*Aquatic Mammals* 2019, *45*(5), 549-562, DOI 10.1578/AM.45.5.2019.549

# Temporary Hearing Threshold Shift in Harbor Porpoises (*Phocoena phocoena*) Due to One-Sixth-Octave Noise Band at 32 kHz

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## Abstract

Temporary hearing threshold shift (TTS) caused by fatiguing sounds in the 1.5 to 16 kHz range has been documented in harbor porpoises (*Phocoena phocoena*). To assess impacts of anthropogenic noise on porpoise hearing, TTS needs to be investigated for other frequencies, as susceptibility appears to depend on the frequency of the fatiguing sound. TTS was quantified after two porpoises (Porpoises F05 and M06) were exposed for 1 hour to a continuous one-sixth-octave noise band centered at 32 kHz, at average received sound pressure levels of 118 to 148 dB re 1 µPa, and at a sound exposure level (SEL) range of 154 to 184 dB re 1 µPa$^2$s. Hearing thresholds for 32, 44.8, and 63 kHz tonal signals were determined before and after exposure to quantify initial TTS and recovery. Porpoise M06's hearing was tested 1 to 4 min after exposure. At 32 kHz, the lowest SEL that resulted in significant $TTS_{1-4}$ (3.4 dB) was 166 dB re 1 µPa$^2$s. At 44.8 kHz, the lowest SEL that resulted in significant $TTS_{1-4}$ (5.2 dB) was 178 dB re 1 µPa$^2$s. The highest $TTS_{1-4}$ (18.3 dB) occurred at 44.8 kHz after exposure to 184 dB SEL. Porpoise F05's hearing was tested 12 to 16 min after exposure. At 32 kHz, the lowest SEL that resulted in significant $TTS_{12-16}$ (3.5 dB) was 184 dB re 1 µPa$^2$s. At 44.8 kHz, the lowest SEL that resulted in significant $TTS_{12-16}$ (1.2 dB) was 178 dB re 1 µPa$^2$s. The highest $TTS_{12-16}$ (8.2 dB) occurred in Porpoise F05 at 44.8 kHz after exposure to 184 dB SEL. At 63 kHz, no TTS could be elicited in either animal. Considering that Porpoise F05 had more time than Porpoise M06 for recovery, the susceptibility of the two porpoises to TTS after exposure to sounds of 32 kHz was similar. In the range investigated so far (1.5 to 32 kHz), susceptibility to TTS appears to increase with increasing frequency below ~6.5 kHz, and to decrease with increasing frequency above ~6.5 kHz.

**Key Words:** anthropogenic noise, audiogram, frequency weighting, harbor porpoise, hearing, hearing damage, hearing sensitivity, odontocete, temporary threshold shift, TTS

## Introduction

The effects of underwater noise from vessel traffic, pile driving, seismic surveys, detonations, and sonar on harbor porpoises (*Phocoena phocoena*) are of particular interest because this odontocete species has a wide distribution area in the coastal waters of the northern hemisphere (Bjorge & Tolley, 2008) and also has acute hearing (i.e., low hearing thresholds) in a wide frequency range (Kastelein et al., 2017b). The harbor porpoise appears to be more susceptible to temporary hearing threshold shifts (TTS) caused by sounds than other tested odontocete species (Finneran, 2015; Tougaard et al., 2016; Houser et al., 2017).

Susceptibility to TTS depends not only on the fatiguing sound's received sound pressure level (SPL) and the exposure duration, but also on the sound's frequency (see Finneran, 2015), so it is important to quantify the effect of various fatiguing sound frequencies on the hearing of the harbor porpoise (National Marine Fisheries Service [NMFS], 2016; Houser et al., 2017). For the regulation of underwater acoustic levels, complete equal-TTS susceptibility contours are desirable, covering the entire frequency range of hearing in the harbor porpoise (0.5 to 140 kHz). Within the 1 to 16 kHz bandwidth, TTS susceptibility has been established (Kastelein et al., 2012, 2013, 2014a, 2014b, 2015a, 2015b, 2017a, 2019): Below 6.5 kHz, TTS susceptibility increased with frequency; but above 6.5 kHz, TTS susceptibility appeared to decrease with frequency, and it is important to know if the decrease in TTS susceptibility continues when the frequency of sound porpoises are exposed to increases above 16 kHz.

The goal of the present study is to increase the known frequency range of TTS susceptibility for harbor porpoises (see Houser et al., 2017) in order to describe the relationship between TTS susceptibility and the frequency of the fatiguing sound. Therefore, TTS and recovery of hearing were quantified in two harbor porpoises after they were exposed to a noise band centered at 32 kHz. The results of the present study contribute to the quantification of equal-TTS susceptibility for the whole functional hearing range of the harbor porpoise. Once this quantification is complete, it will be possible to model research-based auditory weighting curves for odontocetes that echolocate at high frequencies (Wensveen et al., 2014; Southall et al., 2019).

## Methods

### *Study Animals and Site*

The two stranded and rehabilitated harbor porpoises that were used as study animals (~7-y-old female Porpoise F05 and ~4-y-old male Porpoise M06) had been used in a previous study of TTS induced by 16 kHz sounds (Kastelein et al., 2019). The hearing of the study animals in the frequency range tested in the present study (32 to 63 kHz) was probably representative of the hearing of similar-aged harbor porpoises (Kastelein et al., 2017b). The body weights and sizes of the porpoises, and the husbandry conditions are described by Kastelein et al. (2019).

The study was conducted at the SEAMARCO Research Institute, the Netherlands. The animals were kept in a quiet pool complex designed and built for acoustic research, consisting of an outdoor pool (12 m × 8 m; 2 m deep) in which they were exposed to fatiguing sound, connected via a channel to an indoor pool (8 m × 7 m; 2 m deep) in which hearing tests were conducted. For details of the pool, equipment, and water flow, see Kastelein et al. (2019).

### *Acoustics*

*SPL Measurement Equipment and Ambient Noise*—Acoustical terminology follows the standards for underwater acoustics (International Organization for Standardization, 2017). The ambient noise was measured and the fatiguing sound and hearing test signals were calibrated every 2 mo during the study period; for details, see Kastelein et al. (2019). 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 very low; the one-third-octave level increased from 55 dB re 1 μPa at 200 Hz to 60 dB re 1 μPa at 5 kHz. It was similar to the background level at which previous TTS studies had been conducted (see Kastelein et al., 2012, 2019).

*Fatiguing Sound*—The digitized fatiguing sound was produced, transmitted, calibrated, and checked before each exposure session as described by Kastelein et al. (2019). The fatiguing sound consisted of a continuous (duty cycle 100%), one-sixth-octave Gaussian white noise band, centered at 32 kHz (bandwidth: 29.7 to 33.4 kHz). Ideally, a 32 kHz tone would have been used, but in a pool, a pure tone can lead to a very heterogeneous sound field. Therefore, instead of a tonal signal, a very narrow noise band was selected. To determine the fatiguing sound's distribution in the outdoor pool, the SPL of the noise band was measured at 76 locations in the horizontal plane (on a horizontal grid of 1 m × 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 228 measurements in the pool. There were differences in mean SPL per depth (see Figure 1 for an example of the SPL distribution in the pool with mean levels per depth of 145 ± 1 dB at 0.5 m, 148 ± 3 dB at 1.0 m, and 150 ± 2 dB at 1.5 m deep).

To determine the average SPL received by the study animals, the area where they swam during exposure periods (quantified following the methods of Kastelein et al., 2019) was compared to the fatiguing sound's SPL distribution in the pool. The animals swam throughout the entire outdoor pool during exposure to fatiguing sounds, so the average fatiguing sound SPL (average of power sum of 228 measurements in the outdoor pool) was taken to be representative of the SPL received by them.

*Hearing Test Signals*—Linear upsweeps with a duration of 1 s were used as the psychophysical hearing test signals that the study animals were asked to detect before and after exposure to the fatiguing sound (see Kastelein et al., 2019). The center frequencies tested were 32 kHz (the center frequency of the fatiguing sound), 44.8 kHz (half an octave higher than the center frequency), and 63 kHz (one octave higher than the center frequency). The hearing test signals were generated digitally, calibrated, and checked daily, as explained by Kastelein et al. (2019).

### *Experimental Procedures*

One total noise exposure test, consisting of (1) pre-exposure hearing tests starting at 0830 h, (2) fatiguing sound exposure for 1 h in the morning or early afternoon, and (3) a number of post-noise exposure hearing tests in the afternoon, was conducted per day. Pre-exposure hearing tests were performed in the indoor pool, first with Porpoise M06, and then with Porpoise F05. During the hour of fatiguing sound exposure, the animals were in the outdoor pool. Data were collected from January to July 2017, following the

**0.5 m**

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 145 | 144 | 144 | 145 | 144 | 145 | 144 | 145 | 144 | 144 | 145 | |
| 6 | 144 | 145 | 144 | 144 | 146 | 146 | 146 | 144 | 144 | 145 | 144 | |
| 5 | 144 | 143 | 143 | 146 | 145 | 145 | 145 | 146 | 143 | 143 | 144 | |
| 4 | 144 | 144 | 143 | 142 | 145 | | 145 | 142 | 143 | 144 | 144 | |
| 3 | 144 | 143 | 145 | 143 | 144 | 145 | 144 | 143 | 145 | 143 | 144 | |
| 2 | 142 | 144 | 144 | 145 | 147 | 147 | 147 | 145 | 144 | 144 | 142 | |
| 1 | 142 | 143 | 145 | 146 | 145 | 149 | 145 | 146 | 145 | 143 | 142 | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |

a)

**1.0 m**

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 145 | 145 | 145 | 145 | 145 | 148 | 145 | 145 | 145 | 145 | 145 | |
| 6 | 146 | 146 | 146 | 145 | 147 | 147 | 147 | 145 | 146 | 146 | 146 | |
| 5 | 145 | 144 | 145 | 146 | 148 | 148 | 148 | 146 | 145 | 144 | 145 | |
| 4 | 146 | 147 | 146 | 145 | 146 | T | 146 | 145 | 146 | 147 | 146 | |
| 3 | 146 | 145 | 146 | 148 | 144 | 159 | 154 | 148 | 146 | 145 | 146 | |
| 2 | 144 | 146 | 147 | 150 | 143 | 152 | 153 | 150 | 147 | 146 | 144 | |
| 1 | 145 | 147 | 149 | 149 | 141 | 148 | 151 | 149 | 149 | 147 | 145 | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |

b)

**1.5 m**

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 147 | 146 | 149 | 151 | 149 | 150 | 149 | 151 | 149 | 146 | 147 | |
| 6 | 147 | 148 | 148 | 152 | 154 | 152 | 154 | 152 | 148 | 148 | 147 | |
| 5 | 148 | 149 | 148 | 153 | 155 | 148 | 155 | 153 | 148 | 149 | 148 | |
| 4 | 146 | 147 | 152 | 153 | 152 | | 152 | 153 | 152 | 147 | 146 | |
| 3 | 150 | 150 | 148 | 152 | 150 | 147 | 150 | 152 | 148 | 150 | 150 | |
| 2 | 145 | 150 | 150 | 150 | 149 | 146 | 149 | 150 | 150 | 150 | 145 | |
| 1 | 145 | 148 | 150 | 151 | 150 | 147 | 150 | 151 | 150 | 148 | 145 | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |

c)

**Figure 1.** The distribution of one of the five tested SPLs (dB re 1 µPa) in the harbor porpoises' (*Phocoena phocoena*) outdoor pool of the continuous (100% duty cycle) one-sixth-octave noise band centered at 32 kHz (the fatiguing sound), measured at depths of (a) 0.5 m, (b) 1.0 m, and (c) 1.5 m. T = location of the transducer, which was placed at 1 m depth in the center of the pool. The numbers in bold in the grey fields indicate 1 m markings on the side of the pool. The average SPL of all 228 SPL measurements is based on the power sum and was, in this case, 148 ± 3 dB re 1 µPa so that exposure for 1 h resulted in a sound exposure level (SEL) of 184 dB re 1 µPa$^2$s.

protocol developed and explained by Kastelein et al. (2019).

Porpoise M06 was always tested immediately after the fatiguing sound stopped, and Porpoise F05 was always tested after Porpoise M06. The order in which the porpoises were tested was kept constant in order to avoid delays before the first animal was tested, as it was considered important to commence testing within 1 min of the end of exposure. Porpoise M06's hearing thresholds were measured during post-sound exposure (PSE) periods at 1 to 4 min ($PSE_{1-4}$); 4 to 8 min ($PSE_{4-8}$); 8 to 12 min ($PSE_{8-12}$); 60 min if hearing had not recovered after 12 min ($PSE_{60}$); and if hearing had not recovered after 60 min, at 120 min ($PSE_{120}$) after the sound exposure had ended. Porpoise F05's hearing was tested at 12 to 16 min ($PSE_{12-16}$); 16 to 20 min ($PSE_{16-20}$); 20 to 24 min ($PSE_{20-24}$); at 72 min if hearing had not recovered after 24 min ($PSE_{72}$); and if hearing had not recovered after 72 min, at 132 min ($PSE_{132}$) after the fatiguing sound had stopped (see Kastelein et al., 2019). Hearing tests stopped after the hearing threshold was less than 2 dB above the pre-exposure threshold level (this was defined as the hearing being fully recovered). The different average received SPLs of the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz) were tested in random order (5 SPLs for hearing test sound of 32 kHz, 4 SPLs for 44.8 kHz, and 2 SPLs for 63 kHz). Each average received SPL was tested at least four times, except 166 dB SEL at 44.8, which was tested only once due to time constraints.

Control tests were conducted in the same way and under the same conditions as noise exposure tests but without the fatiguing sound exposure. Each control test started with a pre-exposure hearing test session and was followed by exposure to the normal ambient noise in the outdoor pool for at least 1 h with all equipment in place. The transducer was placed in the pool as usual but did not emit sound. Post-ambient exposure (PAE; control) hearing test sessions were then performed. Porpoise M06 was tested 1 to 4 ($PAE_{1\text{-}4}$), 4 to 8 ($PAE_{4\text{-}8}$), and 8 to 12 ($PAE_{8\text{-}12}$) min after the ambient noise exposure period ended, and Porpoise F05 was tested 12 to 16 ($PAE_{12\text{-}16}$), 16 to 20 ($PAE_{16\text{-}20}$), and 20 to 24 ($PAE_{20\text{-}24}$) min after ambient exposure. Four control tests were conducted per hearing test frequency, and they were randomly dispersed among the fatiguing sound exposure tests. On each test day, either a noise exposure test or a control test was conducted.

*Hearing Test Procedures*

A hearing test trial began with one of the harbor porpoises at the start/response buoy. In response to a hand signal, he or she swam to a listening station. The porpoise stationed there for a random period of between 6 and 12 s before the signal operator produced the test signal (in signal-present trials); the porpoise then swam to the start/response buoy to indicate that it had heard the signal. A switch from a test signal level that the porpoise responded to (a hit) to a level that he or she did not respond to (a miss), and vice versa, was called a *reversal*. Each complete hearing test session consisted of ~25 trials (two thirds signal-present and one third signal-absent trials) and lasted for up to 12 min (subdivided into three 4-min periods in the first PSE or PAE session of each animal). In signal-absent trials, a whistle was blown between 6 and 12 s after the animal had stationed on the listening station. The whistle was always heard, and the porpoise always reacted correctly to it by swimming towards the start/response buoy near the trainer where it would receive a fish reward. Only $PSE_{1\text{-}4}$, $PSE_{12\text{-}16}$, $PAE_{1\text{-}4}$, and $PAE_{12\text{-}16}$ hearing session periods with three or more reversals were used for analysis. The methodology is described in detail by Kastelein et al. (2012, 2019).

*Data Analysis*

The mean pre-stimulus response rate for both signal-present and signal-absent trials was calculated as the number of pre-stimuli as a percentage of all trials in each hearing test period. The pre-exposure mean 50% hearing threshold ($PE_{50\%}$) for a hearing test sound was determined by calculating the mean SPL of all (usually 10) reversal pairs obtained during the pre-exposure hearing session.

TTSs for Porpoise M06 after the sound exposure sessions (1 to 4, 4 to 8, 8 to 12, 60, and 120 min) were calculated by subtracting $PE_{50\%}$ from the mean 50% hearing thresholds during $PSE_{1\text{-}4}$, $PSE_{4\text{-}8}$, $PSE_{8\text{-}12}$, $PSE_{60}$, and $PSE_{120}$ periods of the same day. TTSs for Porpoise F05 were calculated in the same way after the sound exposure sessions (12 to 16, 16 to 20, 20 to 24, 72, and 132 min; see Kastelein et al., 2019).

TTSs in the control sessions were calculated by subtracting the mean 50% hearing thresholds obtained during pre-ambient exposure periods from the mean 50% hearing thresholds obtained during the PAE periods of the same day. No TTS occurred in control sessions, so this calculation was close to zero.

We define the onset of TTS as occurring at the lowest SEL at which a statistically significant difference could be detected between the TTS due to the fatiguing sound exposures and the TTS as measured after the control exposures (which was close to zero). The level of significance was established by conducting a one-way ANOVA on the TTS separately for each harbor porpoise and for each hearing test frequency, with the factor SPL (including zero as the control), followed by Dunnett's (1964) multiple comparisons between the control and the other levels of the factor. All analyses were conducted in *Minitab 18*, and the data were conformed to the underlying assumptions of the tests applied (Zar, 1999).

## Results

*Pre-Stimulus Response Rate*

After the 1-h noise exposure periods, the harbor porpoises were always willing to participate in the hearing tests. In a few sessions, the test porpoise moved too slowly from the outdoor (exposure) pool to the indoor (testing) pool, so the minimum of three reversals could not be obtained in the first time period after the fatiguing sound had stopped ($PSE_{1\text{-}4}$ for Porpoise M06 and $PSE_{12\text{-}16}$ for Porpoise F05); data from these sessions were discarded. The mean pre-stimulus response rate for both signal-present and signal-absent trials in the hearing tests varied between 0.4 and 5.6% for Porpoise M06, and between 4.0 and 12.6% for Porpoise F05 (Table 1). The pre-stimulus response rates in the post-exposure periods did not differ much from

**Table 1.** The pre-stimulus response rates of the harbor porpoises (*Phocoena phocoena*) in hearing tests during the pre-exposure periods, after exposure to the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz; PSE = post-sound exposure), and after exposure to ambient noise (control; PAE = post-ambient exposure). All exposure SPLs and hearing test frequencies were pooled for the calculation of percentages. Sample sizes (total number of hearing trials per period) are shown in parentheses.

| Porpoise M06 | Period | | | | | |
|---|---|---|---|---|---|---|
| Fatiguing sound | Pre-exposure | $PSE_{1-4}$ | $PSE_{4-8}$ | $PSE_{8-12}$ | $PSE_{60}$ | $PSE_{120}$ |
| | 1.6% (820) | 2.6% (307) | 2.2% (359) | 2.0% (357) | 1.0% (102) | 5.6% (18) |
| Control | Pre-exposure | $PAE_{1-4}$ | $PAE_{4-8}$ | $PAE_{8-12}$ | | |
| | 0.4% (226) | 3.5% (85) | 2.2% (89) | 2.1% (95) | | |
| **Porpoise F05** | **Period** | | | | | |
| Fatiguing sound | Pre-exposure | $PSE_{12-16}$ | $PSE_{16-20}$ | $PSE_{20-24}$ | $PSE_{72}$ | $PSE_{132}$ |
| | 7.2% (891) | 4.0% (248) | 6.4% (314) | 4.0% (351) | 4.3% (70) | 4.8% (42) |
| Control | Pre-exposure | $PAE_{12-16}$ | $PAE_{16-20}$ | $PAE_{20-24}$ | | |
| | 6.6% (241) | 6.8% (74) | 12.6% (87) | 6.6% (91) | | |

those in the pre-exposure periods and control periods (e.g., these low pre-stimulus response levels are typical for hearing studies at SEAMARCO due to the low noise levels, precise food and body weight control, and the experience of the animals with hearing tests).

*Effect of SPL on TTS*

The ANOVAs showed that the $TTS_{1-4}$ and $TTS_{12-16}$ were significantly affected by the fatiguing sound's SPL when the hearing test frequencies were 32 and 44.8 kHz. Post-hoc Dunnett's comparisons with the controls revealed that the statistically significant onset of TTS varied depending on the animal and the hearing test frequency (Tables 2 & 3).

*TTS in Male Porpoise M06*

With a hearing test signal of 32 kHz, statistically significant $TTS_{1-4}$ occurred in Porpoise M06 after exposure to SELs of 166 dB re 1 $\mu Pa^2s$ and higher (Table 2; Figure 2a); hearing was recovered within 12 min, even after the highest fatiguing sound level tested (Figure 3a). With a hearing test signal of 44.8 kHz, statistically significant $TTS_{1-4}$ occurred after exposure to SELs of 178 dB re 1 $\mu Pa^2s$ and higher (Table 2; Figure 2a). Recovery of hearing occurred within 60 min for exposures up to an SEL of 178 dB re 1 $\mu Pa^2s$, and between 60 and 120 min after exposure to an SEL of 184 dB re 1 $\mu Pa^2s$ (Figure 3b). The critical level (above which the TTS increased strongly) appeared to be around 178 dB re 1 $\mu Pa^2s$. With a hearing test signal of 63 kHz, no $TTS_{1-4}$ occurred, even after exposure to an SEL of 184 dB re 1 $\mu Pa^2s$ (Table 2; Figure 2a). The control sessions showed that the hearing thresholds for all three hearing test signals before and after exposure for 1 h to the low ambient noise were very similar (Figure 3; Table 3).

*TTS in Female Porpoise F05*

With a hearing test signal of 32 kHz, statistically significant $TTS_{12-16}$ occurred in Porpoise F05 after exposure to an SEL of 184 dB re 1 $\mu Pa^2s$ (Table 2; Figure 2b); hearing was recovered within 24 min (Figure 4a). At 44.8 kHz, statistically significant $TTS_{12-16}$ occurred only after exposure to an SEL of 178 dB re 1 $\mu Pa^2s$ or higher (Table 2; Figure 2b). After exposure to the highest SEL (184 dB re 1 $\mu Pa^2s$), recovery of hearing occurred within 132 min (Figure 4b). The critical level (above which the TTS increased strongly) appeared to be around 178 dB re 1 $\mu Pa^2s$. At 63 kHz, no $TTS_{12-16}$ occurred, even at the highest SEL of 184 dB re 1 $\mu Pa^2s$ (Table 2; Figure 2b). The control sessions showed that the hearing thresholds for all three hearing test signal frequencies before and after exposure for 1 h to the low ambient noise were very similar (Figure 4; Table 3).

**Table 2.** Results of one-way ANOVAs on $TTS_{1-4}$ for Porpoise M06 and $TTS_{12-16}$ for Porpoise F05 after exposure for 1 h to the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz) with factor: fatiguing sound level (in dB). Exact *p* values are shown alongside the results of Dunnett's multiple comparisons with the control and the statistically significant TTS onset (indicated in bold in the last column) for each hearing test frequency.

| Porpoise | TTS (min after sound stopped) | Hearing test freq. (kHz) | ANOVA results F values (degrees of freedom), *p* values | SELs (dB) statistically similar to control | SELs (dB) significantly different from control |
|---|---|---|---|---|---|
| M06 | 1-4 | 32 | $F_{5,19} = 26.12$ $p = 0.000$ | 154, 160 | **166**, 178, 184 |
| M06 | 1-4 | 44.8 | $F_{4,12} = 78.97$ $p = 0.000$ | 166, 172 | **178**, 184 |
| M06 | 1-4 | 63 | $F_{2,9} = 2.58$ $p = 0.130$ NS | 166, 184 | None; no TTS |
| F05 | 12-16 | 32 | $F_{5,18} = 9.07$ $p = 0.000$ | 154, 160, 166, 178 | **184***|
| F05 | 12-16 | 44.8 | $F_{4,13} = 54.87$ $p = 0.000$ | 166, 172 | **178**, 184* |
| F05 | 12-16 | 63 | $F_{2,9} = 4.60$ $p = 0.042$ | 166 | **184†**, no TTS |

*TTS in Porpoise F05 was measured 12 to 16 min after the exposure to the fatiguing sound stopped, so if TTS occurred during the exposure, some hearing recovery had probably taken place during the first 12 min after the sound stopped.
†TTS in Porpoise F05 when she was exposed to fatiguing sound at 184 dB SEL and tested at 63 kHz was lower (marginally significant) than in the control (see Figure 2b), so, in fact, no TTS occurred. In all other cases where the TTS was significant, it was higher after sound exposure than in the control tests, as expected.

**Table 3.** Mean $TTS_{1-4}$ in Porpoise M06 and $TTS_{12-16}$ in Porpoise F05 after exposure for 1 h to the fatiguing sound (one-sixth-octave noise band centered at 32 kHz) at several SPLs, quantified at hearing test frequencies 32, 44.8, and 63 kHz (the exposure frequency, half an octave higher, and one octave higher than the exposure frequency), with standard deviations (SD), ranges (in parentheses), and sample sizes (*n*). Results from the control sessions show that no TTS occurred.

| Hearing test frequency (kHz) | SPL dB re 1 µPa | SEL dB re 1 µPa²s | Porpoise M06 Mean $TTS_{1-4}$ | Porpoise M06 SD (range) | Porpoise M06 *n* | Porpoise F05 Mean $TTS_{12-16}$ | Porpoise F05 SD (range) | Porpoise F05 *n* |
|---|---|---|---|---|---|---|---|---|
| 32 | Control | Control | 0.6 | 0.7 (0.0-1.6) | 4 | -0.1 | 1.2 (-1.2-1.3) | 4 |
| | 118 | 154 | 0.8 | 1.0 (-0.5-2.0) | 4 | -0.3 | 0.7 (-1.3-0.3) | 4 |
| | 124 | 160 | 2.1 | 0.4 (1.9-2.6) | 4 | 0.2 | 1.0 (-1.0-1.3) | 4 |
| | 130 | 166 | 3.4* | 1.0 (2.3-4.2) | 4 | 0.4 | 1.3 (-1.4-1.3) | 4 |
| | 142 | 178 | 5.4* | 1.5 (4.2-7.6) | 4 | 1.2 | 0.8 (0.4-2.2) | 4 |
| | 148 | 184 | 6.1* | 0.8 (5.2-6.8) | 5 | 3.5* | 0.5 (2.8-4.1) | 4 |
| 44.8 | Control | Control | 0.2 | 0.3 (0.0-0.6) | 4 | -0.8 | 0.9 (-1.9-0.2) | 4 |
| | 130 | 166 | -0.2 | -- | 1 | 0.0 | -- | 1 |
| | 136 | 172 | 0.8 | 0.9 (0.1-2.0) | 4 | 0.4 | 0.7 (-0.6-1.0) | 4 |
| | 142 | 178 | 5.2* | 2.8 (2.5-9.0) | 4 | 1.2* | 0.7 (0.3-1.9) | 5 |
| | 148 | 184 | 18.3* | 1.7 (16.5-20.5) | 4 | 8.2* | 1.4 (6.1-9.3) | 4 |
| 63 | Control | Control | -0.7 | 0.7 (-1.3-0.0) | 4 | 1.0 | 1.4 (-0.4-2.3) | 4 |
| | 130 | 166 | 0.6 | 0.5 (0.1-1.2) | 4 | 0.0 | 0.5 (-0.5-0.7) | 4 |
| | 148 | 184 | 0.1 | 1.0 (-1.4-1.0) | 4 | -1.1† | 0.9 (-1.8- -0.2) | 4 |

*Significant TTS relative to control sessions
†Initial TTS in Porpoise F05 when she was exposed to fatiguing sound at 184 dB SEL was lower (marginally significant) than in the control (see Figure 2b), so, in fact, no TTS occurred.

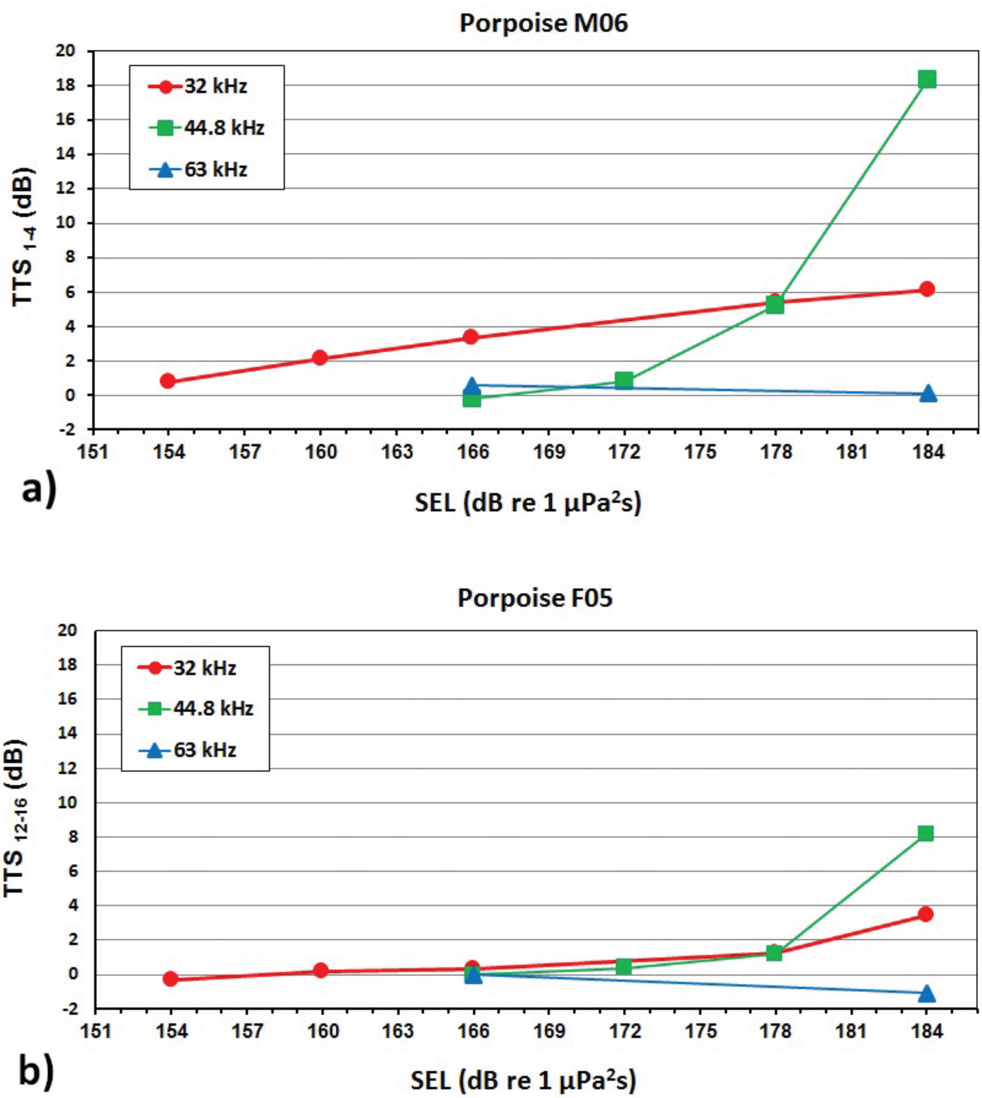


**Figure 2.** (a) $TTS_{1-4}$ in Porpoise M06 and (b) $TTS_{12-16}$ in Porpoise F05 after exposure for 1 h to the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz) at several sound exposure levels (SELs), quantified at hearing test frequencies 32, 44.8, and 63 kHz (the exposure frequency, half an octave higher, and one octave higher than the exposure frequency). Sample size varies per data point shown but is mostly 4 (see Table 3). For average received SPLs (dB re 1 µPa), subtract 36 dB re 1 s from the SEL values. For control values, see Figures 3 & 4 and Table 3.

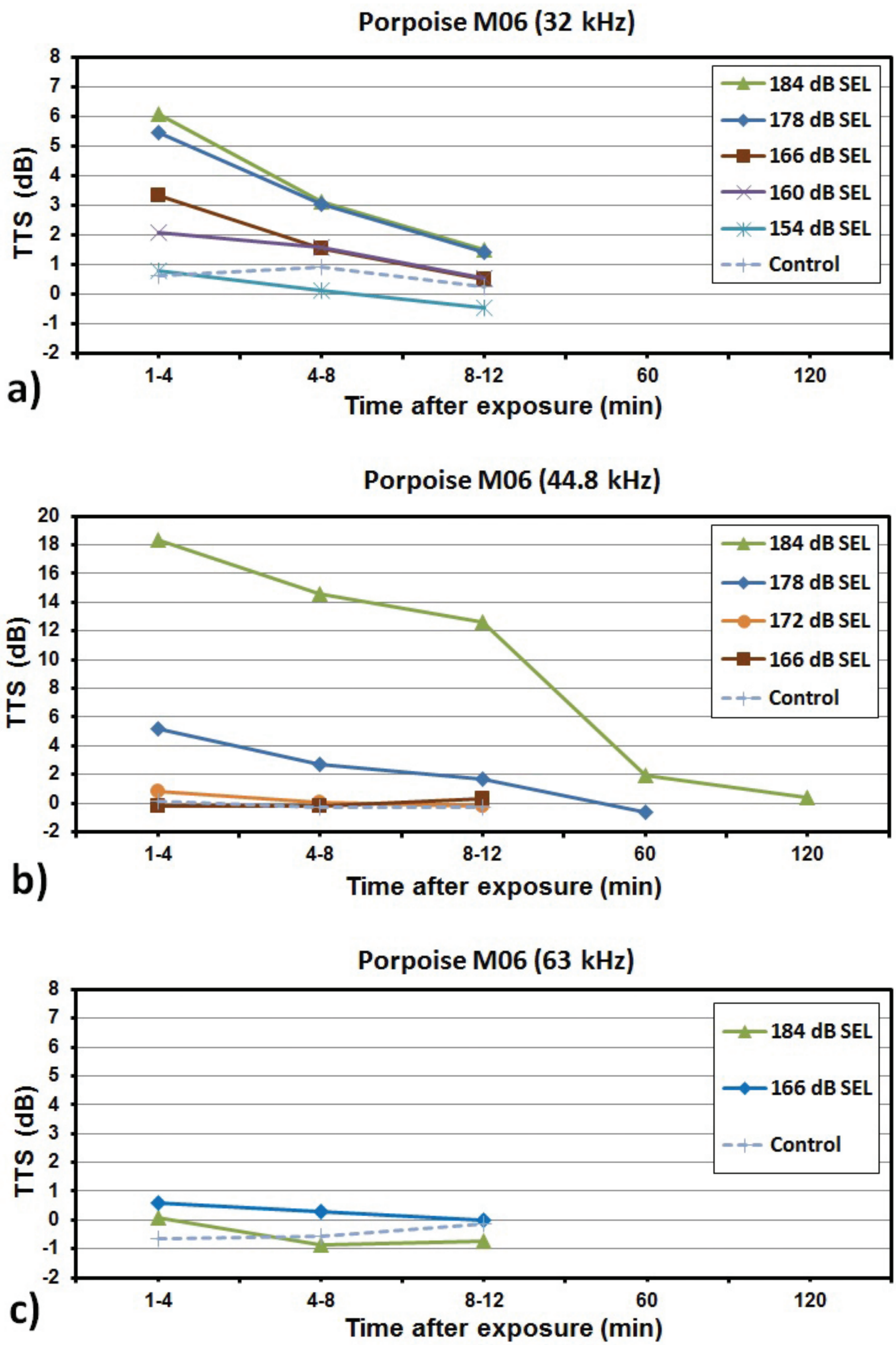


**Figure 3.** Recovery of hearing of Porpoise M06 at (a) 32 kHz, (b) 44.8 kHz, and (c) 63 kHz (no TTS took place, so there was no recovery) after exposure to the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz) at several SELs. For sample sizes and SDs (only for $TTS_{1-4}$), see Table 3. For average received SPLs (dB re 1 µPa), subtract 36 dB re 1 s from the SEL values. Note that the X-axis values are not to scale but depict discrete moments in time.

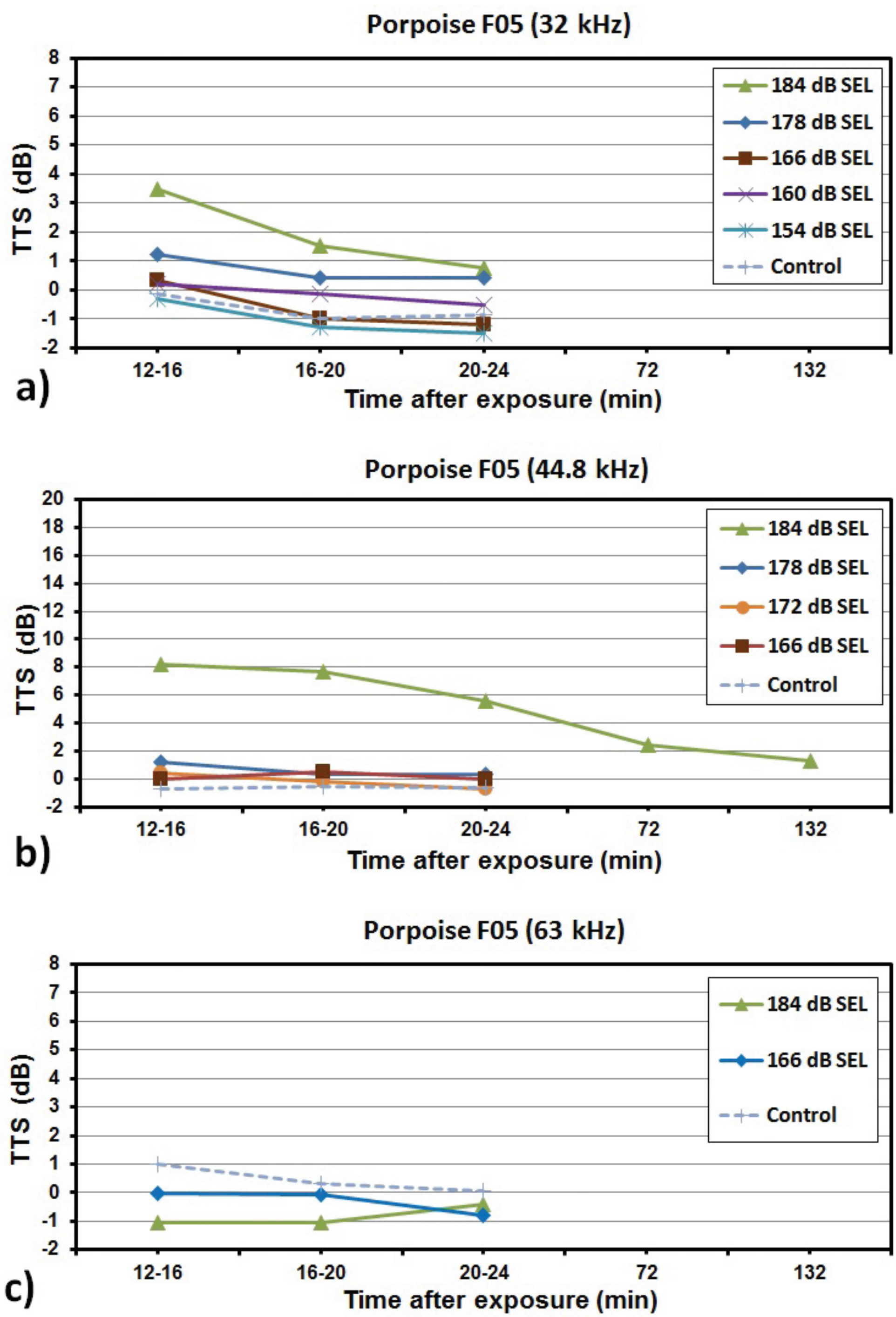


**Figure 4.** Recovery of hearing of Porpoise F05 at (a) 32 kHz, (b) 44.8 kHz, and (c) 63 kHz (no TTS took place, so there was no recovery) after exposure for 1 h to the fatiguing sound (a continuous one-sixth-octave noise band centered at 32 kHz) at several SELs. For sample sizes and SDs (only for $TTS_{12\text{-}16}$), see Table 2. For average received SPLs (dB re 1 µPa), subtract 36 dB re 1 s from the SEL values. Note that the X-axis values are not to scale but depict discrete moments in time.

## Discussion and Conclusions

*Comparison of TTS Between the Study Animals*

Individual differences in susceptibility to TTS cannot be assessed directly for the harbor porpoises in the present study because Porpoise M06 was always tested immediately after the fatiguing sound stopped, and Porpoise F05 was always tested after Porpoise M06 (starting 12 min after the fatiguing sound stopped when her hearing had had time to recover to a certain extent). However, comparison of the $TTS_{8-12}$ measured in Porpoise M06 at the end of his first session (8 to 12 min after the fatiguing sound stopped) with the $TTS_{12-16}$ in Porpoise F05 at the beginning of her first session (12 to 16 min after the fatiguing sound stopped) shows that, for the higher SELs, $TTS_{12-16}$ in Porpoise F05 was ~4 dB greater than $TTS_{8-12}$ in Porpoise M06. Therefore, either Porpoise F05's TTS during the first 4 min after the sound stopped was greater than that of Porpoise M06, Porpoise F05's hearing recovered more slowly than that of Porpoise M06, or both. It is also possible that the observed difference in TTS between the two study animals was related to their slightly different swimming patterns (causing a difference in the SEL they experienced) or to their age difference. Studies on humans and other terrestrial mammals show individual, genetic, and population-level differences in susceptibility to TTS (Kylin, 1960; Kryter et al., 1962; Henderson et al., 1991, 1993; Davis et al., 2003; Spankovich et al., 2014).

*Affected Hearing Frequencies*

Most early TTS studies in marine mammals suggest that the greatest TTS occurs half an octave above the center frequency of the fatiguing noise (Finneran, 2015). The present study supports the findings by Kastelein et al. (2014a, 2019) that the hearing frequency showing the greatest TTS depends on the SEL to which an animal was exposed; but at the higher SELs, the highest TTS was found half an octave above the center frequency of the fatiguing sound. Studies with other odontocete species in which broadband impulsive sounds were used as the fatiguing sound also showed that TTS occurs at frequencies above the peak frequency of the fatiguing sound (Finneran et al., 2002; Lucke et al., 2009; Kastelein et al., 2015a, 2017a). It is likely that broadband exposures at high levels produce broadband TTS with an upward frequency spread, similar to that seen after exposure to pure tones and narrow-band noise (Finneran, 2015).

*Relationship Between the Frequency of the Fatiguing Sound and TTS*

Susceptibility to TTS and its relationship with fatiguing sound frequency can be explored by relating equal-TTS susceptibility data to fatiguing sound frequencies (NMFS, 2016; Houser et al., 2017). Frequency-dependent susceptibility to TTS has been shown for common bottlenose dolphins (*Tursiops truncatus*; Finneran & Schlundt, 2013), Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*; Popov et al., 2011), and belugas (*Delphinapterus leucas*; Popov et al., 2013). Frequency-dependent susceptibility also seems to occur in harbor porpoises. In the present study with the 32-kHz fatiguing sound, 6 dB $TTS_{1-4}$ at 44.8 kHz occurred at a 6 dB higher SEL than that which caused 6 dB $TTS_{1-4}$ after exposure to sounds of 16 kHz in the same porpoise (Kastelein et al., 2019), and at a 20 dB higher SEL than that which caused 6 dB $TTS_{1-4}$ after exposure to sounds of 6 to 7 kHz in another harbor porpoise (identified as Porpoise M02; Kastelein et al., 2014a, using the same psychophysical hearing test technique; Figure 5). Below 6.5 kHz, it appears that susceptibility to TTS increases with increasing frequency; but above 6.5 kHz, it appears that susceptibility to TTS decreases with increasing frequency (based on Kastelein et al., 2019, and the present study). However, there may be individual differences in susceptibility to TTS between Porpoise M02 (exposed to 6 to 7 kHz sweeps; Kastelein et al., 2014a) and Porpoises M06 and F05, which were exposed to a noise band around 16 kHz (Kastelein et al., 2019) and to a noise band centered at 32 kHz (present study). Alternatively, differences in the fatiguing sound type (6 to 7 kHz upsweep vs one-sixth-octave noise band) may have resulted in (or contributed towards) differences in the induced TTSs. The TTS induced in Porpoise M06 when he was exposed in another study to 3.5 to 4.1 kHz 53-C sonar playback sounds (at a slightly lower duty cycle of 96%; Kastelein et al., 2017a) was as expected from TTS studies with Porpoise M02, so, in the 1.5 to 6.5 kHz range, the susceptibility to sound of Porpoise M06 was similar to that of Porpoise M02 (Figure 5).

In most previous TTS studies with harbor porpoises, the fatiguing sounds used differed from those used in the present study. It is unclear whether the hearing frequency (relative to the center frequency of the fatiguing sound) that showed the highest TTS was similar for one-octave noise bands (Kastelein et al., 2012), one-sixth-octave noise bands (Kastelein et al., 2019; present study), narrow-band sweeps (Kastelein et al., 2014b, 2015b), and tonal (continuous wave) sounds (Kastelein et al., 2013, 2014a).

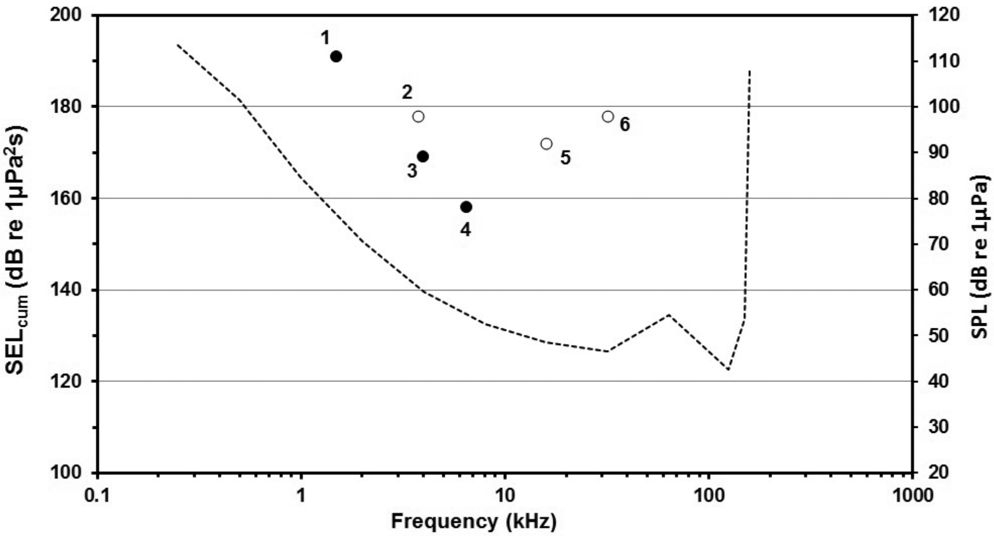


**Figure 5.** The cumulative sound exposure level (SEL$_{cum}$) required to cause a mean TTS$_{1-4}$ of around 6 dB in harbor porpoises after exposure for 1 h to (1) a 1 to 2 kHz sweep at 100% duty cycle (Kastelein et al., 2014b), (2) a 3.5 to 4.1 kHz 53-C sonar playback sound at 96% duty cycle (Kastelein et al., 2017a), (3) a one-octave noise band centered at 4 kHz at 100% duty cycle (Kastelein et al., 2012), (4) a 6.5 kHz tone at 100% duty cycle (Kastelein et al., 2014a), (5) a one-sixth-octave noise band centered at 16 kHz at 100% duty cycle (Kastelein et al., 2019), and (6) a one-sixth-octave noise band centered at 32 kHz at 100% duty cycle (present study). The solid circles are studies with male Porpoise M02, and the open circles are studies with Porpoise M06. Also shown as a dashed line is the audiogram of Porpoise M02 (Kastelein et al., 2010; right-hand Y-axis). All TTSs were measured 1 to 4 min after the fatiguing sound stopped. Numbers 1 through 4 were measured at the center frequency of the fatiguing sound, and numbers 5 and 6 were measured half an octave above the center frequency.

The results of the present and previous TTS studies with harbor porpoises, although representing only part of their total hearing frequency range (1.5 to 32 kHz; Kastelein et al., 2012, 2014a, 2014b, 2017a, 2019), are in agreement with those of Finneran & Schlundt (2013) for bottlenose dolphins and suggest that, like that of bottlenose dolphins, the susceptibility of harbor porpoise hearing to TTS is frequency-dependent. There are very few studies of TTS in harbor porpoises, so TTS susceptibility to fatiguing sounds with frequencies > 32 kHz cannot be predicted. Popov et al. (2011, 2013) showed that susceptibility to TTS in Yangtze finless porpoises did not increase with increasing frequency of the fatiguing sound at frequencies above 45 kHz. The present study suggests that in harbor porpoises that have been exposed to sounds of ~32 kHz, 6 dB TTS occurs at higher SELs than after exposure to sounds of 4, 6.5, and 16 kHz (Kastelein et al., 2012, 2014b, 2015b, 2019; Figure 5). However, although all the TTSs shown in Figure 5 were measured 1 to 4 min after the fatiguing sounds stopped (and are, thus, directly comparable in this regard), the hearing was tested at different frequencies relative to the center frequency of the fatiguing sound. In some studies, the hearing was only measured at the center frequency of the fatiguing sound; and in some cases in which TTS was also measured with hearing test signals half an octave and/or one octave above the center frequency, the 6 dB TTS was sometimes reached first at the center frequency and sometimes at the half an octave above the center frequency. This difference in hearing test signals needs to be taken into account when interpreting the results of the various TTS studies shown in Figure 5. TTS studies in which harbor porpoises are exposed to fatiguing sounds with frequencies > 32 and < 1 kHz are needed to define weighting functions for TTS and permanent hearing threshold shift (PTS) in this species. Also, potential individual differences in TTS susceptibility should be studied by exposing several individuals to the same fatiguing sound.

*Application of Results*

Sufficient TTS data only exists for two odontocete species to try to make a comparison in TTS susceptibility: the bottlenose dolphin (Schlundt et al., 2000; NMFS, 2016; Houser et al., 2017) and the harbor porpoise (see Figure 5). For the bottlenose dolphin, TTS susceptibility has been tested for sounds in the 3 to 60 kHz range, and for the harbor porpoise in the 1.5 to 32 kHz range (Finneran, 2015). Although the data are still scarce and are based on different types of sounds and exposure durations, it appears that harbor porpoises are more susceptible to TTS than bottlenose dolphins in the part of the tested frequency ranges that overlap. For instance, for sounds around 10 kHz, 6 dB TTS is elicited in the harbor porpoise with an SEL that is 20 dB lower than the SEL that elicited 6 dB TTS in bottlenose dolphins.

TTS studies do not confirm the specific SELs at which PTS occurs but can help to define safe sound exposures by providing TTS onset SEL, the rate at which TTS increases per dB fatiguing sound, and critical levels (above which TTS increases dramatically). Extrapolation of the TTS curve of Porpoise M06 in the present study at 44.8 kHz (Figure 2a) to 40 dB (presumed PTS; Southall et al., 2007) yields a rough estimate of the PTS onset SEL for sound around 32 kHz. Regulators can choose a safety level of, for instance, 10 dB below this estimated PTS onset SEL. TTS varies in magnitude and duration, and may compromise feeding, localization, communication, and predator detection in wild harbor porpoises. Therefore, TTS may negatively impact individuals' health and survival even if PTS does not occur. In the long term, TTS (depending on its severity, duration, frequency of occurrence, and affected hearing frequency) is likely to have adverse population effects.

Sounds with frequencies in the 32 kHz range include biological sounds, such as echolocation (Au, 1993), and anthropogenic sounds, including some types of naval and fish-finding sonars (range 20 to 200 kHz; Discovery of Sound in the Sea [DOSITS], n.d.), which are generally used at levels that may induce TTS in harbor porpoises at close range and/or after long exposure durations. Research on the frequency-dependent susceptibility of harbor porpoises to TTS is ongoing in order to quantify the impact of various anthropogenic sounds on their hearing. Once susceptibility to TTS has been quantified for the entire hearing range of the harbor porpoise, it will be possible to generate equal-TTS susceptibility curves (one of which can be used to establish an auditory weighting curve) for harbor porpoises and for other odontocetes that echolocate at high frequencies (Houser et al., 2017; Southall et al., 2019). These curves may aid in the regulation of anthropogenic sound sources by setting safety levels that are specifically tailored to the hearing of these marine mammals.

## Acknowledgments

We thank research assistants Stacey van der Linden, Rowanne Huisman, and Ruby van Kester; students Thaana van Dessel, Tessa Kreeft, Jennifer Smit, and Britt Spinhoven; and volunteers Simone de Winter, Susan Janssen, Lotte Dalmeijer, Kimberly Biemond, and Brigitte Slingerland for their help in collecting the data. We thank Arie Smink for the design, construction, and maintenance of the electronic equipment. We thank Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute, and Erwin Jansen (TNO) who conducted the acoustic measurements. We also thank Nancy Jennings (Dotmoth.co.uk) and two anonymous reviewers for their valuable constructive comments on this manuscript. Funding for this project was obtained from the U.S. Navy's Living Marine Resources program (Contract No. N39430-15-C-1686). We thank Anu Kumar and Mandy Shoemaker for their guidance on behalf of the LMR program. The harbor porpoises were tested under authorization of the Netherlands Ministry of Economic Affairs, with Endangered Species Permit FF/75A/2014/025. We thank Jeroen Vis (Netherlands Ministry of Economic Affairs) for his assistance in making the harbor porpoises available for this project, and the ASPRO group for providing the porpoises.

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