Aquatic Mammals 2025, *51*(1), 13-30, DOI https://doi.org/10.1578/AM.51.1.2025.13

Temporary Hearing Threshold Shift in California Sea Lions (*Zalophus californianus*) Due to a Noise Band Centered at 40 kHz and Comparison with Shifts Due to Lower-Frequency Sounds

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Abstract

California sea lions (*Zalophus californianus*) exposed to anthropogenic noise may experience temporary hearing threshold shift (TTS). The function used in regulations to protect their hearing from such damage in the Pacific Ocean is based on only one datapoint, so more data are needed. To determine their frequency-dependent susceptibility to noise-induced TTS, two California sea lions were exposed for 60 minutes to a continuous one-sixth-octave noise band (NB) centered at 40 kHz as the fatiguing sound, at sound pressure levels of 119 to 143 dB re 1 µPa, resulting in sound exposure levels (SELs) of 155 to 179 dB re 1 µPa^{2}s. TTSs were quantified at the center frequency of the fatiguing sound and up to one octave above that frequency (at 40, 50, 56.5, 63, and 80 kHz). Statistically significant TTS occurred at all hearing test frequencies; higher SELs caused greater TTSs. Significant onset of $TTS_{(1\text{-}4\ min)}$ occurred after exposure to a minimum SEL of 167 dB re 1 µPa^{2}s—a shift of 5.2 dB at hearing frequency 56.5 kHz. At other hearing frequencies, onset of $TTS_{1\text{-}4}$ occurred at SEL 173 dB re 1 µPa^{2}s. $TTSs_{1\text{-}4} \leq 8$ dB recovered within 12 min, and $TTSs_{1\text{-}4}$ of > 8 dB recovered within 60 min. TTSs and hearing recovery patterns were similar in both subjects. Comparison with TTS data for the species' hearing frequency range (0.6 to 40 kHz) shows that after exposure to fatiguing sound frequencies of 0.6, 1, 4, 8, and 16 kHz, the largest $TTS_{1\text{-}4}$ occurred half an octave above the frequency of each of the fatiguing sounds. After exposure to fatiguing sound frequencies 2, 32, and 40 kHz, the largest TTS occurred at the frequency of the fatiguing sounds. Recovery patterns after exposure to the NB at 40 kHz were similar to those after exposure to NBs at 0.6, 1, 2, 4, 8, 16, and 32 kHz. Over almost the entire hearing range, the shape of the audiogram is a poor predictor of the shape of the TTS-onset function. The low TTS-onset SELs show that the hearing of California sea lions is more vulnerable to injury by anthropogenic sound in the oceans than was previously thought.

Key Words: anthropogenic noise, audiogram, auditory weighting, fatiguing sound, hearing damage, hearing recovery, hearing sensitivity, Otariidae, pinniped, temporary hearing threshold shift, TTS

Introduction

Underwater anthropogenic noise in the oceans may have adverse effects on marine animals (Duarte et al., 2021). In marine mammals, high-amplitude sound of sufficient duration can result in short-term reduced hearing sensitivity (temporary hearing threshold shift [TTS]) or permanent hearing damage (permanent hearing threshold shift [PTS]), with negative effects on individual fitness and population dynamics. Regulatory protection of marine mammals from noise requires improved understanding of the vulnerability of their hearing.

The California sea lion (*Zalophus californianus*), a species in the family Otariidae (eared seals), is exposed to noise from anthropogenic activities within its coastal geographic range in the North American Northeast Pacific Ocean (Melin et al., 2018). Understanding the consequences of TTS will help regulatory agencies determine safe and acceptable noise exposure levels for this species (Houser et al., 2017; Southall et al., 2019). TTS in California sea lions has been studied by Kastak et al. (1999, 2005), Finneran et al. (2003), and Kastelein et al. (2021b, 2022a, 2022b, 2024). Fatiguing sounds of different amplitudes and durations result in varying reduced hearing sensitivity at different frequencies and with varying recovery times (Finneran, 2015; Kastelein et al., 2020, 2021a, 2021b). The present study is one of five in a comprehensive research project on California sea lions conducted at SEAMARCO in which TTS was induced by exposure to the following fatiguing sound frequencies: 0.6 and 1 kHz (Kastelein et al., 2022b), 2 and 4 kHz (Kastelein et al., 2021b), 8 and 16 kHz (Kastelein et al., 2022a), 32 kHz (Kastelein et al., 2024), and 40 kHz (present study). In all five studies, the TTS-onset sound exposure level (SEL) was below the TTS-onset function proposed by Southall et al. (2019) for "other marine carnivores in water," which was based on the California sea lion audiogram and data from Kastak et al. (2005). Information on the susceptibility of California sea lions to TTS due to 40 kHz sounds is needed for Environmental Impact Assessments of high-frequency anthropogenic sounds from sources such as depth sounders, fish-finding sonars, underwater data communication devices, and acoustic remote-controlled vehicles.

The goals of the present study, exposing two California sea lions to a fatiguing sound with a center frequency of 40 kHz at several SELs, are (1) to quantify TTS at five hearing frequencies (from 40 kHz to one octave above 40 kHz); (2) to determine the TTS-onset SEL for each hearing frequency; (3) to describe the pattern of hearing recovery after the fatiguing sounds stop; and (4) to assess differences in susceptibility to TTS between the two California sea lions. In the "Discussion," by utilizing TTS data from the entire research project covering most of the hearing range of California sea lions (0.6 to 40 kHz) and in relation to the published audiogram, we (1) compare effects on hearing frequency, (2) compare recovery, and (3) compare TTS-onset SELs with the published TTS-onset function for "other marine carnivores in water" (including Otariidae; Southall et al., 2019).

Methods

A condensed version of the methods is presented here. The subjects, study area, acoustics, experimental procedures, and data analyses are described in more detail by Kastelein et al. (2021b, 2022a, 2022b, 2024).

Subjects and Study Area

The subjects were an adult female California sea lion (F01, age 11 y) and her subadult male offspring (M02, age 5 y). They were healthy and had normal hearing thresholds (Reichmuth et al., 2013; Kastelein et al., 2023).

The study was conducted at the SEAMARCO Research Institute, the Netherlands, in a remote and quiet location. The California sea lions were kept in a pool complex consisting of an outdoor pool and an indoor pool. The indoor pool consisted of a deep part (6 × 4 m; 2 m deep), where the sea lions were kept during the sound exposures and where the hearing tests were conducted, and a shallow part (6 × 3 m; 1 m deep), where the transducer for the fatiguing sounds was placed (see Kastelein et al., 2021b). During sound exposure and control sessions, both sea lions were confined to the deep part of the indoor pool and could not leave the water. During the hearing tests, the sea lion not being tested was kept in the outdoor pool.

Ambient Noise and Sound Pressure Level Measurement

The ambient noise was measured, and the fatiguing sound (in air and underwater) and hearing test signals were calibrated, once every 3 mo during the study period by an independent research organization (TNO, the Hague, the Netherlands).

The California sea lions' listening environment was kept as quiet as possible for hearing tests. The amplitude of the ambient noise in the indoor pool was very low and fairly constant above 0.25 kHz under test conditions (see Kastelein et al., 2024). Test conditions entailed the water circulation system being turned off at least half an hour before the first hearing test was conducted; no rain; and generally wind force Beaufort ≤ 4, depending on the wind direction, with only researchers involved in the hearing tests within 15 m of the pool complex, and those researchers standing still.

Fatiguing Sounds

Digitally generated continuous (100% duty cycle) constant-amplitude one-sixth-octave noise bands (NBs) centered at 40 kHz, without harmonics, were used as the fatiguing sounds (i.e., sounds intended to cause TTS; see Kastelein et al., 2021b).

To produce the NB at 40 kHz at sufficient sound pressure levels (SPLs) to elicit at least 6 dB TTS (a marker of TTS onset; Southall et al., 2019) in the California sea lions, the sound was amplified by a custom-built, high-power, wide-band amplifier and transmitted underwater by a cylindrical transducer (EDO Western Model 337; EDO Corporation, Salt Lake City, UT, USA).

The transducer was suspended in the shallow part of the indoor pool at 1 m depth, 5 cm above the pool floor (see Figure 1). The linearity of the transmitter system producing the fatiguing sound was checked during each calibration and was consistent to 1 dB within a 25 dB range (overlapping the SPL range used in this study).

To quantify the distribution of the fatiguing sounds in the deep part of the indoor pool, the

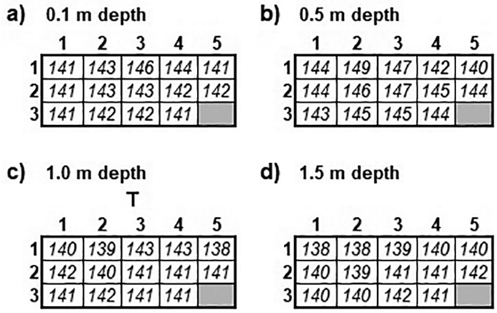


Figure 1. An example, for a source level of 143 dB re 1 µPa, of the sound pressure level (SPL) distribution (values in dB re 1 µPa) in the deep part of the indoor pool (6 × 4 m; 2 m deep; not to scale) during projection of the fatiguing sounds (continuous one-sixth-octave noise bands centered at 40 kHz) at four depths (a through d). Measurements were taken at 14 locations ≥ 1.0 m from the pool wall on a horizontal grid with cells of 1 × 1 m, at four depths per grid cell. These data were used to calculate the average received SPL that the California sea lions (*Zalophus californianus*) experienced during sound exposure. In this example, the mean (± standard deviation) SPL was 143 ± 2.4 dB re 1 µPa (n = 56). The letter **T** in (c) indicates the approximate location of the fatiguing sound transducer (at 1 m depth) in the adjacent shallow part of the indoor pool. The gray area indicates the location of the hearing test signal transducer and baffleboard; this part of the pool could not be accessed by the sea lions (see Kastelein et al., 2021b).

SPL was measured at 56 points (Figure 1). When the fatiguing sound was being projected, the California sea lions generally swam irregularly shaped circles throughout the entire deep part of the indoor pool at all depths, but mostly mid-water at 1 m depth; therefore, the mean SPL experienced by the sea lions was calculated as the power mean SPL of all 56 individual measurement points. SPL varied little with depth or location, resulting in a homogeneous sound field for the fatiguing sound (Figure 1). During sound exposure sessions, the one-sixth-octave NB centered at 40 kHz was projected for 60 min at five source levels, resulting in mean SPLs ranging from 119 to 143 dB re 1 µPa (mean SEL range: 155 to 179 dB re 1 μPa^2s). The highest SPLs used were the highest amplitudes that could be generated without distortion or harmonics.

During occasional and very brief jumps, the California sea lions' heads were completely out of the water. Therefore, though the fatiguing sound was generated underwater, its aerial SPL was also measured with two microphones (Brüel & Kjær [B&K] Model 4135; B&K, Virum, Denmark) with pre-amplifiers (B&K 2669), which were connected to the multi-channel high-frequency analyzer (B&K pulse system LAN-XI 3050) and to a microphone calibrator (B&K 4231). The two microphones were 6 m apart and 30 cm above the water surface. Aerial SPL varied by at most 1 dB between the two microphones, so the mean of the two measurements was used to represent the aerial SPL that the sea lions were exposed to on the rare occasions when their heads were completely out of the water (Table 1).

Before each sound exposure test (see "Experimental Procedures"), the voltage output of the emitting and receiving systems were checked for consistency. If the values were the same as those obtained during SPL calibrations, the sound exposure test was performed.

Hearing Test Signals

The California sea lions were trained to detect signals presented during hearing tests before and after exposure to the fatiguing sound. Narrowband upsweeps (linear frequency-modulated tones) were used as hearing test signals (Finneran & Schlundt, 2007).

The hearing test signal frequencies were 40, 50, 56.5, 63, and 80 kHz: the center frequency of the fatiguing sound, and one third of an octave, half an octave, two thirds of an octave, and one octave above that frequency. The hearing test signals were generated digitally (*Adobe Audition*, Version 3.0; Adobe Inc., San Jose, CA, USA). The linear upsweeps started and ended at ± 2.5% of the center frequency of the hearing test signal and had durations of 1,000 ms, including a linear rise and fall in amplitude of 50 ms. The WAV files used as hearing test signals were projected into the pool using equipment described by Kastelein et al. (2021b). The output drove an acoustic transducer (EDO Western Model 337).

The free-field received SPL of each hearing test signal was measured at the position of the California sea lion's head during the hearing tests. Calibration measurements were conducted with two hydrophones, one at the location of each auditory meatus of a sea lion positioned at the listening station. The linearity of the transmitter system was consistent to 1 dB within a 30 dB range (from 10 dB above the hearing threshold). The SPL at the two locations differed by 0 to 2 dB, depending on the test frequency, and the mean SPL of the two hydrophones was used to calculate the stimulus level during hearing tests.

Experimental Procedures

For the hearing tests, a go/no-go, one-up/one-down staircase method (Cornsweet, 1962) was applied with 2 dB steps, producing a 50% correct detection threshold (Levitt, 1971). Following a correct detection of a signal (a hit), the next

Table 1. The mean, standard deviation (SD), and range of initial temporary hearing threshold shift (TTS_{1-4} in California sea lion F01 and TTS_{12-16} in M02) after exposure for 60 min to ambient noise (control) or to a continuous constant-amplitude one-sixth-octave noise band centered at 40 kHz at several sound exposure levels (SELs), quantified at hearing frequencies 40, 50, 56.5, 63, and 80 kHz. Mean underwater SELs (calculated from mean underwater sound pressure levels [SPLs]) and mean aerial SPLs are shown. TTS levels were calculated as the differences between pre-exposure and post-exposure hearing thresholds. No TTS occurred during control tests; *n* = sample size. *TTS significantly different from control value ($p < 0.05$).

Hearing test frequency (kHz)	SPL in water (dB re 1 µPa)	SEL in water (dB re 1 µPa²s)	SPL in air (dB re 20 µPa)	Sea lion F01 TTS_{1-4} (dB)				Sea lion M02 TTS_{12-16} (dB)			
				Mean	SD	Range	*n*	Mean	SD	Range	*n*
40	Ambient	Control	46	0.8	0.4	0.3-1.3	4	0.7	0.9	-0.1-2.0	4
	131	167	47	1.4	0.3	1.1-1.8	4	-0.4	0.6	-0.8-0.6	4
	137	173	53	8.0*	1.9	6.3-10.6	4	1.0	0.8	-0.2-1.5	4
	143	179	59	11.5*	1.0	10.4-12.5	4	3.6*	1.0	2.2-4.5	4
50	Ambient	Control	46	0.0	1.0	-1.4-0.8	4	-0.2	0.6	-0.9-0.4	4
	131	167	47	1.4	1.0	0.0-2.2	4	-0.1	0.4	-0.5-0.4	4
	137	173	53	5.2*	0.9	4.0-6.1	4	0.7	0.7	0.1-1.6	4
	143	179	59	9.2*	0.8	8.3-10.1	4	5.1*	1.2	3.8-6.3	4
56.5	Ambient	Control	46	1.2	1.2	-0.3-2.6	4	0.7	1.0	-0.2-1.8	5
	119	155	46	0.9	1.2	-0.3-2.0	4	--	--	--	--
	125	161	46	2.8	1.5	1.3-4.9	5	--	--	--	--
	131	167	47	5.2*	2.0	2.9-8.5	5	0.2	0.7	-0.6-1.4	6
	137	173	53	7.4*	1.1	6.3-8.7	5	3.5*	1.1	2.3-4.8	4
	143	179	59	11.2*	0.6	10.4-11.8	4	5.5*	0.5	4.9-6.0	4
63	Ambient	Control	46	0.2	0.8	-0.9-1.2	4	-0.5	1.2	-1.6-1.0	4
	131	167	47	0.3	1.1	-1.3-1.2	4	-0.1	1.0	-1.1-1.3	4
	137	173	53	4.5*	0.2	4.3-4.8	4	0.8	0.6	0.1-1.5	4
	143	179	59	6.6*	0.6	5.9-7.2	4	2.9*	0.2	2.8-3.2	4
80	Ambient	Control	46	-0.1	1.1	-1.3-1.4	4	0.4	0.4	-0.1-0.8	4
	131	167	47	0.7	1.7	-0.8-2.8	4	0.7	0.3	0.2-0.9	4
	137	173	53	5.5*	1.0	4.5-6.9	4	0.6	1.0	-0.7-1.7	4
	143	179	59	6.7*	0.6	5.9-7.1	4	3.6*	1.0	2.4-4.7	4

signal presentation was lowered by 2 dB. This continued until the signal was not detected (a miss). A switch from a hit to a miss is termed a reversal. Following a miss, the next signal levels were increased with 2 dB steps until the signal was correctly detected (the next reversal). The 50% correct detection threshold was the mean of the dB levels of all reversals. No-signal trials (catch trials, in which a whistle indicating the end of the test was the stimulus; see Kastelein et al., 2021b) were presented one-third of the time, and the subsequent signal levels were not changed, regardless of whether the responses to the no-signal trials were correct or incorrect. For each hearing trial, the signal was produced at a random time (4 to 12 s after a sea lion stationed properly at the listening station), and ~25 trials were conducted in each hearing test session, which lasted up to 12 min. When at the listening station, the California sea lions' ears were 1.6 m from the hearing test signal transducer.

One sound exposure test was conducted per day, starting at around 0900 h. A total sound exposure test consisted of (1) a pre-exposure hearing test session, (2) a fatiguing sound exposure, and (3) one or more post-sound exposure (PSE) hearing test sessions. The first PSE hearing test (with the hearing test signal used in the pre-exposure hearing test) commenced within 1 min after the fatiguing sound had stopped for the first California sea lion to be tested (usually F01), and 12 min after the fatiguing sound had stopped for the second sea lion (usually M02). It took less than 1 min for the sea lions to swap places by moving between the indoor and outdoor pools so that testing of the second sea lion could begin without delay.

In addition to the magnitude of TTS soon after sound exposure, subsequent recovery times were recorded. The subscript numbers associated with the PSE periods are the minutes following the cessation of the fatiguing sound, starting with three consecutive 4-min periods (in the first PSE hearing test). The hearing sensitivity of F01 was tested mostly during up to four PSE periods: 1-4 min (PSE_{1-4}), 4-8 min (PSE_{4-8}), 8-12 min (PSE_{8-12}), and 60 min (PSE_{60}) after the fatiguing sound exposure ended. The hearing sensitivity of M02 was tested mostly 12-16 min (PSE_{12-16}), 16-20 min (PSE_{16-20}), and 20-24 min (PSE_{20-24}) after the fatiguing sound exposure ended. Testing was continued until hearing recovery had taken place (defined as a return to mean TTS of < 2 dB).

Control tests were randomly dispersed among the fatiguing sound exposure tests and were conducted in the same way as sound exposure tests, but with exposure to low ambient noise instead of fatiguing sound. The post-ambient exposure (PAE) hearing test session was divided into three consecutive 4-min periods per subject (like the fatiguing sound exposure tests); no PAE tests were conducted after those periods.

To investigate individual differences in susceptibility to TTS, the order in which the California sea lions were tested was reversed in four sessions for one SEL. In these sessions, M02 was tested first at one high SEL: 179 dB re 1 μPa^2s (with the 56.5 kHz hearing test signal, half an octave above the center frequency of the NB).

In general, if no TTS was found at a certain hearing test frequency after exposure to a fatiguing sound with a particular SPL, this frequency was not tested after exposure to lower SPLs. The sample size was generally four for each combination of test parameters (individual sea lion, NB, SPL, and hearing test signal frequency; see "Results"). Data were collected between April and November 2022.

Data Analysis

To check for false positives, the mean incidence of pre-stimulus responses by the California sea lions was calculated as a percentage of the trials in each hearing test session. Both signal-present and signal-absent trials were included in the calculations.

The pre-exposure mean 50% hearing threshold ($PE_{50\%}$) for each test was determined by calculating the mean SPL of all reversal pairs in the pre-exposure hearing test session. TTS_{1-4} (mostly for F01) was calculated by subtracting the $PE_{50\%}$ from the mean 50% hearing threshold during PSE_{1-4}. A similar method was used to calculate TTS_{12-16} (mostly for M02).

We define the onset of TTS as occurring at the lowest SEL at which a statistically significant difference could be detected between the hearing thresholds of the PSE_{1-4} or PSE_{12-16} time periods and the hearing thresholds measured after the control tests (PAE_{1-4} or PAE_{12-16}), both relative to the pre-exposure thresholds. Statistical significance ($p < 0.05$) was established by conducting a one-way ANOVA on the initial TTS (TTS_{1-4} in F01 and TTS_{12-16} in M02), separately for each California sea lion and for each hearing test frequency, with the factor SEL (including the control). When the ANOVA produced a significant value overall, the levels were compared to the control by means of Dunnett multiple comparisons. These analyses were conducted in *Minitab 18*, and data were conformed to the assumptions of ANOVA (equal variances, normal distribution of data and residuals; Zar, 1999). Recovery of hearing and individual differences in susceptibility to TTS are described without inferential statistical analysis.

In two sessions, when F01 was alone in the pool, she swam in a much more regular pattern than when she was with M02. She swam regular clockwise ovals and often breathed in the same location. Her TTS_{1-4} was approximately half that in sessions with both study animals. These two sessions were discarded from the dataset.

Results

When the fatiguing sounds were being generated, the California sea lions mostly took single, short breaths while lifting only their noses out of the water. On a few occasions when the sea lions jumped for respiration during fast swimming, their heads were completely out of the water for < 1 s during sound exposure sessions. Their swimming pattern was very erratic which was usual for when they swam together, even without sound exposure.

Pre-Stimulus Responses

The California sea lions always participated in the hearing tests before and after the 60-min sound exposure and control sessions, and they produced few false positives overall. Pre-stimulus response rates during the pre- and post-exposure hearing test sessions and control tests varied between 5.4 and 12.2% for F01 and between 2.7 and 14.7% for M02.

Effect of Fatiguing Sound Exposure Level on TTS

The one-way ANOVAs to investigate onset of TTS showed that TTS_{1-4} (F01) and TTS_{12-16} (M02) were significantly affected by the fatiguing sound's SEL at all five hearing test signal frequencies ($p = 0.000$; Table 1; Figure 2). Higher SELs resulted in greater TTSs at all hearing frequencies that were tested.

No change in susceptibility to TTS was observed during the study. As expected, the control tests

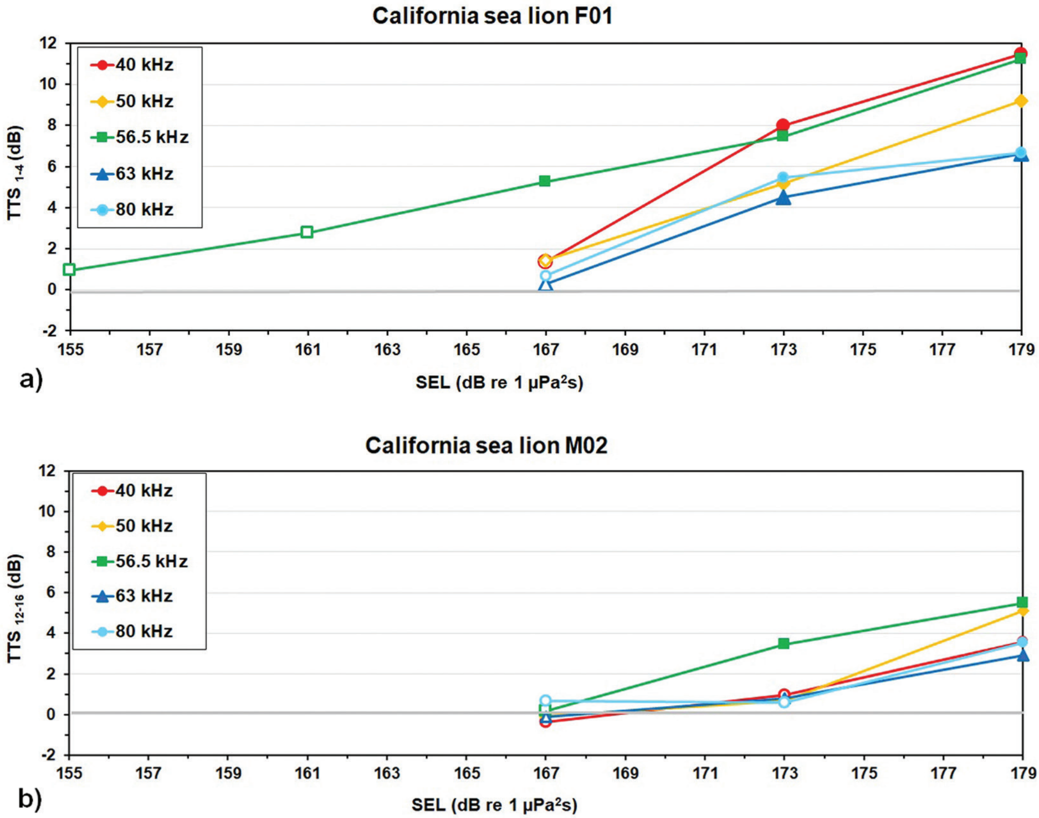


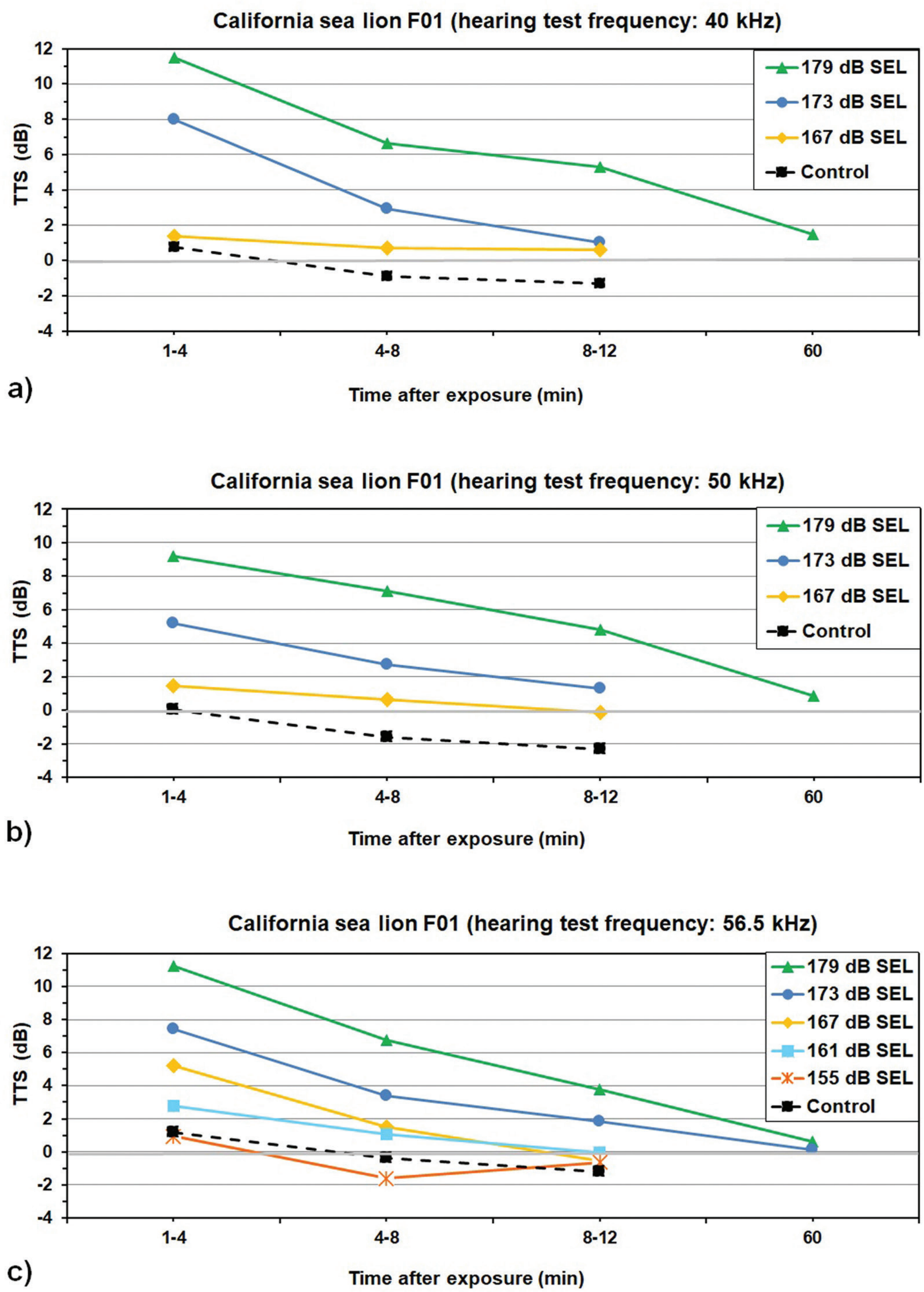
Figure 2. Temporary hearing threshold shifts (TTSs) in California sea lions: mean $TTS_{1\text{-}4}$ in California sea lion F01 (a) and mean $TTS_{12\text{-}16}$ in M02 (b) after exposure for 60 min to a continuous constant-amplitude one-sixth-octave noise band centered at 40 kHz at several sound exposure levels (SELs; dB re 1 $\mu Pa^2 s$), quantified at hearing frequencies 40, 50, 56.5, 63, and 80 kHz (i.e., at the center frequency of the fatiguing sound and up to one octave above that frequency). Open symbols indicate hearing thresholds similar to those in control tests (no statistically significant TTS); solid symbols indicate statistically significant TTS relative to the control tests. Sample size varies per datapoint (see Table 1). For average received sound pressure levels (dB re 1 µPa), subtract 36 dB from the SEL values. For standard deviations and mean control values, see Table 1 and Figures 3 and 4.

showed that the hearing thresholds for all five hearing test signals before and after exposure for 60 min to low ambient noise were similar (Table 1).

TTS at Five Hearing Test Frequencies and Recovery After Exposure to the Fatiguing Sound

With hearing test signal frequencies of 40 and 50 kHz, statistically significant $TTS_{1\text{-}4}$ (i.e., significantly different from control values) occurred in F01 after exposure to SELs of ≥ 173 dB re 1 $\mu Pa^2 s$ (Table 1; Figure 2a). Recovery of hearing occurred within 12 min after exposure to an SEL of 173 dB, and within 60 min after exposure to an SEL of 179 dB re 1 $\mu Pa^2 s$ (Figure 3a & b). With a hearing test signal frequency of 56.5 kHz, statistically significant $TTS_{1\text{-}4}$ occurred after exposure to SELs of ≥ 167 dB re 1 $\mu Pa^2 s$ (Table 1; Figure 2a). Recovery of hearing occurred within 8 min after exposure to an SEL of 167 dB re 1 $\mu Pa^2 s$, within 12 min after exposure to an SEL of 173 dB re 1 $\mu Pa^2 s$, and within 60 min after exposure to an SEL of 179 dB re 1 $\mu Pa^2 s$ (Figure 3c). With hearing test signal frequencies of 63 and 80 kHz, statistically significant $TTS_{1\text{-}4}$ occurred after exposure to SELs of ≥ 173 dB re 1 $\mu Pa^2 s$ (Table 1; Figure 2a), and recovery of hearing occurred within 12 min (Figure 3d & e).

With a hearing test signal frequency of 56.5 kHz, statistically significant $TTS_{12\text{-}16}$ occurred in M02 after exposure to SELs ≥ 173 dB re 1 $\mu Pa^2 s$ (Table 1; Figure 2b) and recovery of hearing occurred within 24 min (Figure 4c). With hearing test signals of 40, 50, 63, and 80 kHz, statistically significant $TTS_{12\text{-}16}$ occurred only after exposure to


California sea lion F01 (hearing test frequency: 40 kHz)
179 dB SEL
173 dB SEL
167 dB SEL
Control
TTS (dB)
12
10
8
6
4
2
0
-2
-4
1-4
4-8
8-12
60
a)
Time after exposure (min)
California sea lion F01 (hearing test frequency: 50 kHz)
179 dB SEL
173 dB SEL
167 dB SEL
Control
TTS (dB)
1-4
4-8
8-12
60
b)
Time after exposure (min)
California sea lion F01 (hearing test frequency: 56.5 kHz)
179 dB SEL
173 dB SEL
167 dB SEL
161 dB SEL
155 dB SEL
Control
TTS (dB)
1-4
4-8
8-12
60
c)
Time after exposure (min)

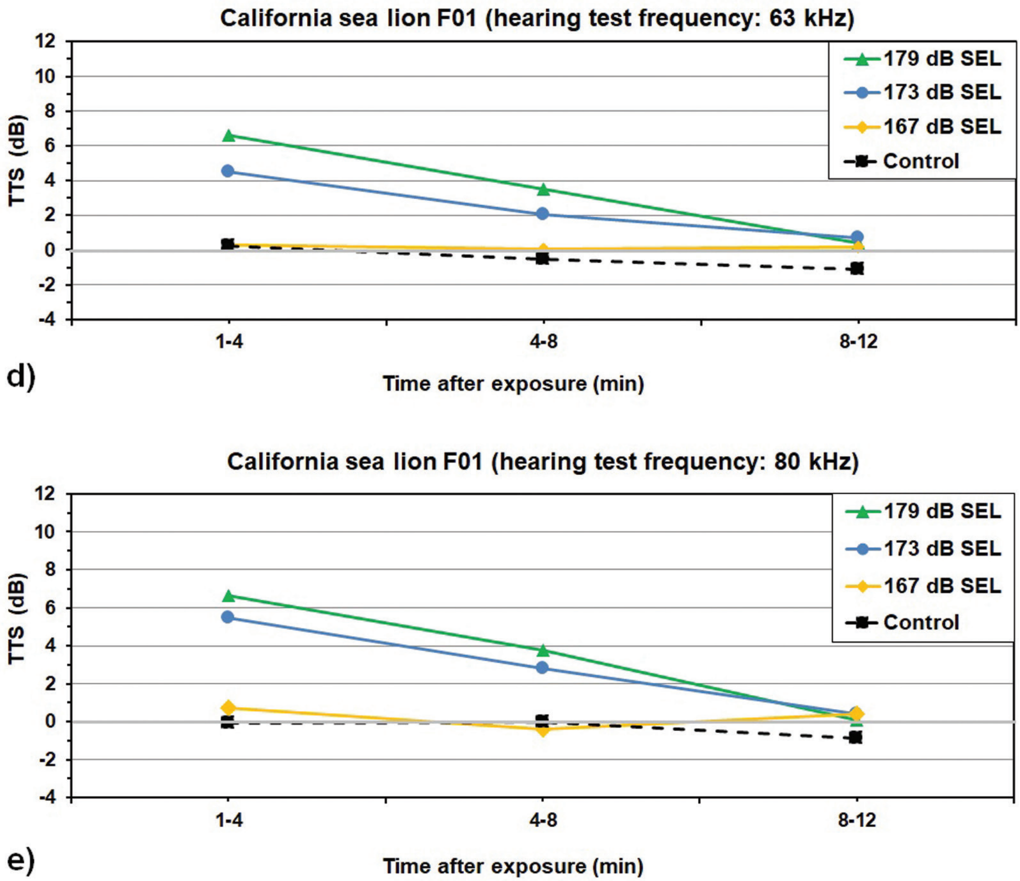
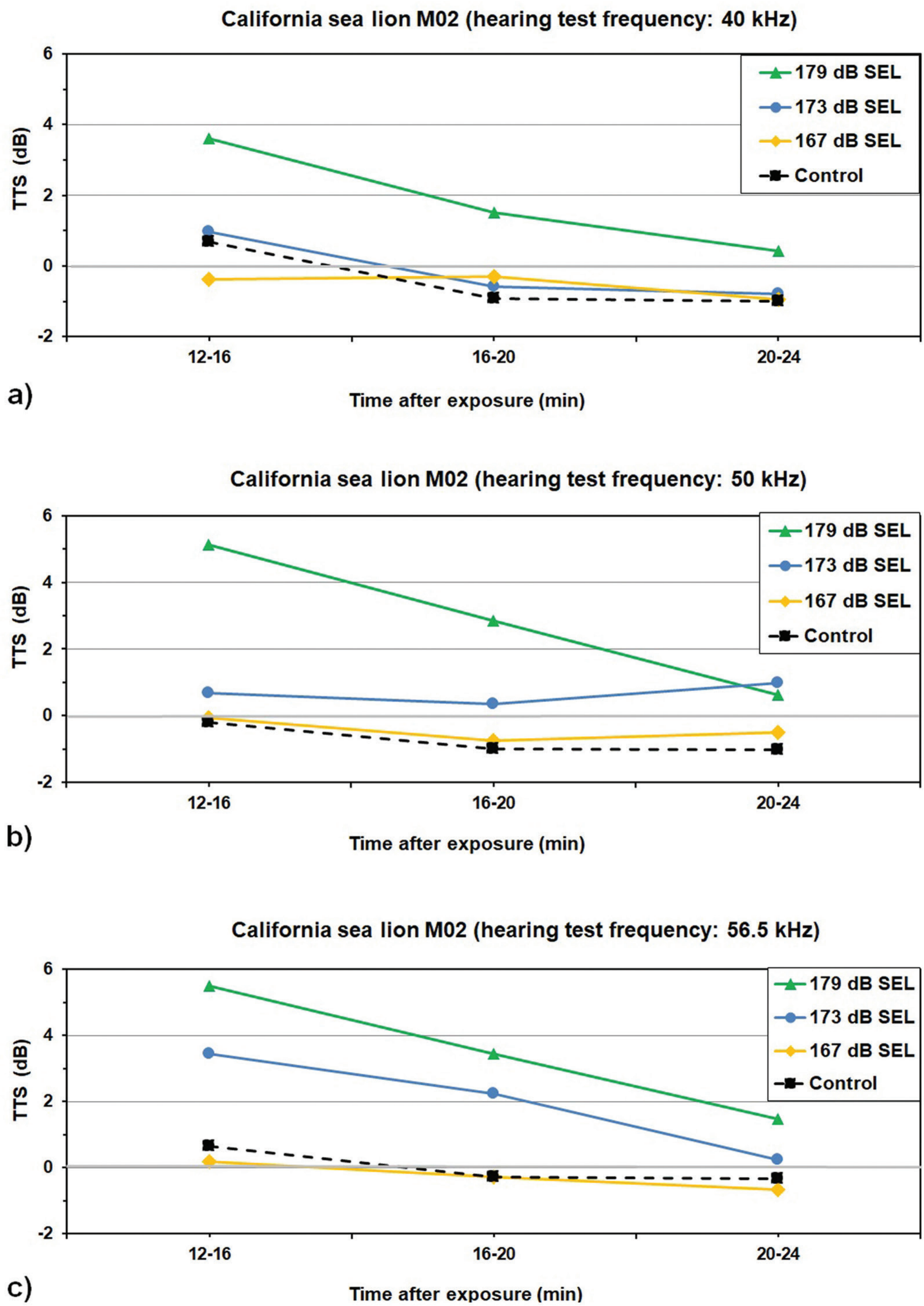


Figure 3. Temporary hearing threshold shifts (TTSs) and recovery in California sea lion F01 tested at 40 kHz (a), 50 kHz (b), 56.5 kHz (c), 63 kHz (d), and 80 kHz (e), after exposure for 60 min to a continuous constant-amplitude one-sixth-octave noise band centered at 40 kHz at several sound exposure levels (SELs; dB re 1 µPa^{2}s). Hearing was considered recovered once mean TTS was < 2 dB. For sample sizes and standard deviations (only for TTS_{1-4}), see Table 1. The x-axis scales in (a), (b), and (c) differ from those in (d) and (e). For average received sound pressure levels (dB re 1 µPa), subtract 36 dB from the SEL values. The mean "TTS" values during control tests (no shifts occurred) are also shown.

the highest SEL of 179 dB re 1 µPa^{2}s. Recovery of hearing occurred within 20 min, except at hearing test frequency 50 kHz, when recovery took 24 min (Figure 4).

Individual Differences in Susceptibility to TTS After Exposure to the Fatiguing Sound

During four sessions, the order in which the California sea lions were tested at hearing test frequency 56.5 kHz after exposure to the NB at SEL 179 dB re 1 µPa^{2}s was reversed. The mean TTS_{1-4} in M02 (9.8 dB; SD = 1.2 dB; n = 4) was only 1.4 dB lower than the mean TTS_{1-4} in F01 (11.2 dB; SD = 0.6 dB; n = 4) after exposure at the same SEL. The recovery patterns were similar (Figure 5a). The mean TTS_{12-16} in F01 (6.0 dB; SD = 0.9 dB; n = 4) was only 0.5 dB higher than the mean TTS_{12-16} in M02 (5.5 dB; SD = 0.5 dB; n = 4) after exposure at the same SEL. The recovery patterns were similar (Figure 5b).


California sea lion M02 (hearing test frequency: 40 kHz)
TTS (dB)
6
4
2
0
-2
179 dB SEL
173 dB SEL
167 dB SEL
Control
12-16
16-20
20-24
a)
Time after exposure (min)
California sea lion M02 (hearing test frequency: 50 kHz)
TTS (dB)
6
4
2
0
-2
179 dB SEL
173 dB SEL
167 dB SEL
Control
12-16
16-20
20-24
b)
Time after exposure (min)
California sea lion M02 (hearing test frequency: 56.5 kHz)
TTS (dB)
6
4
2
0
-2
179 dB SEL
173 dB SEL
167 dB SEL
Control
12-16
16-20
20-24
c)
Time after exposure (min)

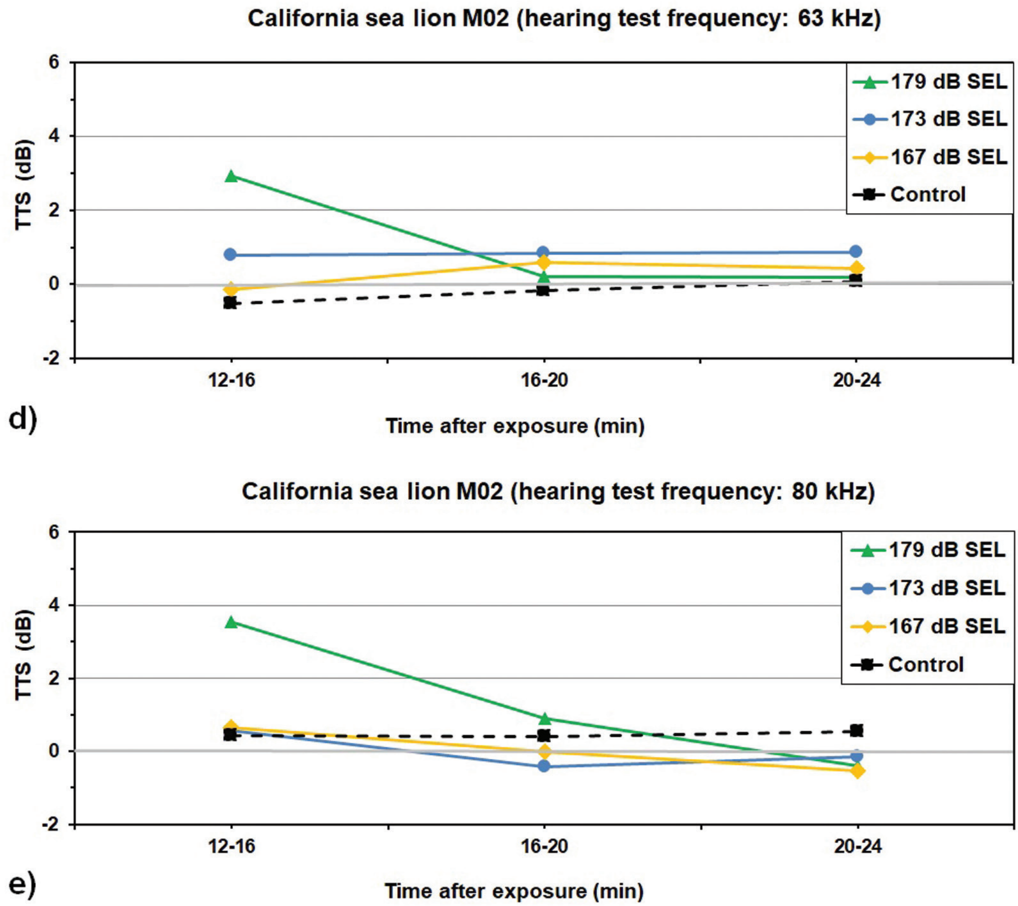


Figure 4. Temporary hearing threshold shifts (TTSs) and recovery in California sea lion M02 tested at 40 kHz (a), 50 kHz (b), 56.5 kHz (c), 63 kHz (d), and 80 kHz (e) after exposure for 60 min to a continuous constant-amplitude one-sixth-octave noise band centered at 40 kHz at several sound exposure levels (SELs; dB re 1 μPa²s). Hearing was considered recovered once mean TTS was < 2 dB. For sample sizes and standard deviations (only for TTS_{12-16}), see Table 1. For average received sound pressure levels (dB re 1 μPa), subtract 36 dB from the SEL values. The mean "TTS" values during control tests (no shifts occurred) are also shown.

Discussion

Baseline Hearing Thresholds, Performance, and Aerial Sound Exposure

During pre-exposure hearing test sessions, the hearing thresholds of the two California sea lions for hearing test signals between 40 and 80 kHz differed from each other by only a few dB (Kastelein et al., 2023), and were similar to the thresholds reported by Reichmuth et al. (2013) and Cunningham & Reichmuth (2016) for another California sea lion at similar hearing test frequencies. This suggests that the hearing of the sea lions in the present study was representative for their species.

The performance of both California sea lions was consistent throughout the study period. For all the TTS measurements, standard deviations were ≤ 2 dB; most were ≤ 1 dB (Table 1). This consistency in TTS was achieved by keeping the ambient noise level low and by taking ample time to allow the sea lions to become accustomed to each new hearing test frequency. The time needed for this varied depending on the individual sea lion and the hearing test frequency. The incidence of pre-stimulus responses (i.e., false positives) by both sea lions was low and similar in all pre-exposure hearing tests, control tests, and hearing tests after exposure to the NB.

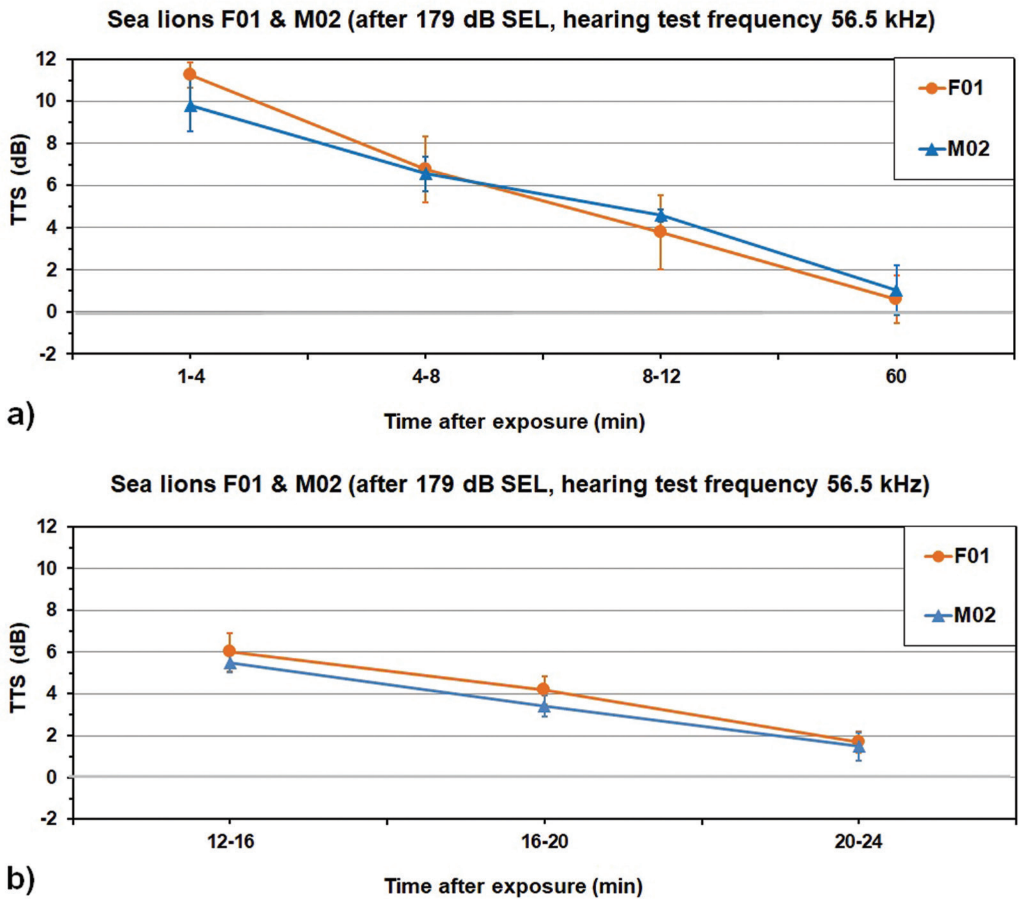


Figure 5. Testing for individual differences in susceptibility to temporary hearing threshold shift (TTS): mean TTS (± standard deviation; *n* = 4) at hearing test frequency 56.5 kHz in California sea lions F01 and M02, measured 1 to 12 and 60 min (a) and 12 to 24 min (b) after exposure for 60 min to the continuous constant-amplitude one-sixth-octave noise band centered at 40 kHz, at a sound exposure level (SEL) of 179 dB re 1 $\mu Pa^2 s$.

Both California sea lions exhibited consistent response patterns in terms of initial TTS and recovery. The susceptibility of individual terrestrial mammals to TTS may change over time (Kujawa & Liberman, 1997; Mannström et al., 2015), but changes were not observed in the present study. Susceptibility to TTS may have remained stable throughout the study period due to the relatively short exposures and relatively low TTSs elicited in the present study compared to those in the studies of Kujawa & Liberman (1997) and Mannström et al. (2015), as discussed by Houser (2021).

When alone during two fatiguing sound exposures, F01 may have predominantly swum at a depth below 0.5 m where lower SPLs occurred (Figure 1). This could account for her lower levels of TTS than when swimming erratically throughout the pool when accompanied by M02. It is also possible that during swimming in a regular swimming path, she was more able to self-mitigate (i.e., reduce her hearing sensitivity when swimming close to the transducer)—an ability observed in odontocetes by Finneran (2018) and Nachtigall et al. (2018)—than when constantly interacting with M02, which made her swimming pattern erratic.

Short breaks in the fatiguing sound can allow hearing to recover and may result in significantly smaller initial TTSs than occur after exposure to fatiguing sounds without breaks (Kastelein et al., 2022a, 2022b). Fatiguing sounds in the present study were continuous (100% duty cycle), but breaks in exposure may have occurred when the California sea lions took breaths. Based on data from harbor seals (*Phoca vitulina*; Kastelein et al., 2018), we assumed that acoustic energy reached the ears as if the entire head was below the water surface as long as the lower jaw (and thus part of the skull) remained below the water surface. Even when their heads were completely out of the water during occasional and very brief jumps, the subjects were exposed to the fatiguing sound just above the water surface, as demonstrated by the SPLs measured in air during sound exposure (Table 1). The building around the pool had hard inner surfaces, which caused the SPL in air 30 cm above the water surface to be fairly homogeneous due to reflections (as evidenced by the similar SPLs measured with the two microphones 6 m apart). When the sea lions jumped for respiration during fast swimming, part of their abdomen usually remained in contact with the water, probably allowing some sound conduction from the water via the body to the ears, as observed in harbor porpoises (*Phocoena phocoena*) by Kastelein et al. (1997). Therefore, it was considered unnecessary to use aerial loudspeakers to project additional fatiguing sound during exposure sessions, and the underwater SELs and TTS measurements are assumed to be accurate.

TTS in Relation to Sound Exposure Level

When significant TTS occurred, higher SELs resulted in greater TTSs at all measured hearing frequencies. Statistically significant TTS_{1-4} onset occurred after exposure for 60 min to an SPL of 131 dB re 1 µPa (SEL of 167 dB re 1 µPa^{2}s); 5.2 dB was measured at 56.5 kHz. The 6 dB TTS_{1-4} onset (defined as "TTS onset" by Southall et al., 2019) is estimated to have occurred after exposure to an SEL of 169 dB re 1 µPa^{2}s (measured at 56.5 kHz).

TTS in California sea lions due to sound around 40 kHz has never been measured before, but TTS-onset SEL was even lower than that after exposure to a one-sixth-octave NB centered at 32 kHz (6 dB TTS_{1-4} after exposure to 179 dB SEL; Kastelein et al., 2024). Thus, despite the fact that hearing sensitivity of California sea lions is decreasing at these frequencies, the vulnerability of hearing seems to increase. Possibly this is due to the fact that these frequencies are transformed into neural signals towards the brain at the base of the cochlea.

Hearing Frequency Affected, Recovery, and Individual Differences in Susceptibility

In guinea pigs (*Cavia porcellus*), the highest TTS occurs at half an octave above the center frequency of the fatiguing sound (Cody & Johnstone, 1981). When F01 was exposed to the NB at 40 kHz at 173 dB SEL and higher, the TTS_{1-4} at 56.5 kHz (half an octave above the center frequency of the fatiguing sound) was similar to the TTS_{1-4} at 40 kHz (the center frequency of the fatiguing sound). Lower, but significant TTS_{1-4} also occurred at 50, 63, and 80 kHz. The consistency of TTS at all the fatiguing sound frequencies that were tested could be because California sea lions have poor frequency discrimination ability in sounds above 32 kHz (Schusterman & Moore, 1978). As with California sea lions, the high-frequency regions of the basal cochlea in humans are most sensitive to noise damage (Ryan et al., 2016). The reason for this is not clear, but it may be related to the high levels of antioxidants found in apical hair cells or to the high rates of metabolic activity in basal hair cells (Sha et al., 2001).

Comparison of results from the five studies making up the present research project on TTS in California sea lions over most of their hearing frequency range shows that hearing reduction in the form of TTS_{1-4} is maximal at half an octave above the center frequency of the fatiguing sound (Table 2; after exposure to 0.6, 1, 4, 8, and 16 kHz; in the remaining three, TTS was present and high), or at its center frequency (2, 32, and 40 kHz; Kastelein et al., 2021b, 2022a, 2022b, 2024, present study). At half an octave above the center frequency, TTS always occurred and was always large; it did not always occur at the center frequency of the fatiguing sound. In harbor porpoises and harbor seals, the hearing frequency showing the highest TTS depends on the SEL (Kastelein et al., 2014, 2019); however, in the present research project, the SEL ranges that could be generated were more limited.

In F01, after exposure to the one-sixth-octave NB at 40 kHz eliciting $TTSs_{1-4} \leq \sim 8$ dB, hearing recovered within 12 min after the sound stopped. $TTSs_{1-4}$ between 8 and 11.5 dB recovered within 60 min. These recovery rates were similar to those found after similar TTSs caused by fatiguing sound with other center frequencies (Kastelein et al., 2021b, 2022a, 2022b, 2024; Figure 6). The scatter in the recovery times per magnitude of TTS_{1-4} is clearly evident.

Testing the hearing of both California sea lions at the same times after the fatiguing sound stopped showed that their susceptibility to TTSs and recovery patterns were similar (Figure 5), as it was after exposure to one-sixth-octave NBs at 0.6, 1, 2, 4, 8, 16, and 32 kHz (Kastelein et al., 2021b, 2022a, 2022b, 2024). The sample size (two genetically related individuals) is too small to draw general conclusions about variability within the species. Studies on humans and other terrestrial mammals show individual, genetic, and population-level differences in susceptibility to TTS (Kylin, 1960; Kryter et al., 1962; Henderson et al., 1993; Wang et al., 2002; Davis et al., 2003; Spankovich et al.,

Table 2. Hearing frequencies most affected by temporary hearing threshold shift (TTS) in California sea lion F01, quantified over most of the hearing range of the species in all five studies that make up the research project (Kastelein et al., 2021b, 2022a, 2022b, 2024, present study). In the eight fatiguing sound frequencies encompassing most of the hearing range, TTS_{1-4} was highest at half an octave above the center frequency of the fatiguing sound (five frequencies; in the remaining three, TTS was present and high), or at its center frequency (three frequencies). This table shows hearing frequencies relative to the center frequency of the fatiguing sound at which statistically significant TTS_{1-4} occurred (*), maximum TTS occurred (Max), and no TTS_{1-4} occurred (no TTS); the SEL at which TTS onset occurred (in italics; dB re 1 µPa²s); and the greatest TTS_{1-4} (in bold; dB; this did not usually occur at the onset SEL); -- = not tested. The red shading indicates the magnitude of greatest TTS in five categories (0-5, 5-10, 10-15, 15-20, and > 20 dB).

	Hearing test frequencies relative to the center frequency of the fatiguing sound					
Center frequency of fatiguing sound (kHz)	Frequency of fatiguing sound	One third octave above	Half octave above	Two thirds octave above	One octave above	Source
0.6	No TTS	--	Max* *207* **6.7**	--	No TTS	Kastelein et al., 2022b
1	* *189* **8.0**	--	Max* *183* **9.6**	--	* *195* **4.5**	Kastelein et al., 2022b
2	Max* *180* **10.5**	--	* *180* **10.2**	--	* *186* **8.2**	Kastelein et al., 2021b
4	* *187* **11.9**	--	Max* *175* **22.4**	--	* *187* **18.9**	Kastelein et al., 2021b
8	* *172* **8.0**	--	Max* *178* **18.0**	--	* *184* **9.5**	Kastelein et al., 2022a
16	No TTS	--	Max* *189* **16.3**	--	* *201* **12.0**	Kastelein et al., 2022a
32	Max* *180* **12.9**	--	* *180* **11.5**	--	* *180* **5.6**	Kastelein et al., 2024
40	Max* *173* **11.5**	* *173* **9.2**	* *167* **11.2**	* *173* **6.6**	* *173* **6.7**	Present study

2014). Further replication with more California sea lions would be needed to assess individual variation in susceptibility to TTS.

TTS-Onset Sound Exposure Level

Exposure of F01 to NBs with eight center frequencies (0.6, 1, 2, 4, 8, 16, 32, and 40 kHz; Kastelein et al., 2021b, 2022a, 2022b, 2024, present study; Figure 7) shows that the lowest SEL causing TTS was mostly half an octave above the center frequency of the fatiguing sound. Taking all frequencies into account, the relatively low vulnerability of California sea lion hearing to 16 kHz sound stands out. The NB at 16 kHz caused TTS at half an octave and one octave above the center frequency of the fatiguing sound, but not at the center frequency, even after exposure to the highest SEL (Kastelein et al., 2022a; Table 2). This suggests not only that the sea lion's hearing is less vulnerable to damage from sounds around 16 kHz, but also that a narrower hearing range is affected by such sounds.

We defined the onset of TTS as occurring at the lowest SEL at which a statistically significant difference could be detected between the hearing thresholds after exposure to the fatiguing sound and after the control. Southall et al. (2019) used the lowest SEL required to elicit 6 dB TTS as a marker of TTS onset, but they gave no rationale for this number; hearing frequency was not

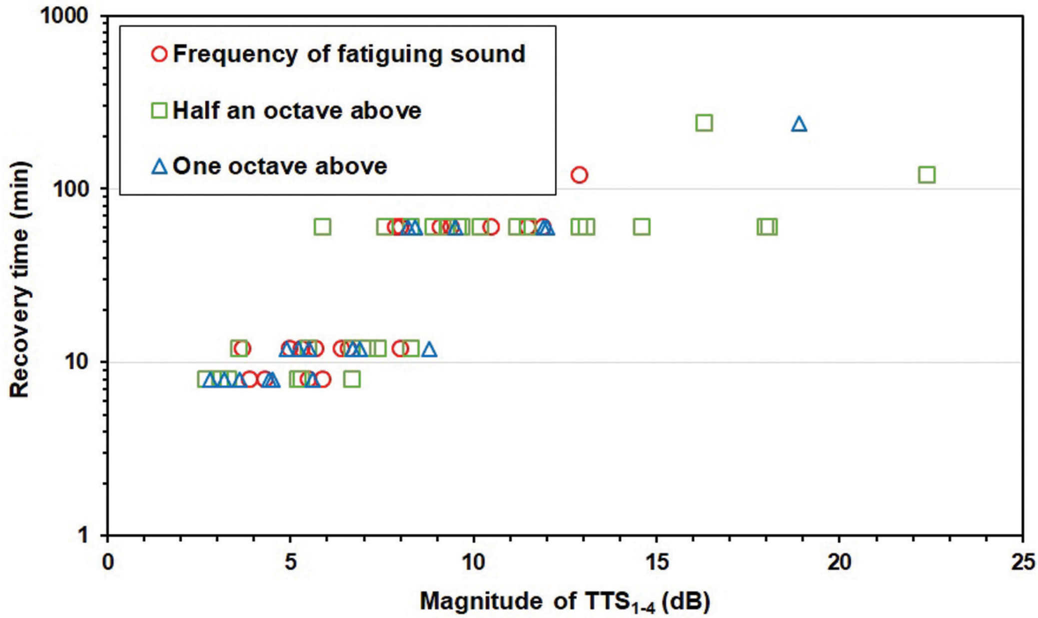


Figure 6. Recovery of hearing: temporary hearing threshold shifts (TTS_{1-4}) in California sea lion F01, quantified after exposure to fatiguing sounds (one-sixth-octave noise bands at eight center frequencies: 0.6, 1, 2, 4, 8, 16, 32, and 40 kHz) over most of the hearing range in relation to hearing recovery times (data from all five studies making up the research project: Kastelein et al., 2021b, 2022a, 2022b, 2024, present study). Note that TTS was measured at discrete moments after the fatiguing sound stopped.

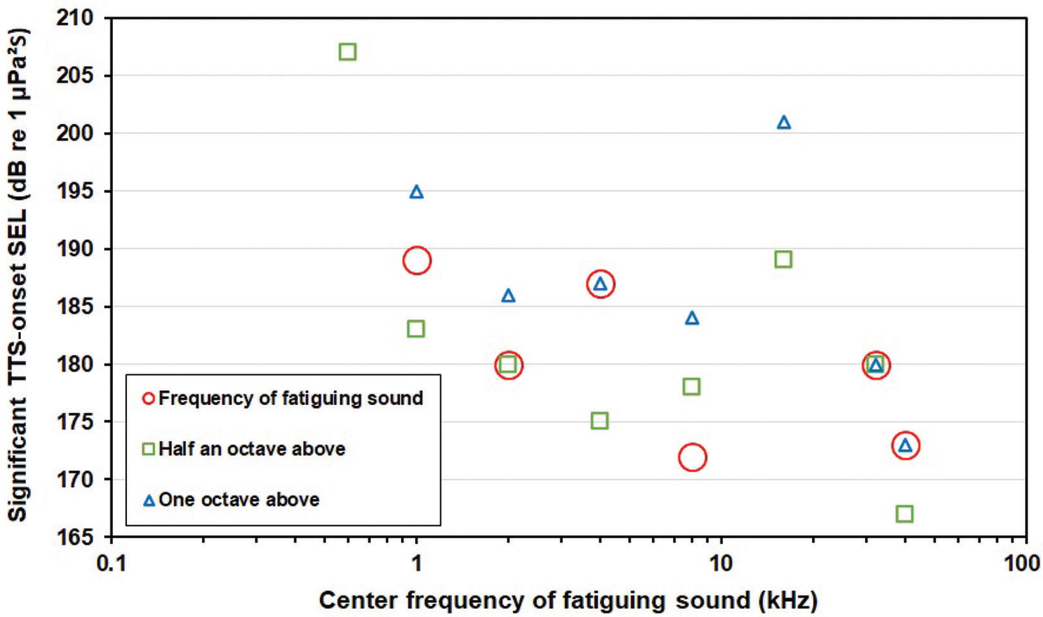


Figure 7. The sound exposure level (SEL) at which the onset of temporary hearing threshold shift (TTS) occurred (i.e., the lowest SEL at which significant TTS_{1-4} occurred relative to the control sessions) for California sea lion F01 tested with three hearing frequencies (at the center frequency of the fatiguing sound, half an octave above, and one octave above that center frequency) after exposure to noise bands with eight center frequencies (0.6 to 40 kHz) (Kastelein et al., 2021b, 2022a, 2022b, 2024, present study)

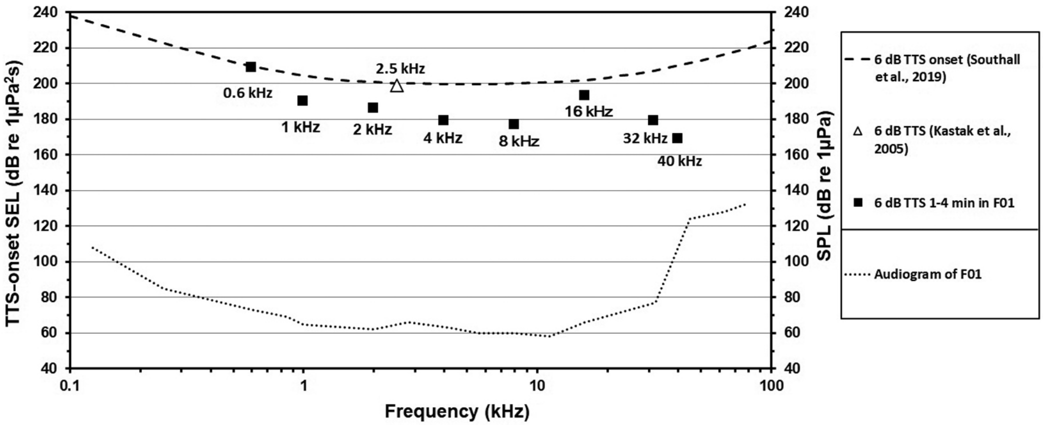


Figure 8. Onset of temporary hearing threshold shift (TTS_{1-4}; defined, following Southall et al., 2019, as fatiguing sound exposure levels [SELs] which elicit 6 dB TTS) in California sea lion F01 for frequencies between 0.6 and 40 kHz in relation to her audiogram (dotted line; Kastelein et al., 2023; right-hand y axis, showing sound pressure levels [SPLs]). The SELs (left-hand y axis) of one-sixth-octave noise bands (NBs) centered at 0.6 and 1 kHz (Kastelein et al., 2022b), 2 and 4 kHz (Kastelein et al., 2021b), 8 and 16 kHz (Kastelein et al., 2022a), 32 kHz (Kastelein et al., 2024), and 40 kHz (present study) caused 6 dB TTS_{1-4} in F01 (■). The published TTS-onset curve for "other marine carnivores in water," including California sea lions (upper dashed line; Southall et al., 2019) was based on a TTS study by Kastak et al. (2005; Δ) in which a California sea lion was exposed to a continuous one-octave NB centered at 2.5 kHz, and on the California sea lion audiograms that had been published before 2018.

specified. By this definition, and considering all hearing frequencies tested, the 6 dB onset of TTS_{1-4} in F01 after exposure to the NB at 40 kHz occurred at an SEL of 169 dB re 1 µPa²s at hearing test frequency 56.5 kHz (Figure 2a).

The results from the entire research project suggest that susceptibility to TTS is frequency-dependent in California sea lions (Figure 8), as it is in other marine mammals in which TTS has been tested: bottlenose dolphins (*Tursiops truncatus*; Finneran & Schlundt, 2013), harbor porpoises (Kastelein et al., 2021a), Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*; Popov et al., 2011), and harbor seals (Kastelein et al., 2020).

F01 was exposed to fatiguing sounds for 60 min in all the studies making up the research project (Kastelein et al., 2021b, 2022a, 2022b, 2024, present study), so 36 dB can be subtracted from the SEL values to obtain the SPL values. Between 0.6 and 16 kHz, the SPL that resulted in 6 dB TTS was 80 to 100 dB above the 50% detection threshold of the sea lion (Kastelein et al., 2021b, 2022a, 2022b, 2023). At 32 kHz (Kastelein et al., 2024) and 40 kHz (present study), the fatiguing SPL that resulted in 6 dB TTS was only 60 and 23 dB, respectively, above her 50% hearing threshold (Figure 8). The results suggest that the shape of the audiogram cannot be used to predict the shape of the TTS-onset function. Therefore, actual TTS-onset SEL threshold measurements should be used.

Towards Improved Protection of California Sea Lions from Underwater Anthropogenic Sound

Except for the TTS caused by a fatiguing sound with a center frequency of 0.6 kHz, SELs at which the 6 dB onset of TTS_{1-4} occurred in F01 (Kastelein et al., 2021b, 2022a, 2022b, 2024, present study) are below the 6 dB TTS-onset levels modeled and predicted by Southall et al. (2019) for "other marine carnivores in water" (Figure 8). Assessment of TTS based on statistical significance suggests even greater susceptibility to TTS than is indicated by the 6 dB onset definition; 6 dB is a useful, simple definition, but it is arbitrary.

Our research project suggests that, for fatiguing sounds above 0.6 kHz, the hearing of California sea lions is more susceptible to injury by anthropogenic noise in the ocean than predicted by Southall et al. (2019). Therefore, to achieve improved protection of the species, a revised TTS-onset SEL function should be defined for California sea lions for underwater sound. Whether the results from the present study can be extrapolated to all otariids, or to all "other marine carnivores in water" as defined by Southall et al. (2019), remains uncertain pending further TTS research with other otariid species.

Acknowledgments

We thank assistants Femke Kuiphof, Luna Korsuize, Renee de Waard, and Dominique Lindemans; students Celyza Wissel, Ramiro Venoaks, Femke Sarens, Madelief Oomen, Elke van den Brink, Fleur van Opstal, Nico Beuzenberg, Jonas Groen, and Marit van den Boogaard; and volunteers Rani van der Vlist, Paul Vermeulen, Amber Verhoef, and Stephanie de Ruijter for their help in collecting the data. We thank Kimberly Tuytens for help with some of the graphs; Arie Smink (Smink Electronics) for the design, construction, and maintenance of the electronic equipment; Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute; Erwin Jansen (TNO, the Hague, the Netherlands) for conducting the acoustic calibration measurements; and Colleen LePrell (University of Texas, Dallas, USA) for her valuable constructive comments on this manuscript. Funding for this study was obtained from the U.S. Navy's Living Marine Resources program (Contract No. N-39430-20-C-2215). We thank Mandy Shoemaker and Anu Kumar for their guidance on behalf of the LMR program. The California sea lions were made available for the research by Blijdorp Zoo, Rotterdam, the Netherlands, and were trained and tested under authorization of the Netherlands Ministry of Economic Affairs, Department of Nature Management.

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