

Effect of Duty Cycle Composition of Intermittent Sound on Temporary Hearing Threshold Shift in a Harbor Porpoise (*Phocoena phocoena*)

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Abstract

Temporary hearing threshold shift (TTS) in mammals depends on aspects of the fatiguing sound causing the shift: frequency, sound pressure level (SPL), exposure duration, and duty cycle (DC). Intermittent fatiguing sounds consist of pulses alternating with inter-pulse intervals (IPIs). With ambient noise below “effective quiet thresholds” (Ward et al., 1976, p. 160) hearing can recover between pulses. Sounds with the same DC can have different combinations of exposure pulse and IPI durations, and it is unclear how DC composition affects TTS. The effects of IPI on TTS and recovery was studied in a harbor porpoise (*Phocoena phocoena*) exposed to one-sixth-octave noise bands centered at 8 kHz with mean SPL of 144 dB re 1 μ Pa and DCs of 50% (cumulative sound exposure level: 177 dB re 1 μ Pa²s) and 100% (continuous; cumulative sound exposure level: 180 dB re 1 μ Pa²s). The 50% DCs were sounds with equal pulse and IPI durations of 10, 8, 6, 4, 2, 1, 0.5, 0.25, and 0.1 s. The TTS_{1–4 min} elicited at 11.3 kHz was similar (~18 dB) for fatiguing sound IPIs between 10 and 4 s, higher (~20 dB) for 2 and 1 s IPIs, higher still (~22 dB) for 0.5 s IPI, and highest (~24 dB) for 0.25 and 0.1 s IPIs. The continuous sound caused 23.8 dB TTS. Hearing recovered during IPIs of 10 to 4 s, less during IPIs of 2 to 0.5 s, and very little during IPIs of $\leq$ 0.25 s. Reverberations of the fatiguing sound in the pool may have added to the TTS caused when IPIs were short. As the effective quiet SPL for 8 kHz sounds in harbor porpoises is unknown, it is unclear which contributions reverberation energy and short recovery times played in causing the high TTS during exposures with IPIs < 4 s. This study supports research indicating reduced TTS after exposure to intermittent sounds relative

to exposures to continuous sounds, and it highlights the importance of quiet intervals between exposures for hearing recovery.

Key Words: anthropogenic noise, effective quiet, Environmental Impact Assessment (EIA), harbor porpoise, hearing damage, hearing loss, intermittent sound, odontocete, recovery of hearing, temporary hearing threshold shift (TTS)

Introduction

The harbor porpoise (*Phocoena phocoena*) is of particular interest when studying the effects of anthropogenic underwater sound on marine mammals, as this odontocete species not only has a large geographic range in the coastal waters of the Northern Hemisphere (Bjorge & Tolley, 2008), but it also possesses hearing over a wide frequency range (0.5 to 140 kHz; Kastelein et al., 2017b). Harbor porpoises are also particularly susceptible to temporary hearing threshold shifts (TTSs) after exposure to fatiguing sounds (sounds causing a hearing threshold shift; Lucke et al., 2009; Finneran, 2015; Tougaard et al., 2015; Houser et al., 2017). In addition, harbor porpoises are the only representative of the very high-frequency (VHF) cetaceans in U.S. Navy/National Marine Fisheries Service (NMFS) criteria and thus play a very important role in noise effects data (NMFS, 2024). Depending on the exposure parameters, sound-induced TTS varies in magnitude and duration, and may compromise feeding, orientation, communication, and predator detection in wild harbor porpoises and other marine mammals that rely mainly on acoustics for these life functions (e.g., Au, 1993). Harbor porpoises have a high metabolism and feeding rate (Wisniewska et al., 2016; Kastelein et al., 2018a,

2018b), so disturbances resulting in small TTSs may impact them disproportionately, especially if such disturbances occur frequently. The cumulative time lost may negatively impact harbor porpoises' foraging, health, reproduction, and survival. As a result, chronic TTSs may have adverse population effects in the long term.

The TTS caused by a fatiguing sound depends on the exposure duration as well as on its sound pressure level (SPL) and frequency (Finneran, 2015). It is important to quantify and understand the effect of fatiguing sounds of various frequencies on the hearing of the harbor porpoise as they are used to generate weighting functions in criteria (Southall et al., 2007, 2019; Tougaard et al., 2015, 2022; NMFS, 2016; Houser et al., 2017). For the regulation of underwater acoustic levels in areas where harbor porpoises occur, complete equal-TTS susceptibility contours are desirable, covering the entire frequency range of hearing in the harbor porpoise (i.e., ~0.5 to ~140 kHz). TTS onset (defined as 6 dB TTS; Southall et al., 2019; Tougaard et al., 2022) sound exposure levels for harbor porpoises due to fatiguing sound in the 0.5 to 88.4 kHz range have been established by Kastelein et al. (2012, 2013, 2014a, 2014b, 2015, 2017a, 2019a, 2019b, 2020a, 2020b, 2020c, 2021a, 2024).

Alongside exposure duration, SPL, and frequency, the duty cycle (DC) of the fatiguing sound plays a role in the resulting TTS. The equal-energy hypothesis (i.e., that exposure to continuous sounds of the same sound exposure level [SEL], regardless of SPL and exposure duration composition, results in the same initial TTS) does not hold for chinchillas (*Chinchilla lanigera*) exposed to intermittent sounds (Saunders et al., 1977; Ward, 1991). That intermittent sounds elicit lower TTS than continuous sounds of the same cumulative SEL has also been observed in marine mammals such as bottlenose dolphins (*Tursiops truncatus*; Mooney et al., 2009; Finneran et al., 2010; Mulsow et al., 2023) and California sea lions (*Zalophus californianus*; Kastelein et al., 2021b, 2022). Several studies with harbor porpoises have also shown effects of the DC of intermittent fatiguing sound on noise-induced TTS, using simulated naval sonar as fatiguing sounds (Kastelein et al., 2014b, 2016, 2017b). However, the sonar pulse durations in those studies were fixed and matched the durations of the pulses used in naval sonars, and only the inter-pulse intervals (IPIs) between the pulses were varied to produce variation in DC. In those studies, the DC had a large effect on the resulting TTS, which showed that recovery of hearing can occur, partly or fully, during the IPIs. However, it is still unclear how the various combinations of durations of pulses and intervals in intermittent fatiguing sounds affect the resulting TTS, or the subsequent recovery pattern.

Therefore, the goal of the present pilot study was to determine the effect of different combinations of durations of pulses and IPIs in intermittent fatiguing sounds with the same DC (50%) on the elicited TTS and recovery in a harbor porpoise. TTS was compared to that resulting from the same fatiguing sound with a 100% DC (continuous), and to control periods in which no sound exposure took place. The study provides data to improve Environmental Impact Assessments and the regulation of effects of exposure to intermittent sound on harbor porpoise hearing.

Methods

Study Subject and Site

The study subject, a previously stranded and rehabilitated adult female harbor porpoise (identified as F05; age: ~12 y, body mass: ~43 kg, body length: 155 cm, girth at axilla: ~85 cm), had participated in previous studies of TTS (Kastelein et al., 2021a, 2024). Her hearing threshold at the frequency tested in the present study (11.3 kHz) is representative of that of similar-aged harbor porpoises (Kastelein et al., 2017b), confirming that her hearing was not compromised by her participation in previous studies. Unfortunately, F05 was only available for a short period of time, so the sample sizes in this pilot study are limited.

The study was conducted at the SEAMARCO Research Institute in the Netherlands. F05 was kept in a quiet pool complex designed and built for acoustic research, consisting of an indoor pool (8 m × 7 m; 2 m deep; Figure 1) in which the study was conducted, connected via a channel (4 m × 3 m; 1.4 m deep; Figure 1) to an outdoor pool (12 m × 8 m; 2 m deep) which F05 had access to when the study was not being conducted. For details of the pool, equipment, and water flow, see Kastelein et al. (2019b).

Equipment Calibration

Acoustical terminology follows International Organization for Standardization (ISO) (2017). The ambient noise was measured, and the fatiguing sound and hearing test signals were calibrated by an external sound measurement company (TNO) just before and at the end of the study period (for calibration methods, see Kastelein et al., 2024). Under test conditions (i.e., water circulation system off, no rain, and Beaufort wind force 4 or below), the ambient noise in the indoor pool was below that of sea state 0.

Hearing Test Signals

The hearing thresholds were tested at 11.3 kHz, the hearing frequency that experienced the highest TTS after exposure to the fatiguing sound (a noise

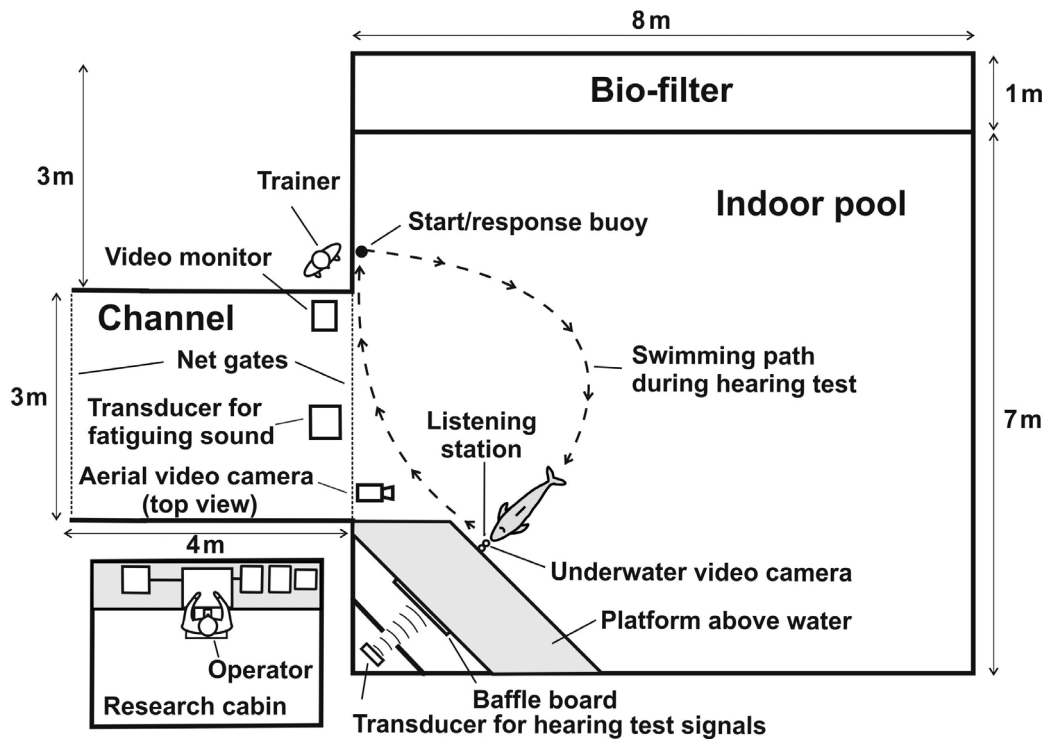


Figure 1. The indoor pool in which the temporary hearing threshold shift study with harbor porpoise F05 was conducted. On each test day, a pre-exposure hearing test was conducted at 11.3 kHz. This was followed, for 1 h, by exposure to a fatiguing sound or, in control sessions, to low ambient noise. Fatiguing sounds were one-sixth-octave noise bands centered at 8 kHz, with either 100% duty cycle (DC), or 50% DC with a particular combination of similar pulse and inter-pulse interval (IPI) durations. Following exposure, one or more hearing tests at 11.3 kHz were conducted to quantify the initial hearing shift and recovery.

band centered at 8 kHz; Kastelein et al., 2024). The hearing test signal was a linear up-sweep which started and ended at $\pm 2.5\%$ of the center frequency. The hearing test signal was generated digitally, and presentations were calibrated and checked daily, as explained by Kastelein et al. (2019b). The hearing test signal duration was 1,000 ms, including a linear rise and fall in amplitude of 50 ms.

Fatiguing Sound

The digitized fatiguing sounds were produced, transmitted, calibrated, and checked before each exposure session, as described by Kastelein et al. (2024). The sounds were transmitted into the indoor pool by an underwater transducer (Model LL1424HP; Lubell Labs, Columbus, OH, USA) through an isolation transformer (Model AC1424HP, Lubell Labs). The transducer was placed at 1 m depth in the channel adjacent to the pool (Figure 1). The fatiguing sound consisted of one-sixth-octave Gaussian white noise band pulses centered at 8 kHz. It was produced

with 100% DC (continuous), and with 50% DC in nine different compositions: combinations of repeated equal-duration pulses followed by IPIs with no transmitted sound, tested in the following order of IPIs: 10, 8, 6, 4, 2, 1, 0.5, 0.25, and 0.1 s. The fatiguing sound pulses had a linear rise and fall in amplitude of 50 ms for 10 to 4 s pulses, 10 ms for 2 to 0.5 s pulses, and 5 ms for 0.25 and 0.1 s exposure sounds. The 50% DC was achieved by matching the durations of the IPIs with the durations of the pulses making up the fatiguing sounds. The rise time period to max amplitude is included as part of the signal; it is not treated as an independent variable.

To determine the fatiguing sound's distribution in the pool, the SPL of the noise band was measured at 40 locations in the horizontal plane (on a horizontal grid of 1 m $\times$ 1 m), and at three depths per location on the grid (0.5, 1.0, and 1.5 m below the surface), resulting in a total of 160 measurements in the pool (see Kastelein et al., 2024). Apart from ~ 1 m around the transducer, the differences

in energetic mean SPL at different locations and depths were minimal. To determine the mean SPL received by F05, the area where she swam during exposure periods was quantified following the methods of Kastelein et al. (2019b).

During fatiguing sound exposure sessions, the noise band was projected for precisely 1 h at one source level (148 dB re 1 μ Pa m), resulting in an energetic mean received SPL experienced by the harbor porpoise of 144 dB re 1 μ Pa (averaged over all 160 measurement locations in the pool). The cumulative sound exposure level (SEL_{cum}) for the 50% DC was 177 dB re 1 μ Pa²s; for the 100% DC noise band, it was 180 dB re 1 μ Pa²s. During the IPLs, reverberations from the pool boundaries (bottom, wall, and water surface) slightly reduced the quiet periods between the pulse transmissions. The average short-term SPL (with rms over 15 ms) in the pool dropped by 60 dB to ambient noise levels with a corresponding reverberation time of ~80 to 90 ms.

Experimental Procedures

On each test day, one sound exposure session or control session was conducted. It consisted of (1) a pre-exposure hearing threshold test starting at ~0830 h; (2) exposure to fatiguing sound or ambient noise (in control sessions) for 1 h, in the morning and/or early afternoon; and (3) a number of post-exposure or post-ambient exposure hearing tests.

Post-exposure hearing tests started within 1 min after the fatiguing sound stopped. F05's hearing thresholds were measured during post-sound exposure (PSE) periods 1 to 4 min (PSE₁₋₄), 4 to 8 min (PSE₄₋₈), and 8 to 12 min (PSE₈₋₁₂), and, if hearing had not recovered then, 60 min (PSE₆₀), 120 min (PSE₁₂₀), 240 min (PSE₂₄₀), and 1,440 min (PSE_{1,440}) after sound exposure ended. Hearing was considered to have recovered when the hearing threshold was $\leq$ 2 dB above the pre-exposure threshold level since fluctuations of $\leq$ 2 dB occurred after control sessions in the quiet conditions of the present study (see "Results") and in previous, similar studies with this subject. The nine 50% DC compositions of the fatiguing sound, and the 100% DC fatiguing sounds, were each tested in one or two sessions.

Control sessions were conducted in the same way and under the same conditions as sound exposure sessions, but without fatiguing sound exposure. Each control session started with a pre-exposure hearing test, which was followed by exposure to the normal ambient noise in the indoor pool for 1 h with the transducer in the pool as usual, but not emitting sound. Post-ambient exposure (PAE; control) hearing tests were performed 1 to 4 min (PAE₁₋₄), 4 to 8 min (PAE₄₋₈),

and 8 to 12 min (PAE₈₋₁₂) after the ambient noise exposure ended. The 14 control sessions were randomly dispersed among the sound exposure sessions.

Hearing Test Procedures

A hearing test trial began with F05 at the start/response buoy; following a hand signal by her trainer, she swam to the listening station which was 1.0 m deep and 2.0 m from the hearing test transducer (Figure 1). She stationed there for a random period of 6 to 12 s before the operator produced the test signal (in signal-present trials). Upon hearing the signal, F05 swam back to the start/response buoy (a "go" response) where she received a food reward. If she did not hear the signal, she stayed at the listening station (a "no-go" response) until she was asked to return to the start/response buoy (by the trainer tapping three times on the side of the pool); no food reward was given. About two thirds of each session consisted of signal-present trials and about one third consisted of signal-absent trials (also called "catch" trials). During signal-absent trials, the trainer used a whistle after F05 had stationed for 6 to 12 s at the listening station to instruct her to return to the start/response buoy, where she received a food reward. Signal-absent trials were included to assess and maintain the subject response bias.

When F05 returned to the start/response buoy before being presented with a test signal (in signal-present trials) or before hearing the trainer's whistle (in signal-absent trials), her response was a pre-stimulus error. The mean incidence of pre-stimulus errors for both signal-present and signal-absent trials was calculated as the number of pre-stimulus errors as a percentage of all trials in each hearing test period.

Following each detection of a hearing test signal, the next signal's level was 2 dB lower; following each undetected signal, the next signal's level was 2 dB higher (staircase method; Cornsweet, 1962). The signal level was not changed following any response to a signal-absent trial (correct or incorrect). A switch from a test signal level that F05 responded to, to a level that she did not respond to, or vice versa, was called a "reversal." Each complete hearing test session consisted of ~25 trials and lasted for up to 12 min. However, the first PSE or PAE sessions were subdivided into three 4-min periods. During pre-exposure and PSE₆₀, PSE₁₂₀, PSE₂₄₀, and PSE_{1,440} hearing test sessions, the goal was to obtain 10 reversals. During each of the 4-min periods within the first PSE and PAE sessions, the goal was to obtain a minimum of three reversals. If the goals were not met, the session was not used for analysis. The methodology

is described in more detail in Kastelein et al. (2019b). Data were collected from September 2022 to January 2023.

Data Analysis

The pre-exposure mean 50% hearing threshold ($PE_{50\%}$) for the hearing test signal was determined by calculating the mean SPL of all reversal pairs obtained during the pre-exposure hearing session. TTSs after the sound exposure sessions (TTS_{1-4} , TTS_{4-8} , TTS_{8-12} , TTS_{60} , TTS_{120} , TTS_{240} , and $TTS_{1,440}$) were calculated by subtracting $PE_{50\%}$ from the mean 50% hearing thresholds during the PSE_{1-4} , PSE_{4-8} , PSE_{8-12} , PSE_{60} , PSE_{120} , PSE_{240} , and $PSE_{1,440}$ periods of the same day (Kastelein et al., 2019b). Similarly, “TTSs” measured on control session days were calculated by subtracting $PE_{50\%}$ from the mean 50% hearing thresholds obtained during the PAE periods of the same day. The value was always close to zero, as no TTS occurred after control sessions.

Results

Motivation and Pre-Stimulus Errors

F05 was always motivated and willing to participate in the hearing tests. The mean incidence of pre-stimulus errors for both signal-present and signal-absent trials varied in the hearing tests between 3.5 and 8.3%, and in the control tests between 2.1 and 7.8%. Incidences of pre-stimulus errors in the pre-exposure, post-exposure, and post-ambient exposure (control) periods were of similar orders of magnitude (Table 1).

TTS and Recovery After Exposure to the Noise Band at 8 kHz at Two Duty Cycles

The TTS_{1-4} elicited in the harbor porpoise was similar (~18 dB) for fatiguing sounds with IPIs between 10 and 4 s, higher (~20 dB) for the 2 and

1 s IPIs, higher still (~22 dB) for the 0.5 s IPIs, and yet higher (~23 dB) for the 0.25 and 0.1 s IPIs (Table 2; Figure 2). The 100% DC (continuous) fatiguing sound of the same SPL caused 23.8 dB TTS. Therefore, hearing recovered a little during exposure to fatiguing sounds with IPIs of 10 to 4 s, less so with IPIs of between 2 and 0.5 s, and very little during IPIs of ≤ 0.25 s. In all but two cases, full recovery of hearing ($TTS \leq 2$ dB) occurred within 240 min post-exposure (Figure 3).

Discussion

Effect of Duration of Inter-Pulse Intervals on Temporary Threshold Shifts

The results from the 50% DC fatiguing sound in the present study suggest that significant hearing recovery can occur in the IPIs when fatiguing sounds are intermittent. TTS was smallest when IPIs were 10 to 4 s long, showing that recovery during exposure was greatest; recovery was less when IPIs were shorter. The TTS_{1-4} after exposure to the fatiguing sound with the two shortest IPIs was similar to that occurring after exposure to the same fatiguing sound at 100% DC (SEL_{cum} was 3 dB higher; Figure 2).

Our experiment was planned so that SPL and SEL_{cum} in all 50% DC exposures were consistent. Hence, exposures with longer IPIs provided more time between pulses for hearing recovery. Higher TTS after exposure to fatiguing sounds with shorter IPIs indicated lack of, or reduced, recovery between pulses. It is unclear how much time is required for recovery of the auditory system to occur (von Benda-Beckmann et al., 2024), but hearing recovery at timescales of minutes to hours depends logarithmically on time (Finneran, 2015). It may be that during shorter IPIs there is insufficient time for any recovery to occur.

Table 1. The incidence of pre-stimulus errors (number of pre-stimulus errors as a percentage of all trials in each hearing test period) by harbor porpoise F05 in hearing tests during pre-exposure periods, in seven post-sound exposure periods (PSE: after exposure to the fatiguing sound, a noise band centered at 8 kHz), and in three post-ambient exposure periods (PAE: after exposure to ambient noise in control sessions). Subscript numbers indicate minutes after exposure ended. All duty cycle compositions were pooled for the calculation of percentages. Sample sizes (total numbers of test and catch trials in all sessions per period) are shown in parentheses.

	Hearing test period							
	Pre-exposure	PSE_{1-4}	PSE_{4-8}	PSE_{8-12}	PSE_{60}	PSE_{120}	PSE_{240}	$PSE_{1,440}$
Fatiguing sound	7.8% (283)	8.3% (109)	4.8% (104)	4.3% (116)	7.2% (318)	6.6% (212)	3.5% (141)	8.2% (73)
Control	Pre-exposure	PAE_{1-4}	PAE_{4-8}	PAE_{8-12}	--	--	--	--
	7.7% (298)	4.0% (99)	2.1% (94)	7.8% (103)	--	--	--	--

Table 2. Temporary hearing threshold shifts (mean TTS_{1-4}) in the first 4 min after exposure and recovery times in harbor porpoise F05 after exposure for 1 h to the fatiguing sound (a one-sixth-octave noise band centered at 8 kHz, with a mean sound pressure level of 144 dB re 1 μ Pa) at two duty cycles: (1) 100% (continuous) or (2) 50% for the nine exposure sound pulse duration–inter-pulse interval compositions. Hearing was quantified at 11.3 kHz (half an octave above the center frequency of the fatiguing sound). One or two sessions were conducted for each duty cycle composition, as shown; SEL_{cum} = cumulative sound exposure level. Recovery times are based on the test periods in which the hearing threshold was documented as ≤ 2 dB above the pre-exposure threshold level, so actual recovery occurred earlier (especially at 1,440 min, as these hearing tests were conducted the day after the day of exposure). The mean and standard deviation (SD) of the control sessions are also shown ($n = 14$), confirming that no TTS occurred after exposure to the ambient noise.

Duty cycle (%)	Duration of pulses in fatiguing sounds (s)	On & off ramps (ms)	Duration of inter-pulse intervals (IPIs) (s)	No. of pulses in 1 h (whole numbers)	SEL_{cum} dB re 1 μ Pa ² s	Mean TTS_{1-4} Session 1 (dB)	Mean TTS_{1-4} Session 2 (dB)	Recovery time (≤ 2 dB TTS) (min)
0	Control	--	--	Control	Ambient noise	0.4 (SD ± 1.1)	--	--
100	Continuous	50	--	--	180	23.8	--	120
50	0.10	5	0.10	18,000	177	22.3	24.2	1,440
50	0.25	5	0.25	7,200	177	23.4	--	1,440
50	0.50	10	0.50	3,600	177	21.5	--	240
50	1	10	1	1,800	177	19.9	--	240
50	2	10	2	900	177	20.4	--	120
50	4	50	4	450	177	18.4	--	120
50	6	50	6	300	177	18.1	--	120
50	8	50	8	225	177	17.6	18.4	240
50	10	50	10	180	177	17.4	18.3	240

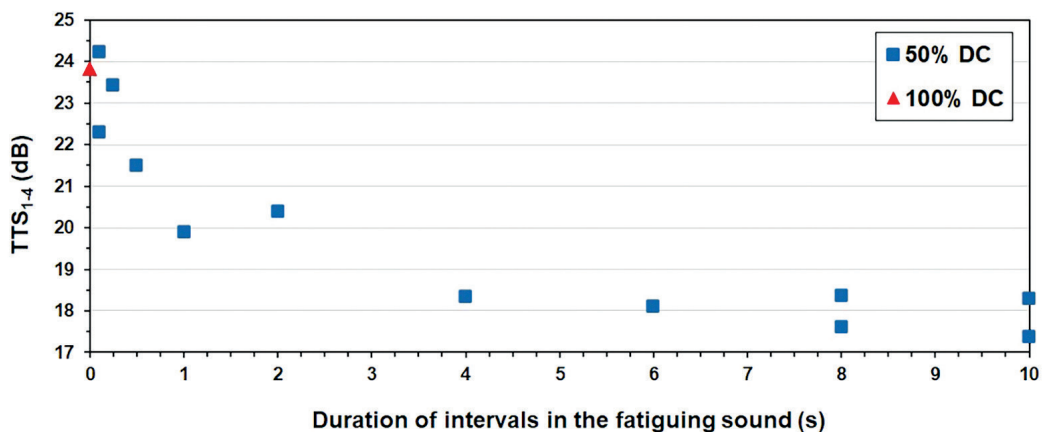


Figure 2. Temporary hearing threshold shifts (TTS_{1-4}) in harbor porpoise F05 in the 4 min after exposure for 1 h to the fatiguing sound (a one-sixth-octave noise band centered at 8 kHz, with a mean SPL of 148 dB re 1 μ Pa) at two duty cycles (DCs). The DC was 100% (continuous; SEL_{cum} 180 dB re 1 μ Pa²s), or 50% (SEL_{cum} 177 dB re 1 μ Pa²s) for the nine pulse duration–inter-pulse interval compositions. Hearing was quantified at 11.3 kHz (i.e., half an octave above the center frequency of the fatiguing sound). One or two sessions were conducted for each DC composition, as shown in Table 2.

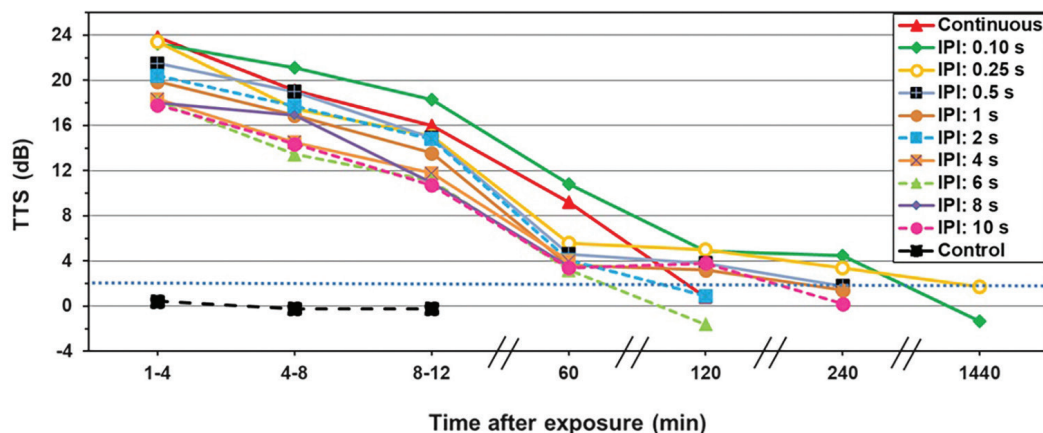


Figure 3. Changes over time in temporary hearing threshold shifts (TTSs), including recovery, in harbor porpoise F05 at hearing test frequency 11.3 kHz, after 1 h exposure to the fatiguing sound (a noise band centered at 8 kHz), at a sound pressure level of 148 dB re 1 μ Pa; 50% duty cycle (DC) composed of nine compositions with different inter-pulse intervals (IPIs) (SEL_{cum} : 177 dB re 1 μ Pa 2 s), and 100% DC (continuous sound; IPI = 0 s; SEL_{cum} : 180 dB re 1 μ Pa 2 s). Each colored line connects the datapoints from one session, except for IPIs 0.1, 8, and 10 s, for which the lines connect datapoints representing means of two sessions (see Table 2). The dashed black line indicates the mean TTS of the control sessions ($n = 14$), confirming that no TTS occurred after exposure to ambient noise. The blue dotted line indicates 2 dB TTS, below which hearing is defined as having recovered. Note that the x-axis is not linear or logarithmic.

Reverberations of the fatiguing sound in the pool may have slightly extended the periods in which the harbor porpoise was exposed to the sound. From human studies, it is known that quiet exposures with up to 22 dB lower SPLs between exposures may hinder recovery of the auditory system if they exceed “effective quiet thresholds” (Ward et al., 1976, p. 160), but these thresholds are unknown for marine mammal species (Finneran, 2015; Schaffeld et al., 2020). The lowest SPL levels at which TTS has been reported in harbor porpoises after 1-h exposures to a continuous one-sixth-octave noise band centered at 8 kHz was 132 dB re 1 μ Pa (at 11.3 kHz; Kastelein et al., 2024) and 123 dB re 1 μ Pa after 1-h exposures to a continuous one-sixth-octave noise band centered at 16 kHz (Kastelein et al., 2019b). The measured times for the exposure sounds in the present study to reach 130 dB re 1 μ Pa and 120 dB re 1 μ Pa after a pulse stopped were 20 and 30 ms, respectively, suggesting that after this time, reverberation was not expected to contribute to further TTS growth (Kastelein et al., 2019b, 2024). After the fatiguing sounds ended, it took ~80 ms for the measured SPL in the pool to reach ambient noise level. Effective quiet thresholds are unknown for harbor porpoises, but the reduction in recovery time was likely to be sometime between 20 and 80 ms. For the shorter IPIs tested in the present study (100 to 250 ms), reverberations within the pool may have significantly extended the effective exposure

time, resulting in shorter effective IPIs (i.e., less time for recovery). This may have contributed to the relatively high TTSs. For longer IPIs tested, the contribution from reverberations was unlikely to be significant.

F05 was only available for a short time, so each DC composition was tested only once or twice. Therefore, care should be taken when interpreting and extrapolating the data. However, in previous TTS studies with the same harbor porpoise, the variation between TTSs after similar exposures was small. TTS_{1-4} in the control sessions of the present study was close to zero and varied little ($n = 14$), and the number of pre-stimulus errors were low. This suggests that the harbor porpoise’s response criteria were stable throughout the study period and supports the validity of the data. However, this pilot study should be repeated with the goal of producing a more extensive dataset.

The findings in the present study are consistent with research in which another harbor porpoise was exposed for 1 h to tonal sweeps from 1 to 2 kHz with a duration of 1 s, and the DC was reduced from 100 to 50% (i.e., the IPI was changed from 0 to 1 s between sweeps). With that change in DC, the initial TTS decreased by 5 dB (Kastelein et al., 2014b), which is similar to the ~4 dB reduction in TTS that was experienced by the harbor porpoise in the present study when the IPI was changed from 0 to 1 s; longer IPIs resulted in even lower initial TTSs.

Some studies of TTS in other odontocete species exposed to intermittent fatiguing sounds indicate similar effects of changes in IPI as found in the present study, whereas other studies indicate no relationship between TTS and recovery, with shorter IPIs between exposures. Mooney et al. (2009) exposed bottlenose dolphins to blocks of three successive downsweeps separated by IPIs of 0.5 s, with each block separated by 24 s, as fatiguing sound to simulate a typical mid-frequency naval sonar application. During multiple intermittent exposures, TTS accumulated, and TTS-onset SELs varied with exposure duration (this could be an effect of the different combinations of SPL and exposure duration used to achieve the same SEL; von Benda-Beckmann et al., 2024). Finneran et al. (2010) measured TTS in a bottlenose dolphin after exposure to a sequence of four 16-s 3 kHz tones at SPLs of 192 dB re 1 μ Pa, with IPIs of 224 s, resulting in a DC of approximately 7%. These exposures were designed to approximate a typical DC from mid-frequency naval sonar, but the temporal spacing of the exposures was increased to allow time for a hearing test between successive exposures. The resulting TTS and recovery were compared to experimentally measured TTS in the same subject exposed to single continuous tones of 16 and 64 s with similar SPLs. The results showed that the exposure to four consecutive 16 s tones produced 3 dB higher TTS than exposure to one 16 s tone, and that one 64 s tone produced a 5 dB higher TTS than exposure to four consecutive 16 s tones. These results indicate the potential for accumulation of TTS after multiple exposures, and for recovery of hearing during the quiet IPIs between exposures (Finneran et al., 2010).

Mulsow et al. (2023) exposed bottlenose dolphins to fatiguing sounds consisting of 10 ms one-sixth-octave bandwidth pulses centered at 8 kHz with SPLs of 175 to 180 dB re 1 μ Pa. The IPIs (2.5, 5, 10, 20, and 40 s) and total number of impulses (40, 80, 160, 320, 640, 1,280, and 2,560) were varied to form combinations producing the same SEL_{cum}. TTS (at 8 and 11.3 kHz) increased with increasing SEL_{cum}, and there was no apparent effect of IPI for exposures with equal SEL. This appears to be consistent with part of the present study, which shows little difference in TTS after exposure to fatiguing sounds with IPIs of 10 to 4 s. The present study indicates that when harbor porpoises are exposed to these fatiguing sounds, shorter IPIs lead to higher initial TTSSs. For shorter IPIs, the present study found approximately a 2 dB difference between fatiguing sounds with 1 to 2 s IPIs and longer IPIs, whereas Mulsow et al. (2023) found similar TTS for IPIs of 1.5 and 2 s and for longer IPIs (up to 20 s) in bottlenose dolphins. However, the present study has

only limited replications, and Mulsow et al. (2023) show substantial variability between exposure conditions and between individuals.

There may be an interaction between increased TTSSs associated with increasing pulse duration and amplitude and recovery during IPIs. Over longer timescales, the recovery rate is correlated with the level of TTS induced (Finneran, 2015). The IPI, therefore, may not be the only factor related to the recovery of hearing rate during the longer IPIs. Finneran et al. (2010) proposed a model to predict TTS in bottlenose dolphins (Modified Power Law [MPL]) after exposure to a particular intermittent sound. This model was adapted to predict patterns of TTS in harbor porpoises exposed to 1 to 2 kHz sonar sounds by using different model parameters (von Benda-Beckmann et al., 2024). Although the 1 to 2 kHz exposure TTS data could be reasonably explained using the MPL model, the model was limited in its ability to predict TTS increases at higher frequencies, and TTS caused by broadband impulsive sounds, highlighting the challenge of finding a parsimonious set of model parameters that can predict the interactive effects of pulse duration, IPI, SPL, and frequency of the fatiguing sound on TTS in marine mammals (von Benda-Beckmann et al., 2024).

Reduced TTS after exposure to intermittent sounds could be achieved via marine mammals' ability to self-mitigate by reducing their hearing sensitivity when they anticipate loud sounds (Nachtigall & Supin, 2013; Finneran et al., 2023, 2024). Conditioned reduction in hearing sensitivity has been demonstrated in a range of marine mammal species, including the harbor porpoise (Nachtigall et al., 2018). The mechanism used to suppress hearing sensitivity may be neural and/or involve the middle ear reflex (Kastelein et al., 2020d; Finneran et al., 2023). It is currently unclear under what conditions marine mammals are able to reduce their hearing sensitivity, whether longer IPIs are required so that they can anticipate the onset of a loud sound, and how long the suppressed sensitivity can be sustained (Finneran et al., 2024). It is possible that both recovery during IPIs and conditioned reduction in hearing sensitivity are combined to result in less TTS during exposures with longer IPIs than during continuous exposures or intermittent exposures with very short IPIs.

Evaluation and Future Research

In Environmental Impact Assessments, the difference between the effects of continuous and intermittent fatiguing sounds on harbor porpoise hearing must be considered (Mooney et al., 2009; Finneran et al., 2010; Kastelein et al., 2014b, 2016, 2017b; Mulsow et al., 2023). The risk of TTS and hearing injury in marine mammals

is often predicted from the anticipated SEL_{cum} (Southall et al., 2019; Tougaard et al., 2022). The present study shows that, as well as SPL and exposure duration which are required to calculate the SEL_{cum} , the composition of the DC is important in estimations of the TTS elicited by intermittent fatiguing sounds. In particular, the duration of the IPIs is important because of the potential that longer IPIs allow hearing recovery to occur even before the end of the exposure. Data from more combinations of alternating (regular or irregular) fatiguing sound pulses and IPIs need to be collected to inform our understanding of the mechanisms' underlying variations in TTS after exposure to various intermittent fatiguing sounds. In addition, studies investigating hearing recovery over short timescales (< 1 s to seconds) would help elucidate the mechanisms for recovery. Finally, studies determining effective quiet thresholds would help to understand to what extent hearing recovery can occur in real-world intermittent or amplitude-modulated exposure conditions.

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Author CRediT Contributions

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Literature Cited

- Au, W. W. L. (1993). *The sonar of dolphins*. Springer-Verlag. <https://doi.org/10.1007/978-1-4612-4356-4>
- Bjorge, A., & Tolley, K. A. (2008). Harbor porpoise *Phocoena phocoena*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 530-532). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00125-5>
- Cornsweet, T. N. (1962). The staircase-method in psychophysics. *American Journal of Psychology*, 75(3), 485-491. <https://doi.org/10.2307/1419876>
- Finneran, J. J. (2015). Noise-induced hearing loss in marine mammals: A review of temporary threshold shift studies from 1996 to 2015. *The Journal of the Acoustical Society of America*, 138(3), 1702-1726. <https://doi.org/10.1121/1.4927418>
- Finneran, J. J., Carder, D. A., Schlundt, C. E., & Dear, R. L. (2010). Temporary threshold shift in a bottlenose dolphin (*Tursiops truncatus*) exposed to intermittent tones. *The Journal of the Acoustical Society of America*, 127(5), 3267-3272. <https://doi.org/10.1121/1.3377052>
- Finneran, J. J., Lally, K., Mulsow, J., & Houser, D. S. (2024). Dolphin short-term auditory fatigue and self-mitigation. *The Journal of the Acoustical Society of America*, 155(3), 2241-2246. <https://doi.org/10.1121/10.0025387>
- Finneran, J. J., Schlundt, C. E., Bowman, V., & Jenkins, K. (2023). Dolphins reduce hearing sensitivity in anticipation of repetitive impulsive noise exposures. *The Journal of the Acoustical Society of America*, 153(6), 3372. <https://doi.org/10.1121/10.0019751>
- Houser, D. S., Yost, W., Burkard, R., Finneran, J. J., Reichmuth, C., & Mulsow, J. (2017). A review of the history, development and application of auditory weighting functions in humans and marine mammals. *The Journal of the Acoustical Society of America*, 141(3), 1371-1413. <https://doi.org/10.1121/1.4976086>
- International Organization for Standardization (ISO). (2017). *ISO 18405:2017 underwater acoustics – Terminology*. ISO.
- Kastelein, R. A., Helder-Hoek, L., & Jennings, N. (2018a). Seasonal changes in food consumption, respiration rate, and body condition of a male harbor porpoise (*Phocoena phocoena*). *Aquatic Mammals*, 44(1), 76-91. <https://doi.org/10.1578/AM.44.1.2018.76>
- Kastelein, R. A., Helder-Hoek, L., & Van de Voorde, S. (2017a). Effects of exposure to 53-C sonar playback sounds (3.5-4.1 kHz) on harbor porpoise (*Phocoena phocoena*) hearing. *The Journal of the Acoustical Society of America*, 142(4), 1965-1975. <https://doi.org/10.1121/1.5005613>
- Kastelein, R. A., Helder-Hoek, L., & Van de Voorde, S. (2017b). Hearing thresholds of a male and a female harbor porpoise (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, 142(2), 1006-1010. <https://doi.org/10.1121/1.4997907>
- Kastelein, R. A., Hoek, L., & Gransier, R. (2016). The cumulative effects of exposure to continuous and intermittent sounds on temporary hearing threshold shifts

- induced in a harbor porpoise (*Phocoena phocoena*). In A. N. Popper & A. Hawkins (Eds.), *The effects of noise on aquatic life II: Advances in experimental medicine and biology* (pp. 523–528). Springer Science+Business Media. https://doi.org/10.1007/978-1-4939-2981-8_93
- Kastelein, R. A., Cornelisse, S. A., Huijser, L. A. E., & Helder-Hoek, L. (2020a). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise bands at 63 kHz. *Aquatic Mammals*, 46(2), 167–182. <https://doi.org/10.1578/AM.46.2.2020.167>
- Kastelein, R. A., Gransier, R., Hoek, L., & Olthuis, J. (2012). Temporary threshold shifts and recovery in a harbor porpoise (*Phocoena phocoena*) after octave-band noise at 4 kHz. *The Journal of the Acoustical Society of America*, 132(5), 3525–3537. <https://doi.org/10.1121/1.4757641>
- Kastelein, R. A., Gransier, R., Hoek, L., & Rambags, M. (2013). Hearing frequency thresholds of a harbor porpoise (*Phocoena phocoena*) temporarily affected by a continuous 1.5 kHz tone. *The Journal of the Acoustical Society of America*, 134(3), 2286–2292. <https://doi.org/10.1121/1.4816405>
- Kastelein, R. A., Gransier, R., Schop, J., & Hoek, L. (2015). Effect of intermittent and continuous 6–7 kHz sonar sweep exposures on harbor porpoise (*Phocoena phocoena*) hearing. *The Journal of the Acoustical Society of America*, 137(4), 1623–1633. <https://doi.org/10.1121/1.4916590>
- Kastelein, R. A., Schop, J., Gransier, R., & Hoek, L. (2014a). Frequency of greatest temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) depends on the noise level. *The Journal of the Acoustical Society of America*, 136(3), 1410–1418. <https://doi.org/10.1121/1.4892794>
- Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Defiliet, L. N., & Huijser, L. A. E. (2020b). Temporary threshold shift in a second harbor porpoise (*Phocoena phocoena*) after exposure to a noise band at 1.5 kHz and a 6.5 kHz continuous wave. *Aquatic Mammals*, 46(5), 431–443. <https://doi.org/10.1578/AM.46.5.2020.431>
- Kastelein, R. A., Helder-Hoek, L., Cornelisse, S., Huijser, L. A. E., & Gransier, R. (2019a). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise band at 32 kHz. *Aquatic Mammals*, 45(5), 549–562. <https://doi.org/10.1578/AM.45.5.2019.549>
- Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., Huijser, L. A. E., & Gransier, R. (2020c). Temporary hearing threshold shift at ecologically relevant frequencies in a harbor porpoise (*Phocoena phocoena*) due to exposure to a noise band centered at 88.4 kHz. *Aquatic Mammals*, 46(5), 444–453. <https://doi.org/10.1578/AM.46.5.2020.444>
- Kastelein, R. A., Helder-Hoek, L., Covi, J., Terhune, J. M., & Klump, G. (2021a). Masking release at 4 kHz in harbor porpoises (*Phocoena phocoena*) associated with sinusoidal amplitude-modulated masking noise. *The Journal of the Acoustical Society of America*, 150(3), 1721–1732. <https://doi.org/10.1121/10.0006103>
- Kastelein, R. A., Helder-Hoek, L., Jennings, N., van Kester, R., & Huisman, R. (2018b). Reduction in body mass and blubber thickness of harbor porpoises (*Phocoena phocoena*) due to near-fasting for 24 hours in four seasons. *Aquatic Mammals*, 45(1), 37–47. <https://doi.org/10.1578/AM.45.1.2019.37>
- Kastelein, R. A., Helder-Hoek, L., Van Acoleyen, L., Defiliet, L. N., & Terhune, J. M. (2024). Temporary hearing threshold shift and testing the equal-energy hypothesis in a harbor porpoise (*Phocoena phocoena*) after exposure to a continuous noise band at 8 kHz, and a revised TTS-onset function. *Aquatic Mammals*, 50(5), 445–459. <https://doi.org/10.1578/AM.50.5.2024.445>
- Kastelein, R. A., Helder-Hoek, L., van Kester, R., Huisman, R., & Gransier, R. (2019b). Temporary hearing threshold shift in harbor porpoises (*Phocoena phocoena*) due to one-sixth-octave noise band at 16 kHz. *Aquatic Mammals*, 45(3), 280–292. <https://doi.org/10.1578/AM.45.3.2019.280>
- Kastelein, R. A., Hoek, L., Gransier, R., Rambags, M., & Claeys, N. (2014b). Effect of level, duration, and inter-pulse interval of 1–2 kHz sonar signal exposures on harbor porpoise hearing. *The Journal of the Acoustical Society of America*, 136(1), 412–422. <https://doi.org/10.1121/1.4883596>
- Kastelein, R. A., Helder-Hoek, L., Defiliet, L. N., Huijser, L. A. E., Terhune, J. M., & Gransier, R. (2021b). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to one-sixth-octave noise bands centered at 2 and 4 kHz: Effect of duty cycle and testing the equal-energy hypothesis. *Aquatic Mammals*, 47(4), 394–418. <https://doi.org/10.1578/AM.47.4.2021.394>
- Kastelein, R. A., Helder-Hoek, L., Defiliet, L. N., Kuiphof, F., Huijser, L. A. E., & Terhune, J. M. (2022). Temporary hearing threshold shift in California sea lions (*Zalophus californianus*) due to one-sixth-octave noise bands centered at 8 and 16 kHz: Effect of duty cycle and testing the equal-energy hypothesis. *Aquatic Mammals*, 48(1), 36–58. <https://doi.org/10.1578/AM.48.1.2022.36>
- Kastelein, R. A., Helder-Hoek, L., Cornelisse, S. A., von Benda-Beckmann, A. M., Lam, F-P. A., de Jong, C. A., & Ketten, D. R. (2020d). Lack of reproducibility of temporary hearing threshold shifts in a harbor porpoise after exposure to repeated airgun sounds. *The Journal of the Acoustical Society of America*, 148(2), 556–565. <https://doi.org/10.1121/10.0001668>
- Lucke, K., Siebert, U., Lepper, P. A., & Blanchet, M-A. (2009). Temporary shift in masked hearing thresholds in a harbor porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. *The Journal of the Acoustical Society of America*, 125(6), 4060–4070. <https://doi.org/10.1121/1.3117443>
- Mooney, T. A., Nachtigall, P. E., & Vlachos, S. (2009). Sonar-induced temporary hearing loss in dolphins. *Biological Letters*, 5(4), 565–567. <https://doi.org/10.1098/rsbl.2009.0099>
- Mulsow, J., Schlundt, C. E., Strahan, M. G., & Finneran, J. J. (2023). Bottlenose dolphin temporary threshold shift following exposure to 10-ms impulses centered at 8 kHz. *The Journal of the Acoustical Society of America*, 154(2), 1287–1298. <https://doi.org/10.1121/10.0020726>

- Nachtigall, P. E., & Supin, A. Ya. (2013). A false killer whale reduces its hearing sensitivity when a loud sound is preceded by a warning. *Journal of Experimental Biology*, 216(16), 3062-3070. <https://doi.org/10.1242/jeb.085068>
- Nachtigall, P. E., Supin, A. Ya., Pacini, A. F., & Kastelein, R. A. (2018). Four odontocete species change hearing levels when warned of impending loud sound. *Integrative Zoology*, 13(2), 160-165. <https://doi.org/10.1111/1749-4877.12286>
- National Marine Fisheries Service (NMFS). (2016). *Technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing: Underwater acoustic thresholds for onset of permanent and temporary threshold shifts* (NOAA Technical Memorandum NMFS-OPR-55). National Oceanic and Atmospheric Administration, U.S. Department of Commerce. www.nmfs.noaa.gov/pr/publications/techmemos.htm
- NMFS. (2024). *Update to: Technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing (Version 3.0): Underwater and in-air criteria for onset of auditory injury and temporary threshold shifts* (NOAA Technical Memorandum NMFS-OPR-71). National Oceanic and Atmospheric Administration, U.S. Department of Commerce. 182 pp.
- Saunders, J. C., Mills, J. H., & Miller, J. D. (1977). Threshold shift in the chinchilla from daily exposure to noise for six hours. *The Journal of the Acoustical Society of America*, 61(2), 558-570. <https://doi.org/10.1121/1.381298>
- Schaffeld, T., Schnitzler, J. G., Ruser, A., Woelfing, B., Baltzer, J., & Siebert, U. (2020). Effects of multiple exposures to pile driving noise on harbor porpoise hearing during simulated flights—An evaluation tool. *The Journal of the Acoustical Society of America*, 147(2), 685-697. <https://doi.org/10.1121/10.0000595>
- Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., Nowacek, D. P., & Tyack, P. L. (2019). Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. *Aquatic Mammals*, 45(2), 125-232. <https://doi.org/10.1578/AM.45.2.2019.125>
- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Jr., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., & Tyack, P. L. (2007). Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquatic Mammals*, 33(4), 411-521. <https://doi.org/10.1578/AM.33.4.2007.411>
- Tougaard, J., Beedholm, K., & Madsen, P. T. (2022). Thresholds for noise induced hearing loss in harbor porpoises and phocid seals. *The Journal of the Acoustical Society of America*, 151(6), 4252-4263. <https://doi.org/10.1121/10.0011560>
- Tougaard, J., Wright, A. J., & Madsen, P. T. (2015). Cetacean noise criteria revisited in the light of proposed exposure limits for harbour porpoise. *Marine Pollution Bulletin*, 90(1-2), 196208. <https://doi.org/10.1016/j.marpolbul.2014.10.051>
- von Benda-Beckmann, A. M., Kastelein, R. A., Lam, F. P. A., de Jong, C. A. F., Wensveen, P. J., & Ketten, D. R. (2024). Susceptibility of harbor porpoise hearing to intermittent sound exposures. In A. N. Popper, J. A. Sisneros, A. D. Hawkins, & F. Thomsen (Eds.), *The effects of noise on aquatic life: Principles and practical considerations* (pp. 1155-1178). Springer. https://doi.org/10.1007/978-3-031-10417-6_177-1
- Ward, W. D. (1991). The role of intermittence in PTS. *The Journal of the Acoustical Society of America*, 90(1), 164-169. <https://doi.org/10.1121/1.401310>
- Ward, W. D., Cushing, E. M., & Burns, E. M. (1976). Effective quiet and moderate TTS: Implications for noise exposure standards. *The Journal of the Acoustical Society of America*, 59(1), 160-165. <https://doi.org/10.1121/1.380835>
- Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Donate, L., Shearer, J., Sveegaard, S., Miller, L. A., Siebert, U., & Madsen, P. T. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, 26(11), 1441-1446. <https://doi.org/10.1016/j.cub.2016.03.069>