

Predicting temporary threshold shifts in a bottlenose dolphin (*Tursiops truncatus*): The effects of noise level and duration

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Noise levels in the ocean are increasing and are expected to affect marine mammals. To examine the auditory effects of noise on odontocetes, a bottlenose dolphin (*Tursiops truncatus*) was exposed to octave-band noise (4–8 kHz) of varying durations (<2–30 min) and sound pressures (130–178 dB re 1 μ Pa). Temporary threshold shift (TTS) occurrence was quantified in an effort to (i) determine the sound exposure levels (SELs) (dB re 1 μ Pa² s) that induce TTS and (ii) develop a model to predict TTS onset. Hearing thresholds were measured using auditory evoked potentials. If SEL was kept constant, significant shifts were induced by longer duration exposures but not for shorter exposures. Higher SELs were required to induce shifts in shorter duration exposures. The results did not support an equal-energy model to predict TTS onset. Rather, a logarithmic algorithm, which increased in sound energy as exposure duration decreased, was a better predictor of TTS. Recovery to baseline hearing thresholds was also logarithmic (approximately –1.8 dB/doubling of time) but indicated variability including faster recovery rates after greater shifts and longer recoveries necessary after longer duration exposures. The data reflected the complexity of TTS in mammals that should be taken into account when predicting odontocete TTS.

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I. INTRODUCTION

Anthropogenic noise in the ocean stems from a variety of sources including shipping, naval sonar, scientific study, oil exploration and drilling, and construction. As usage of the oceans increases, marine noise levels are also expected to rise (National Academy of Sciences, 2005). Serious concern regarding the effects of this noise on marine mammals, as major utilizers of sound in the ocean, has been emerging during the past decade (Richardson *et al.*, 1995; National Academy of Sciences, 2003; Wartzok *et al.*, 2004; National Academy of Sciences, 2005). Excessive noise exposure in marine mammals can induce a variety of adverse behavioral and physiological consequences including changes in hearing sensitivity. In order to mitigate these effects in wild populations, it is necessary to better understand their causes.

Excessive sound exposures may induce both permanent and temporary alterations in hearing thresholds. Permanent threshold changes occur when hearing capabilities do not return to baseline levels. These changes are indicative of hearing damage and are referred to as permanent threshold shifts (PTSs). Temporary threshold shifts (TTSs) demonstrate full recovery of hearing abilities and are generally assumed to be innocuous. These shifts have been demonstrated across vertebrates including fish, reptiles, birds, and mam-

mals (Ward *et al.*, 1958; Saunders and Dooling, 1974; Popper and Clarke, 1976; Mulroy, 1986). Characterizing and understanding how TTS is induced may allow the extrapolation and prediction of PTS levels (Southall *et al.*, 2008). Further, TTS exposure conditions may be considered as a reasonable limit of excessive noise exposure. There is much concern, for obvious reasons, for determining the levels of noise that induce TTS or PTS in humans. As a result, the subject is well studied in some terrestrial mammals, and the variables that relate to TTS (intensity, duration and frequency) are relatively well understood. Thus, models have been developed to predict situations that would induce human TTS and PTS (Ward *et al.*, 1959; Kryter *et al.*, 1966; Ward *et al.*, 1976).

TTS has long been demonstrated in other taxa, but it was not until recently that it was shown that cetaceans are also susceptible to threshold shifts (Schlundt *et al.*, 2000). Further research has shown a relatively robust and resilient marine mammal hearing system and has demonstrated shifts using broadband noise, tones, and seismic waterguns (Finneran *et al.*, 2002; Nachtigall *et al.*, 2003; Finneran *et al.*, 2005). Yet there is much we do not know regarding TTS occurrence and noise effects in cetaceans. For example, do short loud sounds have the same effects as longer quieter sounds of equivalent energy? If we know the intensity and duration of a noise exposure, can we predict TTS?

Answers to these questions require the investigation of a wide range of fatiguing noise levels and durations to develop a predictive model based on empirical evidence. In pinni-

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ped, several studies have done just that (Kastak *et al.*, 2005; 2007). However, in odontocetes, predictive TTS models have been developed based on comparisons across studies that used quite different methodologies and fatiguing stimuli, and the models developed are consequently straightforward but general (Finneran *et al.*, 2005). Thus there is a need for a comprehensive study that encompasses a range of noise level and duration conditions in order to accurately predict the effects of noise on a representative odontocete.

The goal of this study was to examine the relationship between fatiguing noise amplitude and duration in inducing TTS in an odontocete cetacean, and in doing so, to develop a model that predicts the noise levels and durations that would cause TTS and determine if a simple time-intensity trade-off (equal-energy) rule could be applied to these predictions. A secondary goal was tracking the recovery from TTS to establish the recovery rates. To achieve this, the auditory evoked potential (AEP) technique was utilized which allowed for rapid and repeated auditory threshold measurements. Data gathered using the AEP method compare favorably with those obtained using behavioral tests (Yuen *et al.*, 2005; Finneran and Houser, 2006) and have been applied previously in other marine mammal audiometric work including TTS investigations (Nachtigall *et al.*, 2004; Finneran *et al.*, 2007; Nachtigall *et al.*, 2007).

II. MATERIALS AND METHODS

A. Subject and experimental procedure

The subject used in this experiment was an 18-year-old male Atlantic bottlenose dolphin, *Tursiops truncatus*, named Boris. Boris was born and raised in the dolphin breeding colony at the marine mammal research facility in Kaneohe Bay, Oahu, HI. The animal has had substantial cooperative experience with hearing research experiments, including AEP and TTS work (Nachtigall *et al.*, 2003; Nachtigall *et al.*, 2004).

All threshold testing was conducted in the floating open-water sea pens of the Hawaii Institute of Marine Biology, moored off Coconut Island in Kaneohe Bay. The experiment began in May 2004 with the establishment of a baseline audiogram of the subject. Controlled noise exposures for this experiment were introduced in February 2005 and conducted through September 2006 with a total of 57 noise exposures. Exposures were permitted once every 4 days; however, more typically exposures occurred once per week, and often there would be several weeks without exposure sessions. The animal's hearing was monitored and always returned to baseline levels prior to a subsequent exposure. Control sessions were paired with noise exposure sessions and were experimentally identical, excluding the presentation of a fatiguing sound. Because noise exposure sessions were usually presented once per week, a greater number of control and training threshold sessions were conducted, resulting in 82 control sessions (thus some controls were repeated) and 201 days and nearly 300 hearing thresholds measured that were not associated with a fatiguing noise exposure. Noise exposures were permitted with only one subject; thus measurements were often repeated, and data were compared to those of

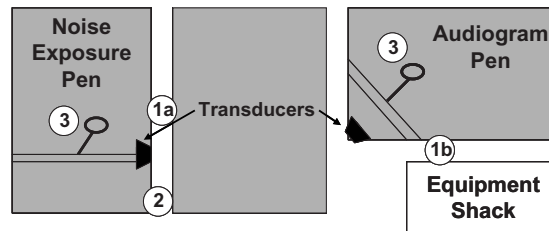


FIG. 1. Diagram of dolphin audiogram threshold testing and fatiguing noise pen experimental setup. (1a, 1b) Trainer positions, (2) assistant position, (3) hoop stations for noise and threshold tests. The equipment shack that housed the AEP and noise exposure equipment is also indicated.

other marine and terrestrial mammals. This ensured that our data were not strongly influenced by a one time occurrence.

Noise sessions consisted of three phases: (1) a pre-exposure threshold measurement to ensure that the subject's threshold was similar to its "baseline," or average threshold, (2) the noise exposure session, and (3) follow-up threshold measurements designed to determine the amount of threshold shift and track the subject's recovery until the subject's hearing returned to the normal threshold range. A threshold shift was determined as the postexposure thresholds, which exceeded +1 standard deviation (SD) of the subject's average threshold. The amount of TTS was measured as a TTS postexposure threshold minus the animal's average threshold. We based all TTS measurements off the subject's mean threshold because between measurements, hearing thresholds often vary slightly (Johnson, 1967; Finneran and Houser, 2006). Using the average threshold allowed us to apply a standard threshold value and TTS level (+1 SD) for each respective frequency examined. All threshold measurements were conducted in the threshold measurement pen using AEPs (Fig. 1). Five AEP records, of 50 s each, were collected per threshold determination; thus a threshold could be estimated in 4–5 min. After the initial threshold measurements, the dolphin voluntarily moved to a separate pen for the fatiguing noise exposure. Immediately after the noise exposure, Boris returned to the threshold measurement pen for the postexposure threshold measurements. These measurements would begin 1–2 min after the cessation of the noise exposure and were conducted with their middle point at 5, 10, 20, 40, and 80 min after noise exposure to thoroughly track the subject's hearing recovery.

B. Evoked potential measurements

At the beginning of each hearing threshold measurement, Boris entered the hearing test pen, and he immediately stationed in front of the trainer. The trainer then gently placed two standard 10-mm gold electroencephalogram (EEG) electrodes, embedded in latex suction cups on the animal. The recording electrode was located 4–10 cm behind the blow-hole, just to the left or right of the animal's midline. The reference electrode was placed on the subject's dorsal fin, which minimized electrical noise from extraneous muscle or nerve movements. Signal conduction was enhanced by the use of standard conductive gel placed between the skin and the electrodes. The animal then returned to station. Upon the trainer's cue, Boris restationed in a hoop 1 m

below the surface and faced a sound projector 2 m away. An acoustic baffle was hung at the surface, 1 m from both the dolphin and the transducer, to prevent extraneous acoustic surface reflections from interfering in the hearing threshold area. The dolphin remained in the hoop for one to three AEP trials (~1–3 min), after which he was recalled to the surface to breathe and receive fish rewards. Boris was then quickly resent to the hoop for the remaining AEP trials. If the hearing thresholds were part of the postexposure threshold measurements, the dolphin was given a break, either resting at the station or being taken out of the test pen, until it was time to begin the next threshold trials.

The sound stimuli were sinusoidally amplitude modulated (SAM) tone bursts digitally generated with a custom LABVIEW program. The tones were converted from digital to analog using an update rate of 200 kHz and a National Instruments PCI-MIO-16E-1 data acquisition (DAQ) card implemented into a desktop computer. Individual tone bursts were 20 ms in duration, presented at a rate of 20 s⁻¹, and for 1000 bursts per trial. On the basis of prior established dolphin modulation rates (Supin and Popov, 1995; Mooney *et al.*, 2006), carrier frequencies were modulated at 1000 Hz and with a modulation depth of 100%. The analog signals were sent from the computer to a custom-built attenuator that could decrease the tones in 1 dB steps. From the signal shaping box, outgoing signals were sent to the projecting transducer, an ITC-1032, and concurrently monitored on a Tektronix TDS 1002 oscilloscope. For each session, thresholds were collected at one of five frequencies: 5.6, 8, 11.2, 16, or 22.5 kHz. Signals typically started at a predetermined start sound pressure level (SPL) of 15–20 dB above the mean threshold and were reduced in 5 dB steps for the remainder of the five trials. If TTS was apparent and thresholds were reached before four to five trials, the SPLs were increased to best track the threshold.

A 30-ms AEP record was collected simultaneously with each stimulus presentation. The received AEPs were amplified and filtered using an Iso-Dam Isolated Biological Amplifier and a Krohn-Hite 3102 filter, both with a bandpass of 300–3000 Hz. They were then digitized by the DAQ card at a rate of 16 kHz. To extract the AEP from noise, 1000 of these records were averaged for each AEP trial.

C. Noise exposure

The noise exposure pen was equipped with a hoop fixed where the subject was required to station for the exposure 2 m from the fatiguing noise transducer. When the subject entered the noise exposure pen, he immediately stationed in front of the trainer. Upon a visual cue from the trainer, the dolphin swam and stationed in the hoop. Typically, several warm-up trials were initiated where the subject was sent to the hoop for 1–2 min with the noise off. When the equipment, animal, and trainer were ready, the trainer directed the fatiguing noise equipment operator to turn the noise on. Because the subject initially demonstrated a startle response that might have inhibited the experiment when an intense fatiguing noise was abruptly turned on, the experimental procedure required the sound to be ramped up from 130 dB re

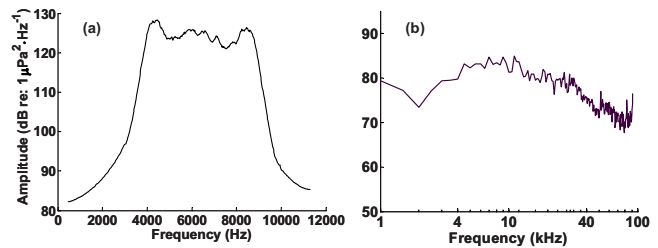


FIG. 2. (Color online) (a) Fatiguing noise spectral density recorded from the hoop calibration position in the noise pen. The octave-band noise is 4–8 kHz with a center frequency of 5.6 kHz. The SPL in this case is approximately 160 dB re 1 μ Pa. (b) Ambient sound at experimental pens in Kaneohe Bay, Oahu, HI measured with a Biomon 8235 and plotted as noise spectral density using a 1024-point FFT. Ten noise samples were averaged to create both plots.

1 μ Pa to 15 dB below the deemed exposure level or a maximum value of 150 dB over the course of a 30-s trial. The animal was then recalled back to the trainer, and the sound was turned up to the planned experimental intensity. The dolphin was then sent back to the hoop to begin what was considered the timed exposure. The warm-up trials were on average 140–145 dB SPL of noise for 30 s and well below TTS levels discussed here and elsewhere (Nachtigall *et al.*, 2004; Finneran *et al.*, 2007). Further, these trials did not substantially increase sound exposure levels (<0.01 dB) re 1 μ Pa²s. For these reasons, they were not likely to affect measured TTS and were not considered part of the noise exposure.

To examine the effects of noise duration and intensity on dolphin hearing, both exposure duration and SPL were varied. Hoop sound exposure duration was set at 30, 15, 7.5, 5.6 (337 s), 3.75, or 1.88 min. All exposure durations were monitored by the trainer who cumulatively noted and controlled the animal's exact time in the hoop for each trial. In doing so, the trainer relayed to the equipment operator the exact time the fatiguing sound could be turned off to get a precise exposure duration (e.g., 1.88 min or 112 s). Fatiguing noise intensities ranged from 130 to 178 dB re 1 μ Pa where, irrespective of the initial ramp-up, SPLs were kept constant throughout the exposure. The fatiguing noise was an octave-band noise of 4–8 kHz (Fig. 2). It was generated by a custom-built white noise generator and then filtered using a custom bandpass filter. Noise was then amplified using a Hafler P3000 amplifier, monitored on the oscilloscope and played through a Massa TR-61A transducer (peak frequency of 5.5 kHz). The noise level was calibrated 11 times throughout the experiment to ensure that no drift occurred in sound levels. To calibrate, a Biomon 8235 hydrophone (–173 dB sensitivity and ± 1 dB from 1 to 40 kHz) was placed in the center of the hoop when the animal was not present. The hydrophone was connected to the oscilloscope to monitor the noise levels, a Fluke 8922A rms voltmeter (1 MHz bandwidth, ± 0.01 dB up to 200 kHz, 1 s integration time), the same DAQ card, and a custom LABVIEW program to record received levels. The noise was then measured with the voltmeter in SPL based on the total rms over the 4–8 kHz band. Received sound pressure varied by ± 0.35 dB (SD) at the 160 dB level across the 11 calibrations. From the SPL (re 1 μ Pa), it was then possible to calculate the noise spectral

density (dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$) from 4 to 8 kHz. Sound exposure level (SEL) (dB re $1 \mu\text{Pa}^2 \text{s}$) was also calculated from the received SPLs for each exposure sound pressure and duration. SPL and SEL are hereafter referred to with the above units.

The exposure schedule was semirandom. Initial exposures were 30 min, and SPL was increased until threshold shifts were induced. Duration was then decreased in order, from 30 to 1.88 min. We then increased the duration (similar to an ABBA session format). Exposures were then remeasured at the shortest durations (1.88 and 3.75 min) using higher SELs than the previous sessions. These sessions were repeated twice. We then increased exposure duration again, this time at the initial SELs. Thresholds shifts were usually investigated at all five frequencies before exposure duration was changed. The time between exposure sessions as well as the variation of exposure duration and SEL likely experimentally precluded some processes that could affect TTS (such as cochlear toughening; Hamernik *et al.*, 2003). Further, the animal was well experienced in TTS studies (Nachtigall *et al.*, 2003; Nachtigall *et al.*, 2004) and likely did not develop unique protective auditory mechanisms for this study.

The dolphin's behavior was continuously monitored during the noise exposure by both the trainer and an assistant. While the trainer was responsible for interacting with the dolphin, the assistant recorded behavioral alterations including number of respirations during surface intervals, latency of time from surface station to the hoop (delay), excessive head or body movement, or any apparent reactions to the fatiguing sound (or reactions within control trials). Because the dolphin had significant experience in TTS, AEP, and other psychoacoustic experiments, his "normal" behavior was well known, and behavioral changes were easily noted. The animal also had significant previous training required to maintain participation in research and husbandry activities, and thus reactions to avoid such activities were expected to be minimized. The dependent variables of respirations, latency, and behavioral modification were measured and analyzed in respective one-way analyses of variance (ANOVAs) to determine if behavioral changes were observed. The assistant also informed the trainer of the duration of the surface intervals and time in the hoop, which were varied somewhat from trial to trial to prevent the dolphin from predicting when each trial and hoop session was over. However, the total time in the hoop for each noise exposure or control session was pre-established and maintained as the exposure time for that session (i.e., 30, 15, ... min). While the animal needed to surface and breathe during exposure sessions, this did not increase SELs because the surface intervals were kept short (45 s) and SPLs were lower at the surface station (10 dB).

D. Data analysis

A 16-ms window of each averaged AEP response to the SAM tones was fast Fourier transformed (FFT) to view the response in the frequency domain. At higher amplitude SPLs (~ 20 dB above threshold), the spectra reflected a well-pronounced peak of $0.1\text{--}0.2 \mu\text{V}$ at the frequency of stimulus

modulation—1000 Hz. At higher sound levels, these peaks were easily distinguishable from background noise; this is because the background noise levels of these spectra were distributed among 50 harmonics across a range of 3 kHz. Thus the magnitude of this noise was a few nV. At SPLs close to threshold, the amplitude of the 1000-Hz spectrum peak was dependent on stimulus sound pressure. Thus, the peak values could be plotted against SPL, and an approximated linear regression could be obtained addressing the peak values. The point where the regression line crossed the abscissa was taken as the theoretical sound level at which no AEP response would be induced and thus was considered the animal's threshold (Nachtigall *et al.*, 2004; Nachtigall *et al.*, 2007). While the entire EFR input-output function of the odontocete was not linear, the oblique portion near threshold was reasonably approximated by regression methods, thus aiding to determine an arbitrary but well established method to estimate response threshold (e.g., Supin *et al.*, 2001; Popov *et al.*, 2005; Nachtigall *et al.*, 2008). Five records were collected for each threshold set, and the points with the highest r^2 value were used in determining the thresholds. While actual threshold measurements were determined off-line, EFRs and FFTs were monitored in real time to assess the animal's AEP response. If both values reached background noise levels for two subsequent trials, SPL was increased 5 dB above the start SPL. This was to ensure the greatest number of reliable data points per threshold estimation within a short period of time.

To determine TTS, postexposure thresholds were compared to the subject's mean (baseline) thresholds for each of the five frequencies tested. These thresholds and their respective standard deviations were calculated from measurements not associated with a noise exposure. More than 40 thresholds were acquired for each frequency. A threshold shift was then determined as a threshold, after a control or actual noise exposure, where the threshold exceeded 1 SD above the mean threshold. These criteria allowed for comparisons to an established threshold and variance. Variance beyond this could then likely be explained by the dependent variable, noise exposure. A TTS was defined as a demonstrated "recovery" back to within ± 1 SD of the mean. These shifts were deemed greater than the day-to-day variation that was found in the baseline thresholds and were distinguishable by comparison to over 300 thresholds measured during the course of the experiment. The consequent recoveries provided confirmation of the shift. All analyses were completed with Excel, MATLAB, and MINITAB software.

III. RESULTS

Baseline hearing thresholds for the dolphin subject were relatively consistent, varying by 2–3 dB SD (mean = 2.8 dB) at a particular frequency [Fig. 3(a) and 3(b)]. Hearing was most sensitive at the higher frequencies (16 and 22.5 kHz) and followed a typical mammalian curve. Baseline thresholds and TTS were primarily explored at 11.2 kHz. The subject demonstrated hearing recovery from all threshold shifts, and baseline thresholds did not significantly increase over the duration of the experiment (Fig. 4).

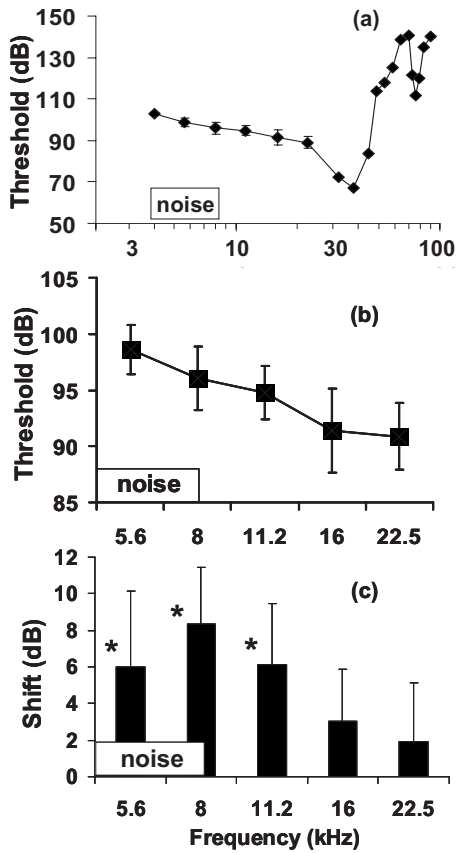


FIG. 3. (a) Audiogram of Boris. (b) Mean hearing thresholds (± 1 SD) of Boris for 5.6–22.5 kHz in SPL (dB re $1 \mu\text{Pa}$). The fatiguing noise band, from 4 to 8 kHz, is depicted at the bottom, relative to the hearing thresholds tested. (c) Mean (± 1 SD) amount of TTS (dB re $1 \mu\text{Pa}$) at each of the five frequencies tested. The * indicates that 5.6, 8, and 11.2 kHz demonstrated mean shifts that were significantly greater than their average threshold (one-way ANOVA and Tukey's pairwise comparison, $p < 0.001$, $F_{5,82} = 16.69$).

No TTS was measured after control conditions in which no sound was presented. The experimental matrix for all exposures ≥ 160 dB and occurrences of TTS are listed in Table I.

A. Threshold shifts and frequency

Temporary threshold shifts were recorded in 26 of 57 noise exposure sessions and at all frequencies tested [Fig.

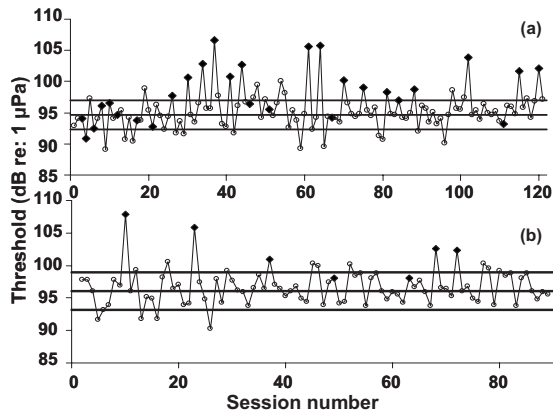


FIG. 4. Thresholds over the duration of the experiment for (a) 11.2 kHz and (b) 8 kHz. Black diamonds indicated thresholds measured after a fatiguing noise exposure. The middle line indicates mean threshold, and top and bottom lines indicate ± 1 SD from the mean.

TABLE I. Noise exposure experimental matrix where the fatiguing sound was octave-band white noise of 4–8 kHz. Parameters listed include audiogram test frequency (kHz), exposure duration (min), noise SPL, SEL, and number of exposures and number of shifts at corresponding test conditions.

Frequency (kHz)	Duration (min)	SPL (dB re $1 \mu\text{Pa}$)	SEL (dB re $1 \mu\text{Pa}^2 \text{s}$)	(No. of exposures-no. of shifts)	
5.6	30	160	192.5	(1-1)	
	15	163	192.5	(1-1)	
	7.5	166	192.5	(1-1)	
	3.75	169	192.5	(1-0)	
	3.75	175	198.5	(1-0)	
	1.875	172	192.5	(1-0)	
	1.875	178	198.5	(1-0)	
	8	30	160	192.5	(1-1)
		15	163	192.5	(1-1)
		7.5	166	192.5	(1-1)
3.75		169	192.5	(1-0)	
3.75		175	198.5	(1-1)	
1.875		172	192.5	(1-0)	
1.875		178	198.5	(1-1)	
11.2		30	160	192.5	(1-1)
		15	163	192.5	(3-2)
		7.5	166	192.5	(3-3)
	5.625	172	197	(1-1)	
	3.75	169	192.5	(1-0)	
	3.75	172	195.5	(1-0)	
	3.75	175	198.5	(3-1)	
	1.875	172	192.5	(1-0)	
	1.875	175	195.5	(1-0)	
	1.875	178	198.5	(3-3)	
16	30	160	192.5	(1-1)	
	15	163	192.5	(1-1)	
	7.5	166	192.5	(1-0)	
	3.75	169	192.5	(1-0)	
	3.75	175	198.5	(1-0)	
	1.875	172	192.5	(1-0)	
	1.875	175	195.5	(1-0)	
	1.875	178	198.5	(1-0)	
	22	30	160	192.5	(1-0)
		15	163	192.5	(1-1)
7.5		166	192.5	(1-0)	
3.75		169	192.5	(1-0)	
3.75		175	198.5	(1-0)	
1.875		172	192.5	(1-0)	
1.875		175	195.5	(1-0)	
1.875		178	198.5	(1-0)	

3(b)]. However, TTS at the higher more sensitive frequencies (16 and 22.5 kHz) did not occur frequently, and no significant increases in the mean threshold postnoise exposure were recorded at those frequencies. Mean postexposure thresholds for 5.6, 8, and 11.2 kHz demonstrated significant increases in hearing thresholds, relative to the baseline hearing threshold (one-way ANOVA, $F_{5,82} = 16.69$, $p < 0.001$; subsequent Tukey's pairwise comparison). These frequencies fell immediately within the center frequency of the fatiguing noise (5.6 kHz) and one-half (8 kHz) and one octave above the noise center frequency. The greatest mean threshold shift oc-

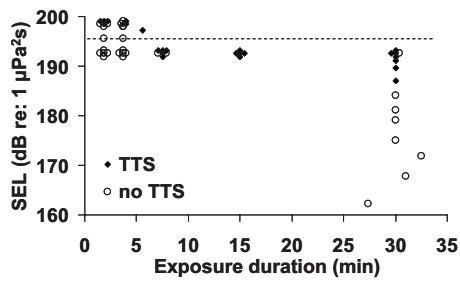


FIG. 5. Sound exposure levels required to induce TTS as the duration of exposure changes at all threshold frequencies tested. Shorter duration exposures required greater SEL to induce TTS. Dotted line indicates an equal-energy line of 195 dB SEL. Black diamonds indicate TTS occurrence; open circles indicate no TTS.

occurred at 8 kHz (8.3 dB SPL) although 5.6 and 11.2 kHz both demonstrated an average TTS of 6 and 6.1 dB SPL, respectively.

Of all the thresholds measured at each selected frequency, TTS was found at 11.2 kHz after 51% of postnoise thresholds ($n=29$) and in 71% ($n=21$) of the postexposures when the SEL was >185 dB. Thresholds after noise exposure were measured in seven instances for each of the other frequencies tested, and TTS occurrences were found to be 43%, 71%, 29%, and 14% for 5.6, 8, 16, and 22.5 kHz, respectively.

B. Threshold shifts and sound exposure levels

Fatiguing sound exposure levels could be adjusted in at least two ways: either by altering the exposure duration or by varying the amplitude of the sound. Generally, as either exposure duration or sound pressure increased, if the other variable remained constant, a greater incidence of TTS could be expected. For example, at the start of the experiment, exposure duration was held at 30 min, but noise SPL and concomitant SELs were gradually increased (Fig. 5). Postnoise exposure thresholds did not demonstrate TTS until approximately 155 dB SPL, or 187 dB SEL. These sound levels induced a relatively small shift (3 dB SPL) at 11.2 kHz. In the following several sessions, as SEL was gradually increased to 192.5 dB (160 dB SPL), the amount of TTS at 11.2 kHz also increased [Fig. 6(a)].

One initial goal of the experiment was to examine the equal-energy hypothesis by keeping SEL constant and by varying exposure duration and sound pressure to determine the effects on TTS. Thus, after TTS was measured at all relevant threshold frequencies (5.6–22.5 kHz) using a 30-min, 160-dB SPL noise exposure, exposure duration was halved and sound pressure was increased by 3 dB, keeping SEL constant, and exposures and thresholds were measured again. However, TTS did not stay constant as exposure duration decreased. Threshold shift occurrence decreased from 80%–86% for 15–30 min exposures to 71% at 7.5 min and to zero significant TTS occurrences at 3.75 and 1.88 min. The amount of TTS also decreased with exposure duration [Fig. 6(a)] and could be predicted by a significant linear relationship ($r^2=0.77$; $p<0.001$; $y=0.34x+2.57$;

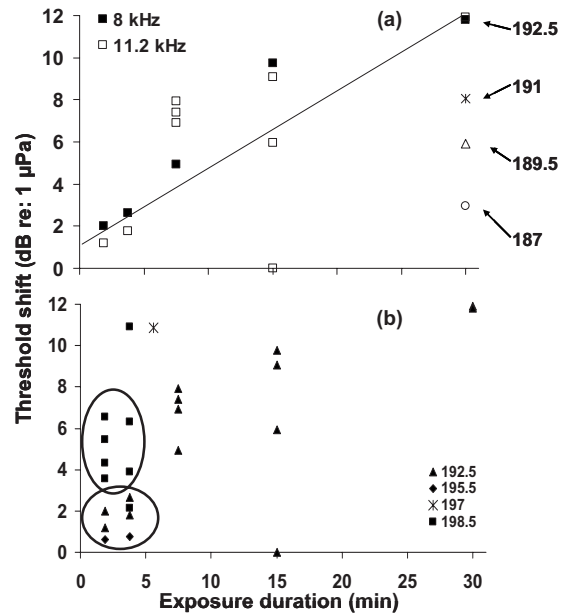


FIG. 6. (a) Amount of threshold shift measured at 8 kHz (closed symbols) and 11.2 kHz (open symbols) for SELs of 192.5 dB and below. Increasing SELs and corresponding symbols are labeled at the right, demonstrating that at constant exposure duration but increasing SEL, TTS increased. A regression of the 192.5 dB SEL data was used to illustrate that with decreasing noise exposure duration, TTS decreased when SEL was held constant ($r^2=0.77$, $p<0.001$, $y=0.34x+2.57$, $n=13$). (b) Amount of TTS for SELs of 192.5 dB and higher. Threshold frequencies are not discriminated, but SEL symbols are labeled to the right. Note that at shorter durations the amount of shift is clustered and higher SELs (top circle) are required to induce significant TTS.

$F_{1,12}=36.29$). Thus, for the same SELs, exposures of 30 min produced nearly 12 dB TTS, whereas 1.88 min of exposure did not generate a shift.

In order to induce TTS at durations of 1.88–3.75 min, fatiguing noise SEL had to be increased from 192.5 to 198.5 dB. Intermediate levels at 195.5 dB SEL did not induce significant amounts of TTS. At 198.5 dB SEL, significant TTS was induced at 8 and 11.2 kHz in seven of eight exposures, with a mean shift of 5.4 dB and one shift of 11 dB [Fig. 6(b)]. Overall, no significant relationship was found between the amount of shift (measured at 5.6, 8, and 11.2 kHz) and SEL ($r^2=0.02$; $p=0.42$). Using the situations in which SEL was increased to induce TTS, threshold shift growth was predicted, revealing a strong positive relationship between SELs and amount of TTS ($r^2=0.96$; $p<0.001$; $TTS=-0.702+1.36$ (SEL); $F_{2,18}=112.2$).

C. Recovery from threshold shifts

Following noise exposures, AEP measurements were recorded for up to 80 min afterward to track the subject's recovery. Following all noise exposure sessions, the subject fully recovered to baseline values within 80 min. When shifts occurred, recovery to within ± 1 SD of the baseline thresholds was typically seen in 20 min (15/26). In only three instances was the subject not within 1 SD of the baseline threshold values by 40 min after the noise exposure. These were either 15- or 30-min exposures at a SEL of 192.5 dB. The shifts were 12, 9.3, and 9.6 dB for 11.2, 11.2, and 5.6 kHz, respectively. Total recovery was rare within

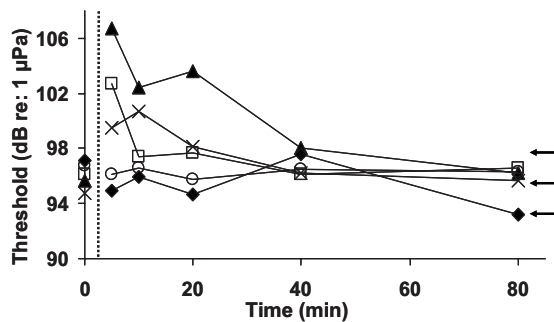


FIG. 7. Thresholds at 11.2 kHz before and after exposures for 192.5 dB SEL for five exposure durations (min): 30 (triangle), 15 (X), 7.5 (open square), 3.75 (open circle), and 1.875 (diamond). Thresholds were measured 5, 10, 20, 40, and 80 min after noise ended. The dotted line indicates noise exposure. Arrows indicate mean threshold ± 1 SD.

10 min of the noise exposure following shifts, only occurring on three occasions, with TTSs of 3.0, 4.7, and 5.8 dB.

Examples of recovery functions after noise exposure are plotted in Fig. 7. In the figure, despite a constant SEL of 192.5, the recovery functions varied for each respective exposure duration and sound pressure session. While the greatest shift was found at the 30-min exposure, the 7.5-min exposure demonstrated greater TTS than the 15 min exposure. However recovery from the 7.5-min exposure was most rapid. Neither the 3.75- nor the 1.88-min exposures induced threshold shifts.

Recovery rates followed a logarithmic function, which was held relatively constant across various methods of analysis (Fig. 8). Greater shifts demonstrated initially steeper slopes of recovery, and lesser shifts reflected more gradual recovery rates. This was best seen by breaking the recovery functions into separate groups (>7 dB shifts, <7 dB shifts, ≥ 15 min exposure, and <15 min exposure). The slopes of these groups varied somewhat but were roughly similar and were calculated as -7.4 , -5.6 , -6.3 , and -6.7 $\log(\text{min})$, respectively, and all were linear in log time. The somewhat steeper slopes of >7 dB shifts and ≥ 15 min exposure may reflect the greater mean shifts of those groups, 8.3 and 7.2 dB SPL, respectively. The shallower slope of the <7 dB shift group was a result of the relatively lower TTS values (mean = 4.6 dB SPL) of the grouping. On average, all recoveries could be approximated by a function of -1.8 dB/doubling of time.

D. Behavioral reactions

The subject's behavior during both the fatiguing noise and the control sessions was monitored and recorded by an assistant; for analysis, behavioral comparisons were made between the control and exposure sessions. Sessions were also divided into groupings of those with 30, 15, ≤ 7.5 min exposures, which were rough proxies for long, moderate, and short duration exposures. No significant difference in overt behavioral changes was found between the exposure and control sessions. However, the subject did exhibit a significant increase in respirations during noise sessions as compared to the control sessions for the longer duration exposures and during noise exposures overall [Fig. 9(a)] (one-

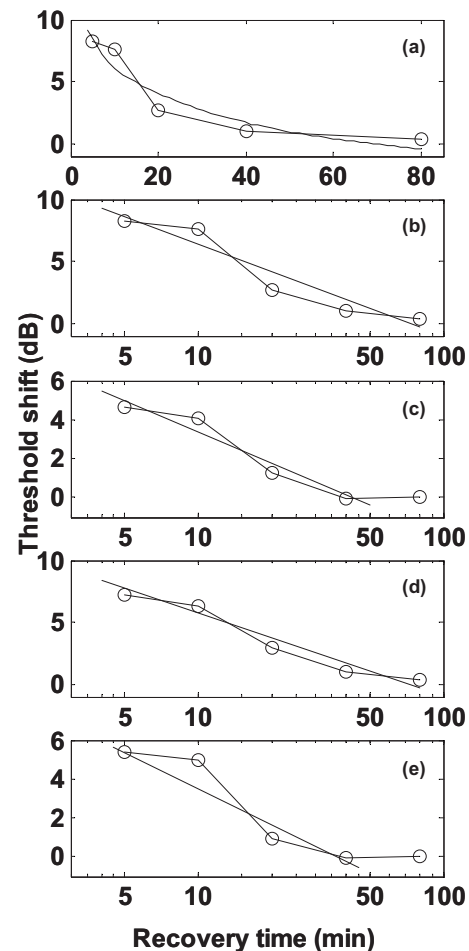


FIG. 8. Threshold shift (dB re 1 μPa) recovery functions demonstrating linear logarithmic recoveries in log time across multiple analysis methods: (a) TTS >7 dB (linear time), (b) TTS >7 dB (log time), (c) TTS <7 dB, (d) TTS from longer duration exposures (30–15 min), and (e) TTS from shorter duration exposures (7.5–1.875 min). The rate of recovery in all cases was approximately -1.8 dB/doubling of time.

way ANOVA and subsequent Tukey's pairwise comparison, $p < 0.001$, $F_{7,4557} = 31.98$). Mean respirations (\pm SD) for these longer durations and all control exposures were 6.14 (± 3.21) and 5.98 (± 3.10), respectively, and 8.81 (± 2.99) and 7.31 (± 3.59) for the equivalent noise exposures. The delay from the intertrial station to the hoop/noise exposure station was also significantly greater during noise exposure sessions, and this was across the groupings of exposure duration ($p < 0.001$, $F_{7,4559} = 25.31$). Mean values for these differences for the groups of 30, 15, ≤ 7.5 min, and all control trials were 6.61 (± 4.48), 6.01 (± 2.85), 5.92 (± 3.64), and 6.41 s (± 4.01 s), respectively. For the noise sessions, delay means were 9.28 (± 5.50), 8.02 (± 3.51), 8.00 (± 3.97), and 8.77 s (± 4.95 s) for the respective groups.

IV. DISCUSSION

The data presented here provide a broad examination of the interaction of fatiguing noise duration and amplitude on TTS in a bottlenose dolphin. Shorter duration exposures were found to require greater amounts of energy (higher SELs) to induce similar amounts of TTS relative to longer duration exposures, indicating that a simple equal-energy ap-

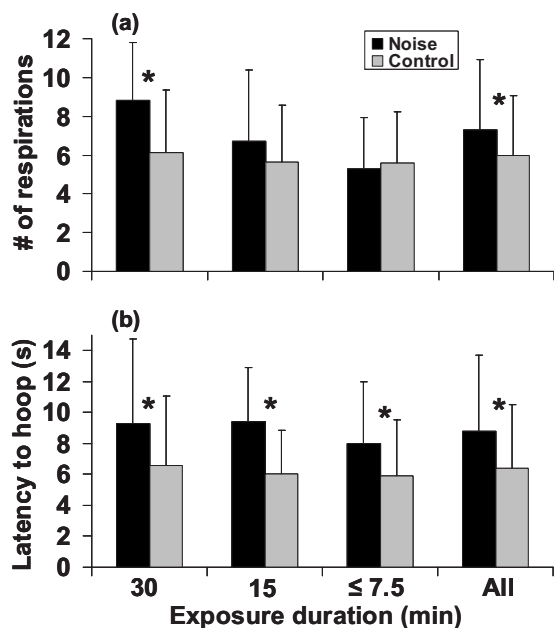


FIG. 9. Mean number of respirations (a) and delay from intertrial stationing pad to hoop station (b) for various noise exposure and control trials. For comparison, we grouped the sessions by the number of trials as well as summed data from all trials of all sessions. There were significantly greater respirations, indicated by the *, during noise sessions with >10 trials and all the sessions grouped together (one-way ANOVA and Tukey's pairwise comparison, $p < 0.001$, $F_{7,4557} = 31.98$). The hoop delay was significantly greater for all groups of noise exposure trials ($p < 0.001$, $F_{7,4559} = 25.31$).

proach does not adequately predict TTS in dolphins. Small behavioral changes in the number of respirations and delay to the exposure station were evident in noise exposure conditions versus control. Mean TTS levels induced here were relatively small compared to those often demonstrated in terrestrial mammals and some other marine mammals (Ward *et al.*, 1959; Finneran *et al.*, 2007; Kastak *et al.*, 2007). However, the data presented here demonstrate the SELs required for TTS onset across a range of exposure durations, and TTS onset can certainly be considered helpful in assessing the effects of noise on wild populations.

The frequency for which the greatest TTS was observed was one-half octave above the center frequency of the noise. Other significant levels of mean TTS were found at the center frequency of the noise and one octave above the center frequency. These trends reflect what has been demonstrated previously with the same animal in similar noise exposure conditions (Nachtigall *et al.*, 2004) as well as results collected with terrestrial mammals and pinnipeds (Ward *et al.*, 1959; Ward, 1962; Kastak *et al.*, 2005), indicating that the frequency trend of odontocete noise-induced TTS appears relatively conserved in marine mammals. The experiment was designed using frequencies below the regions of best auditory sensitivity for a bottlenose dolphin but similar to that of introduced anthropogenic noise. It is likely that at higher frequencies (20–100 kHz) and regions of better sensitivity, TTS levels might have been greater (Mills, 1982). Further, snapping shrimp produce high levels of background noise in Kaneohe Bay, creating an environment for masking [Fig. 2(b)]. In a quieter situation, we would have likely seen greater levels of TTS (Humes, 1980); thus these results may

be somewhat conservative in the amount of TTS induced for the sound levels used. In quieter situations, TTS onset may actually occur at lower exposure levels than predicted by the present study. The dolphin also has relatively poor high frequency hearing (>50 kHz), which seems typical of adult male dolphins (Houser and Finneran, 2006). The animal's hearing within the range of the noise exposure (4–8 kHz) and test conditions (5.6–22.5 kHz) was relatively normal (Nachtigall *et al.*, 2000). There are no data to suggest that the hearing loss outside of the range of the TTS test conditions would affect the amount of TTS at these much lower frequencies examined here.

Exposure duration was also a consideration here. Sound exposure levels were calculated using hoop exposure times. However, for most sessions, the animal had to leave the experimental sound field to breathe. This procedure was not quite an intermittent exposure protocol as the animal was still exposed to noise while he was at the surface, although noise levels were 10 dB SPL lower at the surface station. Because these surface interval durations were minimized and surface sound levels were lower, this protocol did not significantly change SELs (e.g., 192.5 versus 192.7 dB SEL for 30 min exposures, 192.5 versus 192.7 dB for 15 min, 192.5 versus 192.6 dB for 7.5 min, 192.5 versus 192.6 dB for 3.75 min). Thus, it was possible that some very minor TTS recovery occurred during surface intervals, although this was unlikely based on the consistency of SELs and maintenance of relatively high SPLs (150–165 dB) (Ward, 1991).

Based on the SELs that induced TTS, the data were evaluated to determine a model that would predict TTS onset. Several algorithms have been suggested to predict noise levels that induce TTS including the general equal-energy rule, which assumes that as long as noise exposure energy levels are constant, similar threshold shifts will be induced regardless of the noise temporal pattern (Ward *et al.*, 1959). This is often termed the “3-dB rule” as a halving of sound exposure duration and a 3-dB increase in sound intensity maintains a constant energy level and should theoretically induce similar shifts (Kryter *et al.*, 1966). This rule has been employed for human standards (NIOSH, 1998) and has recently been proposed for use in predicting TTS in odontocetes (Finneran *et al.*, 2005). However, despite the fact that it is applied as a general rule and fits in many situations, empirical studies often do not support the equal-energy hypothesis as an accurate means to predict TTS, demonstrating that the trade-off between time and energy is not necessarily linear (Buck *et al.*, 1984; Ward, 1991; Hamernik and Qui, 2001).

Our data generally follow an equal-energy line of 195 dB SEL; however, the TTS instances more often split the line rather than fall upon it (Fig. 5). At shorter duration exposures, such as might occur with a single sonar ping exposure, greater SELs were required to induce TTS relative to longer duration exposures. Further, when SEL was held constant (sound duration decreased but SPLs increased), the amount of TTS did not hold constant as would be predicted by an equal-energy hypothesis [Fig. 6(a)]. Rather, TTS levels also decreased. At shorter duration exposures, increased SELs were required to induce significant levels of TTS [Fig.

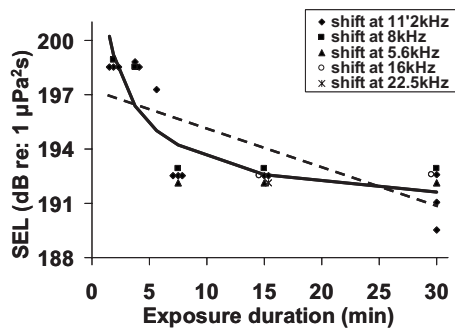


FIG. 10. The SELs required to induce TTS at higher noise levels where threshold frequencies are discriminated. Just TTS occurrence is plotted. Two methods to predict TTS are also graphed: a linear estimation of TTS (dotted line) ($r^2=0.57$, $p<0.001$, $SEL=-0.21T+197.14$, $n=23$) and a logarithmic estimation ($r^2=0.78$, $p<0.001$, $SEL=-6.17 \log(T)+200.21$, $n=23$). Note that in both cases, the slope is positive, indicating that for shorter time durations, greater energy is required to induce TTS.

6(b)]. This noncoherence to the equal energy rule was previously demonstrated in pinnipeds (Kastak *et al.*, 2005; Kastak *et al.*, 2007). These data also indicate that equal-energy levels do not induce similar TTS levels in odontocete cetaceans.

To better predict TTS onset, a model of increasing energy as exposure level decreases appears to fit these data more closely (Fig. 10). Described is both a linear relationship to the threshold shift data, as well as a logarithmic relationship. The linear model does approximate the trend sufficiently well ($r^2=0.57$, $p<0.001$, $SEL=-0.21(T)+197.14$, $F_{1,22}=28.65$), where T =duration of the exposure in minutes. However, the logarithmic estimation does a much better job of predicting the threshold shifts and would apparently make a better model for predicting TTS ($r^2=0.78$, $p<0.001$, $SEL=-6.17 \log(T)+200.21$, $F_{2,21}=78.71$).

Interestingly, although the equal-energy model is often proposed to predict the occurrence of human TTS, there is often a contradiction to this rule, and this is found across taxa, including in humans (Mills *et al.*, 1981), guinea pigs (Buck *et al.*, 1984), and chinchillas (Ward, 1991). Threshold shift occurrence depends on many factors in addition to fatiguing noise energy; these include frequency, intensity, duration, and time intervals of exposure (Bohne and Clark, 1990). Therefore using energy and SEL alone is an insufficient metric for predicting TTS. Although SEL combines both exposure SPLs and duration, these two factors do not necessarily contribute equally to the TTS onset. For example, it is possible that mechanisms that work to reduce TTS for short duration exposures fatigue are reduced for longer duration exposures. It is vital to present both SPL and duration in reporting and predicting TTS. Further, as more information is collected regarding odontocete TTS, it becomes increasingly obvious that the subject of TTS is quite complex. The best way to predict TTS may be to investigate it using a range of variables to determine what exposures produce the same TTS and address an equal-TTS based approach to reducing deleterious noise exposures (Kryter *et al.*, 1966; Ward, 1991).

When TTS onset was examined relative to sensation level (SL), or the difference in decibel between the fatiguing noise SPL and the average threshold, two points were rela-

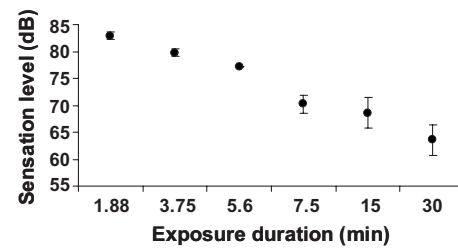


FIG. 11. SL (dB re threshold) at which TTS was induced for various exposure durations. TTS could be induced at much lower SLs for longer duration exposures. Note that the abscissa is categorical.

tively apparent (Fig. 11). First, there was a relationship between SL and exposure duration. As exposure duration decreased, lower SLs were needed to induce TTS. The clarity of the trend may be a means of predicting TTS based on SLs and duration and deserves further investigation. As the trend was negative, it may be important to determine the SLs that induce TTS at much longer duration exposures and if or at what SLs the trend asymptotes. Such predictions may further the understanding of effective quiet (the level at which no duration of exposure will induce TTS) for marine mammals. Second, the SLs of TTS onset for longer duration exposures were similar to SLs of shipping and snapping shrimp noise found in some natural habitats (Johnson, 1967; Erbe, 2002; Aguilar de Soto *et al.*, 2006; Lammers *et al.*, 2008). In other words, both shipping and snapping shrimp sounds may have enough energy to induce TTS if the animal is exposed for a long enough duration. This result implies caution for introducing a constant of noise into the marine environment, but we stress that such sound levels may be naturally encountered by some animals, in some instances.

When considering the behavioral data, it is important to realize that these experiments were primarily designed as hearing investigations, not as investigations of behavioral effects of noise. Thus some caution must be taken when interpreting behavior during these studies and extrapolating to other conditions. We assume that behavioral changes associated with noise exposure indicate an aversion to the fatiguing noise, but this is *only* an assumption. There were no overt behavioral changes that were significantly associated with the presence of the fatiguing noise. However, the dolphin was reinforced throughout his extensive research training and husbandry experience to limit any deviations from expected procedures, and in the interest of the present study, such considerations were taken here. Thus, major behavioral changes were unexpected. However, more subtle changes such as significant increases in respiration rates and delay from the intertrial station to the hoop station were observed (Fig. 9). Fatiguing noise levels at the surface intertrial station were 10 dB lower in SPL than at the hoop. Presumably, this may have been a passive method of deferring noise exposure by the dolphin. Interestingly, only the longer duration exposures reflected higher respiration rates, perhaps implying that potentially the shorter duration exposures, although higher in SPL, may have been less adverse. The only occasion on which the dolphin exhibited an obvious reaction to fatiguing noise exposure was when an amplifier electrically shorted during the exposure, creating an unplanned, unusual, and

relatively loud sound. The dolphin immediately pulled out of the hoop and swam vigorously around the noise exposure pen, burst-pulsing and jaw popping at the transducer and not heeding the trainer for several minutes. However, this was an isolated event and typically the animal stationed properly and observed the trainers' cues. The animal reacted to the unexpected in an unusual way.

Previous TTS studies have often demonstrated more obvious behavioral reactions to noise exposure (Kastak *et al.*, 1999; Schlundt *et al.*, 2000). However, it seems more often that there are only small behavioral changes as these animals are exceptionally well trained. Thus, motivation regarding certain tasks can override presumed reactions to potentially adverse stimuli. Such overriding motivations have been found in wild individuals, for example, pinnipeds raiding fish farms that are equipped with acoustic harassment devices (Quick *et al.*, 2004). The prevalence of such behaviors both in wild and captive animals deserves further attention. Further, our documented behavioral changes were subtle, indicating the importance of detailed observations when examining the effects of noise on marine mammals.

Hearing recovery rates generally followed a logarithmic trend of -1.8 dB recovery/doubling of time. This was similar to some previous results, particularly for shifts that are not greater than 10–15 dB (Nachtigall *et al.*, 2004; Finneran *et al.*, 2007). However, there was variability in the slopes, and greater shifts reflected faster recovery rates. A similar trend was found by Finneran *et al.* (2007), which is not only a confirmation of the logarithmic recovery functions but indicates robustness of both data sets. An interesting note is that the shifts that took 40 min to demonstrate recovery were all of longer duration exposures. This may support the trend that longer duration exposures will often induce greater amounts of TTS, which concurrently requires a greater amount of time for recovery. Similarly, in humans, recovery functions depend somewhat on the exposure situation, and longer duration exposures have demonstrated longer recovery times (Mills, 1982). This may also be demonstrated here. Further, these longer recoveries were recorded on shifts measured at 5.6 and 11.2 kHz, frequencies that did not produce the highest mean TTS. If these shifts were recorded at 8 kHz, greater shifts and longer recoveries might have been found. This underlies the importance of measuring multiple frequencies simultaneously, an important AEP advancement when investigating TTS (Finneran *et al.*, 2007).

V. CONCLUSIONS

This work demonstrates TTS onset in an odontocete across a range of exposure durations and sound levels, and the results indicate that shorter duration exposures often require greater sound energy to induce TTS than longer duration exposures. Recovery functions were relatively consistent but did show some indications that different exposure situations may relate to different recovery rates. The sample size was limited, but repetitive exposures and comparisons between studies increased the robustness of the data. These results are inconsistent with an equal-energy model of TTS supporting the notion that, as in terrestrial mammals, predict-

ing odontocete TTS is quite complicated. It is suggested that TTS onset is considered sufficient to conclude physiological effects of noise exposure in marine mammals. Future investigations should continue to explore the range of variables that relate to threshold shifts to develop an equal-TTS model to better predict and mitigate situations in which anthropogenic noise may affect marine mammals.

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