Underwater Sound Detection Thresholds (0.031-80 kHz) of Two California Sea Lions (*Zalophus californianus*) and a Revised Generic Audiogram for the Species

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Abstract

Unmasked behavioral audiograms of two California sea lions (*Zalophus californianus*), an adult female (F01) and a subadult male (M02), were recorded using narrow-band frequency-modulated hearing test signals. Signals had a duration of 1 s and center frequencies ranging from 0.031 to 80 kHz. Hearing thresholds were measured by varying test signal amplitude according to the up-down staircase method. The resulting underwater audiograms (50% detection thresholds) of the two sea lions were similar and showed the typical mammalian U-shape. Maximum hearing sensitivity (58 and 57 dB re 1 μPa) occurred at 11.3 kHz for F01 and at 8 kHz for M02, respectively. The range of best hearing (defined as < 10 dB from the maximum sensitivity) was from 1 to 16 kHz (four octaves). The detection thresholds for hearing test signal frequencies 0.031, 0.040, and 0.050 kHz were lower than expected, possibly caused by a shift in perceptional modality from auditory to vibrotactile, or due to the difficulty in measuring accurate SPLs of such low frequencies in a pool. Measurements of particle motion deemed detection of these very low frequencies via the vibrissae unlikely. The present study extends the frequency range for which the hearing of California sea lions has been tested. Based on the two audiograms of the present study and audiograms reported by Reichmuth et al. (2013) and Cunningham & Reichmuth (2016), a revised generic audiogram for California sea lions is proposed.

Key Words: anthropogenic noise, audiogram, California sea lion, *Zalophus californianus*, detection threshold, hearing range, hearing sensitivity, low-frequency (LF) sound, Otariidae, pinniped

Introduction

The amphibious pinnipeds, which comprise the families of true seals (phocids), eared seals (otariids), and walruses (odobenids), utilize sound for communication (e.g., Insley et al., 2003), predator detection (e.g., Deecke et al., 2002; Ghai & Insley, 2011), and orientation (e.g., Schusterman et al., 2000). However, to determine the relative importance of sound during these activities for each species, as well as the potential for disturbance by anthropogenic noise (e.g., from shipping, dredging, pile driving, offshore wind turbines, active naval sonar, depth sounders, data communication systems, and acoustic remote-control systems), information is needed on the species' hearing sensitivity both in air and under water.

California sea lions (*Zalophus californianus*) are otariids that occur along the North American west coast, ranging from southern Alaska to central Mexico (Melin et al., 2018). Underwater audiograms of California sea lions have been published for five individuals; their hearing was most sensitive between 0.1 and 50 kHz, but there was high variability between individuals and testing locations (Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016). Due to the small sample sizes, it is not clear whether the variation in hearing sensitivity was due to individual differences (e.g., in age, size, and sex) or differences in measurement methods and study area (e.g., ambient noise levels, behavioral or physiological audiometric technique). Southall et al. (2019) proposed hearing studies on more individuals of this species to investigate individual variation in hearing sensitivity.

To increase the global sample size of hearing-tested California sea lions, we quantified the basic underwater sound detection thresholds of an adult female and a subadult male. Hearing test frequencies between 0.60 and 80 kHz were each tested over a period of 2 to 3 mo as part of a project on temporary hearing threshold shift (TTS; Kastelein et al., 2021, 2022a, 2022b). The following test frequencies were added: 0.063 and 0.125 kHz, as these are associated with underwater shipping noise (van der Graaf et al., 2012); and 0.031 to 0.250 kHz, as additional low-frequency tests were needed to cover the entire hearing range of the species.

While audiograms reflect hearing abilities, it is possible that underwater sounds are detected by a sensory system other than hearing. Kastak & Schusterman (1998) found that for their California sea lions, hearing thresholds for the lowest test frequency (i.e., 75 Hz) were lower than expected. They attributed these findings to a shift in sensory modality: from auditory to vibrotactile detection. Indeed, later research showed that pinnipeds are capable of perceiving water movements and following hydrodynamic trails (e.g., from swimming fish) using their vibrissae (Dehnhardt et al., 1998, 2001; Schulte-Pelkum et al., 2007; Gläser et al., 2011; Hanke et al., 2013). Especially within the near field of a sound projector, particle motion from sound waves may be detected by vibrissae and result in perception of the stimulus (Kastak & Schusterman, 1998; Nedelec et al., 2016).

Herein, we aimed to establish underwater sound detection thresholds for two California sea lions, increasing the number of individuals of this species for which audiograms have been published from five to seven. While testing their hearing, we took the sea lions' vibrotactile detection capabilities into account by quantifying particle motion for the lowest hearing test frequencies. In addition, we aimed to improve the generic audiogram for the species by fitting an equation used by Southall et al. (2019) to the combined detection thresholds of the sea lions from the present study and the studies by Reichmuth et al. (2013) and Cunningham & Reichmuth (2016), as these audiograms were rather similar. The results of this study are an important step towards understanding the relative importance of different sounds to California sea lions, and a vital piece of information for effective protection from disturbance and hearing damage by anthropogenic noise.

Methods

Subjects and Study Area

The subjects were an adult female California sea lion, identified as F01, and her subadult male offspring, identified as M02. During the study, F01 aged from 7 to 11 y old and M02 aged from 1 to 5 y old. F01's total body length was 160 cm, and her body weight varied between 70 and 86 kg, depending on the season. M02's total body length increased from 125 to 165 cm, and his body weight increased from 45 to 72 kg during the study period. Both sea lions were healthy throughout the study. Variation in the subjects' performance was minimized by making weekly adjustments (usually in the order of 100 g) to their daily food ration, based on their body weight, their recent performance in hearing tests and husbandry tasks, and the expected change in water and air temperatures in the following week.

The study was conducted at the SEAMARCO Research Institute, the Netherlands, in a remote and quiet location. The water circulation system was switched off at least 1 h before the first hearing test each day to reduce ambient noise. The sea lions were kept in a pool complex consisting of an outdoor pool (7 × 4 m, 2 m deep), connected via two channels (each 2 × 2 m, 1 m deep) to an indoor pool. The indoor pool consisted of a deep part (6 × 4 m, 2 m deep) in which the hearing tests were conducted, and a shallow part (6 × 3 m, 1 m deep; see Kastelein et al., 2021, for more details of the facility and a top view of the pool complex).

Hearing Test Signal Production, Measurement, and Calibration

The ambient noise was low and constant under test conditions (which consisted of no people moving within 15 m of the pool, water circulation system off, no rain, and generally wind force Beaufort 4 or below), and the hearing test signals were generated digitally (*Adobe Audition*, Version 3.0). The linear upsweeps started and ended at ± 2.5% of the center frequency, and they had durations of 1 s, including a linear rise and fall in amplitude of 50 ms. The center frequencies of the hearing test signals were 0.031, 0.040, 0.050, 0.063, 0.125, 0.250, 0.60, 0.85, 1, 2, 4.2, 5.6, 8, 11.3, 16, 32, 40, 44.8, 63, and 80 kHz. The WAV files used as hearing test signals were played on a laptop computer (Model CX623; Micro-Star International [MSI], Zhonghe District, Taipei, Taiwan), with a program written in *LabVIEW*, to an external data acquisition card (Model USB6251; National Instruments, Austin, TX, USA). The output of the card was controlled in 1 dB steps by the *LabVIEW* program, and it went through a custom-built buffer and low-pass filter, a custom-built variable low-pass filter,

and a custom-built buffer/mixer to the following frequency-range-specific equipment:

- *0.031 to 0.250 kHz* – An equalizer (Model FBQ800; Behringer, Zhongshan, China) and an amplifier (Model TAMP-90; HLLY, Hong Kong), which drove an inductive moving coil transducer (Model J-11; Underwater Sound Reference Division, Newport, RI, USA)

- *0.60 to 16 kHz* – An isolation transformer (Model AC202; Lubell Labs, Columbus, OH, USA), which drove a balanced tonpilz piezoelectric acoustic transducer (Model LL916, Lubell Labs)

- *32 to 80 kHz* – An amplifier (Model TAMP-90, HLLY), which drove a cylindrical piezoelectric transducer (EDO Western, Model 337; EDO Corporation, Salt Lake City, UT, USA)

Harmonics were not detectable at the levels at which the hearing test signals were presented.

The ambient noise was measured and the hearing test signals were calibrated once every 3 mo during the study period by an acoustic consulting agency (TNO). The sound measurement equipment consisted of two hydrophones (Model 8106; Brüel & Kjaer [B&K], Nærum, Denmark) with a multichannel high-frequency analyzer (B&K PULSE, Model LAN-XI 3161) and a laptop computer with B&K PULSE software (*LabShop*, Version 20). The system was calibrated with a pistonphone (Model 4223, B&K), and the sampling frequency was 524.288 kHz. The broadband sound pressure level (SPL; dB re 1 µPa; American National Standards Institute [ANSI], 2013) of each hearing test signal was derived from the 90% received sound exposure and the corresponding 90% time duration (t90; Madsen, 2005). Hearing test signals with frequencies < 0.250 kHz were not filtered. Hearing test signals with frequencies ≥ 0.250 kHz were high-pass filtered (cut-off: 0.1 kHz) with a third order Butterworth filter (18 dB/octave).

The detection thresholds for hearing test signal frequencies 0.031, 0.040, and 0.050 kHz were lower than expected (see "Results"). Therefore, we considered that they may have been detected by a sensory system other than hearing, such as detection of particle motion by the vibrissae (Dehnhardt et al., 1998, 2001; Kastak & Schusterman, 1998; Schulte-Pelkum et al., 2007; Gläser et al., 2011; Hanke et al., 2013). Therefore, the low-frequency hearing test signals (0.031 to 0.25 kHz) were also measured with a vector sensor (Model VHS-100; Ocean

Applied Acoustics, Changshu, China): an epoxy-encased tri-axial accelerometer, with a sensitivity of 0.25 V/(m s⁻²), (-12 dB re 1 V/(m s⁻²)), and an operational bandwidth of 0.02 to 4 kHz. In this sensor, the 9-cm diameter epoxy ball is suspended from rubber bands in a cage, resulting in a mass-spring system with a resonance frequency of 0.01 kHz. The sensor is powered by a 24 V battery. Its weight of 82 g in water (ϱ = 1,000 kg/m³) makes it slightly negatively buoyant. The vector sensor was placed at 1 m depth at the location near the listening station where the sea lion's head was during the hearing tests. The sample frequency was 65.5 kHz. The root-mean-square sound particle acceleration levels (PALs) in x, y, and z directions were averaged over t90. Sound particle acceleration was calculated from the energy sum of the root-mean-square acceleration levels in x, y, and z directions, summed in a bandwidth of 0.02 to 4 kHz. The specified sensitivities of the acceleration channels were checked and confirmed by TNO. For this purpose, the vector sensor was connected to a sinusoidal electro-magnetic shaker. Sensitivity was determined through comparison to the response of a calibrated reference accelerometer (Model 4517, B&K) mounted on the outer shell of the sensor. PAL was measured by the vector sensor. The mean-square sound particle velocity level (PVL) was derived from PAL by integration in the frequency domain.

Experimental Procedures
Experimental procedures have been described in detail by Kastelein et al. (2021, 2022a); a summary is given here. During trials, hearing test signals were produced at a random time 4 to 12 s after the California sea lion being tested stationed itself at the listening station (i.e., by placing its nose against the end cap of a water-filled PVC tube, 154 cm from the transducer and in line with the acoustic axis of the transducer). The sea lions were trained to leave the listening station when they detected the hearing test signal (correct signal response) or wait until they were called back to the start/response buoy by the trainer if they did not hear the signal (correct no-signal response). Each hearing test session consisted of ~25 trials and lasted for up to 12 min per sea lion. The sea lion not being tested was kept in the outdoor pool. Sessions consisted of two thirds signal-present trials and one third signal-absent ("catch") trials, offered in quasi-random order (never more than three consecutive signal-present or signal-absent trials). To prevent unintentional cuing, the operator was out of sight of the sea lion, and the trainer was not aware of the signal type. The end of a signal-absent trial

was indicated to the sea lion by blowing a whistle which was always heard. A psychophysical hearing test technique was used: the "up-down staircase" method (Békésy, 1947; Cornsweet, 1962; Levitt, 1971; Leek, 2001) with 2 dB steps. A switch from a hearing test signal level to which a sea lion responded (a "hit") to a level to which it did not respond (a "miss"), or vice versa, was called a "reversal." The 50% correct detection threshold (Levitt, 1971) was the mean of all available reversal levels per frequency.

We assessed the proportion of false positives as rates of pre-stimulus responses. A "pre-stimulus response" was defined as a California sea lion returning to the start/response buoy before either a hearing test signal (in a signal-present trial) or a whistle (in a signal-absent/catch trial) was produced. Pre-stimulus response data were obtained during the pre-exposure and control hearing test sessions of TTS studies (Kastelein et al., 2021, 2022a, 2022b) and during hearing test sessions in the present study.

The California sea lions did not readily adjust to new hearing test frequencies and found some more difficult to adapt to than others. That is, the subjects' threshold levels only stabilized after the first two or three sessions with each new frequency, which were therefore excluded from the analysis. For four of the frequencies, it took several weeks for thresholds to stabilize in one of the subjects (F01). In these cases, up to five consecutive sessions were excluded from analysis. As the subjects' mean thresholds for previous hearing test frequencies were known to be similar (within a few dB; Kastelein et al., 2021, 2022a, 2022b), testing of each frequency was continued until the thresholds of the two animals became stable (if they were not already). The mean hearing thresholds reported here are based on a total of 100 reversals per frequency.

All hearing tests with the California sea lions were conducted between January 2019 and April 2022. Hearing tests in the 0.60 to 80 kHz range were conducted over 2 to 3 mo per frequency, and hearing tests in the 0.031 to 0.25 kHz range were conducted over a 2-wk period per frequency.

Data Analysis
The sets of hearing thresholds obtained for each subject were compared using paired *t* tests with a significance level of 5%.

The threshold values of the two subjects of this study and those of California sea lion "Ronan" from the studies by Reichmuth et al. (2013) and Cunningham & Reichmuth (2016) were used to derive an equation to describe the general shape of the audiogram for this species. The audiogram of Ronan was used because (1) it is the lowest

audiogram published for California sea lions thus far; (2) it is the most similar to the audiograms obtained in the present study for F01 and M02; and (3) the studies on Ronan are similar to the present study in terms of behavioral measurement technique and low ambient noise levels (Reichmuth et al., 2013; Cunningham & Reichmuth, 2016). Using a manual adjustment approach, the parameters in Equation 2 from Southall et al. (2019) were changed to obtain a close fit to the data. Other equations were initially explored but the best-fitting equation (Equation 1) was in the format of Equation 2 from Southall et al. (2019).

Equation 2 from Southall et al. (2019) was originally based on a generic band-pass filter equation and then modified into an auditory weighting function by Finneran (2016):

$$W(f) = C + 10\log_{10} \{(f/f_1)^{2a} / [1+(f/f_1)^2]^a [1+(f/f_2)^2]^b\}$$

Here, $W(f)$ is the weighting function level in dB re 1 µPa at frequency f in kHz, and C, f_1, f_2, a, and b are fitting parameters describing the shape of the curve (Finneran, 2016; Southall et al., 2019): C is the weighting function gain (in dB) defining the overall vertical position of the curve; f_1 and f_2 (in kHz) are the inflection points of the low- and high-frequency roll-off, respectively; and a and b (dimensionless) define the slope of the low- and high-frequency roll-off, respectively (see p. 3 in Finneran, 2016, and p. 146 in Southall et al., 2019).

Agreement between the data from the three California sea lions (F01, M02, and Ronan) and the equation was quantified using Spearman product-moment correlations.
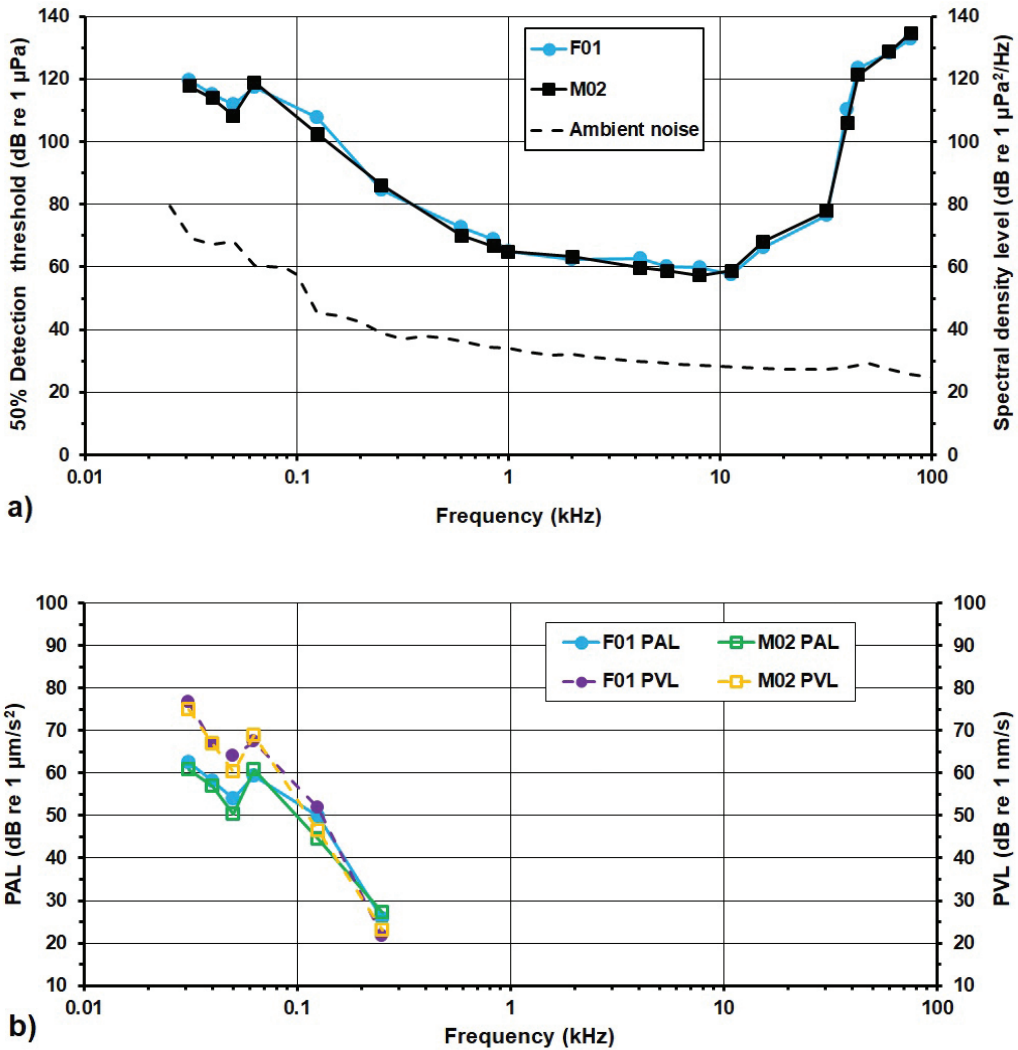
Results

Depending on the hearing test frequency, F01's average pre-stimulus response rate (for both signal-present and signal-absent trials) varied between 3 and 15%, and M02's varied between 5 and 13% (Table 1). These pre-stimulus response rates were considered acceptable.

The underwater audiograms (50% detection thresholds) of the two California sea lions were similar. The mean difference between the two sets of thresholds ± standard deviation (SD) was 0.89 ± 2.35 dB (paired *t* test: $t = 1.65$, degrees of freedom [df] = 18, $p = 0.11$), and both audiograms show the typical mammalian U-shape (Figure 1a). Maximum hearing sensitivity occurred at 11.3 kHz for F01 (i.e., 58 dB re 1 µPa) and at 8 kHz for M02 (i.e., 57 dB re 1 µPa; Table 1). The range of best hearing (defined as < 10 dB from the maximum sensitivity) was from ~1 to 16 kHz (four octaves),

Table 1. Mean 50% underwater sound detection thresholds (± standard deviation) and pre-stimulus response rates of adult female California sea lion F01 and subadult male California sea lion M02 for narrow-band, 1-s upsweep hearing test signals with center frequencies between 0.031 and 80 kHz. Thresholds are expressed as sound pressure levels (SPL; in dB re 1 µPa), particle acceleration levels (PAL; in dB 1 µm/s²), and particle velocity levels (PVL; dB re 1 mm/s). PAL and PVL were measured for 0.031 to 0.250 kHz to investigate the possibility of vibrotactile detection of low-frequency signals. Pre-stimulus response rates (in % of trials) are from pooled signal-present and signal-absent trials. No harmonics were detected in the hearing test signals at these SPLs. $n = 100$ reversals for each threshold.

Hearing test signal		F01				M02			
Center frequency (kHz)	1-s upsweep range (± 2.5% of center frequency) (kHz)	Mean 50% hearing threshold SPL (dB re 1 µPa)	Mean 50% detection threshold PAL (dB 1 µm/s²)	Mean 50% detection threshold PVL (dB re 1 mm/s)	Pre-stimulus response rate (%)	Mean 50% hearing threshold SPL (dB re 1 µPa)	Mean 50% detection threshold PAL (dB 1 µm/s²)	Mean 50% detection threshold PVL (dB re 1 mm/s)	Pre-stimulus response rate (%)
0.031	0.030-0.032	120 ± 2.1	63 ± 2.1	77 ± 2.1	15	118 ± 2.0	61 ± 2.0	75 ± 2.0	11
0.040	0.039-0.041	115 ± 2.1	58 ± 2.1	67 ± 2.1	11	114 ± 2.0	57 ± 2.0	67 ± 2.0	11
0.050	0.049-0.051	112 ± 2.4	54 ± 2.4	64 ± 2.4	8	108 ± 1.9	50 ± 1.9	60 ± 1.9	5
0.063	0.061-0.065	117 ± 1.8	59 ± 1.8	67 ± 1.8	9	119 ± 2.1	61 ± 2.1	69 ± 2.1	8
0.125	0.122-0.128	108 ± 2.2	50 ± 2.2	52 ± 2.2	11	102 ± 2.0	44 ± 2.0	46 ± 2.0	9
0.250	0.244-0.256	85 ± 1.9	26 ± 1.9	22 ± 1.9	11	86 ± 1.8	27 ± 1.8	23 ± 1.8	9
0.600	0.585-0.615	73 ± 2.4	--	--	7	70 ± 2.3	--	--	6
0.850	0.829-0.871	69 ± 1.7	--	--	6	67 ± 2.0	--	--	8
1.0	0.975-1.025	65 ± 1.5	--	--	3	65 ± 1.5	--	--	8
2.0	1.950-2.050	62 ± 1.9	--	--	8	63 ± 1.0	--	--	6
4.2	4.095-4.305	63 ± 1.8	--	--	12	60 ± 1.9	--	--	12
5.6	5.460-5.740	60 ± 2.0	--	--	5	59 ± 1.8	--	--	11
8.0	7.800-8.200	60 ± 2.3	--	--	9	57 ± 2.4	--	--	11
11.3	11.02-11.58	58 ± 1.8	--	--	5	59 ± 2.3	--	--	9
16.0	15.60-16.40	66 ± 2.0	--	--	8	68 ± 1.5	--	--	13
32.0	31.20-32.80	77 ± 1.9	--	--	10	78 ± 1.8	--	--	9
40.0	39.00-41.00	110 ± 1.7	--	--	8	106 ± 2.1	--	--	10
44.8	43.68-45.92	124 ± 2.2	--	--	6	121 ± 2.0	--	--	8
63.0	61.43-64.58	128 ± 2.0	--	--	7	129 ± 1.8	--	--	9
80.0	78.00-82.00	133 ± 2.0	--	--	6	135 ± 2.1	--	--	5

Figure 1. Underwater sound detection thresholds (audiograms) of California sea lions (*Zalophus californianus*) F01 and M02 (see Table 1). The mean 50% detection thresholds for narrow-band frequency-modulated hearing test signals are shown: (a) between 0.031 and 80 kHz in sound pressure level (SPL; dB re 1 µPa, root mean square), and (b) between 0.031 and 0.25 kHz in particle acceleration level (PAL; dB re 1 µm/s²) and particle velocity level (PVL; dB re 1 nm/s²). In (a), the ambient noise in the pool between 0.025 and 80 kHz is shown (the dashed line; right-hand y axis) in dB re 1 µPa²/Hz (spectral density level, derived from ⅓-octave band levels).

and sensitivity fell gradually below 1 kHz and steeply above 32 kHz. The hearing thresholds for 0.063 kHz were as expected, but thresholds of the three lower frequencies were 10 to 15 dB lower than expected based on extrapolation of the rest of the audiogram (Figure 1a).

The thresholds for the low-frequency hearing test signals between 0.031 and 0.25 kHz were also expressed as PAL (dB re 1 µm/s²) and PVL (dB re 1 nm/s) (Figure 1b). The PAL thresholds

of the two California sea lions were similar (mean difference between the two sets of thresholds ± SD = 1.66 ± 3.01 dB; paired *t* test: $t = 1.35$, $df = 5$, $p = 0.23$), as were the PVL thresholds (mean difference between the two sets of thresholds ± SD = 1.50 ± 3.08 dB; paired *t* test: $t = 1.19$, $df = 5$, $p = 0.29$; Table 1). As expected, the PVL thresholds increased at a greater rate than the PAL thresholds as the hearing test frequency decreased (Figure 1b).

Discussion

Evaluation of the Data

The hearing thresholds of the two California sea lions reported herein are suitable for extrapolation to a generic audiogram for the species for several reasons (discussed in detail below): (1) sample sizes were adequate; (2) standard deviations of threshold estimates and rates of pre-stimulus responses (i.e., false positives) were low; (3) masking effects were negligible; and (4) duration of test signals was probably above the temporal integration threshold of the auditory system:

1. In TTS studies with the same California sea lions (Kastelein et al., 2021, 2022a, 2022b), an unmasked pre-exposure hearing threshold was established as a reference level every day prior to the sea lions being exposed to the fatiguing sound intended to result in TTS. The resulting number of sessions per hearing test frequency, including the ambient noise control sessions and each of the SPL levels per fatiguing sound frequency, was five or six. Further replication resulted because baseline thresholds were determined not only at the fatiguing sound's frequency but also at one octave above that frequency. For each of the hearing test frequencies (0.60, 0.85, 1, 2, 4.2, 5.6, 8, 11.3, 16, 32, 40, 44.8, 63, and 80 kHz) measured in the four TTS studies (Kastelein et al., 2021, 2022a, 2022b, In prep.), mean thresholds were based on ~12 hearing test sessions. Thus, the numbers of individual thresholds per frequency reported here are higher than those obtained in other studies in which the main aim was to produce an audiogram (Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016). The repeat measures were often separated by many months. The relatively large sample sizes, stable signal detection criteria (see below), and long data collection periods suggest that, for these California sea lions, the threshold estimations are representative for this species.

2. The 50% correct detection thresholds reported here were for "familiar" signals (in terms of duration and frequency, except during the first sessions with new frequencies) that the sea lions were expecting to hear while actively listening during a specified time. In combination with the sea lions' high motivation in trying to detect the hearing test signals, as indicated by the low pre-stimulus response rates (i.e., between 3 and 15%), this resulted in low standard deviations of the threshold estimates—typically, similar to the 2 dB step size used in the up-down staircase method. Standard deviations of threshold estimates, as well as pre-stimulus response rates, were similar for both sea lions and unrelated to the hearing test frequency (Table 1). This suggests that both sea lions applied the same detection criteria and that these detection criteria were consistent across the full frequency range of hearing test signals and throughout the study period. In addition, their consistently high motivation indicated that the ratio of signal-present to signal-absent trials in our hearing tests was optimal and that the careful weekly adjustments of food rations were appropriate.

3. Ambient noise levels in the pool were consistently low (Figure 1a). If the ambient noise was masking the low-frequency thresholds, then the thresholds would be equal to the spectrum level of the ambient noise (Figure 1a) plus the critical ratio. Southall et al. (2000) found that California sea lion critical ratios between 0.2 and 2.5 kHz ranged from 18 to 22 dB. None of the measured thresholds, between 0.2 and 2.5 kHz at least, were masked by ambient noise. Even if the critical ratio value at 0.031 kHz was the same as that of a harbor seal (*Phoca vitulina*), namely, about 30 dB (Kastelein, unpub. data), the ambient noise in the pool would not be masking the threshold value.

4. Hearing test signal duration can influence hearing thresholds in an effect termed "temporal summation" or "temporal integration." That is, when the signal is shorter than the auditory system's integration time for that signal's frequency (the "time constant"), the amplitude required for its detection increases with decreasing signal duration (Yost, 2000). This effect has been demonstrated in several mammalian species, including humans (Hughes, 1946; Plomp & Bouman, 1959; Watson & Gengel, 1969), cats (*Felis catus*; Costalupes, 1983), bottlenose dolphins (*Tursiops truncatus*; Johnson, 1968), harbor seals (Terhune, 1988; Kastelein et al., 2010b), harbor porpoises (*Phocoena phocoena*; Kastelein et al., 2010a), and California sea lions (in air; Holt et al., 2012). Holt et al. (2012) estimated that, for their lowest frequency tested (i.e., 2.5 kHz), the time constant was 141 ms (or 312 ms when applying the method of

Kastelein et al., 2010b). Assuming that the integration times of California sea lions at very low frequencies are similar to those of harbor seals (Kastelein et al., 2010b), it is possible that longer test signal durations at and below 0.125 kHz would have resulted in lower detection thresholds. However, low-frequency hearing test signals of 2 to 5 s (as were presented to harbor seals by Kastelein et al., 2010b) would have required increasing the duration of the potential trial time beyond 12 s. This would alter the response criteria for signal-absent trials, likely increasing the rate of pre-stimulus responses/false positives. We therefore did not use hearing test signals with durations longer than 1 s.

Unexpectedly Higher Sensitivity for Low-Frequency Sounds

Underwater audiograms of pinnipeds are characterized by two distinct slope patterns at the high-frequency end that are likely a consequence of constraints on the sound pathway and conductive mechanisms (Cunningham & Reichmuth, 2016). These two slope patterns, which were first described for the sea lion Ronan by Cunningham & Reichmuth (2016), were also exhibited by the audiograms established for F01 and M02 in the present study. Their hearing thresholds showed a steep increase with increasing test signal frequency at the high-frequency end: from 32 to 63 kHz, the thresholds increased by approximately 50 dB. At frequencies above 63 kHz, the detection threshold levels increased, but at a lower rate. Overall, the slope pattern parallels the loss of frequency resolution at these high frequencies (Schusterman & Moore, 1978; Cunningham & Reichmuth, 2016). An implication of this is that, along with a requirement for higher amplitudes, the California sea lion's ability to discriminate between different sounds at these high frequencies will decrease the information content of signals at these high frequencies relative to similar signals at lower frequencies. Once the frequency of a signal exceeds that detected by the tonotopic map of the basilar membrane, pitch discrimination is lost (Schusterman & Moore, 1978).

At the low-frequency end of the audiogram, detection thresholds did not increase as steeply with decreasing frequency as expected. Sensitivity for the three lowest frequencies (i.e., 0.031, 0.040, and 0.050 kHz) was ~20 dB greater than expected based on extrapolation of the rest of the audiogram curve at adjacent higher frequencies, which predicts that hearing thresholds at 0.031, 0.040, and 0.050 kHz would be approximately 125, 120, and 117 dB re 1 μPa, respectively (Figure 1a). The low threshold values found for hearing test

frequencies 0.031, 0.040, and 0.050 kHz were neither caused by higher-frequency harmonics, nor by an equipment switch; the same equalizer, amplifier, and transducer were used for all hearing test signals ≤ 0.250 kHz. However, a calibration error may have occurred because the sound field for frequencies below 0.063 kHz is difficult to define in the near field of the transducer when long wave lengths are broadcast in a relatively small pool.

Another possible reason for the low threshold values is a perceptual modality shift. That is, the California sea lions may have used a sensory system other than hearing to detect the low-frequency sounds. Gerstein et al. (1999) found an increase in sensitivity from 0.2 to 0.015 kHz (relative to levels if higher-frequency thresholds were extrapolated to lower frequencies) in the underwater audiogram of the West Indian manatee (*Trichechus manatus*) that they attributed to possible vibrotactile detection of acoustic particle motion. When the sound projector was moved out of the near field, the manatee ("Stormy") could no longer detect these low frequencies, which supported this hypothesis (E. R. Gerstein, pers. comm., 11 October 2022).

Pinnipeds are known to be able to detect particle motion with their vibrissae, allowing them to follow hydrodynamic trails left behind by prey (Dehnhardt et al., 1998, 2001; Schulte-Pelkum et al., 2007; Gläser et al., 2011; Hanke et al., 2013). To investigate if the sea lions detected the low-frequency sounds as particle motion vibrations using their vibrissae (i.e., rather than as sound pressure using their ears), as suggested by Kastak & Schusterman (1998), we measured particle motion as an acceleration component (PAV; in dB re 1 μm/s^2) and as a velocity component (PVL; in dB re 1 nm/s). Dehnhardt et al. (1998) measured PAL (in nm/s^2) and PVL (in μm/s) detection thresholds in a study in which a harbor seal had to detect water movements. In the frequency range 0.03 to 0.10 kHz, the thresholds of the harbor seal were almost two orders of magnitude higher than the California sea lions' acoustic thresholds converted to Dehnhardt et al.'s PAL and PVL units. Harbor seals perform better at hydrodynamic trail following than California sea lions due to the undulated surface structure of their vibrissae, which suppresses vortex-induced vibrations from their own wake (Hanke et al., 2010, 2012; Morrison et al., 2016). Compared to sea lion vibrissae, which are smooth, harbor seal vibrissae experience drag forces that are at least one order of magnitude lower (Hanke et al., 2010). Thus, taking into account that harbor seal vibrissae are likely better at perceiving particle motion than those of sea lions, as well as that the sensitivity of harbor seal vibrissae rapidly drops below 0.25 kHz

(Renouf, 1979), it seems unlikely that the low-frequency sounds were detected by the California sea lions' vibrissae in the present study.

Comparison of California Sea Lion Audiograms
Comparing the data of the present study with the published behavioral audiograms of five California sea lions (Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016), some differences become apparent (Figure 2). For instance, the thresholds obtained during the present study are among the lowest reported for California sea lions thus far, and those from the first study to describe a California sea lion audiogram (Schusterman et al., 1972) were the highest (Figure 2). As there is no standard methodology for behavioral audiometric assessments of marine mammals, the observed differences in hearing thresholds between studies could be due to several factors, including the following:

• *Differences in the ambient noise levels in the testing facilities* – Even though hearing test signals were believed to be unmasked by ambient noise in the previous studies

(i.e., Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016), ambient noise levels in those previous studies were higher than those in the present study.

• *Differences in the time available for the study* – It sometimes took longer for the two California sea lions in this study to achieve maximal sensitivity to new frequencies than it took for harbor seals and harbor porpoises (Kastelein et al., 2009, 2017). The threshold for some hearing test signals continued to descend for weeks. This suggests that at least some differences between published thresholds may be due to differences in the amount of time that was used, or was available, to do the hearing tests. Thresholds may also depend on how experienced the subjects are with psychophysical hearing tests.

• *Differences in threshold calculation* – For instance, Schusterman et al. (1972) used a 75% correct detection criterion; had a 50% correct detection level been applied, as in the present study and the studies by Reichmuth
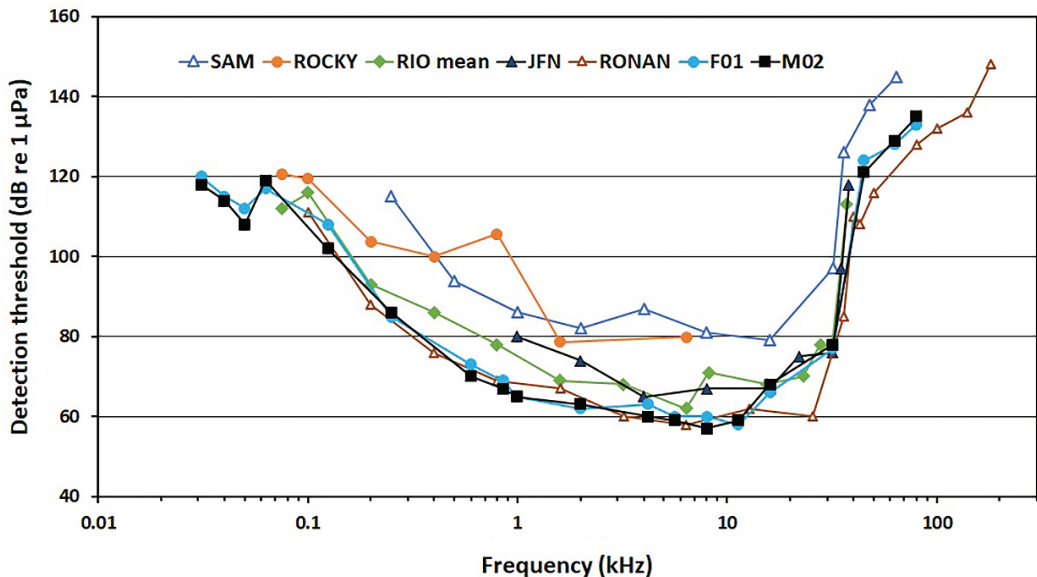
Figure 2. Underwater audiograms of seven California sea lions. Hearing thresholds are shown for F01 and M02 (7 to 11 and 1 to 5 y old, respectively; present study), "Sam" (5 to 6 y old, measured by Schusterman et al., 1972; converted threshold levels obtained from Reichmuth & Southall, 2012), "Rocky" (17 to 19 y old; Kastak & Schusterman, 1998), "Rio" (7 to 15 y old; measured by Kastak & Schusterman, 1998, by Southall et al., 2005, and by Reichmuth & Southall, 2012; mean threshold levels across all stages of testing obtained from Reichmuth & Southall, 2012), "JFN" (2 y old; Mulsow et al., 2012), and Ronan (3 to 6 y old; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016).

et al. (2013) and Cunningham & Reichmuth (2016), their reported thresholds would most likely be several dB lower.

- *Individual differences in hearing sensitivity* – From the present study as well as from previous hearing (TTS) studies with F01 and M02 (Kastelein et al., 2021, 2022a, 2022b), some individual variation in hearing sensitivity became apparent. Therefore, some of the differences between the hearing thresholds of F01, M02, and the previously tested sea lions can likely be attributed to individual differences (e.g., related to age, size, sex, health, acoustic history).

While the sea lions in the previous studies may have had somewhat different hearing sensitivities, it is striking that the sea lions from the present study (F01 and M02) and the most recently tested sea lion before that (Ronan; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016) have very similar, and low, hearing thresholds (Figure 2) despite differences in sex and age. With the studies by Reichmuth et al. (2013) and Cunningham & Reichmuth (2016) being most similar to the present study in terms of behavioral

measurement technique and low ambient noise levels, this suggests that the main cause of differences in hearing thresholds between studies is methodological.

Proposed Generic California Sea Lion Audiogram

Based on an equation from Southall et al. (2019), we propose a new generic California sea lion audiogram (Eq. 2). Parameters in Equation 1 were adjusted manually to obtain a close fit to the audiograms of F01 and M02 (present study), and Ronan (Reichmuth et al., 2013; Cunningham & Reichmuth, 2016), resulting in Equation 2:

$$T(F) = 60 - 10\log_{10}\{(F/0.94)^{4.5}/[1+(F/0.94)^2]^2 \ [1+(F/30)^3]^9\}$$

In Equation 2, T(F) is the threshold level in dB re 1 µPa, and F is the frequency in kHz over the range of 0.031 to 63 kHz. The fit of Equation 2 to the average threshold data (based on the three studies mentioned above) was very good (Figure 3): $r^2 = 0.939$ ($t = 26.45$, $p < 0.000001$, $n = 47$). The high r^2 value reflects the similarity of the threshold values of the three California sea lions and the regularity of the shape of the audiograms over the
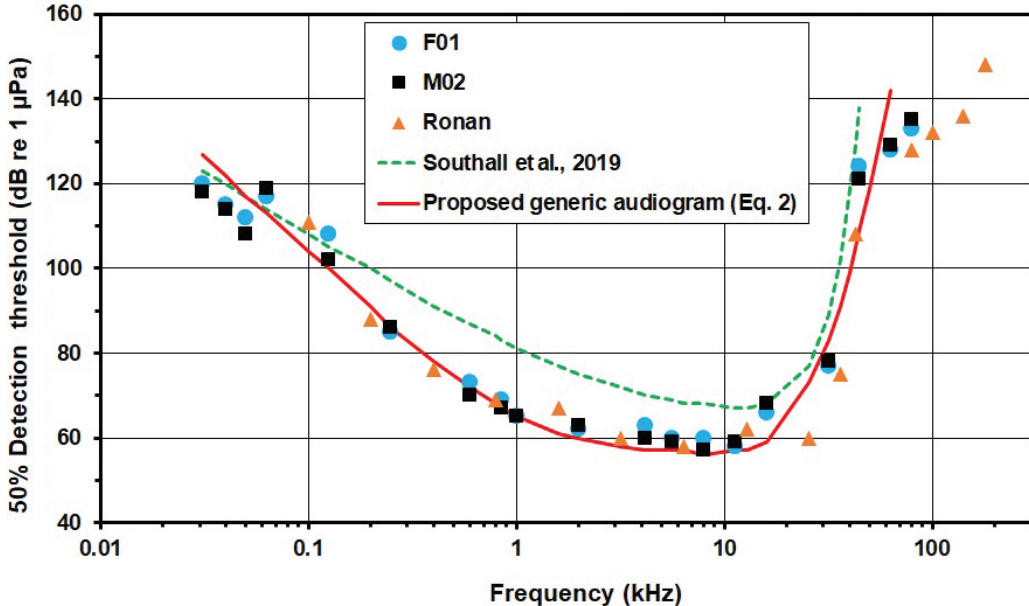
Figure 3. The descriptive equations' fit to the underwater detection thresholds of California sea lions F01 and M02 (this study) and Ronan (Reichmuth et al., 2013; Cunningham & Reichmuth, 2016). The dashed green line depicts the equation for "other marine carnivores in water" from Southall et al. (2019; see Eq. 1). The solid red line depicts the proposed generic audiogram equation (Eq. 2): Threshold (dB re 1 µPa) = 60-10log₁₀ {(F/0.94)⁴·⁵/[1+(F/0.94)²]² [1+(F/30)³]⁹} where F is the frequency (kHz). The proposed equation is a good fit to the data ($r^2 = 0.939$) from 0.031 to 63 kHz.

frequency hearing range (Figures 2 & 3). At and above 80 kHz, the equation produced unrealistically high values, which were therefore dropped from the correlation analyses. A separate equation may be needed to describe the distinct two-slope high-frequency end of California sea lion (and other pinniped) audiograms (Cunningham & Reichmuth, 2016).

We suggest that Equation 2 represents the most accurate generic California sea lion audiogram to date (Figure 3). This audiogram is based on the hearing thresholds measured from the three sea lions with the most sensitive hearing tested to date, as well as across the widest frequency range tested to date (Figures 2 & 3). As such, it is likely more representative for the species than any of the separate or composite audiograms for California sea lions published thus far (i.e., Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005, 2019; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016).

We also suggest that our proposed generic California sea lion audiogram (i.e., the lowest threshold levels for California sea lions) could be adopted as representative of otariid underwater hearing thresholds. This has the advantage of presenting a set of threshold values that are unlikely to be appreciably lower in any other otariid species (e.g., Moore & Schusterman, 1987; Kastelein et al., 2005b). The proposed audiogram model is about 10 dB lower than Southall et al.'s (2019) model for "other marine carnivores in water" (p. 140), which includes otariids. Except at the very highest and lowest frequencies, the proposed generic audiogram is a good fit to the recent California sea lion hearing threshold data (Figure 3). Until audiograms of other otariid species covering their full frequency range become available, using this sensitivity in environmental impact assessments for other otariid species will probably present a conservative approach to assessing potential anthropogenic noise disturbance.

Suggestions for Future Research

Despite sharing their environment and experiencing similar exposure to underwater sounds, fewer hearing studies have been conducted on otariids than on phocids or odontocetes (toothed whales). Recent studies on TTS in California sea lions (Kastelein et al., 2021, 2022a, 2022b) provided evidence that the sound exposure levels needed to cause TTS are lower than those found in the single study (Kastak et al., 2005) that was available to Southall et al. (2019) for the derivation of a noise exposure function. To be able to set underwater noise exposure criteria for otariids

that are as well supported as those for phocids and odontocetes (see Southall et al., 2019), additional data on the hearing of other otariid species are required. Such data include information on hearing sensitivity (as provided by Schusterman et al., 1972; Kastak & Schusterman, 1998; Southall et al., 2005; Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016; present study), but also on how otariids hear in the presence of masking noise (critical ratios, critical bands, noise amplitude modulation; e.g., Southall et al., 2000, 2003; Cunningham et al., 2014), how they hear sounds of different durations (especially pulsed sounds; e.g., Holt et al., 2012), and how they perceive sounds coming from different directions (receiving beam pattern; e.g., Moore & Au, 1975; Kastelein et al., 2005a; Accomando et al., 2020).

The present study also highlighted the need for research into other modalities of sound perception in pinnipeds. Hearing in pinnipeds and other mammals is mainly based on the detection of sound pressure, whereas fish and invertebrates mainly detect the particle motion component of sound (Nedelec et al., 2016; Popper & Hawkins, 2018). Hearing studies such as the present study and those by Kastak & Schusterman (1998) and Gerstein et al. (1999), as well as studies into the hydrodynamic perception capabilities of pinniped vibrissae (Dehnhardt et al., 1998, 2001; Schulte-Pelkum et al., 2007; Hanke et al., 2010, 2012, 2013; Gläser et al., 2011; Morrison et al., 2016), suggest that pinnipeds may detect particle motion in addition to pressure as a means of stimulus detection. The exact mechanism, or mechanisms, by which they do so, however, remain unclear.

Ultimately, information on pinniped sound perception can also be used in studies of California sea lions' general ecology—for example, to estimate at what distances California sea lions can detect conspecifics, echolocation clicks of killer whales (*Orcinus orca*; a predator), and fish (prey). This information can also be used to predict the effects of anthropogenic underwater noise, and to assess the extent to which biologically relevant sounds are masked by anthropogenic noise.

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