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Temporary Hearing Threshold Shift in California Sea Lions (*Zalophus californianus*) Due to a Noise Band Centered at 32 kHz

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Abstract

To determine their frequency-dependent susceptibility to noise-induced temporary hearing threshold shift (TTS), two California sea lions (*Zalophus californianus*) were exposed for 60 min to a continuous one-sixth-octave noise band (NB) centered at 32 kHz as the fatiguing sound, at sound pressure levels of 132 to 156 dB re 1 µPa (sound exposure levels [SELs] of 168 to 192 dB re 1 µPa^{2}s). Using a psychoacoustic technique, TTSs were quantified at the center frequency of the fatiguing sound and at half an octave and one octave above the center frequency (at 32, 44.8, and 63 kHz). When significant TTS occurred, higher SELs resulted in greater TTSs. TTSs and hearing recovery patterns were similar in both sea lions. The mean onset of TTS$_{1\text{-}4\ min}$ (defined as 6 dB TTS) in sea lion F01 is estimated to occur after exposure to an SEL of 179 dB re 1 µPa^{2}s (at hearing test frequency 44.8 kHz). After exposure to an SEL of 180 dB re 1 µPa^{2}s, a mean TTS$_{1\text{-}4\ min}$ of 6.7 dB was measured at hearing test frequency 44.8 kHz. In California sea lions, TTS onset levels are not as closely related (especially at the lower and higher frequencies) to the unmasked hearing thresholds (audiograms) as was previously assumed.

Key Words: anthropogenic noise, audiogram, fatiguing sound, hearing damage, hearing recovery, hearing sensitivity, Otariidae, pinniped, TTS

Introduction

Underwater anthropogenic noise in the oceans has a wide variety of adverse effects on marine animals (Duarte et al., 2021). 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]) in marine mammals. Reduced hearing sensitivity may result in an inability to detect biologically important sounds and may have population-level consequences for mammals that are regularly exposed to high-amplitude noises.

The California sea lion (*Zalophus californianus*), a species in the family Otariidae (eared seals), occurs year-round off the west coast of North America (Melin et al., 2018). In parts of their range, California sea lions are subjected to significant levels of noise from anthropogenic activities. They lead an amphibious life and have good underwater and aerial hearing (Mulsow et al., 2012; Reichmuth et al., 2013; Kastelein et al., 2023). Understanding the parameters of sounds that cause TTS and the consequences for California sea lions of experiencing TTS will help regulatory agencies determine safe and acceptable noise exposure levels for this species, and perhaps for other species of the Otariidae family (as suggested by Houser et al., 2017, and Southall et al., 2019). TTS in California sea lions has previously been studied by Kastak et al. (1999, 2005), Finneran et al. (2003), and Kastelein et al. (2021b, 2022a, 2022b). Comparison with studies on other taxa will help elucidate general principles of TTS in marine mammals (e.g., harbor seals [*Phoca vitulina*] and harbor porpoises [*Phocoena phocoena*]; Kastelein et al., 2012a, 2012b).

Both within and between species, there is variation in the causes and effects of TTS and in recovery times. Fatiguing sounds of different amplitudes and durations result in varying levels of reduced hearing sensitivity at different frequencies, and recovery times also vary (Popov et al., 2014; Finneran, 2015; Kastelein et al., 2020a, 2020b, 2021a, 2021b). The present study is one of five in a comprehensive research project on TTS in California sea lions. Each of the five studies present data on TTS caused by one or two fatiguing sound frequencies as follows: (1) 0.6 and 1 kHz (Kastelein et al., 2022b), (2) 2 and 4 kHz (Kastelein et al., 2021b), (3) 8 and 16 kHz (Kastelein et al., 2022a), (4) 32 kHz (present study), and (5) 40 kHz (ongoing).

The goals of the present study are (1) to quantify TTS in two California sea lions and determine the TTS onset sound exposure level (SEL) after exposure to fatiguing sound with a center frequency of 32 kHz at several SELs; (2) to determine how hearing at three frequencies (corresponding to the center frequency of the fatiguing sound, half an octave above it, and one octave above that frequency) is affected by exposure to the fatiguing sound at each SEL; (3) to describe the pattern of hearing recovery after the fatiguing sound stops; and (4) to assess differences in susceptibility to TTS between the two California sea lions.

Information on the susceptibility of California sea lions to TTS due to 32 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 operated vehicles.

Methods

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

Subjects and Study Area

The subjects were an adult female California sea lion (F01; age 11 y) and her juvenile male offspring (M02; age 5 y). Both sea lions were healthy throughout the study. The subjects had hearing thresholds that were similar to those of other California sea lions (Reichmuth et al., 2013; Kastelein et al., 2023) and, thus, are representative of the species. Both sea lions had participated in previous TTS studies and a basic audiogram study (Kastelein et al., 2021b, 2022a, 2022b, 2023).

The study was conducted at the SEAMARCO Research Institute, the Netherlands, in a remote and quiet location. The California sea lions were kept, and the study was conducted, in a pool complex consisting of an outdoor pool (7 × 4 m; 2 m deep) with a haul-out area above part of the pool, 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) 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, for a top view of the pool complex). The building around the pool had hard (reflective) inner surfaces. 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.

Acoustics

Sound Pressure Level Measurement—The ambient noise was measured, and the fatiguing sound (in air and under water) and hearing test signals were calibrated once every 3 mo during the study period by an acoustic consulting agency (TNO, the Hague, the Netherlands).

Ambient Noise—The California sea lions' listening environment was kept as quiet as possible while their detection thresholds were being measured. The ambient noise in the indoor pool was very low and relatively constant in amplitude above 0.25 kHz under test conditions (Figure 1). Test conditions entailed that the water circulation system was turned off at least half an hour before the first hearing test was conducted; no rain; wind force generally Beaufort ≤ 4, depending on the wind direction; and only researchers involved in the hearing tests within 15 m of the pool complex, with those researchers standing still.

Fatiguing Sound—A digitally generated continuous (100% duty cycle) one-sixth-octave noise band (NB) centered at 32 kHz, without harmonics, was used as the fatiguing sound (i.e., the sound intended to cause TTS; see Kastelein et al., 2021b, for details of equipment and settings).

To produce the NB at 32 kHz at sufficient sound pressure levels (SPLs) to elicit at least 6 dB TTS (the level used as a marker of TTS onset; Southall et al., 2019) in the California sea lions, the sound was amplified by a custom-built, high-power,

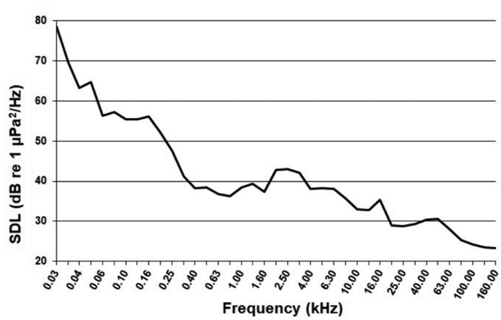


Figure 1. The general underwater ambient noise level in the indoor pool used for California sea lion (*Zalophus californianus*) hearing tests under test conditions. Measurements were recorded as one-third-octave bands and converted to spectrum density levels (SDLs).

wide-band amplifier and transmitted under water 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 2 for the approximate location of the transducer relative to the deep part of the pool). The linearity of the transmitter system producing the fatiguing sound was checked during each calibration and was consistent to 1 dB within a 24 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 (where the California sea lions swam during exposure and control sessions, and where the hearing tests took place), the SPL was measured at 56 points (Figure 2). SPL varied little with depth or location, resulting in a relatively homogeneous sound field (Figure 2). When the fatiguing sounds were being generated, the sea lions usually swam fast at ~1 m depth in clockwise circles and took single, short breaths. Usually when the sea lions surfaced to breathe, which they did by means of a low jump during fast swimming, part of their abdomen remained in contact with the water. They did not swim towards areas with relatively low SPLs, nor did they orient themselves away from the sound source. On occasions when the sea lions surfaced to breathe, their heads were completely out of the water (mean = 1.5 s; standard deviation [SD] = 1.3 s; n = 46 respirations). Therefore, the average SPL of the fatiguing sound experienced by the sea lions was calculated as the power mean of the SPL at all 56 individual underwater measurement points.

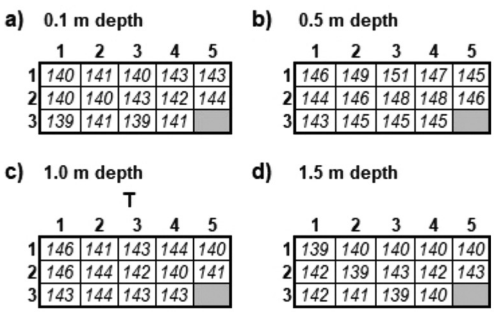


Figure 2. Examples of the sound pressure level (SPL) distribution (values in dB re 1 µPa) in the deep part of the indoor pool (6 × 4 m; 2 m deep; not to scale) during projection of the fatiguing sound: a continuous one-sixth-octave noise band (NB) centered at 32 kHz (a-d). Measurements were taken at 14 locations on a horizontal grid with cells of 1 × 1 m (the outer hydrophone locations were 1.0 m from the pool wall) at four depths per grid cell. These data were used to calculate the average received SPL that the California sea lions experienced during sound exposure. In this example, the mean (± standard deviation [SD]) SPL was 143 ± 3 dB re 1 µPa (n = 56). The power mean was 144 dB re 1 µPa. The letter **T** above a box in (c) indicates the approximate location of a transducer (at 1 m depth) in the adjacent shallow part of the indoor pool. The grey 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, for a scale drawing of the pool).

During sound exposure sessions, the one-sixth-octave NB centered at 32 kHz was projected for 60 min at five source levels, resulting in mean SPLs ranging from 132 to 156 dB re 1 µPa (SEL range: 168 to 192 dB re 1 µPa^{2}s). The highest SPL used represented the highest amplitude that could be generated without distortion or harmonics.

The aerial SPL was measured with two microphones (Brüel & Kjær [B&K] Model 4135; B&K, Virum, Denmark) with pre-amplifiers (B&K Model 2669), which were connected to the multichannel high-frequency analyzer (B&K Pulse System LAN-XI 3050). The system was calibrated with a microphone calibrator (B&K Model 4231). The microphones were placed just next to the pool in two locations (6 m apart), 30 cm above the water surface, while the NB was being projected under water at each of the levels used. Where the aerial SPL was above the ambient noise level, it varied by at most 1 dB between the two measurement locations at the same source level, so the mean of the two measurements was used to represent the aerial SPL that the California sea lions were exposed to while 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. Narrow-band upsweeps (linear frequency-modulated tones) were used as hearing test signals instead of pure tones because sweeps lead to more stable received SPLs at the listening station (Finneran & Schlundt, 2007).

The hearing test signal frequencies were 32, 44.8, and 63 kHz (i.e., the center frequency of the fatiguing sound, half an octave above it, and one octave above that frequency). The hearing test signals were generated digitally using the software *Adobe Audition*, Version 3.0 (Adobe Inc., San Jose, CA, USA). The linear upsweeps started and ended at ± 2.5% of the center frequency and had durations of 1,000 ms, including a 50-ms linear rise and fall in amplitude.

Table 1. The mean, standard deviation (SD), and range of initial temporary hearing threshold shift (TTS_{1-4} in F01 and TTS_{12-16} in M02) after exposure for 60 min to ambient noise (control) or to a continuous one-sixth-octave noise band centered at 32 kHz at several sound exposure levels (SELs), quantified at hearing test frequencies 32, 44.8, and 63 kHz. Mean underwater SELs (calculated from mean underwater sound pressure levels [SPLs]) and mean aerial SPLs are shown for each underwater SPL. 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)	F01 TTS_{1-4} (dB)				M02 TTS_{12-16} (dB)			
				Mean	SD	Range	*n*	Mean	SD	Range	*n*
32	Ambient	Control	46	0.7	0.8	-0.1-1.8	5	-0.3	0.7	-1.3-0.6	5
	138	174	≤ 46	0.6	1.4	-1.1-2.3	4	0.1	0.7	-0.7-0.8	4
	144	180	≤ 46	3.9*	0.4	3.5-4.5	4	0.3	0.9	-1.0-0.8	4
	150	186	46	5.9*	1.3	4.6-7.6	4	0.5	0.5	-0.1-1.1	4
	156	192	48	12.9*	2.4	9.7-15.5	4	4.3*	1.4	2.5-5.9	6
44.8	Ambient	Control	46	0.9	0.6	0.1-1.7	5	0.0	1.1	-1.2-1.4	4
	132	168	≤ 46	1.2	1.0	0.2-2.2	4	0.7	1.1	-0.6-1.8	4
	138	174	≤ 46	1.2	0.8	0.0-1.7	4	1.2	0.7	0.2-1.7	4
	144	180	≤ 46	6.7*	1.1	5.1-7.6	4	0.7	1.0	-0.3-2.8	10
	150	186	46	8.9*	1.6	6.4-11.1	8	0.5	0.9	-0.8-2.0	7
	156	192	48	11.5*	1.4	9.1-12.6	5	3.4*	0.9	2.2-4.4	4
63	Ambient	Control	46	0.7	0.7	-0.2-1.3	4	0.1	1.2	-1.5-1.7	5
	138	174	≤ 46	1.1	0.2	0.8-1.3	4	--	--	--	--
	144	180	≤ 46	2.8*	0.4	2.3-3.3	4	-0.2	0.6	-0.7-0.4	4
	150	186	46	3.6*	0.2	3.3-3.8	4	--	--	--	--
	156	192	48	5.6*	1.0	4.3-6.4	4	0.9	0.7	0.3-1.8	4

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. The 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 found to be consistent to 1 dB within a 30 dB range (measured from 10 dB above the hearing threshold). The SPL at the two locations differed by 0 to 2 dB, depending on the test frequency. 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 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 until the signal was correctly detected (the next reversal). The 50% correct detection threshold was the mean of the dB levels of all of the reversals. No-signal trials (catch trials in which a whistle indicating the end of the test was the stimulus) 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 California 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 sea lions' ears were 1.6 m from the hearing test signal transducer.

One total 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 (using the same hearing test signal as 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 to be tested (usually M02). It took less than 1 min for the sea lions to swap places by moving between the indoor and outdoor pools, so testing of the second sea lion could begin without delay.

In addition to the magnitude of TTS immediately 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 continued until hearing recovery had taken place. Recovery was 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 (similar to 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. In these sessions, M02 was tested first at two high SELs: (1) 180 and (2) 192 dB re 1 μPa^2s (with a 44.8 kHz hearing test signal, half an octave above the NB).

In general, if no TTS was found at a certain hearing test frequency after exposure to the 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, NB, SPL, and hearing test signal frequency; see "Results"). The data were collected between October 2021 and February 2022.

Data Analysis

To check for false positives within a hearing test session, the mean rate of pre-stimulus responses by the subjects were calculated as a percentage of the trials. Both signal-present and signal-absent trials were included in the calculations (see Kastelein et al., 2021b).

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 defined 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 post-exposure hearing thresholds were compared to the control thresholds using a Dunnett multiple comparisons post-hoc test. These analyses were conducted in *Minitab 18*, and the data conformed to the assumptions of the tests used (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.

Results

Pre-Stimulus Response Rate

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. The pre-stimulus response rates of F01 during the pre- and post-exposure hearing test sessions and control tests varied between 2.6 and 8.0% (mean = 5.4%; SD = 2%; n = 10). The pre-stimulus response rates by M02 during the pre- and post-exposure hearing test sessions and control tests varied between 3.2 and 6.7% (mean = 5.7%; SD = 1%; n = 10).

Effect of Fatiguing Sound Exposure Level on TTS

The one-way ANOVAs to investigate onset of TTS showed that TTS_{1-4} (F01) was significantly affected by the fatiguing sound's SEL at all three hearing test signal frequencies ($p = 0.000$; Table 1). In M02, TTS_{12-16} was significantly affected by the fatiguing sound's SEL at hearing test frequencies 32 kHz ($p = 0.000$) and 44.8 kHz ($p = 0.001$), but not at 63 kHz ($p = 0.228$).

No change in susceptibility to TTS was observed during the study. As expected, the control tests showed that the hearing thresholds for all three hearing test signals before and after exposure for 60 min to low ambient noise were very similar (Table 1).

TTS and Recovery After Exposure to the Fatiguing Sound

With hearing test signal frequencies of 32, 44.8, and 63 kHz, statistically significant TTS_{1-4} was elicited in F01 after exposure to SELs ≥ 180 dB re 1 µPa^{2}s (Table 1; Figures 3a & 4). With a hearing test signal of 32 kHz, recovery of hearing occurred within 8 min after exposure to SELs of 180 and 186 dB re 1 µPa^{2}s and within 120 min after exposure to an SEL of 192 dB re 1 µPa^{2}s (Figure 4a). With a hearing test signal of 44.8 kHz, recovery of hearing occurred within 8 min after exposure to an SEL of 180 dB re 1 µPa^{2}s and within 60 min after exposure to SELs of 186 and 192 dB re 1 µPa^{2}s (Figure 4b). With a hearing test signal of 63 kHz, recovery always occurred within 8 min (Table 1; Figure 4c).

With hearing test signals of 32 and 44.8 kHz, statistically significant TTS_{12-16} was elicited in M02 after exposure to an SEL of 192 dB re 1 µPa^{2}s (Table 1; Figures 3b, 5a & 5b). Recovery of hearing occurred within 20 min. With a hearing test signal of 63 kHz, statistically significant TTS_{12-16} could not be elicited (Table 1; Figures 3b & 5c).

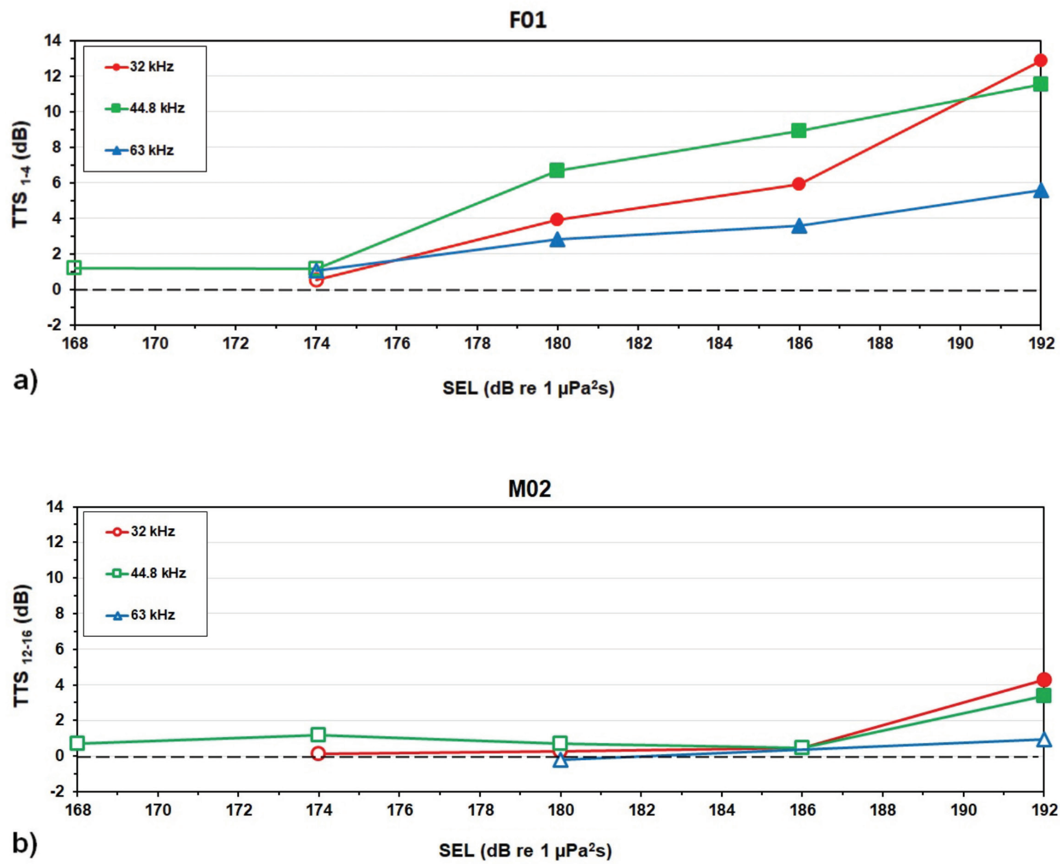


Figure 3. Temporary hearing threshold shifts (TTS) in California sea lions: mean TTS_{1-4} in F01 (a) and mean TTS_{12-16} in M02 (b) after exposure for 60 min to a continuous one-sixth-octave NB centered at 32 kHz, at several sound exposure levels (SELs), quantified at hearing test signal frequencies 32, 44.8, and 63 kHz (i.e., at the center frequency of the fatiguing sound, half an octave above it, and one octave above it). Open symbols indicate thresholds similar to those in control tests (no TTS); solid symbols indicate statistically significant TTS relative to the control tests. Sample size is at least 4 but varies per data point (see Table 1). For average received SPLs (dB re 1 µPa), subtract 36 dB from the SEL values. For standard deviations and mean control values, see Table 1 and the dashed lines in Figures 4 and 5.

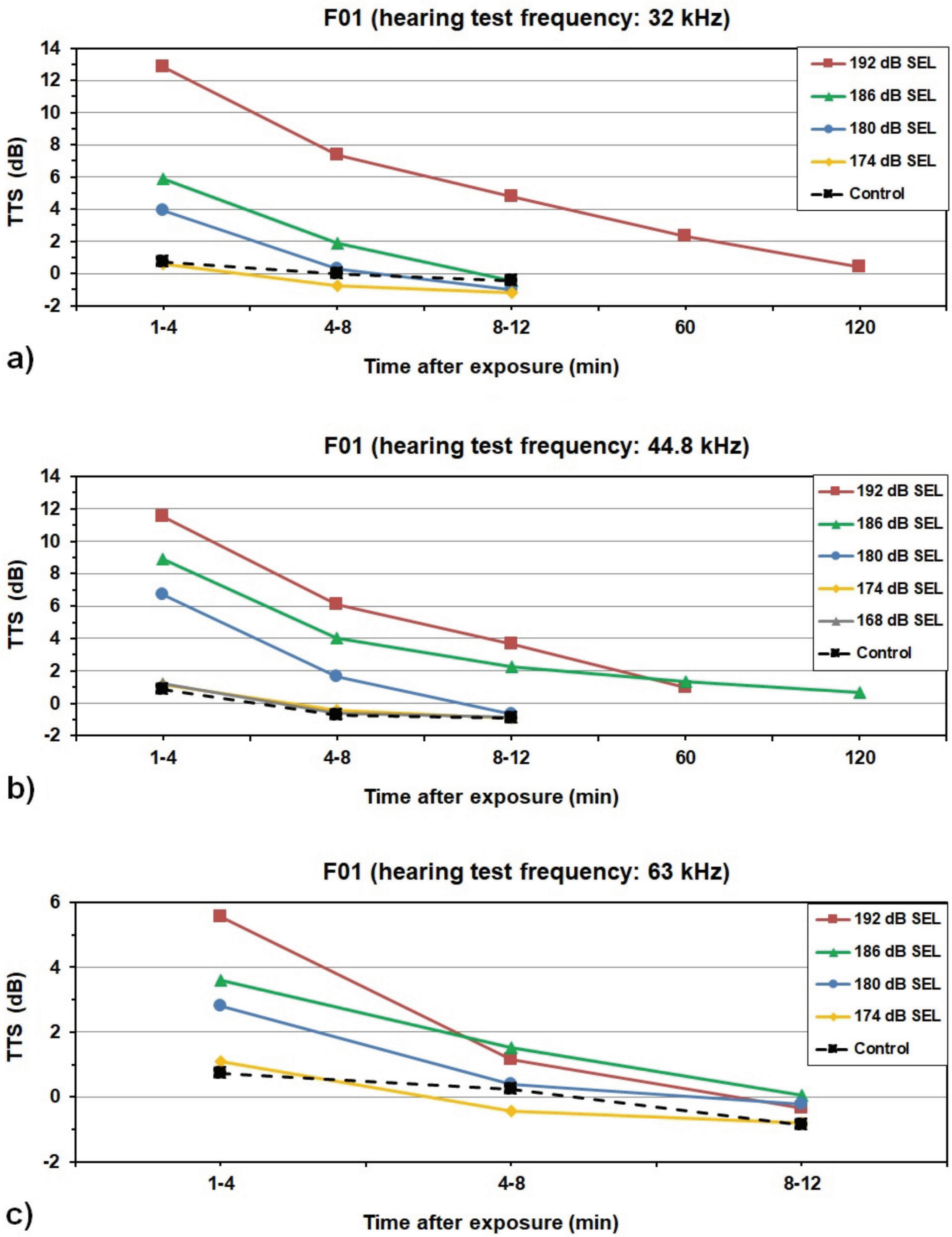
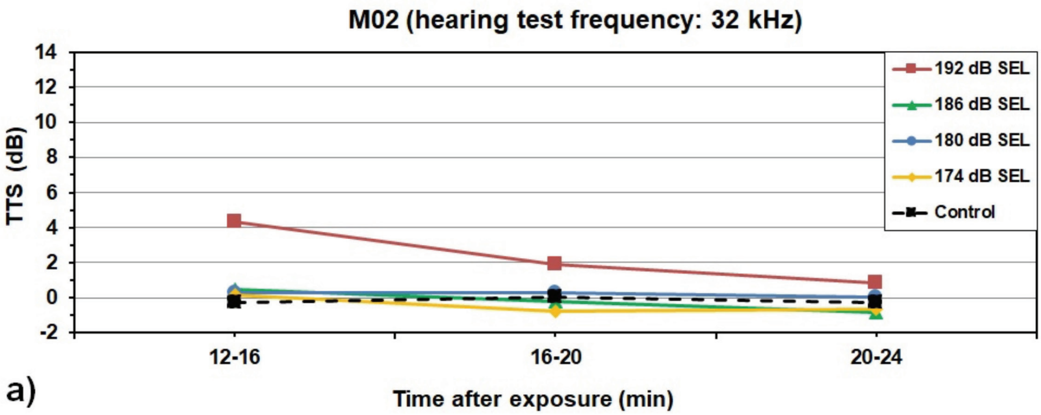
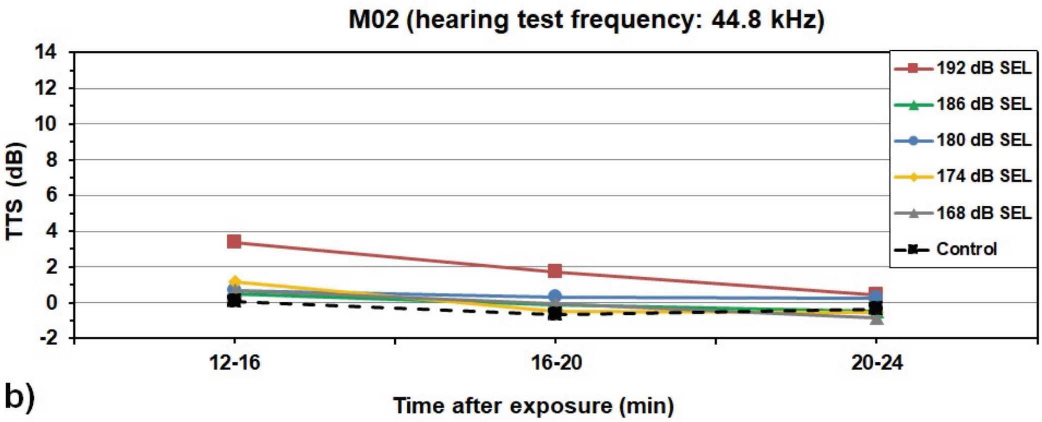


Figure 4. TTS and recovery in California sea lions: changes over time in the mean TTS of F01 tested at hearing test signal frequencies 32 kHz (a), 44.8 kHz (b), and 63 kHz (c) after exposure for 60 min to a continuous one-sixth-octave NB centered at 32 kHz at several SELs. Hearing was considered recovered once TTS was < 2 dB. For sample sizes and SDs (only for TTS_{1-4}), see Table 1. The x- and y-axis scales in (c) differ from those in (a) and (b). For average received SPLs (dB re 1 µPa), subtract 36 dB from the SEL values. The mean "TTS" values during control tests (no shifts occurred) are also shown as black squares connected by dashed lines.



a)



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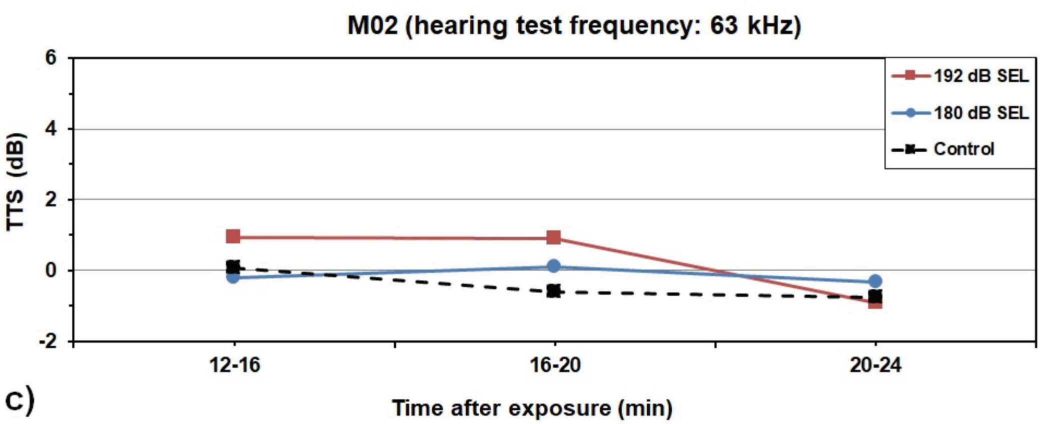

c)

Figure 5. TTS and recovery in California sea lions: changes over time in the mean TTS of M02 tested at hearing test signal frequencies 32 kHz (a), 44.8 kHz (b), and 63 kHz (c) after exposure for 60 min to a continuous one-sixth-octave NB centered at 32 kHz at several SELs. No TTS was detected at hearing test signal frequency 63 kHz. For sample sizes and SDs (only for TTS_{12-16}), see Table 1. The y-axis scales in (c) differ from those in (a) and (b). For average received SPLs (dB re 1 µPa), subtract 36 dB from the SEL values. The mean "TTS" values during control tests (no shifts occurred) are also shown as black squares connected by dashed lines.

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 44.8 kHz after exposure to the NB at SEL 180 dB re 1 µPa²s was reversed. The mean TTS_{1-4} in M02 (8.2 dB; SD = 2.0 dB; *n* = 4) was 1.5 dB higher than the mean TTS_{1-4} in F01 (6.7 dB; SD = 1.1 dB; *n* = 4) after exposure at the same SEL. The recovery patterns were similar (Figure 6a)—recovery was complete in both California sea lions within 12 min. The mean TTS_{12-16} in F01 (1.6 dB; SD = 1.0 dB; *n* = 4) was also similar (i.e., TTS_{12-16} did not occur) to the mean TTS_{12-16} in M02 (0.7 dB; SD = 1.0 dB; *n* = 4) after exposure at the same SEL (Figure 6b).

During a further four sessions, the order in which the California sea lions were tested at hearing test signal frequency 44.8 kHz after exposure to the NB at SEL 192 dB re 1 µPa²s was reversed. The mean TTS_{1-4} in M02 (11.5 dB; SD = 1.1 dB; *n* = 4) was very similar to the mean TTS_{1-4} in F01 (11.5 dB; SD = 1.4 dB; *n* = 5) after exposure at the same SEL. The recovery patterns were also similar (Figure 7a). The mean TTS_{12-16} in F01 (5.3 dB; SD = 0.9 dB; *n* = 4) was 1.9 dB higher than the mean TTS_{12-16} in M02 (3.4 dB; SD = 0.9 dB; *n* = 4) after exposure at the same SEL, but the recovery patterns were similar (Figure 7b).

Discussion

Baseline Hearing Thresholds, Performance, and Aerial Sound Exposure

During pre-exposure test sessions, the hearing thresholds of the two California sea lions for hearing test signals between 32 and 63 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 other California sea lions at similar hearing test frequencies (Figure 8). 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 < 2.5 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

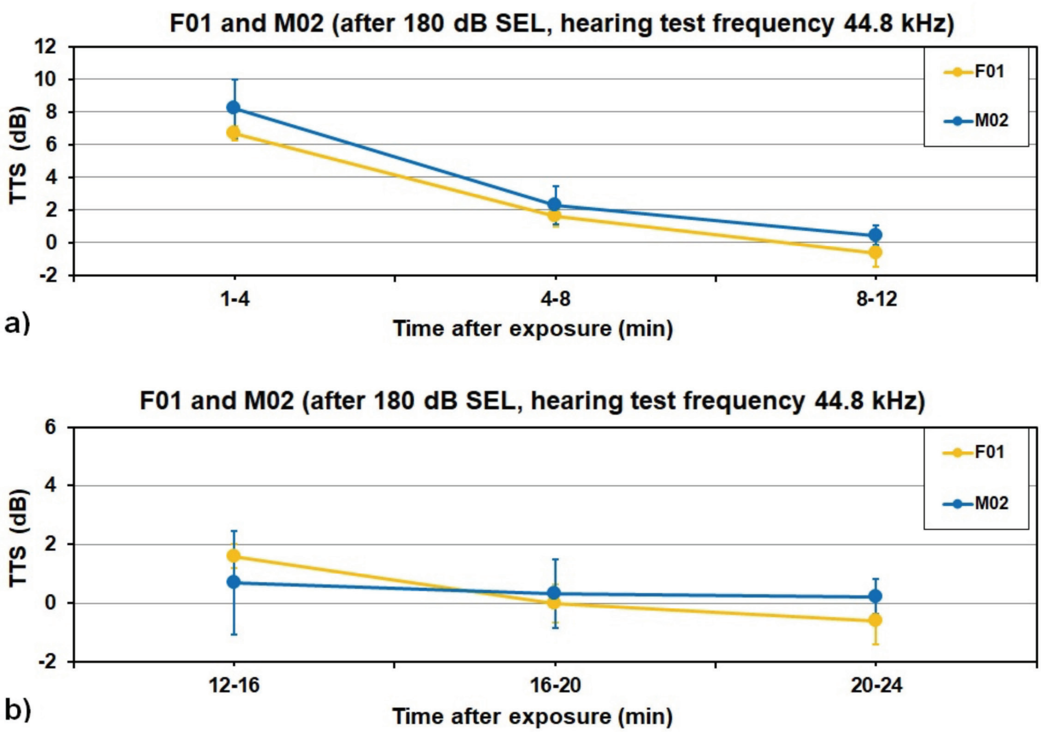

Figure 6. Individual similarity in susceptibility to TTS in California sea lions: mean TTS (± SD; *n* = 4) at hearing test frequency 44.8 kHz in F01 and M02, measured 1 to 12 min (a) and 12 to 24 min (b) after exposure for 60 min to the continuous one-sixth-octave NB centered at 32 kHz at an SEL of 180 dB re 1 µPa²s. The x- and y-axis scales differ in (a) and (b).

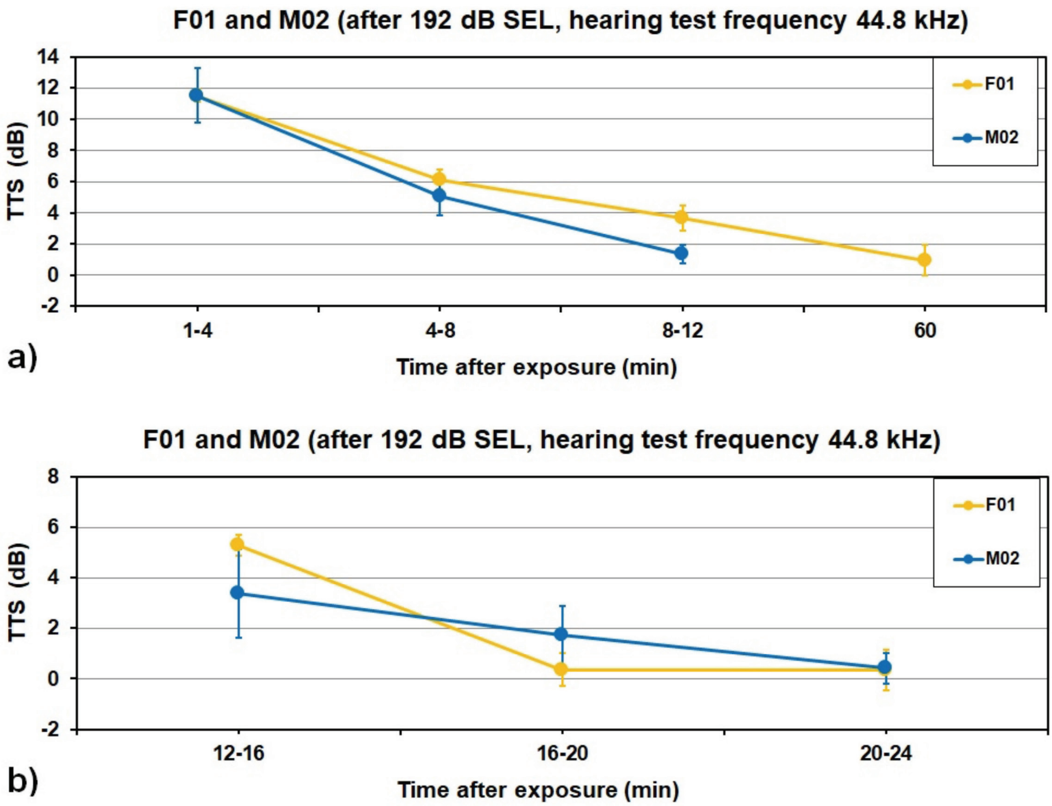

Figure 7. Individual similarity in susceptibility to TTS in California sea lions: mean TTS (± SD; $n = 4$) at hearing test frequency 44.8 kHz in F01 1 to 60 min after exposure, in M02 1 to 12 min after exposure (a), and in both sea lions 12 to 24 min after exposure (b) for 60 min to the continuous one-sixth-octave NB centered at 32 kHz at an SEL of 192 dB re 1 µPa²s.

each new hearing test frequency by measuring the basic hearing threshold until it stabilized and was close to that of the other sea lion. The time needed for this varied depending on the individual sea lion and the hearing test frequency. Mean pre-stimulus response rates (i.e., false positives) by both sea lions were low and similar in all pre-exposure hearing tests, control tests, and hearing tests after exposure to the fatiguing sound, showing that performance was consistent.

The two California sea lions exhibited similar patterns of 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).

Short breaks in the fatiguing sound can allow hearing to recover and may result in significantly smaller 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 lifted their heads out of the water to take breaths. Based on data from harbor seals (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 surfacings (low jumps), the California sea lions were exposed to the fatiguing sound transmitted from the water, as demonstrated by the SPLs measured in air during sound exposure (Table 1). In addition, the building around the pool had hard inner surfaces, which caused the SPL in air 30 cm above the water surface to be relatively homogeneous

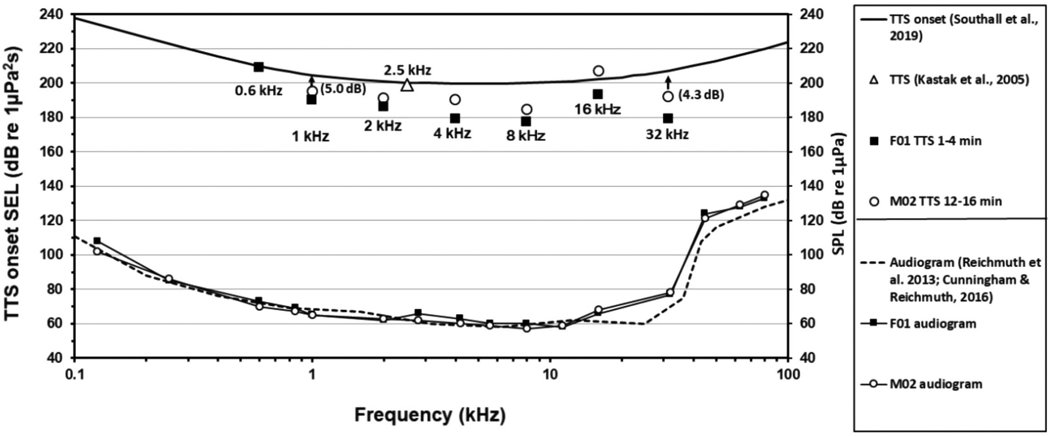

Figure 8. Onset of TTS in relation to the audiogram of the California sea lion: the SELs (left-hand y-axis) of one-sixth-octave NBs centered at 0.6 and 1 kHz (Kastelein et al., 2022b), 2 and 4 kHz (Kastelein et al., 2021b), 8 and 16 kHz (Kastelein et al., 2022a), and 32 kHz (present study) that caused 6 dB $TTS_{1\text{-}4}$ in F01 (■) and 6 dB $TTS_{12\text{-}16}$ in M02 (O). No $TTS_{12\text{-}16}$ could be elicited in M02 after exposure to the NB at 0.6 kHz. The maximum SEL at which the NB at 1 kHz could be produced only elicited 5 dB $TTS_{12\text{-}16}$ in M02, and the maximum SEL at which the NB at 32 kHz could be produced only elicited 4.3 dB $TTS_{12\text{-}16}$ in M02, so, in both cases, to cause 6 dB TTS, the SEL would have had to be slightly higher (as indicated by the arrows above the open circles). In this figure, the lowest SEL required to cause 6 dB TTS is defined as a marker of TTS onset (upper solid line; Southall et al., 2019). Also shown are the audiogram of a California sea lion (dashed line; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016) and the audiograms of F01 and M02 used in the present study (right-hand y-axis, showing SPLs; Kastelein et al., 2023).

due to reflections (as evidenced by the similar SPLs measured by two microphones which were 6 m apart). Typically when the sea lions surfaced during fast swimming (usually for respirations), part of their abdomen remained in contact with the water. Therefore, it was considered unnecessary to use aerial loudspeakers to project additional fatiguing sound during exposure sessions, and our underwater SELs and TTS measurements are assumed to be accurate.

Hearing Frequencies Affected by Exposure to the Fatiguing Sound at Each Exposure Level

When F01 was exposed to the NB at 32 kHz, $TTS_{1\text{-}4}$ occurred not only at the center frequency of the fatiguing sound and at half an octave higher (i.e., at 44.8 kHz), but also, to a lesser extent, at one octave higher (63 kHz; Table 1 & Figure 3A). For most of the fatiguing sound center frequencies tested with these California sea lions for this research project, a similar pattern was observed, though in most cases the greatest TTS occurred at half an octave above the center frequency (Cody & Johnstone, 1981; Kastelein et al., 2021b, 2022a, 2022b); in the present study, it occurred at the center frequency (only 1.4 dB higher than the maximum TTS measured with the hearing test frequency half an octave above the center frequency of the fatiguing sound). The hearing frequency most affected depends not only on the frequency, but also on the SEL of the fatiguing sound (Kastelein et al., 2019).

Like most other fatiguing sounds that have been tested with California sea lions (Kastelein et al., 2021b, 2022a, 2022b), the 32 kHz fatiguing sound elicited TTS in a wide frequency band (Table 1), showing that even narrow-band fatiguing sounds may result in TTS occurring over a range of adjacent frequencies. This should be considered in environmental impact assessments.

Hearing Recovery After the Fatiguing Sound Stopped

Hearing recovery in the California sea lions was similar to that after exposure to fatiguing sounds centered at 2 and 4 kHz (Kastelein et al., 2021b)—TTSs up to 6.7 dB recovered within 8 min, TTSs up to 12 dB took an hour to recover, and only the highest TTS measured (12.9 dB) took over an hour to recover. Kastak et al. (2007) exposed a California sea lion for 1.5 to 50 min to a continuous octave-band noise centered at 2.5 kHz in air at SPLs between 94 and 133 dB re 20 µPa, but they started testing their subject 10 to 15 min after sound exposure stopped and did not test it again the same day, unless initial TTS was higher than 20 dB. The TTSs of < 20 dB recovered within 24 h, and six instances of TTS

> 20 dB required a longer recovery time. These TTSs followed a linear recovery rate of 8.8 dB per log(min) (Kastak et al., 2007), suggesting that a TTS of 25 dB would require almost 11 h and 40 min to recover. In the present study, initial TTSs (TTS_{1-4}) were tested almost immediately after sound exposure stopped (1 to 4 min), and initial TTSs measured by Kastak et al. (2007) would have been higher if they had been measured sooner after the sound stopped. This may explain the longer recovery time observed for TTSs > 20 dB by Kastak et al. (2007).

Individual Differences in Susceptibility to and Recovery from TTS

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 (Figures 6 & 7). In fact, susceptibility to TTS and recovery in both subjects was similar after exposure to NBs at 0.6, 1, 2, 4, 8, 16, and 32 kHz (Kastelein et al., 2021b, 2022a, 2022b, present study). However, the sample size (two individuals) is too small to draw general conclusions about variability within the species, and F01 and M02 are genetically related (mother and son). 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., 2014). Therefore, further replication with more California sea lions is needed to assess individual differences.

TTS Onset Sound Exposure Level

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. However, Southall et al. (2019) used the lowest SEL required to elicit 6 dB TTS as a marker of TTS onset, although the rationale for the choice of 6 dB was not mentioned, and the hearing frequency was not specified. By this definition, and considering all hearing test frequencies, the 6 dB onset of TTS_{1-4} in F01 after exposure to the NB at 32 kHz occurred at an SEL of 179 dB re 1 $\mu Pa^2 s$ (at 44.8 kHz; Figure 3a). The 6 dB onset of TTS_{12-16} (quantified after some recovery of hearing had occurred) in M02 after exposure to the NB at 32 kHz was not reached, but a 4.3 dB TTS occurred after exposure to an SEL of 192 dB re 1 $\mu Pa^2 s$ (at 32 kHz; Figure 3b). These results from the present study, combined with 6 dB TTS onset SELs after exposure to fatiguing sounds centered at 0.6, 1, 2, 4, 8, and 16 kHz (Kastelein et al., 2021b, 2022a, 2022b), 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., 2020b).

The 6 dB TTS onset SEL for F01 in the present study for the NB at 32 kHz (179 dB re 1 $\mu Pa^2 s$ at 44.8 kHz) was much lower than expected if the TTS onset curve roughly followed the shape of the California sea lion audiogram (the TTS onset SEL for M02 was also lower than expected). At all three hearing test frequencies for F01, significant TTS occurred already at an SEL of 180 dB re 1 $\mu Pa^2 s$ (SPL 144 dB re 1 μPa for 1 h). A similar pattern of lower (or similar) 6 dB TTS onset SELs after exposure to a fatiguing sound at 32 kHz than to one at 16 kHz was found in harbor seals (Kastelein et al., 2020a): the TTS onset SEL of two harbor seals to a one-sixth octave NB at 32 kHz was between 176 and 181 dB re 1 $\mu Pa^2 s$ (SPLs of 140 and 145 dB re 1 μPa for 1 h) at a hearing frequency of 45 kHz (Kastelein et al., 2020a). TTS onset SELs at these high fatiguing sound frequencies may be low because the hearing frequencies at which the highest TTSs occurred are close to the upper frequencies of the California sea lions' and harbor seals' audiograms, where hearing becomes much less sensitive. Observing all the TTS onset SELs of these two pinniped species, it could also be concluded that the TTS onset SEL for F01 for 16 kHz (Figure 8) is unexpectedly high and that the ones for 32 kHz are normal.

There is fairly good agreement that the extended high frequencies are highly vulnerable to noise injury, with deficits commonly reported in studies on humans exposed to occupational noise and music. One of the theories is that all sound has to pass through the base to get to its best frequency at the basilar membrane, and damage to the base (where the high frequencies are transformed into electrical signals to the brain) could occur because of the way mechanical energy travels along the basilar membrane. The base of the cochlea is also more metabolically active and has higher free radical production than the rest of the basilar membrane (Fettiplace & Nam, 2019).

Hearing loss, whether permanent or temporary (but repeated), may compromise an individual California sea lion's fitness and/or survival. With the exception of TTS after exposure to an NB centered at 0.6 kHz, all SELs at which the 6 dB onset of TTS_{1-4} has been observed in F01 so far (Kastelein et al., 2021b, 2022a, 2022b, present study) are below the 6 dB TTS onset levels modeled and predicted by Southall et al. (2019), as are most of the $TTS_{12\text{-}16}$ onset SELs of M02 (Figure 8). This means that California sea lions are more susceptible to TTS than predicted and that they experience TTS as a result of exposure to sounds of lower SELs than predicted. Therefore, we suggest that the TTS onset SEL function for Otariidae (marine mammal group OCW; Southall et al., 2019) should be adjusted. Once the final fatiguing sound frequency of our research program has been tested (40 kHz), we will propose an updated TTS onset function for California sea lions.

The low TTS onset levels seen at the very highest frequencies within the hearing range of California sea lions (32 kHz), as well as in harbor seals (32 and 40 kHz; Kastelein et al., 2020a) and Yangtze finless porpoises (testing 32, 64, and 128 kHz; the lower the frequency of the fatiguing sound at the same SEL, the higher the initial TTS; Popov et al., 2011), show that TTS onset levels are not as closely related (especially at the lower and higher frequencies) to the unmasked hearing thresholds (audiograms) as was assumed, based on very few available data by Southall et al. (2019).

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