Underwater temporary threshold shift in pinnipeds: Effects of noise level and duration

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Behavioral psychophysical techniques were used to evaluate the residual effects of underwater noise on the hearing sensitivity of three pinnipeds: a California sea lion (*Zalophus californianus*), a harbor seal (*Phoca vitulina*), and a northern elephant seal (*Mirounga angustirostris*). Temporary threshold shift (TTS), defined as the difference between auditory thresholds obtained before and after noise exposure, was assessed. The subjects were exposed to octave-band noise centered at 2500 Hz at two sound pressure levels: 80 and 95 dB SL (*re*: auditory threshold at 2500 Hz). Noise exposure durations were 22, 25, and 50 min. Threshold shifts were assessed at 2500 and 3530 Hz. Mean threshold shifts ranged from 2.9–12.2 dB. Full recovery of auditory sensitivity occurred within 24 h of noise exposure. Control sequences, comprising sham noise exposures, did not result in significant mean threshold shifts for any subject. Threshold shift magnitudes increased with increasing noise sound exposure level (SEL) for two of the three subjects. The results underscore the importance of including sound exposure metrics (incorporating sound pressure level and exposure duration) in order to fully assess the effects of noise on marine mammal hearing. [DOI: 10.1121/1.2047128]

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I. INTRODUCTION

The pinnipeds (seals, sea lions, and walruses) are amphibious carnivores that spend a significant amount of time foraging at sea. All pinnipeds tested thus far are sensitive to sound in air and under water; therefore, they are likely to be susceptible to the harmful effects of loud noise in both media. It has recently been shown that moderate levels of underwater noise can induce a temporary reduction of hearing sensitivity (temporary threshold shift or TTS) in some marine mammals, provided that the exposure duration is relatively long. Noise-induced TTS has been examined in some pinnipeds and odontocete cetaceans (dolphins and other toothed whales) exposed to fatiguing stimuli of varying durations and bandwidths (Finneran *et al.*, 2000; 2002; Kastak and Schusterman, 1996; Kastak *et al.*, 1999; Nachtigall *et al.*, 2003; 2004; Schlundt *et al.*, 2000). In these studies the magnitude of TTS was generally small (<20 dB), and hearing sensitivity recovered rapidly. While it would be helpful to predict the auditory effects of different noise exposures on the hearing of marine mammals, there are no data from which extrapolation can be made from small TTS at low-level, short-duration noise exposures to TTS resulting from louder, longer exposures. Data that show relationships between sound level and TTS exist for some terrestrial mammals, but models of TTS growth in these subjects have not been applied to marine mammals.

One purpose of TTS experiments with marine mammals is to provide data that will aid regulatory agencies in determining potentially harmful levels of anthropogenic noise. Because exposure to anthropogenic noise in the marine environment is sporadic and interrupted, it is necessary to examine variables associated with varying noise sound pressure levels, intermittence of exposure, and total acoustic energy of exposure, in order to accurately predict the effects of noise on marine mammal hearing.

Various models of the effects of interrupted noise exposures on TTS have been proposed (Harris, 1991; Kryter, 1994). An equal energy model predicts that two noise exposures will induce similar threshold shifts if the exposures are matched in sound energy, regardless of the temporal patterning of exposure. Thus, according to an equal energy rule, a doubling of exposure duration and a 3-dB increase in amplitude should induce similar threshold shifts. Use of the 3-dB duration-level exchange rate for determining noise risks under intermittency of exposure is advocated in the most recent noise exposure criteria put forth by the U.S. Department of Health and Human Services (NIOSH, 1998).

A modified equal energy, or 5-dB rule, was formulated under the assumption that some recovery occurs during periods of exposure intermittency; thus, a doubling in exposure duration could be approximated by a 5-dB increase in amplitude. Though incorporated into various noise exposure criteria, exchange rates based on acoustic energy have been called into question by numerous studies (Harding and Bohne, 2004; Patuzzi, 1998; Strasser *et al.*, 2003). Because energy-based exchange rules cannot consistently predict the degree of noise-induced hearing loss, the influence of other acoustic characteristics on TTS must be examined. Specifically, the frequency and amplitude distribution, temporal patterning, and bandwidth/duration properties (e.g., continuous vs impulsive) of fatiguing sounds appear to all be important in determining the potential for noise-induced hearing loss (Ahroon *et al.*, 1993; Hamernik *et al.*, 1991; 1993; 2002).

The goal of this study was to examine the interactions between noise amplitude and duration in inducing TTS in pinnipeds under water, partly to determine whether a simple time-intensity trade-off rule can be applied to marine mammal noise exposure criteria. The experiments reported here were intended to build upon data obtained earlier from the same three subjects (Kastak *et al.*, 1999), using octave-band noise exposure levels of 65–75-dB SL (sensation level, referenced to absolute auditory threshold at center frequency). This study employed octave-band noise at 80 and 95 dB SL, with net exposure durations ranging from 22 to 50 min. It is important to note here that, as in the previous study, the sound levels chosen were based upon the hearing sensitivity of the subjects. Therefore, the absolute exposure conditions across subjects differed by up to 22 dB (the difference between pure-tone thresholds for the sea lion and harbor seal). Threshold shift was assessed at the center frequency of the exposure octave band, as well as one-half octave above the center frequency, where other studies have reported maximal threshold shifts (McFadden, 1986; Moore *et al.*, 2002). Results were analyzed by examining the relationship between TTS and sound pressure level and exposure duration. Additionally, a third metric, sound exposure level, was used to clarify some of the variability in TTS levels that was not explainable by sound pressure level or duration alone. The data reported here will contribute to the understanding of pinniped TTS and to the prediction of certain auditory effects of intense noise exposure on free-ranging marine mammals.

II. METHODS

A. Subjects

Three pinnipeds were used in this study: a 16-years-old female California sea lion (*Zalophus californianus*), a 14-years-old male harbor seal (*Phoca vitulina*), and a 7-years-old female northern elephant seal (*Mirounga angustirostris*). All three subjects had extensive experience performing acoustic signal detection tasks, and each had previously undergone audiometric testing in water (Kastak and Schusterman, 1996; Southall *et al.*, 2000). The animals were housed at the University of California, Santa Cruz, Long Marine Laboratory in outdoor concrete pools filled with running seawater. All audiometric testing and noise exposures were conducted with the approval of the UCSC Chancellor's Animal Research Committee.

B. General procedure

Auditory thresholds were obtained from each subject prior to noise exposure (baseline thresholds), immediately following noise exposure (exposure thresholds), and 24 h following noise exposure (recovery thresholds). Each test sequence spanned 2 days in order to incorporate all testing conditions. Two series of experiments were completed. In the first experiment, net noise exposure duration was held constant at 22 min and noise amplitude was held constant at 80 dB SL. Prior to testing, hearing thresholds at 2500 Hz were obtained for each subject. All noise levels (in SL) were referenced to the mean of these baseline hearing thresholds. The fatiguing stimulus was an octave band of continuous, Gaussian white noise centered at 2500 Hz. Thresholds were measured at the center frequency and at a frequency one-half octave above center frequency (3530 Hz). Twelve test sequences were completed for each of the two testing conditions. In the second experiment, the noise level was held constant at 95 dB SL, while the exposure duration was varied from 25 to 50 min. Thresholds were measured at 2500 Hz for both exposure durations and at 3530 Hz for the 50-min exposures. Eight replicates were completed for each of the three testing conditions.

C. Threshold testing

The stimuli used for threshold testing were 500-ms pure tones (40-ms rise/fall times) that were generated by and manually triggered from a function generator (Stanford Research Systems DS345—40-kHz update rate, 16-bit precision). Signals were attenuated (HP 350C), amplified (Realistic MPA-20), and projected from one of two underwater transducers (NUWC J-9 or Lubell Laboratories LL-1424). The projectors were suspended in the circular test pool (7.5-m diameter, 2.5-m depth) by a PVC harness that was moved along a steel pipe support for positioning. The projector was positioned approximately 5 m behind the testing apparatus, at a depth of about 1 m.

Calibration was conducted daily before and after noise exposure, in the absence of the subjects, by placing a hydrophone (H-56 or International Transducer Corporation ITC-8212) in the position occupied by the subjects' heads during testing. Calibration tones were projected via the function generator from one of the two projecting transducers. The received signal was measured using a PC-based signal analysis software package (SPECTRA PLUS, Pioneer Hill) through the PC sound card. Because of the reverberant characteristics of the testing environment, signal levels were mapped at multiple locations surrounding the center position to ensure that spatial variability in the tonal signal was not greater than 3 dB in the sound field surrounding the chin station.

Underwater thresholds for each animal were estimated using behavioral psychophysical techniques. The subjects were trained using operant conditioning to respond by pressing a paddle when presented a pure tone and to withhold response in the absence of a tone (go/no-go procedure). At the beginning of a trial, the subject was signaled by a trainer to dive to the test apparatus, which consisted of a chin cup (to prevent movement of the subject's head) and a response paddle. The position of the subject's head while stationed in the chin cup was approximately 1 m below the surface of the water. The "go," or paddle press response, when occurring in the presence of a signal, was recorded as a hit. Withholding response, or a "no-go," in the absence of a signal, was recorded as a correct rejection. Responding in the absence of a signal was recorded as a false alarm, and failure to respond to a signal was scored as a miss. Hits and correct rejections were reinforced with a piece of fish. Subjects were recalled without reinforcement following false alarms and misses. The trial sequence was balanced (i.e., the number of signal-present trials equaled the number of signal-absent trials), and the first-order conditional probability of either trial type was 0.5 (modified from Gellermann, 1933).

The first signal trial of each session was preselected at a level of 20–30 dB above the estimated threshold, ensuring a hit. On subsequent signal trials, the level was decreased by 4 dB following each hit, until the first miss. Following the first miss, the step size was changed to 2 dB, and the signal level was increased following a miss and decreased following a hit (staircase procedure). Each change in the direction of the signal adjustment constituted a reversal. Thresholds were defined as the mean of ten reversals, corresponding to 50% correct detections (Dixon and Mood, 1948).

D. Noise exposures

The subjects had previously been trained to station in front of a platform used to project moderate levels of band-limited noise under water (Kastak *et al.*, 1999). Conditioning techniques were used to gradually increase the noise exposure durations and levels tolerated by the subjects. A single projector (Ocean Engineering Enterprises DRS-8) was mounted on the exposure apparatus, which was placed against the side of the testing pool, approximately 4 m from the testing apparatus. The distance between the subject's head and the noise projector was 0.5 m.

Continuous, Gaussian white noise was generated using the PC software package COOLEDIT (Syntrillium Software) and digitally filtered over the octave band to ensure that the noise spectrum was flat to within ±3 dB. The noise was projected from the DRS-8 transducer. Calibration of the noise stimuli took place daily before and after noise exposure using the same procedure described for calibrating the test stimuli. Figure 1 shows a typical exposure spectrum recorded in the absence of the subject, at the position occupied by the subject's head during exposure. Received octave band levels were either 80 or 95 dB SL. Sound pressure levels corresponding to these SLs differed because of the differences in auditory sensitivity of the three subjects. For the 80-dB SL condition, SPLs were 159 dB *re*: 1 μPa for the sea lion, 137 dB *re*: 1 μPa for the harbor seal, and 149 dB *re*: 1 μPa for the elephant seal. SPLs corresponding to 95-dB SL were 174 dB *re*: 1 μPa for the sea lion, 152 dB *re*: 1 μPa for the harbor seal, and 164 dB *re*: 1 μPa for the elephant seal. The net exposure durations were 22 min (80-dB SL), 25, and 50 min (95-dB SL).

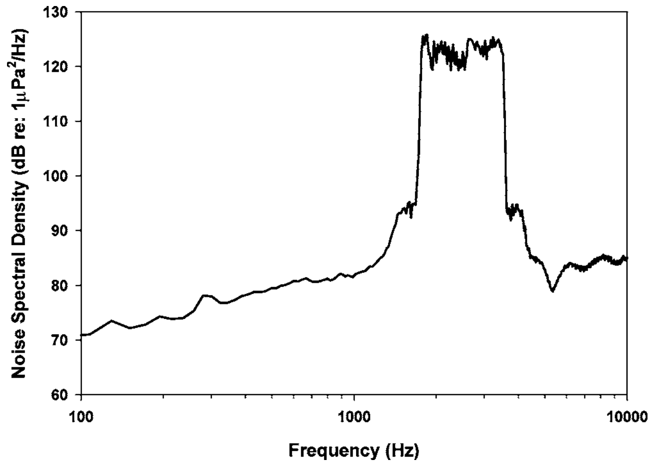

FIG. 1. Noise spectral density of the fatiguing stimulus, recorded from the calibration position in the test pool. The center frequency of the octave band is 2500 Hz and the octave-band level is approximately 159 dB *re*: 1 μPa.

For each exposure condition, the number and duration of dives into the noise field were matched within subjects. Because each of the subjects had to surface to breathe, making sound exposure intermittent, surface intervals between dives were controlled as carefully as possible, to minimize recovery effects and to avoid variability during sequence replications. Net exposure duration was determined by subtracting surface intervals from the overall exposure duration. Across all exposures, the sea lion spent an average of 75% of the total exposure interval on station in the noise field, the harbor seal spent 87%, and the elephant seal spent 84%.

E. Control sessions

During control sessions, subjects completed entire testing sequences, without exposure to noise, for net durations corresponding to each experimental exposure condition (22, 25, or 50 min). Surface intervals in control sessions were similar to those in experimental sessions. Control sequences were conducted to ensure that physiological, motivational, or emotional factors related to session length, dive duration, or satiation, as opposed to the presence of fatiguing noise, could be eliminated as causative factors for observed threshold shifts. During the first experiment, each subject completed a total of six control sequences, each with a sham exposure of 22 min. During the second experiment, each subject completed a total of ten control sequences, four with sham exposures of 25 min and six with sham exposures of 50 min.

F. Data analysis

Threshold shifts were calculated by subtracting pre-exposure thresholds from those obtained immediately following noise exposure. Recovery was assessed by comparing thresholds obtained 24 h following noise exposure to both baseline and exposure thresholds. A within-subjects, repeated measures design was used. If an overall significant difference between thresholds among the three conditions was found using a one-way, repeated measures ANOVA, a Student–

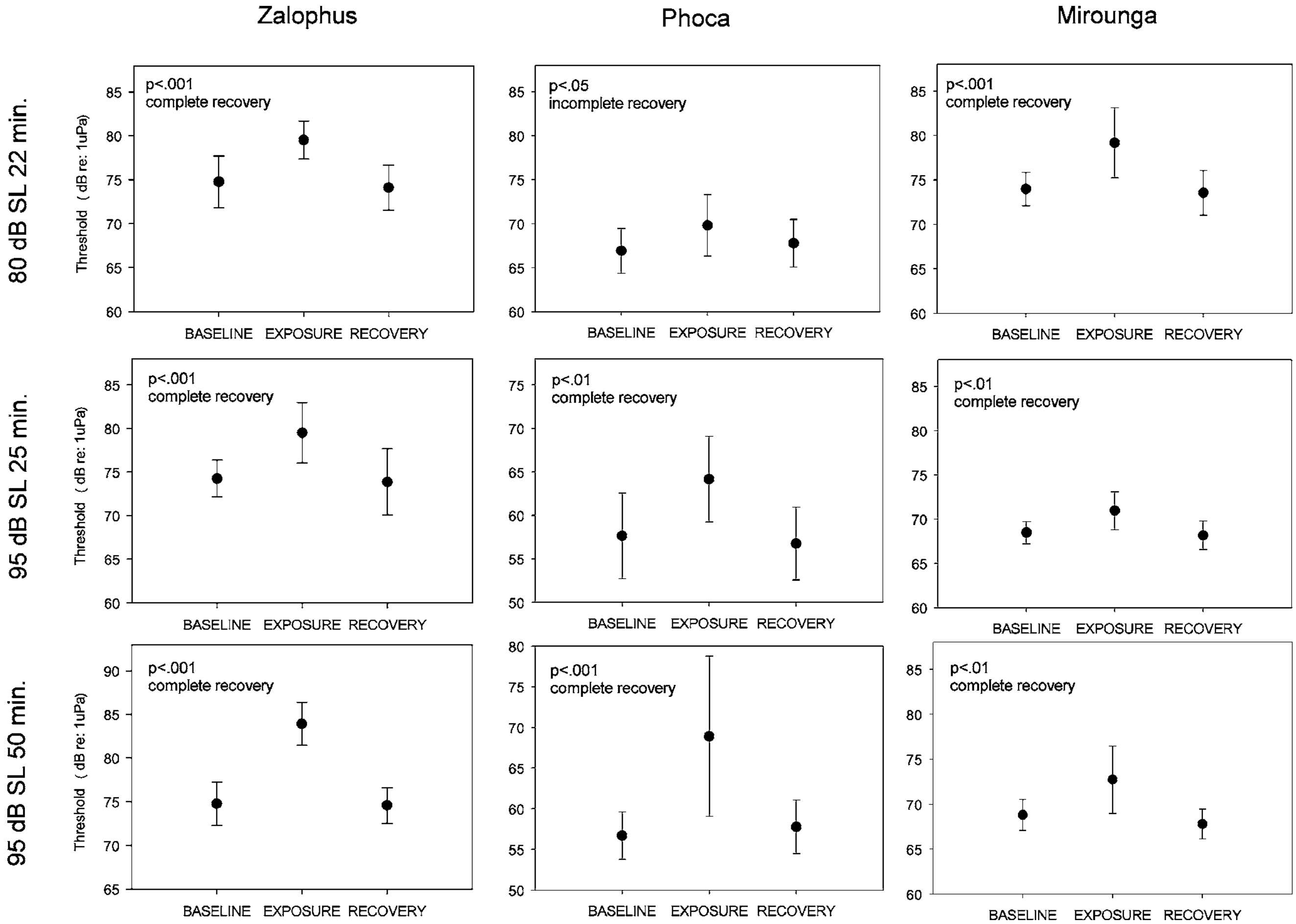

FIG. 2. Baseline (pre-exposure), exposure, and recovery thresholds for a sea lion, a harbor seal, and an elephant seal exposed to octave-band noise centered at 2500 Hz. The test frequency was 2500 Hz. The *p* values indicate statistical significance of comparisons between conditions. In all cases, exposure thresholds were significantly greater than baseline thresholds, and there was no difference between baseline and recovery thresholds. In all but one case, recovery thresholds were significantly lower than exposure thresholds. Points refer to mean thresholds obtained over multiple sessions; error bars denote standard deviations.

Newman–Keuls test was performed for each individual comparison. Mean threshold shifts in experimental and control conditions were compared using a Student's *t*-test, as were differences between control session shifts and a hypothetical condition of 0-dB shift. For purposes of analyzing the effects of exposure duration, the 22- and 25-min conditions were combined. This grouping is justified in that the 3-min difference between the exposure conditions translates into a negligible difference in sound energy or sound exposure level of approximately 0.5 dB.

III. RESULTS

A. Exposure vs control conditions

When tested at the center frequency of the exposure band, all subjects showed evidence of a significant mean threshold shift under all exposure conditions (Fig. 2). Sessions used to estimate thresholds for each of the subjects generally lasted about 15 min; therefore, it was common to find that recovery occurred during these sessions. Recovery was usually seen as a progressive decrease in the level of signals required to elicit a "go" response. Because all of the tracking data for a given session (ten reversals) were used to estimate thresholds, it is likely that the mean TTS levels presented here are underestimates of TTS that would have been recorded at earlier postexposure levels. For example, TTS_2, the threshold shift measured 2 min following exposure, is commonly cited as representing the peak postexposure TTS (Hirsch and Ward, 1952); threshold shifts recorded 15 min later are usually smaller in magnitude.

There was a statistically significant relationship between exposure condition and threshold—mean exposure thresholds were greater than mean baseline thresholds and recovery thresholds. Auditory sensitivity recovered fully within 24 h, with the exception of the 2.9-dB mean threshold elevation following recovery in the harbor seal (for the 22-min, 80-dB SL, 137-dB *re*: 1-μPa condition). Figure 3 shows that threshold shifts measured one-half octave higher than the noise band center frequency were significantly smaller than those measured at center frequency for the sea lion and elephant seal, but were not significantly different for the harbor seal.

B. TTS growth with sound pressure level and duration

Threshold shifts as a function of increasing noise exposure level are shown in Fig. 4. For the sea lion and harbor

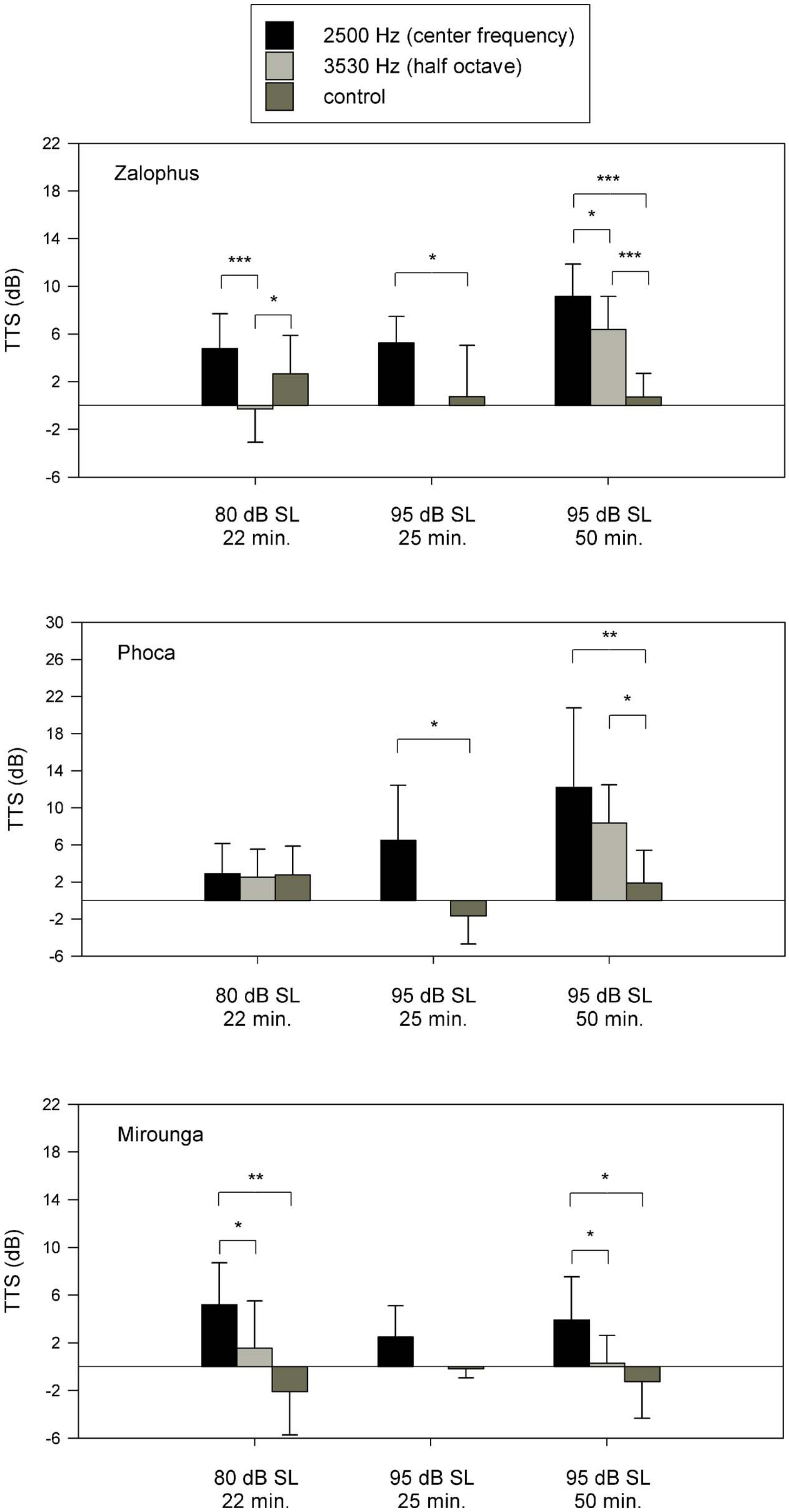

FIG. 3. Mean threshold shifts for three exposure levels and three exposure durations. Threshold shifts were measured at 2500 or 3530 Hz following exposure to octave-band noise centered at 2500 Hz. Control sequences duplicated the exposure sequences, with the exception that no noise was presented. Brackets show differences between individual groups of data. ($^{*}=p<0.05$; $^{**}=p<0.01$; $^{***}=p<0.001$; all other comparisons are not significant.)

seal, threshold shifts at center frequency increased by 0.5 and 3.6 dB, respectively, when duration was held constant (22–25 min) and noise SPL was increased from 80 to 95 dB SL. Neither of these differences was statistically significant. For the elephant seal, the magnitude of threshold shift decreased by 2.7 dB when the noise SPL was increased from 80 to 95 dB SL. This difference was also not significant.

Threshold shifts as a function of noise exposure duration are shown in Fig. 5. Threshold shifts increased significantly with an increase in exposure duration from 20 to 50 min, with exposure level held constant at 95 dB SL for the sea lion (3.9 dB). For the harbor seal, the difference between mean threshold shifts at 25 and 50 min at 95-dB SL was 5.7 dB. However, because of high levels of variability, the difference was not significant. Similarly, a difference of 1.4 dB for the elephant seal under the same conditions was not significant. Doubling the exposure duration (+3-dB sound exposure level) had a greater effect on threshold shift

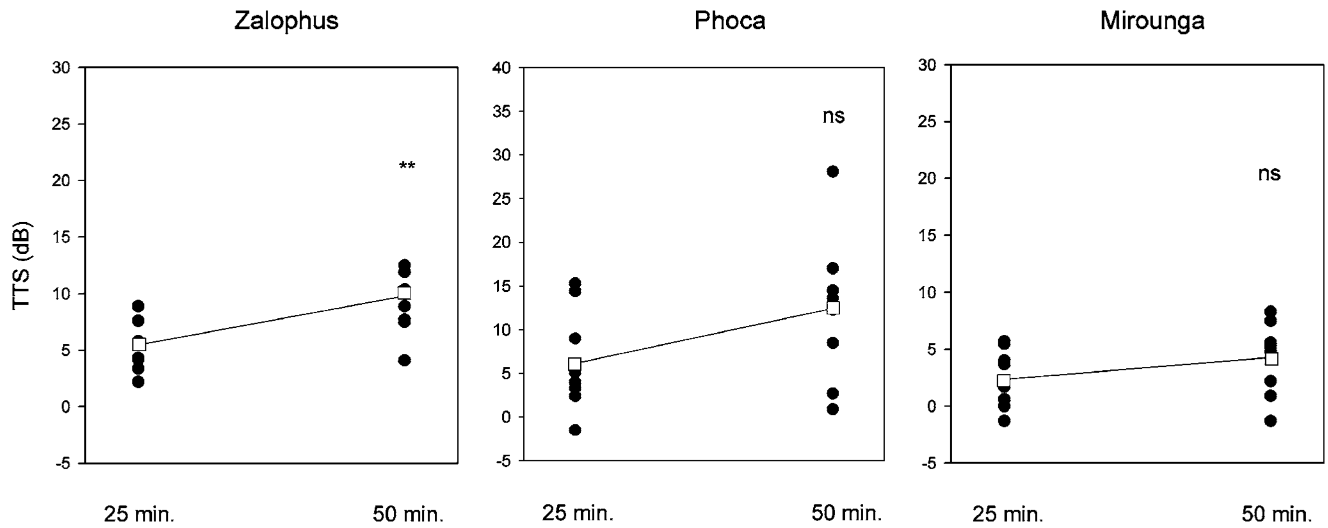

FIG. 4. Threshold shifts at center frequency of noise band following 25 and 50 min of 95-dB SL noise exposure. Points denote individual threshold shifts determined from test sequences. Open squares denote mean threshold shifts. ($^{**}=p<0.001$; ns=not significant.)

than an increase of 15 dB in exposure level, even though for two subjects the change failed to meet statistical significance.

C. Sound exposure level

Figure 6 shows TTS magnitude plotted against sound exposure level (SEL), a metric that incorporates both sound pressure level and duration. SEL is calculated as 10 times the logarithm of the integral, with respect to duration, of the mean-square sound pressure, referenced to 1 $\mu\mathrm{Pa}^2$ s. Using this metric, 0-dB SEL corresponds to a continuous sound whose rms sound pressure equals the reference pressure of 1 μPa at a duration of 1 s (Morfey, 2001). For the sea lion and the harbor seal, there was a significant linear relationship between SEL and TTS magnitude, with slopes of 0.16- and 0.39-dB TTS per dB SEL. These slopes are smaller than slopes of exposure level vs TTS that have been obtained in similar studies (Carder and Miller, 1972; Mills *et al.*, 1979; Ward *et al.*, 1958), illustrating that a linear fit to the data, though significant, is inadequate to describe the relationship between sound exposure and threshold shift at the low threshold shift magnitudes obtained in this study. For the elephant seal, the slope of the regression line was not significantly different from zero.

A curvilinear fit, modified from the exponential form of an equation developed by Maslen (1981) to describe the relationship between asymptotic threshold shift and sound pressure level, has the advantage of illustrating the relationship between shift and sound exposure at low levels, with a lower asymptote of 0-dB shift. The equation used in this study was

$$\mathrm{TTS} = (10m1)\log_{10}(1 + 10^{(\mathrm{SEL}-m2)/10}).$$

The parameter $m1$ corresponds approximately to the slope of the linear portion of the curve relating noise level to threshold shift, while $m2$ corresponds to the x intercept of the extrapolation of the linear portion of the curve, or what can be considered the approximate onset of TTS. In all cases, the fit of this curve was better than that of a simple exponential.

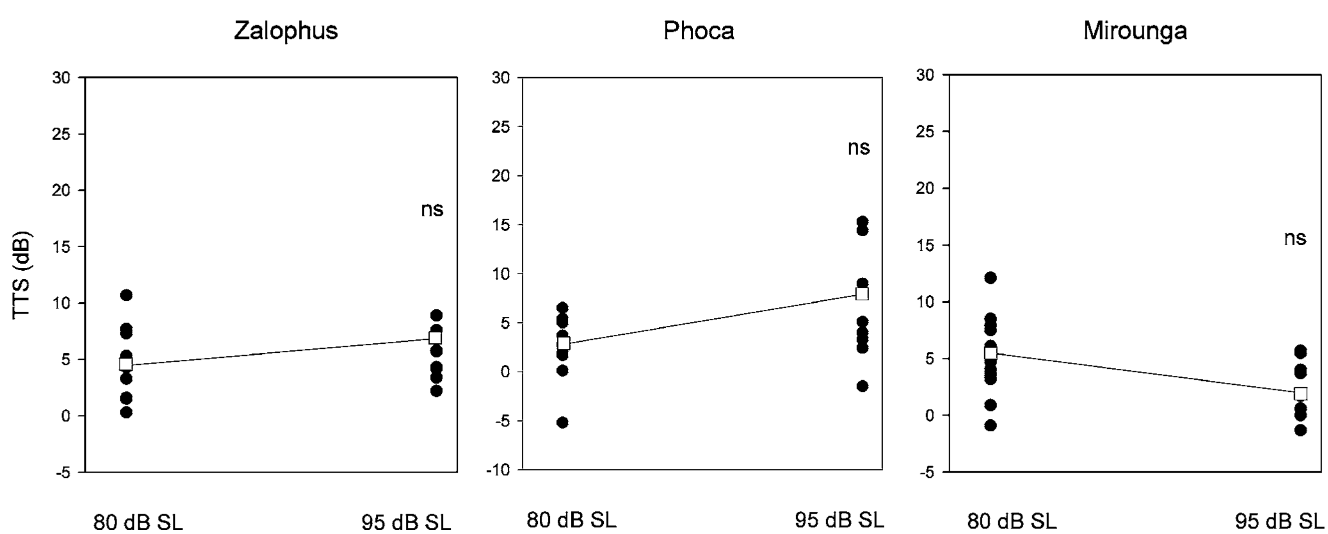

FIG. 5. Threshold shifts at center frequency of noise band following 22 min of exposure at 80-dB SL and 25 min of exposure at 95-dB SL. Points denote individual threshold shifts determined from test sequences. Open squares denote mean threshold shifts. (ns=not significant.)

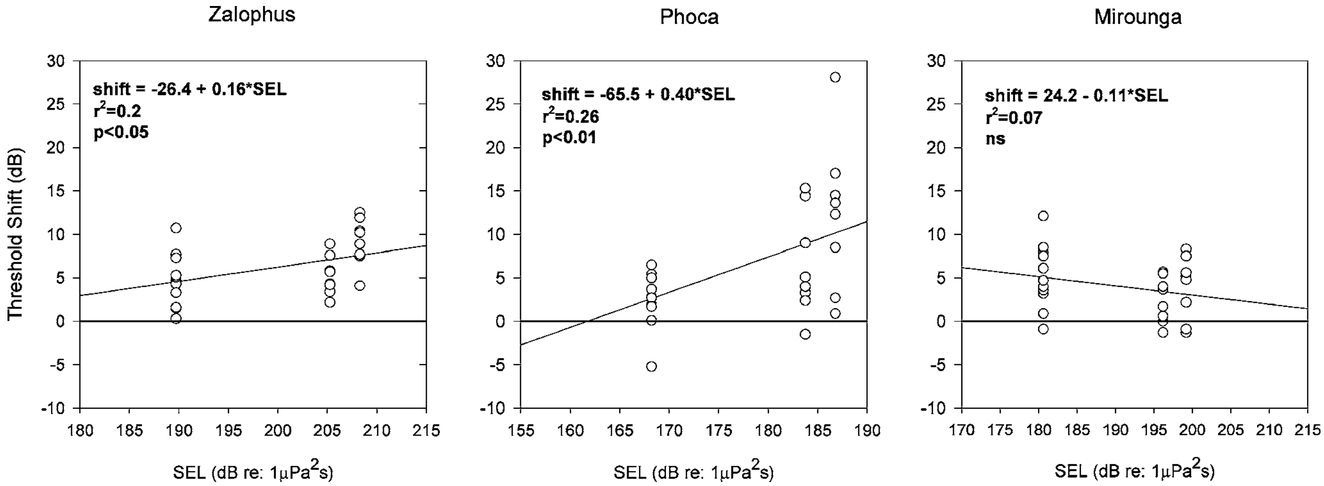

FIG. 6. Linear regression plots of TTS vs sound exposure level at center frequency of noise band for the three subjects. Line slopes, significance, and *r*-squared values are provided in the legends. The horizontal lines are zero-shift lines provided for reference.

When curves of this form are applied to the center frequency TTS data obtained from the sea lion and harbor seal, the value of $m2$ is 205.6 dB *re*: 1 μPa^{2}s for the sea lion (r^2=0.27;$F_{1,26}$=9.45;$p<0.01$) and 182.3 dB *re*: 1 μPa^{2}s for the harbor seal (r^2=0.30;$F_{1,26}$=11.05;$p<0.01$). The best fits resulting in $m2$ estimates were obtained by fixing $m1$ at 2 dB/dB. Poorer fits were obtained at both higher and lower values of $m1$ ranging from 1.0 to 3.0, values that we considered reasonable limitations based on data from terrestrial animals. An attempt to fit this equation form to the elephant seal center frequency data did not converge on estimates for either $m1$ or $m2$, probably because of outlying threshold shift values at low exposure levels.

Better fits to all three data sets were obtained by including the half-octave shifts along with center frequency shifts (Fig. 7). The best-fit curves have essentially unchanged parameters for the sea lion ($m2$=206.5;r^2=0.32;$F_{1,46}$=27.07,$p<0.0001$) and the harbor seal ($m2$=183.1;r^2=0.37;$F_{1,46}$=21.77,$p<0.0001$). With the half-octave threshold shifts included, the elephant seal data provided an estimate for $m2$ of 203.9 with $m1$ fixed at 2.0; however, the fit was still nonsignificant.

In order to determine whether differences in TTS onset represented by differences in individual hearing levels can be normalized to allow a combination of data from subjects with varying sound detection thresholds, SELs were converted to SL, in the same way that the absolute noise exposure levels were determined. Normalization here simply provides a common reference so that, with exposure levels equalized, the effects of duration can be examined. For example, the harbor seal's detection threshold for a 2500-Hz, 500-ms pure tone was about 57 dB *re*: 1 μPa. The sound exposure level of a tone of this duration at threshold is 54 dB *re*: 1 μPa^2 s. Likewise, SELs for the sea lion and elephant seal at threshold were 75.5 and 66.3 dB *re*: μ Pa^2 s, respectively. When the thresholds are subtracted from the onset of TTS, the differences are 129.1 dB for the harbor seal, 131 dB for the sea lion, and 137.6 dB for the elephant seal.

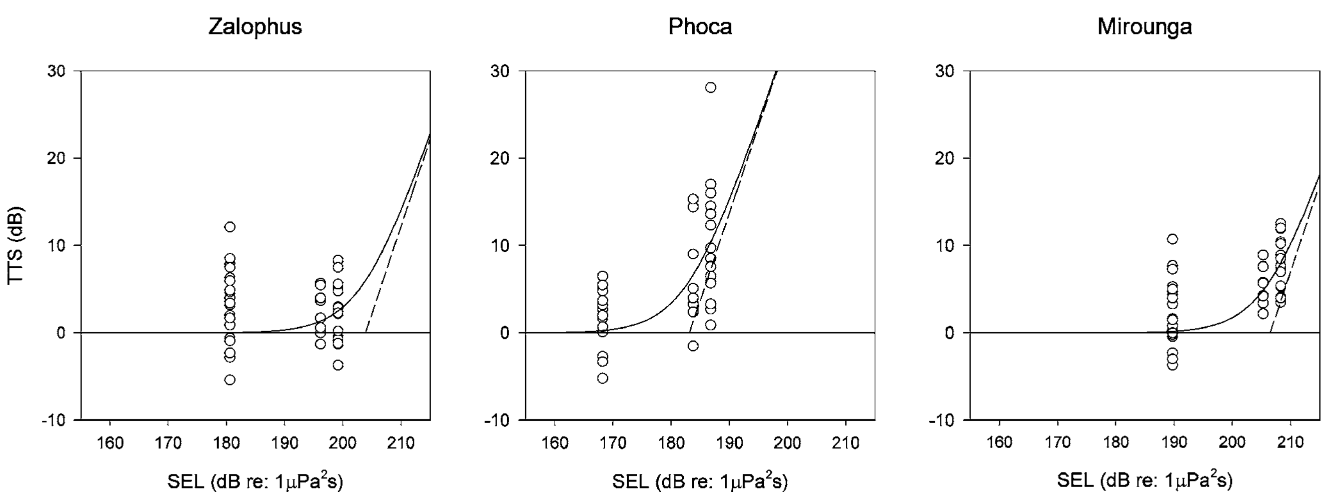

FIG. 7. Nonlinear regression plots of TTS vs sound exposure level at center frequency of noise band and one-half octave higher for the three subjects. See the text for an equation and significance of the model parameters. Solid curves represent exponential increase of TTS with increasing SEL. The horizontal lines are zero-shift lines. Dotted straight lines project TTS onset to linear portion of curve at higher exposure levels.

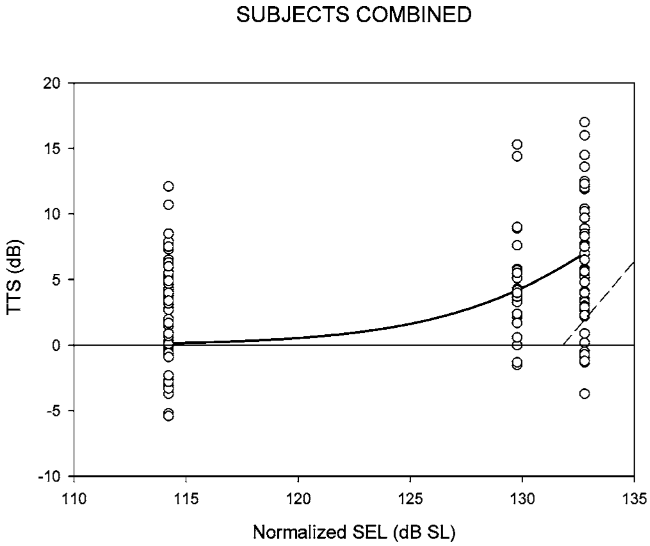

FIG. 8. Combined nonlinear regression plot of TTS vs normalized sound exposure level (referred to individual thresholds; includes half-octave data). See the text for details.

A curve fit to the normalized data combined for all subjects (r^2=0.13; $F_{1,142}$=21.9; $p<0.0001$) is shown in Fig. 8. The parameter $m1$ is again fixed at 2, and the resulting estimate for $m2$ is 131.8 $\mathrm{SL}_{(e)}$ (the subscript e denotes that sensation level is referred to a threshold sound exposure level).

IV. DISCUSSION

Building upon results from previous work with the same subjects (Kastak *et al.*, 1999), the data presented here show that TTS can be induced in pinnipeds under water following exposure to moderate levels of noise for durations of up to 50 min. The mean threshold shifts in this experiment were generally small relative to experimentally induced threshold shifts in other mammals, with mean (statistically significant) shifts ranging from 2.49 to 12.2 dB, and maximum individual threshold shifts of 28.1 dB (harbor seal), 12.5 dB (sea lion), and 12.1 dB (elephant seal). A linear relationship between the amplitude of the fatiguing stimulus and TTS has been shown in some, but not all species, but primarily at durations and levels greater than those used in this study (see, e.g., Smith *et al.*, 2004). Because at low threshold shift levels there is a curvilinear rather than a linear relationship between noise level and threshold shift, extrapolating these data in order to predict TTS at higher exposure levels should be approached cautiously. Applying a simple linear model to describe the relationship between TTS and SEL at low exposure levels will most likely result in underestimates of TTS at longer exposure durations and higher noise levels. Like a simple linear model, the adapted exponential model used here is limited in terms of predictive power. The limitations arise not through the use of the model itself, but from the highly variable, relatively low TTS levels and the small number of sound exposure levels used. Nonetheless, the increase in TTS of 2 dB per dB SEL in this study is approximately the same as values from prior studies of humans (Mills *et al.*, 1979; Ward *et al.*, 1958). The significance of this result must be taken with caution, however, because of the high degree of variability and the relatively small number of SELs used. As more data are obtained by using higher sound exposure levels, different patterns of intermittency, and additional subjects, the fit of this or other models should improve.

Increasing the noise exposure duration and amplitude independently resulted in increases in the magnitude of the threshold shift for two of the three subjects of this experiment. Increasing the exposure duration from 25 to 50 min had a greater effect on threshold shifts than increasing the exposure level from 80 to 95 dB SL. These results are inconsistent with an equal energy model (3-dB exchange rate), and suggest that moderate levels of long duration sounds may have a greater impact on hearing than equal-energy sounds of greater amplitude but shorter duration. Preliminary results from the same subjects tested in air also support this conclusion (Kastak, 2003; Kastak and Insley, 2005); however, more testing at various combinations of exposure level and duration needs to be completed before definitive conclusions can be reached.

Also of interest is the finding that mean threshold shifts one-half octave above center frequency were smaller than the corresponding shifts at center frequency in all subjects, contrasting with previous findings (McFadden, 1986) which showed a maximal shift one-half octave above the frequency of the exposure stimulus. The half-octave effect has been shown to occur after exposures to pure tones; in fact, TTS at the exposure frequency may not be evident, even in the presence of a significant threshold shift one-half octave higher. Consistent with observations of this effect, Schlundt *et al.* (2000), using brief tones as fatiguing stimuli, found that threshold shifts measured in odontocetes (bottlenose dolphins and beluga whales) generally occurred at frequencies above the exposure frequency. This type of upward spread in affected frequency has been attributed to the basalward spread in the peak of the cochlear traveling wave under the influence of an increasingly intense sinusoid, and partially attributed to cochlear amplification (McFadden and Yama, 1983; McFadden, 1986; Moore *et al.*, 2002). Although Nachtigall *et al.* (2004) recently found maximal threshold shifts approximately one-half octave above the upper limit of a 7-kHz-wide noise band in bottlenose dolphins, this finding has not been shown by some other studies using bands of noise (e.g., Neilsen *et al.*, 1986). It is possible that exposure to bands of noise does not result in a shift in the peak of the cochlear partition response because of phase differences between individual frequency components, explaining why some experiments fail to demonstrate this effect.

Although the limited evidence from this study does not support an equal-energy exchange model, threshold shifts *were* proportional to overall sound exposure level, indicating an effect of noise energy. There are two interesting findings associated with this relationship. First, assuming that threshold shift magnitudes have a lower asymptote at 0 dB, and that a curvilinear, modified exponential curve describes the relationship between SEL and threshold shift, there should be an increase of approximately 2-dB threshold shift per dB of sound exposure level, at noise levels moderately more intense than those used in this study. This 2-dB relationship appears to hold for all three subjects and may be tentatively used to predict threshold shifts at much higher noise levels. Second, there is a consistency in TTS onset, represented by the second parameter of the fit equation, in sound exposure level (SEL). When the noise levels are referenced to each subject's hearing level, these numbers fall within ±4 dB of a mean value of 132.5-dB $SL_{(e)}$, while the combined data provide an overall onset level of 131.8-dB $SL_{(e)}$. It is important to note that the normalization procedure for sound exposure level was conducted to show that the effects of increasing duration appear to be the same for all subjects, regardless of baseline hearing level, and not to make any inferences about the relationship between an auditory threshold and the sound energy resulting in TTS. In this case, auditory threshold is simply a benchmark that equalizes exposures between subjects with different hearing sensitivities. Testing at a number of different sound pressure level/duration combinations will help to determine whether these numbers can be used as onset levels for TTS in pinnipeds.

In most respects, noise-induced threshold shifts in pinnipeds follow trends similar to those observed in other mammals. The data are characterized by variable shifts at low noise levels; increasing shifts with increasing exposure duration, sound levels, and sound exposure levels; and complete, rapid recovery of sensitivity. In many cases, complete recovery appeared to occur within 15 min of noise cessation, and in no case was there an overall, long-term change in thresholds (indicating permanent threshold shift or PTS), despite numerous, repetitive noise exposures (Southall *et al.*, 2005). In the absence of better predictive models, the data included here indicate that sound exposure levels resulting in TTS onset range from about 183 to 206 dB *re*: 1 μPa^2 s, these levels being dependent on absolute hearing sensitivity. Future studies examining the effects of noise on pinniped hearing will likely have to rely on longer duration or more intense stimuli in order to adequately assess models that relate sound energy or sound exposure level to TTS. Additionally, because the pinniped auditory system functions amphibiously, future studies should examine the effects of airborne noise on pinniped hearing. Data generated by this and other studies should be taken into account by regulatory agencies attempting to mitigate the adverse effects of noise on these marine mammals.

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