHz), and upper-frequency limit of hearing, which extends to 76 kHz at 60 dB re 20 μ Pa (Heffner and Heffner 1985b; Neff and Hind 1955). It is really at low frequencies (\leq 1 kHz) that the sea otter diverges markedly from the terrestrial carnivore pattern. In this range, aerial thresholds for the sea otter are 17–37 dB higher than those reported for the ferret (Kelly et al. 1986).

The aerial hearing of the sea otter, while divergent at low frequencies from other terrestrial carnivores, is nearly identical to that of the California sea lion at all but the highest frequencies. The low-frequency thresholds of the two species fall within 5 dB of one another, and the range of best hearing is also the same, with the sea otter showing slightly better sensitivity than the sea lion. The idea that the sea lion and the sea otter have aerial hearing that is evolutionarily convergent is supported by their similarities to one another and by their differences relative to other closely related species. The sea lion lineage diverges from that of phocid (true) seals with respect to low-frequency hearing (Mulson and Reichmuth 2010; Reichmuth et al. 2013) and the sea otter diverges from the terrestrial mustelids within the same frequency range (Heffner and Heffner 1985a; Kelly et al. 1986). This suggests a selective pressure related to similar amphibious lifestyles, which has influenced aerial hearing despite significant time differences in transitions from terrestrial forms (>20 my for the sea lion versus <5 my for the

sea otter). Improved understanding of auditory anatomy in sea otters would help to resolve the origin of this apparent low-frequency attenuation of sound (e.g., a closure mechanism to protect the ear from water entry, hypertrophy of middle ear structures).

The sea otter's ability to detect sounds under water is also most similar to that of the California sea lion, as compared to two other species of phocid pinnipeds. However, in contrast to their well-matched hearing thresholds for airborne sounds, the sea otter is significantly less sensitive (5–35 dB) than the sea lion across the frequency range of hearing in water. This relative deficit is particularly evident at frequencies below 8 kHz, where the decline in hearing sensitivity with decreasing frequency is atypically shallow. While the differences between the taxa cannot be fully explained at this time, it is likely that the sea lion's enhanced hearing sensitivity in water is attributable to the much longer aquatic history of the species. This suggests the presence of auditory adaptations (e.g., through selective pressure for the detection of biologically significant underwater sounds), non-auditory adaptations (e.g., through selective pressures related to submergence, swimming, or diving in cold, fluid environments), or both types of adaptations, which may be present in sea lions to a similar or greater extent than in sea otters. A detailed description of the bony and soft tissue auditory anatomy of sea otters—and some additional information about the auditory anatomy of sea lions—will be required to further explore this issue. The findings of such an exploration would provide significant insight into the evolutionary biology of aquatic hearing in mammals.

Hearing in noise

The utility of measuring critical ratios to describe the ability of an animal to detect a signal that is coincident with noise is that the ratios hold across noise levels (Fay 1988) and media (air or water; Fay 1988; Southall et al. 2000, 2003a). Additionally, significant background noise is present in most typical environments used by animals. Relatively low critical ratios suggest specialization for detecting signals in noise, while relatively high critical ratios suggest a poor ability to resolve the signal of interest from the acoustic background. Critical ratios have been measured for many birds and mammals (for review, see Fay 1988) as well as many marine mammals (for review, see Richardson 1995b; Reichmuth 2012), providing a framework for comparative studies of auditory masking.

The relatively high critical ratios determined in the present study (25–34 dB) indicate that the auditory system of the sea otter is not specialized for operating in noisy conditions. This is in contrast to the relatively low critical ratios measured for other marine carnivores, including

California sea lions, harbor seals, northern elephant seals, and spotted seals (Southall et al. 2000, 2003a; Sills et al. 2014), which indicate a refined ability for signal processing in noise. The data for the sea otter do follow the expected trend of increasing critical ratios with increasing frequency from 2 to 22.6 kHz, the highest frequency tested. Over this span, the sea otter's critical ratios are quite similar to those of cats (Costalupes 1983a) and increase at a rate of 2.9 dB/octave, compared to the well-established mammalian trend of 3 dB/octave (Fay 1988). The lack of predicted decline in critical ratios at lower frequencies suggests that sounds below 2 kHz are more difficult for sea otters to resolve from spectrally overlapping background noise, or conversely, that low-frequency noise can more easily mask signals of interest in the same frequency range. While there are no critical ratio data presently available for other mustelids, the sea otter critical ratios below 2 kHz are more similar to those of some rodents (e.g., Mongolian gerbil, *Meriones unguiculatus*; Kittel et al. 2002) than they are to terrestrial or marine carnivores. Although the critical ratios for the sea otter were measured in air, they are expected to be the same under water, despite differences in absolute hearing sensitivity between the two media.

Ecological considerations

Given that sea otters, like sea lions, are semi-aquatic mammals with what appear to be primarily air-adapted ears (Nummela 2008), they can be considered hearing generalists with a fairly broad range of hearing that extends to more than 30 kHz. This is not surprising given that other carnivores also have sensitive high-frequency hearing, and that many vocalizations produced by sea otters contain spectral energy extending across the frequency range of hearing, with peak energy focused in the range of best hearing (McShane et al. 1995; Ghouh and Reichmuth 2012). In air, their vocalizations are used during several types of social interactions (Kenyon 1969; McShane et al. 1995). Significantly, their loudest and most common calls are used to establish and maintain contact between mothers and their dependent pups (Sandegren et al. 1973) in dynamic conditions when other sensory cues are unavailable. Additionally, sea otters are known to be acoustically vigilant to potential threats while hauled out or at the surface (Scammon 1874), reinforcing the idea that there are selective pressures for the retention of sensitive aerial hearing in this species. At this point, it remains difficult to determine whether sea otters have any degree of specialization for underwater hearing as a result of their aquatic lifestyle, in part because it is not possible to know how sea otters might compare to fully terrestrial carnivores listening for sounds under water.

It is interesting to consider whether the sea otter's relatively poor sensitivity to low-frequency sounds might be a byproduct of adaptations for subsurface foraging. Sea otters acquire benthic prey at depths of less than 40 m (Bodkin et al. 2004), but they dive repeatedly and—depending on habitat quality—spend more than a third of their time involved in foraging activities to support their high metabolism (Yeates et al. 2007). Adaptations to protect the ear during diving could be shared with sea lions, whose ancestors foraged in nearshore coastal habitats similar to those used by sea otters today (Riedman 1990). It is possible that such changes to outer and/or middle ear structures could differentially attenuate the transmission of low-frequency sounds in both media, as the observed reduction in low-frequency hearing is not likely to be attributable to sensori-neural adaptations of the inner ear. The idea that these adaptations may have evolved for non-sensory reasons is perhaps the most likely explanation for the convergence in the hearing capabilities of sea otters and sea lions. Unlike sea lions that actively pursue their prey under water, sea otters bring their food to the surface between dives and spend the majority of their time at sea with their primary sensory structures above the water's surface. The differences in foraging behavior between the species, and corresponding differences in the presumed significance of underwater sound, make it less likely that selective pressures related to hearing have influenced sea otters and sea lions in the same way.

Conservation implications

Given the paucity of relevant information about the auditory sense of sea otters, even the most basic information can be applied to considerations of anthropogenic noise and associated disturbance in the coastal waters they inhabit. The auditory profiles describing aerial and underwater hearing obtained in this study—while based on a single subject—provide a useful, conservative measure of hearing for the species. The upper and lower frequency limits of these data can be used to distinguish sound sources of relevance to sea otters from those of lesser concern. The description of relative sensitivity within the audible frequency band can illustrate the different perceptual effects of various sound frequencies and suggest why certain sounds may be more salient to sea otters than others. The finding that audiogram shape is not dramatically different in air and under water for sea otters implies that a common set of parameters concerning hearing can be generally applied to both airborne and waterborne sounds. Perhaps most importantly, hearing thresholds obtained in quiet conditions and in the presence of noise (to establish critical ratios) can be used to estimate the distances over which many sounds may be detected by a hypothetical sea otter in different noise backgrounds. This basic approach, which relies on appropriate measurement

of signals and noise, estimates of sound propagation in representative environments, and audiometric data such as those obtained in this study, can be applied in conservation and management contexts (see, e.g., Erbe and Farmer 2000; Southall et al. 2003b; Dooling and Popper 2007).

Another management tool that has been suggested for marine mammals with respect to anthropogenic sounds is the development of auditory weighting functions for groups of species with similar hearing capabilities (Southall et al. 2007). Such weighting functions establish the relevant bandwidth for noise exposure assessments by compensating for the differential frequency response of the auditory system, and allowing sounds of lesser concern to be identified and de-emphasized. The information about hearing sensitivity obtained in the present study allows sea otters—for the first time—to be appropriately considered in the context of existing (Southall et al. 2007) and proposed (Finneran and Jenkins 2012) weighting functions for other marine mammals. In terms of measuring anthropogenic sound, and predicting auditory effects resulting from exposure to anthropogenic sound, we suggest that sea otters can be reasonably grouped with sea lions and other otariid pinnipeds based on the similarities in their measured audiograms.

While sea otters share similar hearing capabilities with otariid pinnipeds, their differences in ecology and physiology become important at the level of behavioral effects associated with sound exposure. Because sea otters require prolonged periods of undisturbed rest at the surface to counterbalance extremely high metabolic costs associated with foraging at sea (Yeates et al. 2007), these animals are particularly vulnerable to even brief intervals of disturbance. Specifically, disturbance from airborne sounds or activity at the surface causes long metabolic recovery times to more energetically efficient resting states (Yeates 2006) and imposes especially high costs on reproductive females (Thometz et al. 2014). These physiological limitations, as well as life history constraints such as strong fidelity to small home ranges, may impede a sea otter's ability to respond to sounds or disturbance in ways that are available to other marine species. As little is known about the effects of anthropogenic sound on the behavior of sea otters, more research on this topic is needed.

Conclusions

1. Although sea otters are adapted for an aquatic lifestyle and spend most of their lives at sea, they have retained aerial hearing sensitivity that is comparable to that of terrestrial carnivores.
2. At low frequencies, the hearing of sea otters is not as sensitive as expected and there is marked reduction in

sensitivity at frequencies below 1 kHz; as a result, their audiograms in air and under water most closely resemble those of sea lions.

3. Overall, the sensitivity of sea otters to underwater sounds is reduced compared to other amphibious marine mammals (seals and sea lions), especially at low frequencies.
4. Sea otters lack a refined ability to detect signals embedded in background noise, as seen in other marine carnivores.
5. These hearing profiles for sea otters improve understanding of evolutionary biology, sensory ecology, and conservation practice; nevertheless, more data are needed including hearing data for additional subjects, description of auditory structures, and observations of the behavioral effects of various sound exposures.

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Ethical standards Animal welfare considerations were consistent with the current laws of the United States. Federal authorization for sea otter research was granted by the US Fish and Wildlife Service under scientific research permit MA186914-0. The animal protocols associated with 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.

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