Aquatic Mammals 2025, *51*(5), 28-37, DOI https://doi.org/10.1578/AM.51.5.2025.28

Critical Ratio Measurements Can be Used to Assess Effective Quiet Thresholds in Harbor Seals, Harbor Porpoises, and California Sea Lions

John M. Terhune[1] and Ronald A. Kastelein[2]

[1]*Department of Biological Sciences, University of New Brunswick, 355 Campus Circle Road, Saint John, NB, E2L 4L5, Canada*
E-mail: terhune@unb.ca
[2]*SEAMARCO, Julianalaan 46, 3843 CC, Harderwijk, The Netherlands*

Abstract

Effective quiet is a sound pressure level (SPL) that will never cause temporary hearing threshold shifts (TTSs), even after long exposures. TTS is typically measured after the end of a fatiguing sound exposure when some recovery may have occurred during the threshold measurement. Using published data from 24 studies from the SEAMARCO Research Institute, we examined the recovery from TTS of harbor seals (*Phoca vitulina*), harbor porpoises (*Phocoena phocoena*), and California sea lions (*Zalophus californianus*) to assess whether the measurement procedures to determine initial TTSs were compromised by recovery from TTS. When initial $TTS_{1\text{-}4}$ (measured 1 to 4 min post exposure) was < 6.0 dB, recovery occurred in 42, 50, and 57% of sessions (respectively for each species) at 4 to 8 min post exposure. By 8 to 12 min post exposure, the complete recovery rates were 65, 86, and 92% (respectively for each species). A certain amount of recovery from TTS occurs during the post-exposure hearing threshold determination. Rapid recovery from small TTSs makes determination of the effective quiet SPL threshold difficult to measure. An alternative to quantifying unmasked hearing sensitivity to assess small TTSs may be quantifying the critical ratio (CR; the difference in dB between a tonal signal detection threshold and the spectrum level of the masking noise at that frequency) at the beginning and just before the end of the fatiguing sound exposure. If the CR measured just before the fatiguing sound ends is higher than the CR measured just after the fatiguing sound began, then that difference will be the magnitude of TTS that has occurred. Using CR measures will avoid recovery occurring during the measurement process. CR determinations can be made using more trials than during the 1- to 4-min post-exposure hearing tests and should result in more accurate measurements of TTSs. Determining effective quiet SPL thresholds allows the identification of "safe" received SPLs that do not cause TTS. This information will be useful in environmental assessments of anthropogenic sounds. However, even "safe" SPLs may reduce the ability of mammals to hear signals by causing acoustic masking.

Key Words: critical ratio, effective quiet, fatiguing sound levels, hearing thresholds, marine mammals, masking, temporary threshold shift

Introduction

Anthropogenic sounds may have negative effects on marine mammals because exposure to high-amplitude and/or long-duration sounds can result in a temporary hearing threshold shift (TTS) in which the detection threshold of a mammal is raised (Finneran, 2015). Such a shift interferes with the detection of sounds that could be important to the animal and, thus, may interfere with behavioral functions such as courtship, mating, social interactions, prey detection, and orientation (Duarte et al., 2021). Recovery from small TTSs (< ~6.0 dB) can take minutes, but recovery from large TTSs (> ~20.0 dB) can take hours or days. Sound exposures resulting in TTSs have been measured for a few marine mammal species (e.g., Kastak et al., 2005; Finneran, 2015; Southall et al., 2019; Kastelein et al. references cited in Table 1) to provide guidance for regulatory noise exposure limits (Southall et al., 2019).

TTS in marine mammals is typically measured by determining the unmasked hearing detection threshold and then exposing the animal to a fatiguing sound at a specific sound pressure level (SPL) for some duration (resulting in a sound exposure level [SEL]). Following cessation of the fatiguing sound, the unmasked detection threshold is determined. TTS is present if the second threshold is higher than the threshold measured before exposure

Table 1. Numbers of individual initial temporary hearing threshold shift ($TTS_{1\text{-}4}$) determinations that were between 2.0 and 15.9 dB for harbor seals (*Phoca vitulina*), harbor porpoises (*Phocoena phocoena*), and California sea lions (*Zalophus californianus*). The fatiguing sounds were narrow Gaussian noise bands (except for the harbor seal at 6.5 kHz which was exposed to a tonal sound), and the exposure time was always 60 min. The initial TTSs were estimated 1 to 4 min after the cessation of the fatiguing sound. FF = fatiguing sound center frequency (kHz); 0, 1/3, 1/2, 2/3, and 1 refer to the fraction of an octave that the hearing test frequency at which TTS was measured was above the FF.

Species	FF (kHz)	Number of TTS determinations at each hearing test frequency octave above FF					Kastelein et al. references
		0	1/3	1/2	2/3	1	
Harbor seal	0.5					1	2020e
Harbor seal	1.0			3			2020e
Harbor seal	2.0	13		12		18	2020e
Harbor seal	4.0	13					2012b
Harbor seal	6.5	31		16			2019a
Harbor seal	16.0	8		9			2019c
Harbor seal	32.0	23		11			2020d
Harbor seal	40.0	15	15		4		2020f
Harbor porpoise	0.5	3					2021a
Harbor porpoise	1.5	6		17		13	2020b
Harbor porpoise	4.0	11					2012a
Harbor porpoise	8.0	7		8		3	2024a
Harbor porpoise	16.0	20		14		5	2019d
Harbor porpoise	32.0	16		5			2019b
Harbor porpoise	63.0	27		16			2020a
Harbor porpoise	88.4	12	6	11			2020c
California sea lion	0.6	1		12		1	2022b
California sea lion	1.0	8		15		5	2022b
California sea lion	2.0	24		20		17	2021b
California sea lion	4.0	16		13		11	2021b
California sea lion	8.0	16		17		10	2022a
California sea lion	16.0			17		10	2022a
California sea lion	32.0	12		18		12	2024b
California sea lion	40.0	8	10	22	8	9	2025

to the fatiguing sound (e.g., Kastak et al., 2005; Finneran et al., 2010; Kastelein et al. references cited in Table 1). The accuracy of hearing threshold determinations in marine mammals is typically within ~2.0 to 3.0 dB (e.g., Finneran et al., 2010; Kastelein et al., 2023). For environmental assessment purposes concerning marine mammals, variation in measuring low levels of TTSs led to the practical definition of the "onset" of TTS as a shift of at least 6.0 dB (Schlundt et al., 2000; Southall et al., 2019). A TTS of 6.0 dB is assumed to interfere with the perception of sounds of importance to marine mammals—that is, signals. Statistically significant levels of TTS can be measured below 6.0 dB, however (Kastelein et al. references cited in Table 1).

Noise can cause acoustic masking if it overlaps in frequency and time with the signal (Jeffress, 1970). Masking interferes with the distance at which a signal can be detected, and small increases in the degree of masking can result in disproportionate

decreases in detection distance. For example, in deep water where spherical spreading of sound occurs, the received SPL decreases (theoretically) by 6.0 dB for every doubling of the distance between the signal source and the receiver. Thus, relative to the maximum communication distance in quiet surroundings, a 6.0 dB increase in the background noise reduces the communication distance by half in deep water (Terhune & Killorn, 2021). Similarly, if a mammal experiences a 6.0 dB TTS (i.e., its hearing sensitivity is temporarily reduced by 6.0 dB), then in quiet surroundings its maximum communication or sound detection distance is reduced by ~50%. Thus, large TTSs can result in severe reductions in sound detection by marine mammals (Finneran, 2015; Southall et al., 2019). Temporary hearing loss estimations are used in environmental impact assessments of anthropogenic sound sources, especially if large TTSs are likely to occur.

Not all anthropogenic sounds result in TTS in marine mammals. "Effective quiet" refers to sound levels below a SPL threshold which does not cause TTS or delay recovery from TTS (Ward et al., 1976). Anthropogenic sounds in the ocean can cause TTS, so it is important to determine the effective quiet SPL thresholds that are likely to result in TTS or prohibit the recovery from TTS in marine mammals. Effective quiet thresholds can be approximated by determining the lowest SPL and exposure durations that result in small TTSs (Finneran & Branstetter, 2013). Such information will be useful in assessing the potential impact of anthropogenic noise sources for environmental protection purposes.

Our aim is to examine the hearing recovery patterns of three species of marine mammals from different families: harbor seals (*Phoca vitulina*), harbor porpoises (*Phocoena phocoena*), and California sea lions (*Zalophus californianus*). The study animals experienced small TTSs in a set of parallel studies conducted at the SEAMARCO Research Institute in The Netherlands. For all three species, the experimental conditions in which similar sound exposures and TTS determination procedures were used were similar (Kastelein et al. references cited in Table 1). These studies indicated that small TTSs often recovered 8 to 12 min after cessation of the fatiguing sound. This suggested that the methods currently used to quantify TTS might not be appropriate for measuring effective quiet threshold SPLs. Herein, we will (1) assess whether the measurement procedures to determine TTSs were compromised by recovery by studying TTS recovery patterns; (2) assess whether recovery from TTS is related to fatiguing sound frequency or hearing test frequency; and (3) suggest improved methods to measure very small TTSs so that the effective quiet SPL threshold can be quantified. Measuring recovery patterns of TTS levels below 6.0 dB will help assess the validity of adopting that level as a TTS "onset" level for environmental impact assessments (Southall et al., 2019). Determining SPLs that do not result in TTS, even after long exposures to continuous, variable, or intermittent anthropogenic sounds, will aid in developing regulatory limits to protect marine mammals from temporary reductions in hearing sensitivity.

Methods

Data Sources

TTS and recovery were quantified in three marine mammal species (harbor seals, harbor porpoises, and California sea lions) at the SEAMARCO Research Institute (Kastelein et al. references cited in Table 1). The methods used involved measuring the unmasked hearing threshold of the subject using the go/no go staircase technique, exposing the subject for 1 h to a continuous constant-amplitude fatiguing sound (usually a noise band [NB]), and then measuring the unmasked hearing threshold after cessation of the sound to determine if there was a TTS. This was done with the NBs at various SPLs across the hearing frequency range of each species. Post-exposure thresholds were determined in at least three time periods: 1 to 4 min, 4 to 8 min, and 8 to 12 min after cessation of the fatiguing sound. During each of the 4-min periods, the goal was to obtain a minimum of three reversals (of correct detections and misses and vice versa). If this goal was not met, the session was not used for analysis. In the resulting publications (Kastelein et al. references cited in Table 1), $TTS_{1\text{-}4}$, $TTS_{4\text{-}8}$, and $TTS_{8\text{-}12}$ were calculated from repeating the number of sessions until at least 60 reversals in total were obtained, typically in four to six sessions. If TTS was still present in the 8- to 12-min period, thresholds were determined 60 to 72 min post exposure, or even later, until hearing had fully recovered. The threshold measurement accuracy was estimated to be ± 2.0 dB; therefore, $TTS_{1\text{-}4}$ was assumed to have occurred if the post-exposure threshold was ≥ 2.0 dB higher than the pre-exposure threshold. Similarly, recovery from TTS was assumed to have occurred once the unmasked threshold was < 2.0 dB above the pre-exposure threshold. Full details of the experimental procedures are presented in the individual studies. The methodology is described in more detail by Kastelein et al. (2012b, 2019b, 2021b). Note that the analyses performed in this study were made using data from individual sessions (see "Data Analyses" section).

The SEAMARCO studies were not designed to measure fatiguing sound exposures resulting in very small TTSs. TTS was measured at the center frequency of the fatiguing sound and at hearing frequencies up to one octave above that frequency (Kastelein et al. references cited in Table 1) and

was often highest when measured half an octave above the center frequency of the fatiguing sound (Kastelein et al., 2019a). The data included in the analyses of the present study were limited to sessions in which the initial $TTS_{1\text{-}4}$ magnitudes were between 2.0 and 15.9 dB. TTSs of ≥ 16.0 dB were too few to permit meaningful analyses. Hearing recovery was measured 4 to 8 min and 8 to 12 min after cessation of the fatiguing sound for each of the individual sessions.

Two harbor seals, three harbor porpoises, and two California sea lions were exposed to eight fatiguing sound center frequencies and up to five hearing test signal frequencies, as outlined in the Kastelein et al. references cited in Table 1. For each species, most of the determinations were from one individual, with a few TTS thresholds from a second or third individual (Kastelein et al. references cited in Table 1). The numbers of threshold determinations for the harbor seals, harbor porpoises, and California sea lions were 195, 229, and 317, respectively.

Data Analyses

For each individual threshold measurement, the TTS magnitudes at 4 to 8 and 8 to 12 min post exposure were subtracted from the $TTS_{1\text{-}4}$ magnitude at 1 to 4 min post exposure to determine if recovery had occurred. The numbers of the samples that did or did not recover (threshold < 2.0 dB above the pre-exposure threshold) were determined per dB level of the initial $TTS_{1\text{-}4}$ and graphed for visual inspection. The proportions of TTSs that recover during the 4- to 8-min and 8- to 12-min post-exposure measurement times will indicate whether or not recovery from TTS could be compromising the measurement process in a significant manner. The proportions of samples that did, or did not, recover were determined for initial $TTS_{1\text{-}4}$ magnitudes that were 5.9 dB or lower and 6.0 dB or higher. The less than, or greater than, 6.0 dB TTS threshold categories were chosen to reflect the practical definition of the "onset" of TTS used by Southall et al. (2019) to assess potential anthropogenic noise environmental impacts. Determining the recovery patterns for TTSs below 6.0 dB will help assess the validity of adopting that level as a practical TTS "onset" level for environmental impact assessments (Southall et al., 2019).

The rates of recovery from TTS associated with the fatiguing frequencies and hearing test frequencies were examined using general linear model (GLM) analyses with the packages 'tidyverse,' 'lme4,' and 'DHARMa' in *R* (R Core Team, 2023). The dependent variable (recovery) was the number of dB that the initial $TTS_{1\text{-}4}$ levels had dropped to in the 8- to 12-min periods. Within each species, only the fatiguing sound frequencies that had hearing frequency data at both 0 and 0.5 octaves above the fatiguing frequency were included in the analyses (Table 1). The dataset was too unbalanced to include other fatiguing frequencies or hearing frequencies that were 0.33, 0.66, or 1.0 octaves above the fatiguing frequencies.

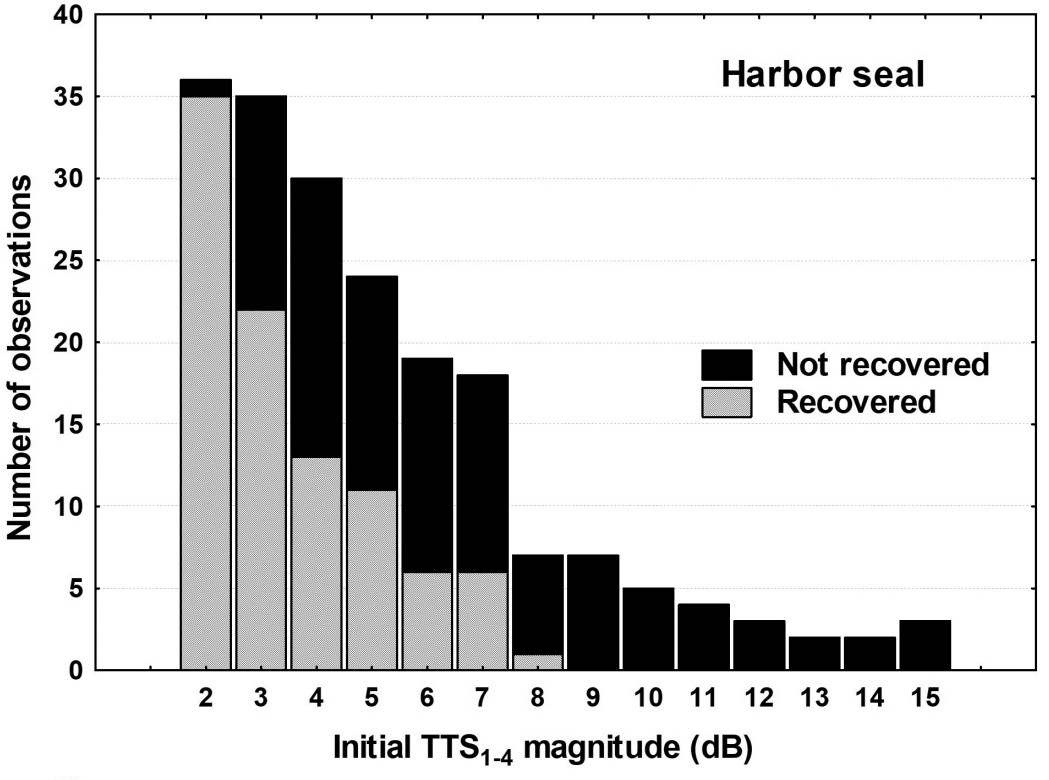
Results

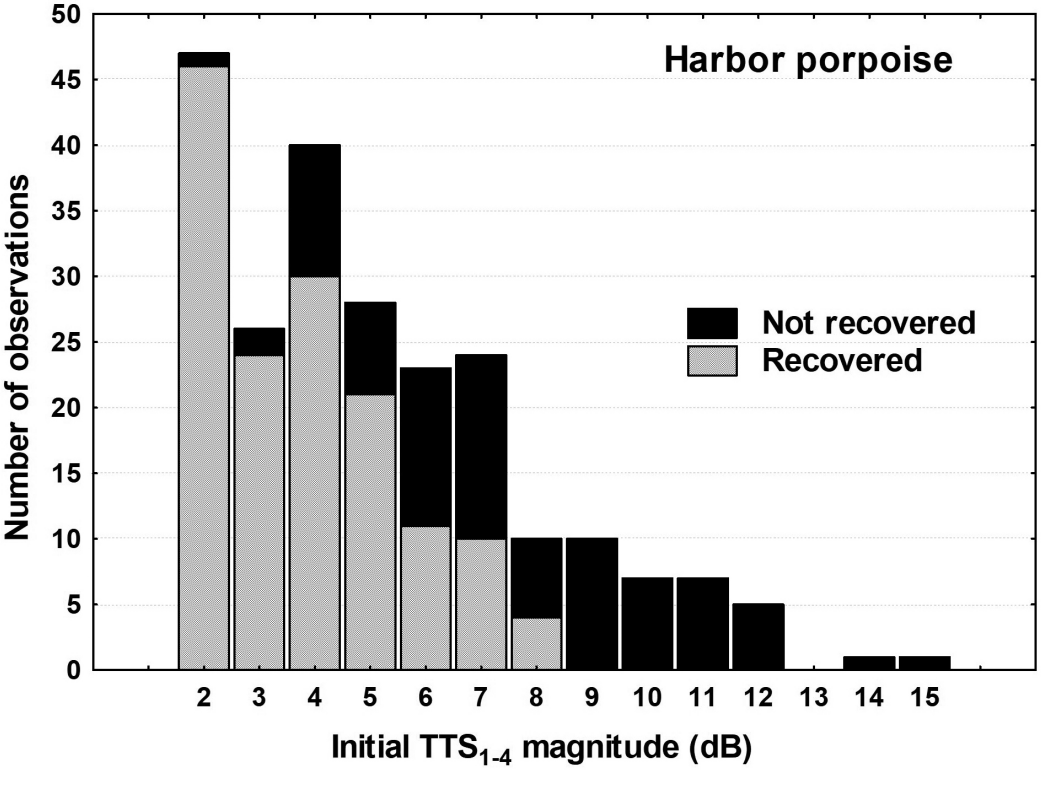
For all three species, there was substantial recovery from small $TTSs_{1\text{-}4}$ by 8 to 12 min post exposure (Figure 1). When the initial $TTS_{1\text{-}4}$ magnitudes were ≤ 5.9 dB, close to half the cases had recovered (TTS < 2.0 dB) by 4 to 8 min post exposure, and 65 to 93% had recovered by 8 to 12 min post exposure (Table 2). In a few cases, there was complete recovery from initial $TTS_{1\text{-}4}$ magnitudes that were well above 6.0 dB (Figure 1).

For all three species, examinations of the 'DHARMa' residuals (R Core Team, 2023) did not indicate any problems. McFadden's Pseudo R^2 values were 0.26, 0.42, and 0.54 for the harbor seal, harbor porpoise, and California sea lion analyses, respectively. The statistical significances of the R^2 values were all $p < 0.00001$. There were very strong relationships between recovery and the initial $TTS_{1\text{-}4}$ levels for all three species, and weaker relationships with the fatiguing sound frequency and recovery for harbor porpoises and California sea lions (Table 3). The hearing octave was not a significant factor in all three species.

Table 2. Full recovery (% of TTS < 2.0 dB) of $TTS_{1\text{-}4}$ with initial TTS less than or greater than 6.0 dB at two post-fatiguing sound times for harbor seals, harbor porpoises, and California sea lions. The number of times TTS was measured in each species at each magnitude is shown in parentheses.

	Full recovery, 4-8 min post exposure		Full recovery, 8-12 min post exposure	
Species	$TTS_{1\text{-}4}$ ≤ 5.9 dB	$TTS_{1\text{-}4}$ ≥ 6.0 dB	$TTS_{1\text{-}4}$ ≤ 5.9 dB	$TTS_{1\text{-}4}$ ≥ 6.0 dB
Harbor seal	42% (125)	1% (70)	65% (125)	36% (70)
Harbor porpoise	50% (141)	6% (88)	86% (141)	28% (88)
California sea lion	57% (122)	4% (195)	93% (122)	28% (195)


Harbor seal
Number of observations
Not recovered
Recovered
0
5
10
15
20
25
30
35
40
2 3 4 5 6 7 8 9 10 11 12 13 14 15
Initial TTS1-4 magnitude (dB)


Harbor porpoise
Number of observations
Not recovered
Recovered
0
5
10
15
20
25
30
35
40
45
50
2 3 4 5 6 7 8 9 10 11 12 13 14 15
Initial TTS1-4 magnitude (dB)

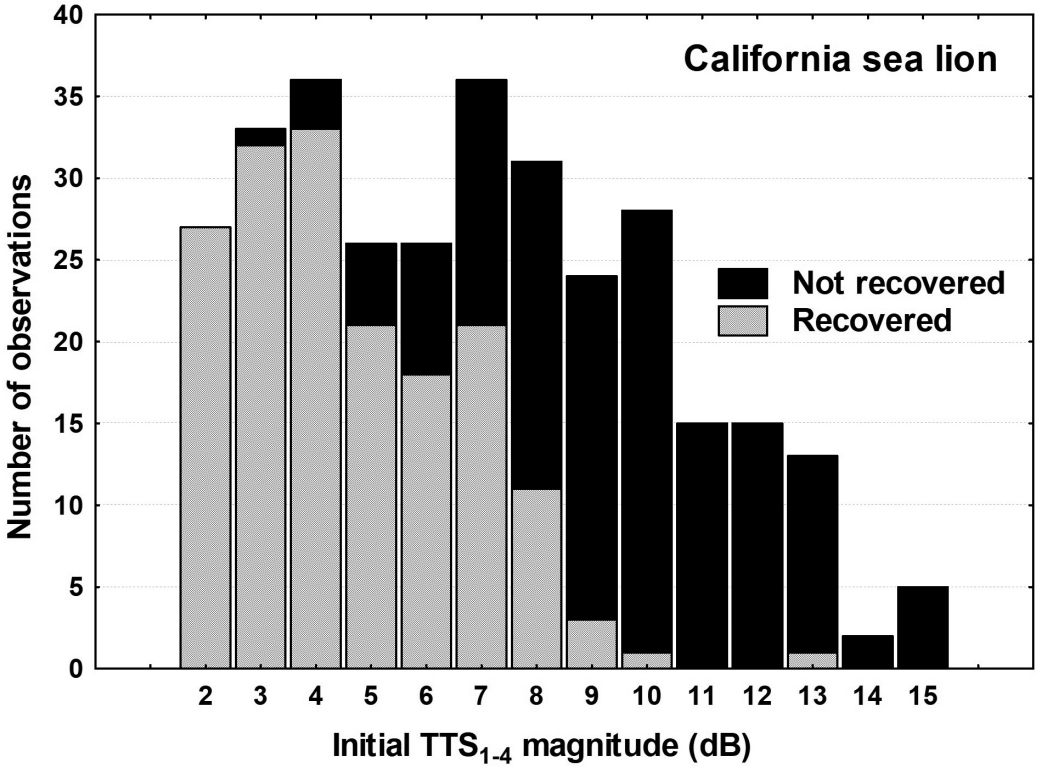


Figure 1. The numbers of observations in which initial temporary hearing threshold shifts ($TTS_{1\text{-}4}$, measured 1 to 4 min after exposure to fatiguing sounds of various frequencies and tested at various hearing frequencies) had recovered by 8 to 12 min post exposure in harbor seals (*Phoca vitulina*), harbor porpoises (*Phocoena phocoena*), and California sea lions (*Zalophus californianus*). The light grey areas indicate complete recovery while the black areas indicate a lack of recovery (i.e., TTSs were ≥ 2.0 dB by 8 to 12 min post exposure). Note that the majority of $TTS_{1\text{-}4}$ below 4.0 dB had recovered before the end of the 8- to 12-min measurement period. Results are based on the studies shown in Table 1.

Table 3. Coefficients of the general linear model (GLM) analyses of recoveries from TTS after 8 to 12 min related to the initial $TTS_{1\text{-}4}$ level (TTS), fatiguing frequency, and hearing test octave. Only hearing test frequencies that included both 0.0 and 0.5 octaves higher than the fatiguing sound frequency were included in the analyses (see Table 1). Sample sizes for the harbor seals, harbor porpoises, and California sea lions are 125, 165, and 192, respectively. Statistically significant ($p < 0.05$) variables are in bold.

Species	Variable	Estimate	SE	z	*p*
Harbor seal	**Intercept**	2.778	0.651	4.268	**< 0.00002**
Harbor seal	**TTS**	-0.649	0.134	-4.865	**< 0.00001**
Harbor seal	Frequency	0.00003	0.000002	1.619	0.105
Harbor seal	Octave	0.475	0.499	0.952	0.341
Harbor porpoise	**Intercept**	5.541	0.829	6.685	**< 0.00001**
Harbor porpoise	**TTS**	-0.704	0.110	-6.383	**< 0.00001**
Harbor porpoise	**Frequency**	-0.00002	< 0.00001	-2.194	**0.028**
Harbor porpoise	Octave	-0.682	0.449	-1.519	0.129
California sea lion	**Intercept**	6.281	0.967	6.498	**< 0.00001**
California sea lion	**TTS**	-0.967	0.126	-7.114	**< 0.00001**
California sea lion	**Frequency**	0.000044	0.00001	2.741	**0.0061**
California sea lion	Octave	0.366	0.00048	0.750	0.453

Discussion

Variability in the Dataset

The intent of the original SEAMARCO TTS studies (Kastelein et al. references cited in Table 1) was to examine the onset of, and recovery from, TTS after the 60-min exposures to the continuous fatiguing sound. At each fatiguing sound frequency and hearing test frequency, the low SELs were expected to result in no or small TTSs. If no or very small $TTS_{1\text{-}4}$s occurred, then that SEL was not examined further, and higher SELs were presented in subsequent trials. The hearing test frequencies that were examined varied with species and fatiguing sound frequencies (Kastelein et al. references cited in Table 1) and were limited by the time available during the various studies. As a result, the dataset analyzed in this study was unbalanced, which resulted in some fatiguing frequencies and hearing test frequencies being presented to only one or two species; this precluded some comparative analyses.

The data used herein are from individual threshold measurements (i.e., only from one sound exposure per day), while the thresholds reported in the resulting publications (Kastelein et al. references cited in Table 1) were derived from a number of exposures (typically 3 to 5) which were combined to obtain ~60 reversals. Also, the TTS values reported in the resulting publications (Kastelein et al. references cited in Table 1) included some individual measures in which the $TTS_{1\text{-}4}$s were < 2.0 dB and are not included in this study.

The GLM analyses revealed a strong negative relationship between the initial $TTS_{1\text{-}4}$ and the recovery by 8 to 12 min post exposure in all three species (Table 3). The low $TTS_{1\text{-}4}$s often had fully recovered at that point, which was not the case for the higher $TTS_{1\text{-}4}$. For the harbor seals, there was no relationship between recovery and the fatiguing frequency; for the harbor porpoises, there was a very weak negative relationship between recovery and the fatiguing frequency; and for the California sea lions, the relationship was very weak and positive. There were no relationships between the hearing test octave and recovery in all three species (Table 3). These results support our assumption that once TTS has occurred, the recovery is not influenced by the original fatiguing sound frequency or the hearing test frequency. Thus, within each species, all of the recoveries from TTS are considered to be independent of the fatiguing sound frequencies and hearing test frequencies for the results presented in Table 2 and Figure 1.

Recovery Patterns

The recovery patterns indicate that recovery from small $TTS_{1\text{-}4}$s can take place during the first 4-min measurement period. An implication of this is that these $TTS_{1\text{-}4}$ magnitudes may be underestimated because some recovery occurred before the measurements could be completed. This is an important constraint in determining the effective quiet threshold SPL. TTSs 8 to 12 min post exposure are invalid for that purpose if any recovery has occurred, or if the $TTS_{1\text{-}4}$ was underestimated. In both these situations, the effective quiet threshold will be overestimated.

Difficulties in accurately measuring low levels of TTS (Schlundt et al., 2000) led Southall et al. (2019) to adopt 6.0 dB TTS as a practical measure of TTS "onset" threshold. The high levels of recovery (to TTS < 2.0 dB) from TTS < 6.0 dB after 8 to 12 min post exposure in all three species in the present study suggest that the arbitrary 6.0 dB "onset" threshold is an appropriate value. While animals with 6.0 dB TTS will experience hearing reduction, the effect is relatively short-lived. There will be some variability associated with determining the SPL of the effective quiet thresholds. Once effective quiet threshold SPLs and 6.0 dB TTS "onset" threshold are established, there is likely to be a small zone of uncertainty between these two measures. SPLs in this region are likely to occasionally create small TTSs that recover quickly following the end of the fatiguing sound exposure.

Using Critical Ratios to Measure Small TTSs

To determine the effective quiet threshold SPL (Martin et al., 2020), it is necessary to measure TTSs before the end of the exposure to the putative fatiguing sound. We propose that this can be accomplished by measuring critical ratios (CRs) in the presence of the fatiguing sound. The CR is the difference, in dB, between the tonal detection threshold and the spectrum level at that frequency of a continuous masking NB (Scharf, 1970). To determine if a TTS has occurred, the CR is measured immediately after the fatiguing sound begins and, thus, before TTS has occurred. Then, after a long exposure, 6 h for example, the CR is measured again while the low-level fatiguing sound is still present. If the CR measured just before the fatiguing sound ends is higher than the CR measured just after the fatiguing sound began, then the difference will be the highest TTS that has occurred. If a TTS has occurred during the exposure period, then the second CR measure will be higher than the first by an amount equal to the TTS. This procedure assumes that it will take some time after the start of the low-level fatiguing sound for TTS to develop. It would not

be applicable using moderate to high-amplitude fatiguing sound exposures that would create TTS within a few minutes. Also, this procedure is not applicable to impulsive fatiguing sounds because CR estimates require continuous constant-amplitude masking noise (bands).

The advantage of measuring TTS using CRs is that the CR threshold measured just before the fatiguing sound ends can be based on a larger number of trials than the 1- to 4-min post-exposure measure—that is, the threshold calculations can be based on reversals that occur over a 1- to 12-min period rather than just the 1 to 4 min post exposure. This will increase the accuracy of the detection threshold determinations relative to those measured with fewer trials. If CR is measured in the presence of the low-level fatiguing sound, there is no opportunity for recovery during the measurement period. If the fatiguing sound SPL is too low to create a TTS, then the initial and last CR values will be similar. In this case, the noise level (and SPL value) will be below the effective quiet threshold. In a series of sessions in which the putative fatiguing sound level is varied in amplitude per session, it will be possible to determine the highest SPL at which ≤ 2.0 dB TTS occurs (after a long-duration exposure); this is the effective quiet threshold SPL.

The durations over which TTS measurements to quantify the effective quiet threshold are conducted are important. For marine mammals exposed to continuous anthropogenic sounds, 24-h exposures would be appropriate. This may be possible for cetaceans in pools or net pens but is less practical for pinnipeds. Though wild pinnipeds often remain at sea for considerable periods of time, for captive animals in pools, restricted opportunities to haul out and rest may result in stress. Exposures lasting 6 h may be more practical for pinnipeds. This is a sufficient amount of time to ensure that TTS is unlikely to occur due to longer exposures, although a 24-h continuous exposure to the fatiguing sound is often considered to be appropriate in effective quiet determinations (Martin et al., 2020).

Amplitude-modulated or intermittent fatiguing sounds cause smaller TTSs than continuous sounds (e.g., Kastelein, 2021b). Thus, in a worst-case scenario, the largest TTSs would be caused by a fatiguing NB that was continuous and of constant amplitude. Effective quiet threshold SPLs derived from exposure to such sounds would be very conservative in that those SPLs would not be expected to cause TTSs, especially if the fatiguing sound fluctuated in amplitude.

Measuring the effective quiet thresholds across the hearing frequency range of a species by using CR determinations will be less time-consuming than quantifying TTS (Kastelein et al. references cited in Table 1) because with CRs, an accurate determination of the presence or absence of TTS can be made during a single fatiguing sound exposure. Previously, four to six exposures at each SEL were required to obtain a sufficient number of reversals to calculate the unmasked threshold levels immediately after the cessation of the fatiguing sound (Kastelein et al. references cited in Table 1).

Anthropogenic sound SPLs below the effective quiet threshold could still be capable of masking or behavioral disruption (e.g., Kastelein et al., 2009; Southall et al., 2021). In environmental impact assessments, it will be important to distinguish between (1) SPLs that are "safe" with respect to creating TTS and (2) lower SPLs that can still result in masking.

Conclusion

Using CR increases to measure small TTSs and the effective quiet threshold SPL would avoid recovery that occurs during TTS measurements made in quiet surroundings after the end of the fatiguing sound. CR thresholds can be measured using more trials than can be conducted during the 1- to 4-min post-exposure TTS measurement periods; therefore, the TTS measurements are likely to be more accurate. Continuous constant-amplitude fatiguing sounds result in higher TTSs than intermittent sounds because in intermittent sound exposures some hearing recovery occurs during the time between sounds (e.g., Kastelein et al., 2021b, 2022a). Using continuous constant-amplitude fatiguing sounds with SPLs that just begin to result in TTS will provide a conservative measure of the effective quiet threshold SPL. No TTS will be elicited during exposures of intermittent or variable-amplitude sounds at the same SPL. Determining effective quiet thresholds at hearing frequencies at and above the fatiguing sound center frequencies will identify SPLs that are "safe" in that they will not cause TTS. Such data will be useful in environmental impact assessments because many anthropogenic sounds have amplitudes below the effective quiet threshold so TTS generation will not be an issue.

Acknowledgments

We thank all staff, students, and volunteers who helped with the data collection. Funding was provided from various agencies acknowledged in the individual publications along with the following more recent sources. For the harbor porpoise studies, funding was provided by Ecowende, a joint venture of Shell, Eneco, and Chubu Electric Power (in regard to the Hollandse Kust West wind

park) via WaterProof B.V. (Contract ID 196). We thank project managers Joost Brinkkemper and Irna Huisjes (WaterProof B.V.) for their guidance. For the harbor seal studies, funding was provided by the Netherlands Ministry of Defense via TNO (Contract No. 3100416476). We thank Frans-Peter Lam for his guidance on behalf of TNO. For the California sea lion studies, funding was provided by 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. Elizabeth Henderson and three reviewers are thanked for their valuable comments on an earlier draft of this review. We thank EnerGeo Alliance for sponsoring the Open Access publication of this study.

Literature Cited

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., Gordon, T. A. C., Halpern, B. S., Harding, H. R., Havlik, M. N., Meekan, M., Merchant, N. D., Miksis-Olds, J. L., Parsons, M., Predragovic, M., Radford, A. N., Radford, C. A., Simpson, S. D., Slabbekoorn, H., . . . Juanes, F. (2021). The soundscape of the anthropocene ocean. *Science*, *371*(6529), eaba4658. https://doi.org/10.1126/science.aba4658

Finneran, J. J. (2015). Noise-induced hearing loss in marine mammals: A review of temporary threshold shift studies from 1996-2015. *The Journal of the Acoustical Society of America*, *138*(3), 1702-1726. https://doi.org/10.1121/1.4927418

Finneran, J. J., & Branstetter, B. K. (2013). Effects of noise on sound perception in marine mammals. In H. Brumm (Ed.), *Animal communication and noise* (Vol. 2, pp. 273-308). Springer. https://doi.org/ 10.1007/978-3-642-41494-7_10

Finneran, J. J., Carder, D. A., Schlundt, C. E., & Dear, R. L. (2010). Growth and recovery of temporary threshold shift at 3 kHz in bottlenose dolphins: Experimental data and mathematical models. *The Journal of the Acoustical Society of America*, *127*(5), 3256-3266. https://doi.org/10.1121/1.3372710

Jeffress, L. A. (1970). Masking. In J. V. Tobias (Ed.), *Foundations of modern auditory theory* (Vol. 1, pp. 85-114). Academic Press. https://doi.org/10.1016/B978-0-12-691901-1.50008-5

Kastak, D., Southall, B. L., Schusterman, R. J., & Reichmuth Kastak, C. (2005). Underwater temporary threshold shift in pinnipeds: Effects of noise level and duration. *The Journal of the Acoustical Society of America*, *118*(5), 3154-3163. https://doi.org/10.1121/1.2047128

Kastelein, R. A., Helder-Hoek, L., & Gransier, R. (2019a). Frequency of greatest temporary hearing threshold shift in harbor seals (*Phoca vitulina*) depends on fatiguing sound level. *The Journal of the Acoustical Society of America*, *145*(3), 1353-1362. https://doi.org/10.1121/1.5092608

Kastelein, R. A., Cornelisse, S. A., Huijser, L. A. E., & Helder-Hoek, L. (2020a). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise bands at 63 kHz. *Aquatic Mammals*, *46*(2), 167-182. https://doi.org/10.1578/AM.46.2.2020.167

Kastelein, R. A., Gransier, R., Hoek, L., & Olthuis, J. (2012a). Temporary threshold shifts and recovery in a harbor porpoise (*Phocoena phocoena*) after octave-band noise at 4 kHz. *The Journal of the Acoustical Society of America*, *132*(5), 3525-3537. https://doi.org/10.1121/1.4757641

Kastelein, R. A., Gransier, R., Hoek, L., Macleod, A., & Terhune, J. M. (2012b). Hearing threshold shifts and recovery in harbor seals (*Phoca vitulina*) after octave-band noise exposure at 4 kHz. *The Journal of the Acoustical Society of America*, *132*(4), 2745-2761. https://doi.org/10.1121/1.4747013

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Defillet, L. N., & Huijser, L. A. E. (2020b). Temporary threshold shift in a second harbor porpoise (*Phocoena phocoena*) after exposure to a noise band at 1.5 kHz and a 6.5 kHz continuous wave. *Aquatic Mammals*, *46*(5), 431-443. https://doi.org/10.1578/AM.46.5.2020.431

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Huijser, L. A. E., & Gransier, R. (2020c). Temporary hearing threshold shift at ecologically relevant frequencies in a harbor porpoise (*Phocoena phocoena*) due to exposure to a noise band centered at 88.4 kHz. *Aquatic Mammals*, *46*(5), 444-453. https://doi.org/10.1578/AM.46.5.2020.444

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S., Huijser, L. A. E., & Gransier, R. (2019b). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise band at 32 kHz. *Aquatic Mammals*, *45*(5), 549-562. https://doi.org/10.1578/AM.45.5.2019.549

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S., Huijser, L. A. E., & Terhune, J. M. (2019c). Temporary hearing threshold shift in harbor seals (*Phoca vitulina*) due to a one-sixth-octave noise band centered at 16 kHz. *The Journal of the Acoustical Society of America*, *146*(5), 3113-3122. https://doi.org/10.1121/1.5130385

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S., Huijser, L. A. E., & Terhune, J. M. (2020d). Temporary hearing threshold shift in harbor seals (*Phoca vitulina*) due to a one-sixth-octave noise band centered at 32 kHz. *The Journal of the Acoustical Society of America*, *147*(3), 1885-1896. https://doi.org/10.1121/10.0000889

Kastelein, R. A., Helder-Hoek, L., Defillet, L. N., Terhune, J. M., & Jennings, N. (2025). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to noise bands centered at 40 kHz and comparison with shifts due to lower frequencies. *Aquatic Mammals*, *51*(1), 13-30. https://doi.org/10.1578/AM.51.1.2025.13

Kastelein, R. A., Helder-Hoek, L., Van Acoleyen, L., Defillet, L. N., & Terhune, J. M. (2024a). Temporary hearing threshold shift and testing the equal-energy hypothesis in a harbor porpoise (*Phocoena phocoena*) after exposure to a continuous noise band at 8 kHz, and a revised TTS-onset function. *Aquatic Mammals*, *50*(5), 445-459. https://doi.org/10.1578/AM.50.5.2024.445

Kastelein, R. A., Helder-Hoek, L., Van Acoleyen, L., Defillet, L. N., & Terhune, J. M. (2024b). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to a noise band centered at 32 kHz. *Aquatic Mammals*, *50*(2), 107-121. https://doi.org/10.1578/AM.50.2.2024.107

Kastelein, R. A., Helder-Hoek, L., van Kester, R., Huisman, R., & Gransier, R. (2019d). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise band at 16 kHz. *Aquatic Mammals*, *45*(3), 280-292. https://doi.org/10.1578/AM.45.3.2019.280

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Defillet, L. N., Huijser, L. A. E., & Gransier, R. (2021a). Temporary hearing threshold shift in a harbor porpoise (*Phocoena phocoena*) due to exposure to a continuous one-sixth-octave noise band centered at 0.5 kHz. *Aquatic Mammals*, *47*(2), 135-145. https://doi.org/10.1578/AM.47.2.2021.135

Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Defillet, L. N., Huijser, L. A. E., & Terhune, J. M. (2020e). Temporary hearing threshold shift in harbor seals (*Phoca vitulina*) due to one-sixth-octave noise bands centered at 0.5, 1, and 2 kHz. *The Journal of the Acoustical Society of America*, *148*(6), 3873-3885. https://doi.org/10.1121/10.0002781

Kastelein, R. A., Helder-Hoek, L., Defillet, L. N., Huijser, L. A. E., Terhune, J. M., & Gransier, R. (2021b). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to one-sixth-octave noise bands centered at 2 and 4 kHz: Effect of duty cycle and testing the equal-energy hypothesis. *Aquatic Mammals*, *47*(4), 394-418. https://doi.org/10.1578/AM.47.4.2021.394

Kastelein, R. A., Helder-Hoek, L., Defillet, L. N., Kuiphof, F., Huijser, L. A. E., & Terhune, J. M. (2022a). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to one-sixth-octave noise bands centered at 8 and 16 kHz: Effect of duty cycle and testing the equal-energy hypothesis. *Aquatic Mammals*, *48*(1), 36-58. https://doi.org/10.1578/AM.48.1.2022.36

Kastelein, R. A., Helder-Hoek, L., Defillet, L. N., Van Acoleyen, L., Huijser, L. A. E., & Terhune, J. M. (2022b). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to one-sixth-octave noise bands centered at 0.6 and 1 kHz. *Aquatic Mammals*, *48*(3), 248-265. https://doi.org/10.1578/AM.48.3.2022.248

Kastelein, R. A., Helder-Hoek, L., Van Acoleyen, L., Defillet, L. N., Huijser, L. A. E., & Terhune, J. M. (2023). Underwater sound detection thresholds (0.031-80 kHz) of two California sea lions (*Zalophus californianus*) and a revised generic audiogram for the species. *Aquatic Mammals*, *49*(5), 422-435. https://doi.org/10.1578/AM.49.5.2023.422

Kastelein, R. A., Parlog, C., Helder-Hoek, L., Cornelisse, S., Huijser, L. A. E., & Terhune, J. M. (2020f). Temporary hearing threshold shift in harbor seals (*Phoca vitulina*) due to a one-sixth-octave noise band centered at 40 kHz. *The Journal of the Acoustical Society of America*, *147*(3), 1966-1976. https://doi.org/10.1121/10.0000908

Kastelein, R. A., Wensveen, P. J., Hoek, L., Au, W. W. L., Terhune, J. M., & de Jong, C. A. F. (2009). Critical ratios in harbor porpoises (*Phocoena phocoena*) for tonal signals between 0.315 and 150 kHz in random Gaussian white noise. *The Journal of the Acoustical Society of America*, *126*(3), 1588-1597. https://doi.org/10.1121/1.3177274

Martin, S. B., Lucke, K., & Barclay, D. R. (2020). Techniques for distinguishing between non-impulsive sound in the context of exposure for marine mammals. *The Journal of the Acoustical Society of America*, *147*(4), 2159-2176. https://doi.org/10.1121/10.0000971

R Core Team. (2023). R*: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Scharf, B. (1970). Critical bands. In J. V. Tobias (Ed.), *Foundations of modern auditory theory* (Vol. 1, pp. 159-202). Academic Press. https://doi.org/10.1016/B978-0-12-691901-1.50010-3

Schlundt, C. E., Finneran, J. J., Carder, D. A., & Ridgway, S. H. (2000). Temporary shift in masked hearing thresholds of bottlenose dolphins, *Tursiops truncatus*, and white whales, *Delphinapterus leucas*, after exposure to intense tones. *The Journal of the Acoustical Society of America*, *107*(6), 3496-3508. https://doi.org/10.1121/1.429420

Southall, B. L., Nowacek, D. P., Bowles, A. E., Senigaglia, V., Bejder, L., & Tyack, P. L. (2021). Marine mammal noise exposure criteria: Assessing the severity of marine mammal behavioral responses to human noise. *Aquatic Mammals*, *47*(5), 421-464. https://doi.org/10.1578/AM.47.5.2021.421

Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., Nowacek, D. P., & Tyack, P. L. (2019). Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. *Aquatic Mammals*, *45*(2), 125-232. https://doi.org/10.1578/AM.45.2.2019.125

Terhune, J. M., & Killorn, D. (2021). A method for preliminary assessment of the masking potential of anthropogenic noise to baleen whale calls. *Aquatic Mammals*, *47*(3), 283-291. https://doi.org/10.1578/AM.47.3.2021.283

Ward, W. D., Cushing, E. M., & Burns, E. M. (1976). Effective quiet and moderate TTS: Implications for noise exposure standards. *The Journal of the Acoustical Society of America*, *59*(1), 160-165. https://doi.org/10.1121/1.380835