Underwater temporary threshold shift induced by octave-band noise in three species of pinniped

David Kastak, Ronald J. Schusterman, Brandon L. Southall, and Colleen J. Reichmuth Long Marine Laboratory, University of California, 100 Shaffer Road, Santa Cruz, California 95060

(Received 11 November 1998; revised 4 April 1999; accepted 14 April 1999)

Pure-tone sound detection thresholds were obtained in water for one harbor seal (*Phoca vitulina*), two California sea lions (Zalophus californianus), and one northern elephant seal (Mirounga angustirostris) before and immediately following exposure to octave-band noise. Additional thresholds were obtained following a 24-h recovery period. Test frequencies ranged from 100 Hz to 2000 Hz and octave-band exposure levels were approximately 60-75 dB SL (sensation level at center frequency). Each subject was trained to dive into a noise field and remain stationed underwater during a noise-exposure period that lasted a total of 20-22 min. Following exposure, three of the subjects showed threshold shifts averaging 4.8 dB (*Phoca*), 4.9 dB (*Zalophus*), and 4.6 dB (Mirounga). Recovery to baseline threshold levels was observed in test sessions conducted within 24 h of noise exposure. Control sessions in which the subjects completed a simulated noise exposure produced shifts that were significantly smaller than those observed following noise exposure. These results indicate that noise of moderate intensity and duration is sufficient to induce TTS under water in these pinniped species. © 1999 Acoustical Society of America. [S0001-4966(99)05907-X]

PACS numbers: 43.80.Nd [WWLA]

INTRODUCTION

Noise-induced temporary threshold shift (TTS) is the reversible elevation in auditory threshold that may occur following overstimulation by a loud sound (see Ch. 14 in Yost, 1994, for a brief review). In mammals, noise-induced TTS involves structural and/or metabolic fatigue to the supporting, transducing, and processing elements within the peripheral and central auditory systems (Ward, 1997). The magnitude and duration of TTS are related to the level, duration, spectral distribution, and temporal pattern of the fatiguing stimulus. In addition, biological variables such as age, sex, and individual differences in auditory sensitivity may interact in complicated ways with these acoustic characteristics. Studies of TTS in nonhumans have generally been conducted on rodents, cats, and primates (Clark, 1991). These experiments, however, all involved airborne test and fatiguing stimuli; therefore, the few generalities developed from them may apply only to mammals with air-adapted hearing under conditions in which the fatiguing stimulus is also airborne. When human divers were tested underwater, for instance, the resultant levels of TTS were much higher than originally predicted (Smith and Wojtowicz, 1985). Thus the fatiguing effects of underwater noise on auditory sensitivity remain largely unexplored, particularly for animals adapted to hear in this medium.

The ears of marine mammals are modified from those of their terrestrial ancestors and are adapted to function in the naturally noisy environment of the ocean. Speculation that marine mammals have evolved a certain degree of protection from noise-induced hearing loss is consistent with a viewpoint that recognizes the evolution of these animals in such an acoustically challenging environment. If marine mammals do show diminished TTS susceptibility relative to terrestrial mammals, then concern about potential marine habitat degradation related to anthropogenic noise (Richardson et al., 1995) may be exaggerated. If, however, the marine mammal ear is not particularly adapted to resist the damaging effects of noise, this concern is well placed. Thus an opposing viewpoint might consider marine mammals especially sensitive to acoustic overstimulation, given increasing levels of oceanic noise pollution. Considering the implications for conservation reflected by these two opposing viewpoints, it is extremely important to conduct studies of TTS in marine mammals.

Investigation into the effects of noise on marine animals, in terms of behavioral reactions to loud sounds and measurable losses in auditory sensitivity, may help to define zones of impact within which there may be significant immediate and/or short-term noise effects. Individual exposure events are not likely to have dramatic long-term or fitness consequences, except for cases of extremely high exposure level resulting in acoustic trauma. However, these events may result in short-term impairment in the ability to communicate, navigate, forage, and detect predators. Additionally, behavioral reactions to noise exposure such as startle responses or avoidance may interrupt ongoing behaviors, and have consequences as severe as mother-offspring separation.

Long-term noise effects, on the other hand, cannot be directly evaluated through TTS experiments. While permanent threshold shifts (PTS) may be caused by repeated temporary shifts over a long period of time, the magnitude of PTS cannot be predicted from the degree of TTS induced in single exposure events (Melnick, 1991; Yost, 1994). Exposure conditions with the potential to induce PTS are much more likely to compromise individual fitness, and, when viewed on a larger scale, affect the health of marine mammal populations. It will be necessary to develop new models or to expand upon current models in order to determine the relationships between frequent or numerous TTS events and PTS. These models can be invoked only when sufficient information regarding TTS in marine mammals is made available.

The experimental approach to TTS assessment involves the determination of a subject's auditory thresholds prior to and immediately following exposure to a fatiguing stimulus. Thresholds may be determined behaviorally (through classically or operantly conditioned responses to acoustic stimuli), or physiologically, by measuring evoked potentials (see Clark, 1991 for a review). Fatiguing stimuli can be pure tones, bands of noise, or impulsive sounds. Repeated threshold estimates over time provide an indication of the rate of recovery of TTS. Many of these procedures cannot be conducted with marine mammals because threshold determination, being largely voluntary, is time consuming, and large populations of test-sophisticated subjects do not exist.

Data on TTS have been obtained for two marine mammal species, the bottlenose dolphin (Tursiops truncatus) and harbor seal (Phoca vitulina). Threshold shift in bottlenose dolphins was examined following exposure to short-duration, intense, pure tones (Ridgway et al., 1997). The harbor seal TTS data were obtained fortuitously, in air, and under somewhat uncontrolled conditions following long-term exposure to broadband noise (Kastak and Schusterman, 1996). The research reported herein was designed in part to replicate in water the earlier in-air harbor seal TTS. The primary goal of the current study was to determine minimum levels of continuous noise that would induce a measurable, recoverable shift in auditory threshold for one harbor seal (Phoca vitulina), two California sea lions (Zalophus californianus), and one northern elephant seal (Mirounga angustirostris) under water. In accordance with concern about anthropogenic noise (most of which is low frequency in nature), both the fatiguing stimuli and test tones used in this experiment were at or below 2000 Hz. Additionally, the duration of noise exposure was adjusted in such a way that fatiguing stimuli of moderate rather than high intensity could be used.

I. METHODS

A. Subjects

One male harbor seal (*Phoca vitulina*), age 10, two female California sea lions (*Zalophus californianus*) ages 12 and 21, and one female northern elephant seal (*Mirounga angustirostris*), age 4, were the subjects of these experiments. Subjects were housed at Long Marine Laboratory in Santa Cruz, California, in free-flow seawater tanks. All experiments were conducted with the approval of the University of California Chancellor's Animal Research Committee (CARC).

B. General procedure

We used a repeated measures design to compare auditory thresholds obtained in sessions prior to noise exposure ("baseline" thresholds); immediately following noise exposure ("exposure" thresholds); and following a recovery pe-

riod of 24 h ("recovery" thresholds). Subjects were usually tested over the course of two consecutive days to include all three conditions.

C. Threshold testing

The apparatus and design for threshold testing is described in detail elsewhere (Kastak and Schusterman, 1998). Testing took place in a 7.5-m diameter, 2.5-m deep concrete tank. The testing apparatus was a PVC platform mounted at one side of the tank. A chin-cup located at the base of the apparatus was the positioning point for the subject. A moveable opaque door served to delineate trials by opening to reveal a plastic response paddle. Pure-tone signals (500-ms duration, rise/fall times of 40 ms) were produced by a function generator, amplified, attenuated (in 4- or 2-dB increments) and manually triggered. Tones were projected through a J-9 underwater transducer positioned approximately 5 m behind the position of the subject's head. We used an up-down or staircase procedure in which an initial suprathreshold tone was attenuated by 4 dB following each correct detection (HIT), defined by the subject touching the response paddle with its nose. Following the first failure to detect (MISS), the signal level was increased by 2 dB. The 2-dB step size was used for the remainder of the test. The signal level was subsequently increased by one step following each MISS and decreased by one step following each HIT. Thresholds were defined by the signal level corresponding to 50% correct detections, according to the method outlined in Dixon and Mood (1948). Catch trials (signal absent trials) were incorporated into threshold sessions in order to obtain estimates of response bias. The proportion of catch trials was 0.5 for the harbor seal and sea lions, and was sufficient to maintain the percentage of false alarms (responses in the absence of a signal) at levels of 10%-20%. The elephant seal was relatively conservative with respect to reporting a signal, therefore the proportion of catch trials was occasionally decreased from 0.5 to 0.3 in order to attempt to maintain comparable false alarm rates between subjects.

D. Noise exposure regimes

Each subject was trained to submerge and place its muzzle into a plastic chin cup mounted on the front of a separate PVC platform, ensuring that no movement of the head would occur during noise exposure. Initially, the subjects dove into a noise field of low intensity, and this intensity was gradually increased as each subject became more tolerant of the noise. The chin cup was 51 cm from two University UW-30 underwater speakers mounted on the apparatus and positioned on either side of the animal's head. Gaussian white noise was first passed through a variable filter, with high and low pass cutoffs separated by one octave, and then projected from the University speakers. The sound field was uniform (i.e., did not change in level or spectral composition) in the area occupied by the subjects' heads, and was measured before and after exposure sessions with an H-56 hydrophone and PC-based spectral analysis software (SpectraPlus, Pioneer Hill). Because of transducer response and tank reverberation, noise spectra were not completely

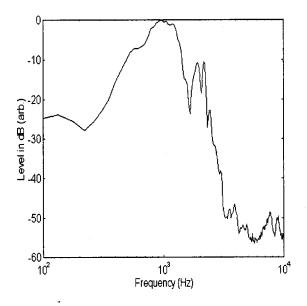


FIG. 1. Example of spectrum for 1000-Hz centered noise recorded at the position of the animal's head.

flat within the band of interest (see Fig. 1), and there was some spread of energy into adjacent octave bands. Only the noise level in the designated octave band was used for calibration.

The noise levels used for each noise-exposure period were referenced to sensation level, or the subject's baseline threshold. The harbor seal was exposed to octave-band noise (OBN) with center frequencies of 100 Hz (threshold testing at 100 Hz), 500 Hz (threshold testing at 500, 750, and 1000 Hz), and 1000 Hz (threshold testing at 1000 Hz). Center frequencies were 1000 Hz for corresponding threshold testing at 1000 Hz and 2000 Hz for threshold testing at 2000 Hz for the sea lions. The elephant seal was exposed to OBN with a center frequency of 1000 Hz with corresponding threshold testing at 1000 Hz. Exposure levels were approximately 60 dB SL (sensation level at center frequency) for the harbor seal, and ranged from approximately 55 to 65 dB SL for the sea lions. Because several preliminary exposures at levels of 55-65 dB SL failed to induce TTS in the elephant seal, the majority of noise exposures for this subject used levels of 70–75 dB SL. The duration of exposure was 20 min for the harbor seal and sea lions, and 22 min for the elephant seal.

During the diving regime, the subjects were intermittently reinforced with fish for remaining in the noise field. The subjects occasionally surfaced to breathe during the exposure period. These surface intervals were timed, and cumulative time spent at the surface was added to the total exposure time, so that the subjects were exposed to OBN for a net time of 20 or 22 min.

E. Control sessions

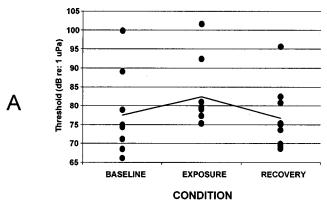
In order to ensure that physiological or behavioral changes associated with voluntary diving (as opposed to noise exposure) did not affect auditory thresholds, several control sessions were conducted. In the control procedure, an initial threshold was obtained in the usual manner, and then a simulated noise-exposure session was conducted, during which the subject stationed for a net time of 20 or 22 min at the noise apparatus with no fatiguing stimulus present. Following the mock exposure session, a "recovery" threshold was obtained in the same manner as in the experimental procedure.

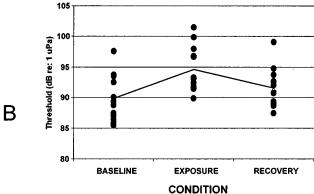
Nine matched sets of baseline/noise/recovery thresholds were collected for the harbor seal, along with 11 control sets. There were 12 sets each of experimental and control thresholds collected for the older sea lion, and 11 experimental and 6 control sets collected for the elephant seal.

F. Analysis

Comparisons were made between thresholds obtained under baseline, exposure, and recovery conditions. These comparisons were based on thresholds pooled over all frequencies tested. Measures of threshold shift under exposure and recovery conditions are expressed relative to baseline thresholds, with positive values indicating a loss of sensitivity (i.e., TTS) and negative values indicating a sensitivity gain relative to the baseline condition. Statistical comparisons between the thresholds of each subject were conducted by using a one-way repeated measures ANOVA as a preliminary test for significant differences among the three conditions. When an overall difference was detected, a Student-Newman-Keuls test was performed on each pairwise comparison to detect differences between conditions (Glantz and Slinker, 1990). A Student's t-test was used to compare mean threshold shifts under test and control conditions.

We applied a signal detection analysis to the data collected from the harbor seal, primarily because of an apparent shift in response bias. This bias was evidenced by an elevated false alarm rate following noise exposure. The analysis was performed in the following way: indices of detectability (d') were calculated for pre-exposure threshold values, using a value of 0.5 (our definition of "threshold") for the probability of correct detection P(y|sn), and the false alarm rate during the "reversal" or staircase phase of the session as P(y|n). We subsequently determined the signal level which would be required to produce the same d'value during post-exposure sessions (i.e., how much more intense must a signal be following exposure to reach the same sensation level as a signal before exposure?). This was done by determining the post-exposure P(y|sn) corresponding to the pre-exposure d' value, given the post-exposure P(y|n). This is not a threshold correction for false alarms based on high threshold theory (Swets et al., 1964); rather it is movement along an ROC curve corresponding to an assumed post-exposure change in response bias. We then determined the theoretical increase in signal level corresponding to the change in P(y|sn) for exposure sessions versus baseline sessions, using psychometric functions obtained previously for this subject. Because the sea lion and elephant seal false alarm rates did not correlate with session type, this analysis was performed on the harbor seal data only.





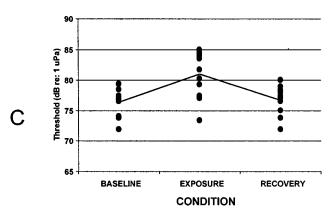


FIG. 2. Underwater pure-tone detection thresholds (in dB re: 1 μ Pa) for (A) the harbor seal (*Phoca vitulina*), (B) the California sea lion (*Zalophus californianus*), and (C) the northern elephant seal (*Mirounga angustirostris*), measured before noise exposure (baseline), immediately following noise exposure (exposure), and following a 24-h recovery period (recovery). The line connects mean thresholds for each condition. Note: test frequencies have been pooled for each condition (see text).

II. RESULTS

Thresholds for the harbor seal are shown in Fig. 2(A). The average threshold shift relative to baseline thresholds for this subject following noise exposure was 4.8 dB (range =1.8–9.2 dB) and the average shift following the recovery period was -0.8 dB. When the matched values for baseline, exposure, and recovery sessions were compared, there were significant differences between baseline and exposure thresholds (q=5.98; p<0.01), and between exposure and recovery thresholds (q=6.93; p<0.01). Baseline and recovery thresholds were not significantly different.

False alarm rates for the harbor seal were usually higher

on exposure (0.28; range=0.0-0.64) vs both baseline (0.13; range=0.0-0.44) and recovery (0.16; range=0.0-0.56) sessions. Nine out of 11 individual exposure sessions (82%) showed an increase in false alarm responding over respective baseline sessions. In one post-noise session there was no change in false alarm rate, and in one exposure session the false alarm rate was lower than in the corresponding baseline session. For computational simplicity, p(y|sn) values of 0.0 were changed to 0.01 before d' values were calculated (problems introduced by this adjustment will be addressed in Sec. III). The average d' for threshold signals in baseline sessions was 1.41 (range=0.14-2.33, s.d.=0.67). The average change in signal level required to match d' values for baseline and recovery sessions was about 3 dB, resulting in a mean corrected threshold shift of nearly 8 dB rather than the originally calculated value of nearly 5 dB. These adjustments assume an average psychometric function slope of about 0.25 normal deviate (probit) per dB. This number was obtained from prior psychoacoustic testing of the harbor seal using a method of constant stimuli.

Data for the harbor seal indicate that following similar dives without noise exposure, thresholds increased by an average of 1.0 dB for the harbor seal. Figure 3(A) shows that the degree of threshold shift on experimental sessions was significantly elevated compared to the control condition $(t_{18}=2.45, p<0.05)$.

Threshold shifts relative to baseline thresholds for the older sea lion following noise exposure averaged 4.9 dB (range=2.9–6.7 dB). Thresholds obtained following the recovery period showed an average shift of 1.7 dB. A comparison of the matched values between the three experimental conditions [Fig. 2(B)] showed significant differences between baseline and exposure thresholds (Student–Neuman–Keuls q=12.87; p<0.01); between exposure and recovery thresholds (q=8.25; p<0.01); and between baseline and recovery thresholds (q=4.64; p<0.05).

On 12 control sessions, this sea lion showed an average threshold increase of 2.0 dB. The degree of threshold shift on experimental sessions was significantly elevated compared to the control condition [t_{22} =3.04; p<0.01; Fig. 3(B)].

The younger sea lion showed a marginal average threshold shift following noise exposure, but daily performance on exposure sessions was variable, and shifts were generally small and statistically unreliable. In addition, this subject did not complete a sufficient number of controls sessions to statistically compare performance with experimental sessions.

Figure 2(C) shows thresholds obtained under the three conditions for the elephant seal. Shifts following exposure averaged 4.6 dB (range=-0.4–12.3 dB), and shifts following recovery averaged -0.4 dB. Exposure thresholds were significantly higher than baseline thresholds (q=6.37; p<0.01) and recovery thresholds (q=5.85; p<0.01). There was no significant difference between baseline and recovery thresholds.

The mean threshold shift for the elephant seal was -2.1 on control sessions. As shown in Fig. 3(C), threshold shifts on test sessions were significantly elevated compared to shifts on control sessions (t_{15} =3.38; p<0.01).

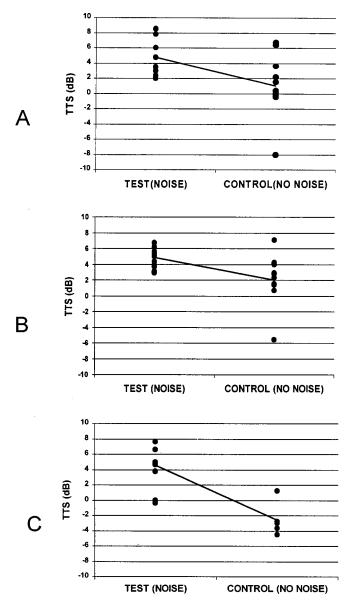


FIG. 3. Threshold shifts in experimental (diving with noise) and control (diving without noise) sessions for the harbor seal (A), sea lion (B), and elephant seal (C). The line connects mean shifts for experimental and control sessions.

III. DISCUSSION

This is the first report of underwater noise-induced temporary threshold shift in pinnipeds. Ridgway et al. (1997) reported TTS induced by intense tones in bottlenose dolphins (Tursiops truncatus); however, the methods differed significantly from those used in this study in the following ways: the fatiguing stimuli in the Ridgway et al. study were intense short-duration tones rather than bands of noise. Furthermore, the data obtained from dolphins (Ridgway et al., 1997) represent shifts in masked thresholds rather than in absolute thresholds, because of high background noise levels in San Diego Bay, where the tests took place. While the effect (if any) of temporary hearing impairment on masked thresholds is not known for certain, some research has shown that the magnitude of measurable TTS decreases as the masker level increases (Parker et al., 1976). Assessment of TTS under such circumstances is difficult because a noise masker decreases the *measured* level of TTS irrespective of whether temporary fatigue has occurred. Thus the underwater masked threshold shifts obtained by Ridgway *et al.* (1997) may underestimate the true threshold shifts (i.e., shift in absolute thresholds) and hence, the degree of fatigue to the dolphin auditory system that can potentially be induced by loud environmental noise.

It should also be noted that Ridgway *et al.* (1997) used a free operant psychophysical procedure (Egan *et al.*, 1964) that makes false alarm rates difficult to quantify, and therefore this approach is not particularly amenable to any sort of signal detection analysis. Shifts in response criteria, such as those shown by our harbor seal, cannot be evaluated without unambiguous estimates of false alarm responding.

Similar to the TTS study on dolphins (Ridgway et al., 1997) we also found that the trained responses of our seals and sea lions were often disrupted by exposure to noise, especially during the early phases of the TTS experiments. These changes mirror those shown by one of the sea lions the harbor seal, and the elephant seal tested. The disruptions in pinniped behavior were reflected in hauling out, aggression directed at the apparatus and at the trainer, and refusal to station at the apparatus during noise exposure. These altered behaviors in the form of increased levels of aggression and/or avoidance of a location in which food had been received prior to noise exposure (bite plates or chin cups associated with acoustic testing) should be examined more closely in both lab and field settings. For instance, if marine mammals in the wild avoid breeding grounds or feeding locations following exposure to loud sounds (shipping noise, sonars, etc.), regardless of whether a temporary loss of hearing has occurred, there can be dramatic fitness effects (e.g., loss of reproductive output), especially if the animals become sensitized to the noxious stimuli (but see Perry et al., 1998, for negative findings).

A second effect that may be considered separately from hearing loss in the classical sense is a change in response bias, for example, the increase in false alarm responding exhibited by the harbor seal in the present study. Marine mammals participating in psychophysical tasks are frequently trained to adopt a rather strict response criterion; that is, false alarm rates are typically very low (Schusterman, 1974). This was indeed the case for the harbor seal, whose average false alarm rate for absolute thresholds taken over a range of eight frequencies was 0.07 (Kastak and Schusterman, 1998), and whose baseline false alarm rate in this study averaged 0.13. The data from this study are also consistent with a previous increase in false alarm responding by the same subject following long-term exposure to airborne noise (Kastak and Schusterman, 1996). The cause of this animal's postexposure change in responding is not clear. In the earlier study of hearing loss in air (Kastak and Schusterman, 1996), we hypothesized that the seal's anomalous responses were due to tinnitus; however, the requisite tests (for example, those described by Jastreboff, 1990) have not been conducted and would be methodologically taxing. An alternative explanation for the increase in false alarm rate is related to the testing procedure. The up-down psychophysical procedure that we used is designed to concentrate signal levels around threshold. Following noise exposure, the sensation level of the tones presented on the first few trials would have been lower than expected by the subject because of the threshold shift. These weak signals may have led the seal to adopt a more liberal response criterion. The increased tendency to respond would have been reinforced if the subject responded fortuitously to signals that were actually below sensation level. Because signal levels in the up—down procedure are predictably weak (i.e., close to threshold), this method is particularly prone to such changes in response criterion. Regardless of the cause, criterional shifts could have dramatic consequences for free-ranging animals, in the form of responding inappropriately to conspecific signals, acoustic cues from potential predators and prey, or irrelevant, nonbiological sound.

The reader should keep in mind that the spread in thresholds depicted in Figs. 2 and 3 is partly a function of pooling thresholds of different frequencies. In addition, there was greater variability observed in baseline thresholds than was obtained in previous studies using the same subjects (Kastak and Schusterman, 1998). A probable cause of the increased threshold variance was a difference in psychophysical methods. In the Kastak and Schusterman (1998) study, most thresholds were estimated by the method of constants, while in this study, thresholds were always estimated using an abbreviated up—down staircase method, sometimes with a fairly large initial step size. The rationale for selecting the latter procedure was to obtain thresholds rapidly, before the onset of recovery.

We encountered one potential problem in the noise exposure regime directly related to the fact that noise exposure and threshold testing took place under water. The subjects surfaced to breathe, and generally returned to the noise apparatus immediately. However, each subject occasionally remained at the surface for a protracted interval, and it was clear that the noise could be avoided by adopting this strategy. Although surface intervals generally accounted for 20%-25% of the total exposure time, the duration and number of each surface interval varied dramatically both within and between individuals. The effects of this intermittence could theoretically range from none (consistent with an equal energy hypothesis) to reducing the TTS to 75%-80% of its value relative to 100% exposure time (consistent with an on-fraction hypothesis). The actual effect is likely to lie somewhere in between. There are several options for dealing with the complication of intermittence. One is to adjust the noise intensity and the dive durations so that the subjects are exposed to louder sounds for a continuous short period of time. We are currently working on this strategy with the northern elephant seal, which has been trained to submerge in a noise field for extended periods (12 min +) on a single breath. The second and perhaps more favorable strategy is to expose the subjects to noise in air, and obtain thresholds either in air or underwater. In this way the exposure could be better controlled, in that (1) reduced reverberation would allow easier manipulation of the fatiguing stimulus, and (2) the subjects would not have to withdraw from the sound field in order to breathe. Given that stimulus levels reaching the inner ear (in terms of sensation level) can be equated, data generated from airborne TTS studies should be comparable to those generated from studies taking place in water. Moreover, threshold shifts induced by aerial noise such as rocket flights, sonic booms, explosions, etc., have the potential to affect behavior the same way that TTS induced by underwater noise does. Indeed, temporary deafness caused by atmospheric noise can impact behavior under water as well as in air. It would be useful to quantify these effects in terms of "safe" exposure levels for airborne as well as underwater sound.

A second problem occurring during extended submersion has to do with behavioral changes in response to the dive *per se*, rather than to the noise exposure. These behavioral changes may be reflected in the small but statistically insignificant threshold shifts obtained for the pinniped subjects in the control procedures following mock noise exposures. We are unable at present to pinpoint the cause of these shifts, but can speculate that changes in motivational state following extended submersions may be at least partially responsible for threshold changes following dives.

Another difficulty in interpreting the pinniped TTS data lies in the timing between noise offset and threshold determination. Maximum TTS has been shown to occur approximately 2 min following exposure (TTS₂), yet it is difficult to precisely determine magnitudes of TTS₂ in nonhuman subjects (Yost, 1994). In this study, final threshold determination for all subjects occurred approximately 6–10 min following exposure, with the longest time intervals occurring for the elephant seal. Thus it is likely that we underestimated TTS in these subjects by up to several dB, when compared with standard TTS results.

Noise exposure criteria for marine mammals may be based on several different models that are based on both the characteristics of the noise and the auditory capabilities of the species of concern. The simplest of these criteria involves the zone of audibility, which is the area around a source within which the sound can be heard by a marine mammal. These zones can be estimated using propagation models or measurements in conjunction with estimated ambient noise levels and data on auditory thresholds and critical ratios. Audibility, however, does not imply dramatic behavioral change or auditory damage, so these models are of limited use in defining exposure criteria. In terms of behavioral changes, the zone of responsiveness is the area around a source within which an observable response to the noise occurs. This zone is likely to be smaller than the zone of audibility. Again, measures of behavioral responses are of limited use because of the potential for habituation or sensitization; lack of consistency in defining a behavioral response; and interactions of noise responses with other behavioral variables such as motivational state. Zones of hearing loss, within which auditory damage is likely to occur, can be calculated only by defining the parameters involved in TTS. These models will be more complicated, in that interactions between received sound levels and the duration of exposure will influence the degree of potential threshold shift at a given distance. For this reason, more detailed evaluations of intensity/duration interactions must be made.

The goal of these experiments was not to determine

"safe" exposure levels for marine mammals to underwater sound. Rather, it was to demonstrate that TTS can be induced in pinnipeds on a repeatable and controlled basis. The threshold shifts obtained for our subjects were small in magnitude, but consistent and replicable. From these results we conclude that octave band noise levels below about 60 dB SL are unlikely to result in a measurable TTS, while moderate exposures of 65-75 dB SL reliably produce small amounts of TTS in three of the four experimental subjects. Clearly these animals do not have special mechanisms that protect against noise-induced hearing loss. We are currently developing modifications of the techniques used in this study to examine the role of intermittence and interactions between sound duration and intensity in inducing TTS. These techniques and results, as well as those of subsequent experiments, will ultimately play a role in defining anthropogenic noise-exposure criteria for pinnipeds and other marine animals.

ACKNOWLEDGMENTS

This work was financially supported by Grants Nos. N000149510936 and N000149910164 from the Office of Naval Research to Ronald Schusterman. The authors gratefully acknowledge the help of the Pinniped Research in Cognition and Sensory Systems group at Long Marine Laboratory, especially Jim Grayson who provided valuable assistance conducting experiments. Two anonymous reviewers provided thoughtful comments on an earlier version of this manuscript.

- Clark, W. W. (1991). "Recent studies of temporary threshold shift (TTS) and permanent threshold shift (PTS) in animals," J. Acoust. Soc. Am. 90, 155-163
- Dixon, W. J., and Mood, A. M. (1948). "A method for obtaining and analyzing sensitivity data," J. Am. Stat. Assoc. 43, 109-126.

- Egan, J. P., Greenberg, G. Z., and Schulman, A. I. (1964). "Operating characteristics, signal detectability, and the method of free response," in Signal Detection and Recognition by Human Observers, edited by J. Swets (Wiley, New York), pp. 316-347.
- Glantz, S. A., and Slinker, B. K. (1990). Primer of Applied Regression and Analysis of Variance (McGraw-Hill, New York).
- Jastreboff, P. J. (1990). "Phantom auditory perception (tinnitus): Mechanisms of generation and perception," Neurosci. Res. 8, 221–254.
- Kastak, D., and Schusterman, R. J. (1996). "Temporary threshold shift in a harbor seal (Phoca vitulina)," J. Acoust. Soc. Am. 100, 1905-1908.
- Kastak, D., and Schusterman, R. J. (1998). "Low frequency amphibious hearing in pinnipeds: Methods, measurements, noise and ecology," J. Acoust. Soc. Am. 103, 2216-2228.
- Melnick, W. (1991). "Human temporary threshold shift (TTS) and damage risk," J. Acoust. Soc. Am. 90, 147-154.
- Parker, D. E., Tubbs, R. L., Johnston, P. A., and Johnston, L. S. (1976). "Influence of auditory fatigue on masked pure-tone thresholds," J. Acoust. Soc. Am. 60, 881-885.
- Perry, E. A., Boness, D. J., and Insley, S. J. (1998). "A study of sonic boom effects on seals breeding on Sable Island, Canada," J. Acoust. Soc. Am.
- Richardson, W. J., Greene, Jr., C. R., Malme, C. I., and Thomson, D. H. (1995). Marine Mammals and Noise (Academic, San Diego).
- Ridgway, S. H., Carder, D. A., Smith, R. R., Kamolnick, T., Schlundt, C. E., and Elsberry, W. R. (1997). "Behavioral Responses and Temporary Shift in Masked Hearing Threshold of Bottlenose Dolphins, Tursiops truncatus, to 1-second Tones of 141 to 201 dB re 1 µPa," Technical Report 1751, Revision 1, Naval Command, Control and Ocean Surveillance Center, RDT&E Division, San Diego.
- Schusterman, R. J. (1974). "Low false-alarm rates in signal detection by marine mammals," J. Acoust. Soc. Am. 55, 845-848.
- Smith, P. F., and Wojtowicz, J. (1985). "Temporary auditory-threshold shifts induced by twenty-five-minute continuous exposures to intense tones in water," Report 1063, Naval Submarine Medical Center.
- Swets, J. A., Tanner, Jr., W. P., and Birdsall, T. G. (1964). "Decision processes in perception," in Signal Detection and Recognition by Human Observers, edited by J. Swets (Wiley, New York), pp. 3-57.
- Ward (1997). "Effects of high-intensity sound," in Encyclopedia of Acoustics V. III, edited by Malcolm Crocker (Wiley, New York), pp. 1497-
- Yost, W. A. (1994). Fundamentals of Hearing: An Introduction, 3rd ed. (Academic, San Diego).