

Marine Mammal Noise Exposure Criteria: Updated Scientific Recommendations for Residual Hearing Effects

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This publication is dedicated with great respect and admiration to Dr. Jeanette Thomas who was an original panel member, valued colleague, and dear friend. Jeanette was a champion of marine mammal science who set higher standards for all in terms of scholarship, integrity, and professionalism. She was a stellar role model, particularly for young women in science; an insightful editor; and a dedicated professor and mentor. She will ever continue to inspire us.

Abstract

This article evaluates Southall et al. (2007) in light of subsequent scientific findings and proposes revised noise exposure criteria to predict the onset of auditory effects in marine mammals. Estimated audiograms, weighting functions, and underwater noise exposure criteria for temporary and permanent auditory effects of noise are presented for six species groupings, including all marine mammal species. In-air criteria are also provided for amphibious species. Earlier marine mammal hearing groupings were reviewed and modified based on phylogenetic relationships and a comprehensive review of studies on hearing, auditory anatomy, and sound production. Auditory weighting functions are derived for each group; those proposed here are less flattened and closer to audiograms than the Southall et al. M-weightings. As in Southall et al., noise sources are categorized as either impulsive or non-impulsive, and criteria use multiple exposure metrics to account for different aspects of exposure. For continuous (non-impulsive) noise

sources, exposure criteria are given in frequency-weighted sound exposure level (SEL, given in units relative to 1 $\mu\text{Pa}^2\text{-s}$ or (20 $\mu\text{Pa}^2\text{-s}$) for water and air, respectively). Dual exposure metrics are provided for impulsive noise criteria, including frequency-weighted SEL and unweighted peak sound pressure level (SPL, given in units relative to 1 μPa or 20 μPa for water and air, respectively). Exposures exceeding the specified respective criteria level for any exposure metric are interpreted as resulting in predicted temporary threshold shift (TTS) or permanent threshold shift (PTS) onset. Scientific findings in the last decade provide substantial new insight but also underscore remaining challenges in deriving simple, broadly applicable quantitative exposure criteria for such diverse taxa. These criteria should be considered with regard to relevant caveats, recommended research, and with the expectation of subsequent revision.

Key Words: hearing, marine mammals, noise exposure, TTS, PTS, weighting, criteria

Introduction and Overview

Scientific evaluation of how anthropogenic (human-generated) noise influences marine mammals extends back nearly half a century (Payne & Webb, 1971). Increasing knowledge and concern for animal welfare have led regulators and industry to consider what noise exposure levels from specific human activities are likely to harm marine animals, especially the marine mammals (cetaceans, pinnipeds, other marine carnivores, and sirenians) which are the focus herein (e.g., National Marine Fisheries Service [NMFS], 1995; High Energy Seismic Survey [HESS], 1999; for a more detailed review, see Houser et al., 2017). Scientific advisory organizations have also reviewed and evaluated the available science in terms of its implications (and limitations) for regulatory policies for ocean noise (e.g., National Research Council [NRC], 1994, 2000, 2003, 2005; International Council for the Exploration of the Sea [ICES], 2005). These efforts stimulated substantial scientific research and increased appreciation for the complexity of the underlying issues that had to be addressed to broadly predict the potential effects of noise. Verboom & Kastelein (2005) proposed hearing-weighted exposure thresholds for discomfort, temporary threshold shift, and hearing injury for exposure to continuous sounds for harbor seals and harbor porpoises. However, prior to 2007 and largely because of limited data, noise exposure criteria had not been formulated or broadly proposed for different types of marine mammals and different types of anthropogenic noise sources.

In 2002, the U.S. National Marine Fisheries Service (NMFS) Ocean Acoustics Program assembled a panel of scientists to address this challenging task. They reviewed all available information and developed methods to evaluate and quantify noise exposure levels for different anthropogenic sources expected to cause (1) behavioral responses of varying severity and (2) reductions in auditory sensitivity changes, including both temporary threshold shifts (TTS) and permanent threshold shifts (PTS). This resulted in the auditory exposure criteria described in Southall et al. (2007). The purpose of the present article is to advance and update these criteria to better predict the risk of TTS and PTS onset from noise exposure in marine mammals.

Southall et al. (2007) acknowledged the limitations of their approach given the limited underlying data and the need to extrapolate findings from terrestrial to marine mammals. Their focus was limited to marine mammals under the jurisdiction of the NMFS, resulting in the inclusion of cetaceans (whales, dolphins, and porpoises) and most pinnipeds (seals and sea lions), but the exclusion of walrus, polar bears, sea otters, and sirenians

(manatees and dugongs). Despite these limitations, the initial process was an important step, providing specific scientific recommendations to inform regulatory decision-making and serving as a foundation for future criteria.

Elements of Southall et al. (2007) were derived from approaches used to develop damage risk criteria for human hearing (Kryter et al., 1966; Kerr et al., 2017). Historically, this research on hearing damage focused on laboratory animal species as models for human hearing and hearing damage, particularly for PTS studies (Clark, 1991). Prior to Southall et al. (2007), few formal criteria had been proposed for protecting hearing of multiple, mixed species in any heterogeneous taxa. There are still no comparable criteria for terrestrial wildlife. Southall et al. recognized that small terrestrial laboratory animals were likely poor models for large mammals with specialized ears adapted to a different medium. However, in the absence of direct information, extrapolations were used to support the development of the original criteria.

The Southall et al. (2007) noise exposure criteria were presented within an analytical framework that (1) categorized marine mammals into groups based on what was known about their hearing, (2) distinguished noise types with differing potential to affect hearing based on acoustical characteristics, and (3) utilized multiple exposure metrics to account for properties of sound that were expected to have the greatest influence on hearing. An important step in the analytical framework involved weighting functions to account for the frequency-dependent effects of noise for different marine mammal hearing groups. Such weightings for human hearing have a complex history, with multiple weighting curves developed for different applications. Weighting functions originally were developed for efficient telephony (see Houser et al., 2017), with later application to models of noise-induced human annoyance (e.g., Schomer, 1977). Weighting procedures were also intended to simplify operational criteria for preventing noise-induced hearing loss (von Gierke, 1965). Southall et al. (2007) provided auditory weighting functions to account for differential auditory sensitivity of different marine mammal hearing groups as a function of sound frequency. Given the extremely limited data available, the basis for deriving any auditory weightings for any group, but especially those with little or no direct hearing measurements, was debated extensively. Eventually, Southall et al. supported the use of deliberately broad weighting functions to discount exposure for noise at frequencies outside the presumed audible range, with explicit caveats and research recommendations to support the improvement of the criteria.

Regulatory approaches prior to Southall et al. (2007) generally failed to account for frequencies that animals heard relatively well or poorly. The weighting functions for a wide range of marine mammal species explicitly derived by Southall et al. were intended to be relatively coarse compared to the audiogram—admitting all frequencies that an animal could presumably hear but smoothing the transition to frequencies it could not hear. This approach, which used exponential functions, was based conceptually on a human weighting filter designed for high amplitude noise (human C-weighting) (Schomer, 1977; Harris, 1998). These “M-weighting” filters were developed for five marine mammal groups (low-, mid-, and high-frequency cetaceans, plus pinnipeds in water and pinnipeds in air) and allowed estimation of noise exposures that accounted for differential hearing sensitivity of each marine mammal hearing group to noise at different frequencies. Despite acknowledged limitations and the coarse nature of their design, the novel M-weighting filters became a *de facto* standard in some regulatory applications (e.g., Finneran & Jenkins, 2012; Bureau of Ocean Energy Management [BOEM], 2016).

Similar weightings have been proposed separately for laboratory animals (Bjork et al., 2000; Lauer et al., 2012), but none have been systematically applied or standardized for any other broad taxa of non-human animals. Various other approaches utilizing data on hearing sensitivity to predict frequency-specific sensitivity to noise exposure were explored by different taxa of free-ranging animals within the same time-frame, including Delaney et al. (1999) for strigiform owls, Verboom & Kastelein (2005) for harbor porpoises and harbor seals, Nedwell et al. (2007) for various aquatic species, and Terhune (2013) for harbor porpoises. There is some support for the use of auditory threshold functions for predicting behavioral responses to sound (i.e., animals cannot react if they cannot hear a sound); however, clear relationships between absolute auditory sensitivity and predisposition to hearing damage have yet to be demonstrated. Consequently, Southall et al. (2007) chose not to base weighting functions directly on auditory sensitivity, a conclusion that was revisited here.

The panel of subject-matter experts who contributed to Southall et al. (2007) was reconvened with some modifications¹ to consider all relevant available literature and update and expand the Southall et al. (2007) exposure criteria for TTS/PTS onset for all marine mammal species. The intent is to provide the best scientific interpretation and application of the available information within different marine mammal hearing groups while acknowledging data limitations for specific topics and for some hearing groups. As in Southall et al., the approach herein was to use

available data to reasonably predict criteria for which effects are likely rather than necessarily proposing the most “protective” criteria. This is evident in the use of median values from available hearing and TTS-onset data and the use of median values from other hearing groups to estimate values for hearing groups for which no data exist, rather than using the lowest measured onset for any threshold or particular effect for any individual measured or represent the hearing group or other groups for which no such data exist. Policy and regulatory applications depend on a host of factors (e.g., population status, legal/regulatory considerations, and/or individual species issues for which differences may be justified). It is therefore important that for criteria to be most broadly useful in a variety of these contexts, they aim to quantify risk as a function of exposure at a population level rather than simply predicting the most severe possible consequence for any individual. A detailed discussion of this issue and potential implications is provided. It is acknowledged that additional data on intra- and interspecific variation in hearing and noise effect data are needed to more fully specify how risk varies as a function of exposure. Herein, acoustic criteria are defined for effects that are probable rather than possible. Subsequent criteria should use these data to more fully characterize risk probability as a function of exposure (e.g., in terms of percent likelihood of a certain effect) rather than as discrete levels above which effects are probable. With a probabilistic approach, managers could objectively evaluate the associated risk they were willing to accept on a case-by-case basis and in light of other factors. The need for additional supporting data and more explicit consideration of variation in hearing and TTS data within and between species in deriving and interpreting group-specific weighting and noise exposure functions is discussed.

These noise criteria are the latest in a series of previous and ongoing efforts to evaluate and predict the risk of various kinds of effects of noise on marine mammals. The initial such assessment was by Verboom & Kastelein (2005) for a few species of interest. Subsequent exposure criteria have been developed for single species (e.g., Tougaard et al., 2015), while others have focused on a broader number of species but primarily considered specific types of exposures (e.g., Finneran & Jenkins, 2012). The noise criteria here represent the next step in a sequential process of evolution of the criteria proposed by Southall et al. (2007), substantially modified with new analytical methods by Finneran (2016), and recently adopted as U.S. regulatory guidance by the NMFS (2016, 2018).

While the quantitative process described herein and the resulting exposure criteria here are based

on, and in many respects are identical to, those derived by Finneran (2016) and adopted by the NMFS (2016, 2018), there are a number of significant distinctions. The exposure criteria here appear in a peer-reviewed publication and include all marine mammal species for all noise exposures, both under water and in air for amphibious species. NMFS (2016, 2018) provides regulatory guidance only for the subset of marine mammals under their jurisdiction and do not include criteria for aerial noise exposures, an important consideration in many locations for which some earlier assessments were made (Finneran & Jenkins, 2012). The exposure criteria here, while based on the Finneran (2016) quantitative method and consistent with the NMFS (2016, 2018) guidance where they overlap, are thus more broadly relevant, peer-reviewed, and less subject to potential changes in national regulatory policy. The later point was made evident in the re-evaluation and requisite reissuance of the NMFS (2016) guidance resulting from political pressure exerted in the form of a federal executive order (NMFS, 2018).

Further, the criteria here include a comprehensive review of all available data on direct measures of hearing, auditory anatomy, and emitted sound characteristics for all marine mammal species. Variation at many levels, by individual, age/sex class, health status, life history strategy, local area, population, species, and taxon (genus, family, etc.) is fully expected and should be directly incorporated when sufficient data are available. These data are used to evaluate and, in some cases, modify and expand the hearing group characterizations more subjectively derived by Finneran (2016) from the original Southall et al. (2007) groups. Six marine mammal hearing groups, two of which have different criteria depending upon the medium, are proposed here: three cetacean groups, phocid pinnipeds (true seals), other marine carnivores (comprising otariid pinnipeds, walrus, polar bears, and sea otters), and sirenians (manatees and dugongs) (as in Finneran, 2016). Two additional cetacean groups are identified for which some evidence exists to warrant additional division, with specific recommendations given for research for further evaluation. This is consistent with the approach taken by Southall et al. (2007) with regard to the proposed future segregation of phocid and otariid pinnipeds, which was later adopted. It should be noted that this results in some proposed differences in the terminology of hearing groups relative to those used in Finneran (2016) and NMFS (2016, 2018). These proposed differences in nomenclature may be confusing, but we believe they are justified (see the “Marine Mammal Hearing Groups and Estimated Group Audiograms” section and Appendices 1-6) and will support future criteria as new information emerges.

Southall et al. (2007) defined sound sources as “pulses” or “non-pulses” based on their characteristics at the source using a simple, measurement-based approach proposed by Harris (1998). As a simplifying measure, impulsive noise types (e.g., pile driving and seismic airguns) were distinguished based on their characteristics at the source without regard for well-known propagation effects that might change their appropriate characterization to non-impulsive at greater ranges. Here, we retain the same source categorization for impulsive and non-impulsive sources (as in Table 1, Southall et al., 2007) but note that the respective exposure criteria (impulsive or non-impulsive) should be applied based on signal features likely to be received by animals rather than by signal features at the sound source. Specific methods by which to estimate the transition from impulsive noise to non-impulsive noise are being developed in a parallel effort by some of the authors here and by other members of this panel.

The same dual exposure metrics used by Southall et al. (2007, Appendix A) are used here for impulsive noise criteria: (1) *frequency-weighted sound exposure level* (SEL), defined here as ten times the logarithm to the base ten of the ratio of the time integral of the square of the instantaneous frequency-weighted sound pressure to the reference value of $1 \mu\text{Pa}^2\text{-s}$ or $(20 \mu\text{Pa}^2)\text{-s}$ for water and air, respectively, and (2) *unweighted peak sound pressure level* (hereafter peak SPL), defined as 20 times the logarithm to the base ten of the ratio of the maximum absolute value of the instantaneous unweighted sound pressure to the reference value of $1 \mu\text{Pa}$ or $20 \mu\text{Pa}$ for water and air, respectively. These two metrics are applied under the condition that exceeding either threshold by the specified level is sufficient to result in the predicted TTS or PTS onset. The different exposure metrics are required to account for different aspects of exposure level and duration: SEL is a measure of sound energy of exposure accumulated over time and over multiple exposures, whereas SPL is a measure of absolute maximum exposure. For impulsive exposures, both criteria are defined for all marine mammal groups. However, for non-impulsive exposures, only frequency-weighted SEL criteria are given here, replacing the dual exposure metric approach proposed by Southall et al. (2007). Given the typically much longer duration of most common non-impulsive noises (e.g., vessel noise and dredging) relative to any embedded transient components and given the very high peak SPL values required to induce TTS/PTS, there are virtually no scenarios for which the SEL criterion would not be met prior to an exposure exceeding what would be the associated dual-metric peak SPL criteria

(which are thus not given). The assumption here is that SEL values will be calculated over the entire duration of a discrete noise exposure and/or will be cumulative over multiple repeated noise exposures that occur in sufficiently rapid succession. While a 24-h intermittency period has previously been proposed to “reset” the SEL accumulation (Southall et al., 2007) as a precautionary approach, limited subsequent data (see Finneran, 2015) suggest that in some instances a shorter interval would be more appropriate in terms of considering multiple exposures as discrete events rather than continuing to accumulate noise energy. This is an important area of needed research discussed later in greater detail.

Human occupational damage risk criteria for hearing loss, in addition to considering discrete noise exposures, are designed to provide sufficient protection for hearing over decades to working lifetimes, assuming that the majority of potentially damaging exposure is likely to be experienced in the workplace, with time for recovery in relative silence between shifts (Baughn, 1973; American Academy of Audiology, 2003; Daniell et al., 2003; Kerr et al., 2017). There is clearly a similar need for distinct and different marine mammal exposure criteria that consider potential long-term hearing loss produced by cumulative exposure over years, decades, or lifetimes. Despite this, the criteria presented herein remain limited to identifiable noise exposure events on much shorter time scales. Unfortunately, the available data for marine mammals are inadequate to predict long-term noise-induced hearing loss (NIHL) from cumulative exposure, and there are no measurements of cumulative received exposures available over the required time-scales for individuals and populations. Criteria for long-term noise exposure will require data on hearing effects of longer-term exposures and on the durations of quiet required to recover from these effects (e.g., Ward et al., 1976).

The derivation of hearing group-specific weighting functions and TTS/PTS onset involves five general processes, each with a number of basic steps, assumptions, and, in many cases, requisite extrapolations. These processes are as follows:

1. Identify marine mammal hearing groups using available data on hearing, auditory anatomy, and sound production.
2. Estimate hearing parameters for each species grouping and estimate group audiograms.
3. Derive group-specific auditory weighting and noise exposure functions using generic band-pass filter equations and group-specific hearing and TTS data.

4. Calculate group-specific TTS onset using either exposure functions (SEL) or extrapolation methods from TTS-onset measurements (SPL).
5. Calculate group-specific PTS onset (both SEL and SPL) using estimates of TTS growth rates.

Following a synthesis of recent scientific data on hearing and the effects of noise that are collectively relevant to this process (see next section), the first two processes are described in the “Marine Mammal Hearing Groups and Estimated Group Audiograms” section. The derivation of auditory weighting and exposure functions and the calculation of associated TTS- and PTS-onset levels are described in the “Marine Mammal Auditory Weighting and TTS Exposure Functions” section.

Finally, key research requirements to improve quantitative methods for evaluating the auditory effects of noise on marine mammals are identified and discussed in the “Research Recommendations” section.

Recent Progress in Understanding Marine Mammal Hearing and the Effects of Noise on Hearing

Substantial progress has been made in quantifying marine mammal hearing and the effects of noise on hearing for a range of taxa since the review provided by Southall et al. (2007). Recent reviews of TTS (Finneran, 2015) and auditory masking (Erbe et al., 2016) in marine mammals summarize the current state of knowledge in these fields. Herein, we consider recent scientific data, organized as it relates to specific sections of the proposed exposure criteria, including absolute hearing capabilities, auditory weighting functions, and the fatiguing effects of noise. (**Note:** Common names are used within the main text, and taxonomic references for all species are provided within corresponding appendices.)

New Research on Marine Mammal Absolute Hearing Capabilities

Numerous studies have been published in the past decade on absolute (unmasked) hearing capabilities in various marine mammals, both in water and in air (primarily for pinnipeds). These data are reviewed here, with particular emphasis on previously untested species and increased sample sizes within species.

There are still no direct measurements of underwater hearing available for any mysticete, and such measurements are unlikely to be obtained in the near future. Anatomical data and modeling can be used to estimate audible ranges and frequencies of

best hearing but cannot be used to estimate hearing sensitivity or generate empirical audiograms. Anatomical advances relevant to evaluating baleen whale hearing include suggested hearing ranges for right, bowhead, and humpback whales based on histology and computerized tomography (CT) of inner ears (Ketten, 1994; Parks et al., 2007b; Mountain et al., 2008; Tubelli et al., 2012a); identification of potential fatty sound conduction pathways to the inner ear in minke whales (Yamato et al., 2012); estimated hearing ranges and best hearing frequencies from CT scanning and histology-based finite element modeling (FEM) for minke whales (Tubelli et al., 2012b); and estimated hearing profiles using FEM modeling from CT scans of fin whales (Cranford & Krysl, 2015).

Several recent studies provide direct information to describe underwater hearing in odontocete cetaceans. These include audiograms for the bottlenose dolphin (Popov et al., 2007), white-beaked dolphin (Nachtigall et al., 2008), Indo-Pacific humpback dolphin (Li et al., 2012), beluga whale (Finneran et al., 2009; Castellote et al., 2014; Popov et al., 2015), killer whale (Branstetter et al., 2017), short-finned pilot whale (Schlundt et al., 2011), long-finned pilot whale (Pacini et al., 2010), Gervais' beaked whale (Cook et al., 2006; Finneran et al., 2009), and Blainville's beaked whale (Pacini et al., 2011). New audiometric data are also available for two high-frequency specialists: (1) the harbor porpoise and (2) finless porpoise (Popov et al., 2006, 2011; Kastelein et al., 2010, 2012a, 2015a).

The phenomenon of auditory gain control has been discovered in several cetaceans. Auditory gain control during echolocation has been demonstrated for the false killer whale (Nachtigall & Supin, 2008), bottlenose dolphin (Mooney et al., 2011), and harbor porpoise (Linneschmidt et al., 2012). Changes in hearing thresholds following conditioning with an auditory cue warning of the impending arrival of loud sounds have also been measured in the false killer whale (Nachtigall & Supin, 2013), the bottlenose dolphin (Nachtigall & Supin, 2014, 2015), the beluga whale (Nachtigall et al., 2016a), and the harbor porpoise (Nachtigall et al., 2016b). These studies reveal an apparent level of plasticity in hearing sensitivity, which presumably provides a temporary reduction in susceptibility to noise exposure. Evidence of auditory gain control, while intriguing, remains challenging to integrate into noise exposure criteria. Whether the ability to adjust hearing sensitivity affords "protection" to odontocetes exposed to noise in contexts where it may be predictable is unknown. However, these results support the observation that four different echolocating species found in widely divergent environments have additional adaptive and protective mechanisms to tolerate noise

exposure (see Nachtigall et al., 2018). This suggests that they may be able to learn to change their hearing sensation levels when warned that loud sounds are about to occur. This could render the exposure criteria presented herein somewhat conservative in such scenarios, although additional research is needed to further evaluate this.

Recent studies provide new hearing data for phocid pinnipeds, with complete underwater and in-air audiograms published for harbor seals (Kastelein et al., 2009; Reichmuth et al., 2013), spotted seals (Sills et al., 2014), and ringed seals (Sills et al., 2015). New hearing data are also available for otariid pinnipeds, with in-air measurements for Steller sea lions (Mulsow & Reichmuth, 2010) and underwater and in-air audiograms for California sea lions (Mulsow et al., 2011, 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013). Reichmuth et al. (2013) reviewed amphibious hearing abilities in phocid and otariid pinnipeds. Audiometric data for other marine mammal groups not included in the original criteria are also now available for some marine carnivores, including sea otters (Ghoul & Reichmuth, 2014) and polar bears (Nachtigall et al., 2007; Owen & Bowles, 2011), as well as sirenians, including the West Indian manatee (Gerstein et al., 1999; Mann et al., 2005; Gaspard et al., 2012) and Amazonian manatee (Klishin et al., 1990).

These studies augment earlier research considered by Southall et al. (2007). Increasing knowledge of marine mammal hearing abilities informs the designation of marine mammal hearing groups (see "Marine Mammal Hearing Groups" section). Further, some of the new hearing data contribute to the audiograms estimated for each hearing group (see "Marine Mammal Auditory Weighting and TTS Exposure Functions" section). All available marine mammal hearing data, as well as data on anatomy and sound production relevant for evaluating audible range, are discussed in the "Marine Mammal Hearing Groups" section, with a description of the evaluation methods and assumptions used in the detailed syntheses provided in the Appendices.

Recent Studies Relevant to Auditory Weighting Functions

Largely in response to the need to improve upon the marine mammal auditory weighting functions derived by Southall et al. (2007), a number of subsequent studies have evaluated frequency-dependent aspects of hearing, with the goal of informing derivation of weighting functions. Weighting functions for humans have been derived from idealized versions of equal loudness functions, which describe perception of relative sound amplitude across the frequency range of human hearing (Fletcher &

Munson, 1933; Yost, 2000; Houser et al., 2017). To obtain these functions, experimental subjects are asked to compare sounds of various frequencies and levels to a sound of known level at a reference frequency. The resulting family of curves defines human loudness perception. Direct measurements of equal loudness in marine mammals are limited to a single study of equal loudness in bottlenose dolphins (Finneran & Schlundt, 2011) that parallels the methods used to derive auditory weighting functions in humans.

Equal latency functions (describing the latency of response to a stimulus across a range of frequencies) correlate well with loudness in humans and have been proposed as a method for estimating equal loudness functions in laboratory animals. Within marine mammals, reaction times to supra-threshold tones have been measured in bottlenose dolphins, harbor porpoises, and pinnipeds (Reichmuth et al., 2013; Wensveen et al., 2014; Mulsow et al., 2015). Finally, studies of frequency-specific temporal integration also provide insight into the derivation of weighting functions given their relationship to equal latency, direct measurements of which are used to evaluate relative differences in perception relevant to weighting functions. Recent studies have quantified these parameters in harbor porpoises (Kastelein et al., 2010) and several pinniped species (Holt et al., 2012).

Recent Marine Mammal TTS Data

One of the most active areas of research on the effects of noise on marine mammal hearing has been TTS studies using non-impulsive noise as reviewed by Finneran (2015). Many of these studies address data needs articulated by Southall et al. (2007) regarding TTS-onset, growth, and frequency-specific differences in these parameters. Recent TTS studies have included six of the eight marine mammal groups to be identified herein, with studies both under water and in air for the amphibious marine carnivores. No studies have been conducted to date on any aspect of TTS in mysticetes or sirenians.

Extensive research on TTS from non-impulsive noise exposure has been conducted on several odontocete cetacean species since Southall et al. (2007), including the bottlenose dolphin (Mooney et al., 2009; Finneran et al., 2010; Finneran & Schlundt, 2010, 2013), beluga whale (Popov et al., 2014), harbor porpoise (Kastelein et al., 2011, 2012b, 2013a, 2013b, 2014a, 2014b, 2015b), and finless porpoise (Popov et al., 2011). Recent TTS studies in pinnipeds have also been conducted using non-impulsive noise (Kastak et al., 2007; Kastelein et al., 2012c, 2013a).

A few TTS studies have also been conducted in marine mammals using impulsive noise sources.

These studies are more limited than those using non-impulsive sources, in part because of methodological challenges in generating these signals within laboratory settings in ways that approximate their characteristics as experienced by animals in the field. However, progress in this area addresses a major knowledge gap from Southall et al. (2007). New studies include those on the bottlenose dolphin (Finneran et al., 2015), harbor porpoise (Lucke et al., 2009; Kastelein, 2013; Kastelein et al., 2015a), and several pinniped species (Reichmuth et al., 2016) exposed to seismic pulses or impulsive pile-driving noise.

Recent Studies of Auditory Masking in Marine Mammals

As discussed above, the exposure criteria developed here focus on the residual effects of noise exposure (TTS/PTS) rather than simultaneous interference from noise, including auditory masking. Exposure criteria for identifying masking analogous to standards for preventing speech interference in humans (e.g., Kryter, 1994) are clearly relevant to broader anthropogenic noise issues for marine mammals. While issues related to masking are not considered in depth here, sufficient progress has been made that explicit masking criteria within specific contexts may soon be possible (see Erbe et al., 2016). Recent empirical studies have considered masking in a wide range of marine mammal species (Lemonds et al., 2011, 2012; Branstetter et al., 2013), including harbor porpoises (Kastelein & Wensveen, 2008), manatees (Gaspard et al., 2012), spotted and ringed seals (Sills et al., 2014, 2015), California sea lions (Cunningham et al., 2014), and sea otters (Ghoul & Reichmuth, 2014).

Marine Mammal Hearing Groups and Estimated Group Audiograms

Marine Mammal Hearing Groups

Numerous authors have recognized that differences in frequency-specific hearing sensitivity among different animals influence how they are affected by noise exposure. Southall et al. (2007) proposed relatively broad marine mammal hearing groups, each containing many species that still had some expected differences among them, based on what was known or inferred about these differences. Within these groupings, procedures were developed to derive applicable group-specific weighting functions and to more narrowly predict the effects of noise exposure. This was intended to account for biological differences in frequency sensitivity that had previously been ignored in regulatory applications.

Southall et al. (2007) defined five groups of marine mammals, based on phylogenetic

relationships and a combination of auditory, physiological, and behavioral characteristics (where known). These groups included three subdivisions of the cetaceans (mysticete whales, dolphins, and porpoises) corresponding to typical frequency ranges of known or estimated hearing sensitivity and sound production parameters, as well as common auditory anatomical features: *low-frequency cetaceans* (baleen whales), *mid-frequency cetaceans* (including most odontocetes), and *high-frequency cetaceans* (including a subset of odontocetes specialized for high frequencies). Seals and sea lions (pinnipeds) comprised the other hearing group with their amphibious nature resulting in functional hearing groups for *pinnipeds in water* and *pinnipeds in air*.

These initial groupings accounted for gross frequency-specific differences in hearing, but it was clear from the outset that subsequent modifications were necessary and inevitable. For instance, Southall et al. (2007) suggested that additional hearing groups would likely be justified in future noise exposure criteria (e.g., separation of phocid and otariid pinnipeds) as additional information on both hearing capabilities and the effects of noise on hearing became available. Southall et al. also focused on species regulated by the NMFS, which excluded a number of species, including sirenians (manatees and dugongs), walrus, sea otters, and polar bears. Furthermore, the inability to account for what were expected to be numerous sources of inter- and intraspecific variation within hearing groups was identified as clearly important but lacking a sufficient empirical basis. The absence of data in many related areas to address these issues was acknowledged by Southall et al., along with a strategic research plan to improve future criteria.

A revised set of marine mammal hearing groups and associated frequency-weighting functions were proposed by Finneran (2016) for U.S. Navy regulatory compliance processes. This approach was subsequently used in a U.S. regulatory policy guidance document (NMFS, 2016, 2018) for evaluating the potential effects of underwater noise exposure for marine mammal species specifically under their jurisdiction. Similar marine mammal hearing groups are identified here, with several notable distinctions. While cetaceans retain their three-part grouping, phocid seals and all other marine carnivores are now considered separately in terms of both underwater and aerial hearing, as these species are amphibious (in-air criteria were not proposed by NMFS, 2016, 2018). Furthermore, a modified nomenclature for marine mammal hearing groups is proposed, accounting for further divisions identified within the mysticete and odontocete cetaceans (discussed below). While we argue that there is evidence to support further segregation of marine

mammal groupings, at present, there are insufficient data to explicitly develop distinct exposure criteria because of the absence of TTS/PTS-onset data with which to do so. Southall et al. (2007) faced a similar problem with regard to the phocid and otariid pinnipeds, which were originally grouped together despite some evidence supporting their segregation. Herein, a similar approach is taken. The basis for further segregation is identified, and additional research needs to inform these assessments as further distinctions are presented.

To re-evaluate the segregation of marine mammal species into appropriate hearing groups, published literature describing audiometry, auditory anatomy, and sound production were reviewed and evaluated for all marine mammal species (Appendices 1-6). Audiometric data included measurements of hearing sensitivity across species-typical frequency ranges obtained using behavioral (psychophysical) methods and measurements of hearing sensitivity (primarily over mid- and high-frequency hearing ranges) obtained using neurophysiological methods. Auditory anatomy was considered with respect to basic ear types defined by sound conduction mechanisms and morphology of middle and inner ear structures, as well as by cochlear type where possible. Additionally, quantitative predictions of low- and/or high-frequency hearing limits derived from auditory models were evaluated.

Several characteristics of sound production were also considered for each marine mammal species. Frequency information regarding social sound emissions was summarized for all species where data were available. Further, for odontocete cetacean species that echolocate, frequency content of known or suspected echolocation clicks was described. In addition, the types of clicks produced while searching for prey (based on Fenton et al., 2014) were also considered in relation to hearing group distinctions. The logic, methods, and source data for species categorized into hearing groups are detailed within each appendix (each corresponding to the hearing groups described below, with aerial and underwater characteristics for the amphibious marine carnivores appearing in combined appendices). In addition to validating the species groupings presented here, these appendices enable identification of species for which few or no data are available, or for which available data are in conflict. In these cases, groupings are based on extrapolation to the most closely phylogenetically related species.

It is important to note that while many types of studies provide insight into possible hearing characteristics, only behavioral (psychophysical) audiometry provides direct measurements of hearing that include the entire auditory perceptual system. Further, unlike neurophysiological methods, behavioral audiometry can be effectively used to measure

hearing at low frequencies (subject to availability of a suitably large enclosure) and, thus, can describe the complete shape of hearing sensitivity curves. These studies are inherently costly, limited to few individuals, and constrained to species that can reasonably be studied in long-term captivity. Such data are therefore available for only 15% of marine mammal species but have high value to the development of frequency-specific weighting functions. Consequently, behavioral audiometric data for marine mammals have been vetted to ensure that only data from healthy individuals with apparently normal hearing are used to develop weighting functions. Such data are exclusively applied in the derivation of estimated group audiograms (see “Estimated Group Audiograms for Marine Mammals” section). Neurophysiological measurements of auditory evoked potentials (AEPs), obtained from recording electrodes, are reported for all marine mammal studies that present frequency-specific response thresholds (typically obtained with narrow-band clicks or sinusoidally amplitude-modulated stimuli). These data are limited in the frequencies that can be tested and are not always similar to behavioral hearing thresholds that involve the complete hearing process through to perception. For marine mammal species tested thus far, AEPs do not adequately describe the lowest-frequency portion of their hearing. However, they do provide reliable estimates of high-frequency hearing limits and, thus, inform understanding of the hearing range, which varies by hearing group.

Anatomical data provide useful information about similarities and differences in auditory structures among marine mammal species. A complete review of marine mammal auditory anatomy is beyond the scope of this article. Herein, the defining features of the auditory pathway are considered, including the basic type of mammalian ear exhibited by each species (see Fleischer, 1978; expanded by Nummela, 2008) and descriptions of cochlear types (e.g., Ketten & Wartzok, 1990; Ketten, 1992; Manoussaki et al., 2008). These data provide a basis for rough groupings of species in the absence of any audiometric information. In addition, quantitative estimates of low- and high-frequency hearing limits derived from anatomical models have been included for which these data are available and are tied to the type of models used to generate the information. Additional details regarding anatomical modeling methods applied to different hearing groups are provided within each respective appendix. At present, auditory models applied to marine mammals include those based on cochlear spiral radii ratios (Manoussaki et al., 2008; Ketten & Mountain, 2014; Racicot et al., 2016), basilar membrane thickness-to-width ratios (e.g., Ketten, 2000; Parks et al., 2007b), basilar membrane frequency place maps (Ketten,

1994; Ketten & Mountain, 2014), finite element models of sound pressure passing through the head to the bony structures encasing the ear (Cranford & Krysl, 2015), and sound pressure transductions and transfers through the structures of the middle ear (Tubelli et al 2012a, 2012b). Additionally, measures of middle ear stiffness provide information that supports models of middle-ear transfer functions, providing relative information on frequencies associated with best sensitivities (e.g., Miller et al., 2006; Zosuls et al., 2012). All auditory models seek to describe how sound stimulates portions of the auditory pathway and how these structures transform acoustic energy into mechanical and thence neural stimuli. These models have inherent constraints and limitations—no one anatomical model provides complete audiometric data because the final percept that is “hearing” requires a series of coupled elements. Therefore, readers are strongly advised to consider the hearing limits predicted by various auditory models in the context of how many of the multiple, specific components are modeled and their role as well as the methodology employed. In many cases, models using similar approaches and common, defined anatomical elements with realistic stimuli that do not grossly exceed normal conditions will provide the most reliable insight into probable hearing and hearing differences across species.

Information concerning the sounds produced by different species has been used to make basic inferences about auditory sensitivity. This approach should be used with caution, in part because the hearing abilities of animals have likely not evolved exclusively to support communication (e.g., Fay & Popper, 2012), and peak hearing sensitivity generally does not necessarily correspond directly to predominant frequencies present in species-typical vocalizations (e.g., Ladich & Yan, 1998; Pytte et al., 2004; Arch & Narins, 2008; Velez et al., 2015). However, it is likely that most animals are able to hear social sounds produced by conspecifics in at least part of the frequency range occupied by the dominant energy in their sounds. Echolocating species tend to show enhanced hearing sensitivity in frequency regions associated with centroid or peak spectra of their echolocation clicks (e.g., Wartzok & Ketten, 1999; Ketten, 2000; Surlykke & Nachtigall, 2014). The Appendices include the frequency ranges of reported frequencies for sounds used for communication by marine mammals. The Appendices also separate information about the frequency content of echolocation clicks produced by odontocete species. Because these signals tend to be broadband, centroid or peak frequency data (rather than overall frequency range) are reported where possible. While it is acknowledged that these may be imperfect predictors, information about the

frequency content of sound emissions can provide at least some indirect information regarding the range of hearing for a given species, and similarities in sound emissions in related species can be used to hypothesize similarities in hearing abilities.

A distinguishing acoustic feature of odontocete species is the type of click they emit when searching for prey. We have followed the convention established by Fenton et al. (2014) by describing these clicks as multiple pulse (MP), frequency-modulated (FM), broadband high frequency (BBHF), or narrow-band high frequency (NBHF). Among the odontocetes, the NBHF click type has been particularly useful in parsing a number of high-frequency specialized species from other odontocetes as it is only present within species in this group. Further, the presence of FM click types in a number of odontocete species provide one line of evidence for a potential future split beyond that presently proposed. Given these considerations and taking into account all available information regarding audiometry, anatomy, and sound production characteristics—with particular emphasis on frequency ranges of hearing—eight discrete hearing groups are identified, including (1) LF cetaceans, (2) HF cetaceans, (3) VHF cetaceans, (4) sirenians (SI), (5) phocid carnivores in water (PCW), (6) phocid carnivores in air (PCA), (7) other marine carnivores in water (OCW), and (8) other marine carnivores in air (OCA) (Table 1).

There are several new distinctions in group nomenclature compared to those in some earlier criteria used by Southall et al. (2007), Finneran (2016), and NMFS (2016, 2018). The use of *carnivores* as opposed to *pinnipeds* reflects the inclusion of several non-pinniped marine mammal taxa. The distinction between *HF* and *VHF cetacean* groups (as opposed to mid- and high-frequency) reflects the regions of best hearing sensitivities within these groups, often including frequencies approaching or exceeding 100 kHz; these frequencies would be more appropriately described within marine bioacoustics as high to very high. Further, as discussed in more detail below, a number of anatomical and sound production properties suggest a potential distinction of *very low* (VLF) and *LF cetaceans* among mysticetes. Some evidence also suggests a potential segregation of *mid-frequency* (MF) and *HF cetaceans* in addition to the distinction of HF and VHF cetaceans. Subsequent noise exposure criteria may consider deriving explicit auditory weighting functions for these additional groups. If supported by future research, this would be analogous to our present use of multiple weighting functions among marine carnivores rather than the single weighting function used for all pinnipeds in Southall et al. (2007).

Low-Frequency (LF) Cetacean Hearing Group

The LF cetacean group contains all of the mysticetes (see Appendix 1 for more details on issues discussed below). The absence of direct hearing data for this taxon continues to warrant substantial caution in attempting to predict their hearing capabilities and any potential susceptibility of their hearing to noise exposure. Audible frequency ranges estimated for baleen whales from vocalization frequencies and anatomical modeling, limited anecdotal observations of spontaneous responses to tonal signals in free-ranging animals, as well as the phylogenetic distinctions from odontocete cetaceans support the general designation of the mysticetes as a discrete, LF-oriented hearing group. The pinna is absent (as for all cetaceans); the external auditory canal is thin and partially occluded; a distinct conical wax plug is present on the lateral side of the tubular, everted tympanic membrane; and the auditory pathway may involve specialized fats (Yamato et al., 2012). The mammalian middle ear for all LF cetacean species is the mysticete type (Nummela, 2008), which is characterized by tympanic and enlarged periotic bones that are fused anteriorly and posteriorly, as well as massive ossicles that are loosely articulated and a voluminous, hyper-inflated middle ear cavity (Ketten, 1992). For mysticete species that have been evaluated, the cochlea is distinct in that the basilar membrane is exceptionally broad at the apical end. This cochlea has been termed type M (mysticete), although more recent data argue for probable subdivisions within this group that need to be further explored (Ketten, 1992; Ketten et al., 2016).

Within this group, several lines of evidence suggest that some whales may be more sensitive to very low frequencies (see Ketten, 1992, 2000; Edds-Walton, 1997) and, therefore, may form a distinct category. The relatively larger mass of blue, fin, bowhead, and right whales compared to other baleen whales, and the VLF components of most of their vocalizations, combined with anatomical characteristics including relatively larger basilar membranes and larger cochlear radii ratios (Ketten et al., 2016), suggest that some of these species may be specialized for the use of very low frequencies. Thus, these species may be distinguished from other species such as minke and humpback whales, which more commonly use higher sound frequencies in species-typical vocal communication. However, as noted above, many mammalian species possess best hearing above the lower end of their vocalization frequency range. Recent anatomical modeling of auditory structures in some mysticete species is generally consistent with the expectation of hearing sensitivity exceeding vocal range (Tubelli et al., 2012a; Cranford & Krysl, 2015) as is anatomical modeling of cochlear radii ratios conducted by Ketten &

Table 1. Proposed marine mammal hearing groups, applicable auditory weighting functions, genera or species within each proposed group, and the associated appendix within which available data on hearing, auditory anatomy, and sound production are reviewed

Marine mammal hearing group	Auditory weighting function	Genera (or species) included	Group-specific appendix
Low-frequency cetaceans	LF	Balaenidae (<i>Balaena</i> , Eubalaenidae spp.); Balaenopteridae (<i>Balaenoptera physalus</i> , <i>B. musculus</i>)	1
		Balaenopteridae (<i>Balaenoptera acutorostrata</i> , <i>B. bonaerensis</i> , <i>B. borealis</i> , <i>B. edeni</i> , <i>B. omurai</i> ; <i>Megaptera novaeangliae</i>); Neobalenidae (<i>Caperea</i>); Eschrichtiidae (<i>Eschrichtius</i>)	
High-frequency cetaceans	HF	Physeteridae (<i>Physeter</i>); Ziphiidae (<i>Berardius</i> spp., <i>Hyperoodon</i> spp., <i>Indopacetus</i> , <i>Mesoplodon</i> spp., <i>Tasmacetus</i> , <i>Ziphius</i>); Delphinidae (<i>Orcinus</i>)	2
		Delphinidae (<i>Delphinus</i> , <i>Feresa</i> , <i>Globicephala</i> spp., <i>Grampus</i> , <i>Lagenodelphis</i> , <i>Lagenorhynchus acutus</i> , <i>L. albirostris</i> , <i>L. obliquidens</i> , <i>L. obscurus</i> , <i>Lissodelphis</i> spp., <i>Orcaella</i> spp., <i>Peponocephala</i> , <i>Pseudorca</i> , <i>Sotalia</i> spp., <i>Sousa</i> spp., <i>Stenella</i> spp., <i>Steno</i> , <i>Tursiops</i> spp.); Montodontidae (<i>Delphinapterus</i> , <i>Monodon</i>); Plantanistidae (<i>Plantanista</i>)	
Very high-frequency cetaceans	VHF	Delphinidae (<i>Cephalorhynchus</i> spp.; <i>Lagenorhynchus cruciger</i> , <i>L. australis</i>); Phocoenidae (<i>Neophocaena</i> spp., <i>Phocoena</i> spp., <i>Phocoenoides</i>); Iniidae (<i>Inia</i>); Kogiidae (<i>Kogia</i>); Lipotidae (<i>Lipotes</i>); Pontoporiidae (<i>Pontoporia</i>)	3
Sirenians	SI	Trichechidae (<i>Trichechus</i> spp.); Dugongidae (<i>Dugong</i>)	4
Phocid carnivores in water	PCW	Phocidae (<i>Cystophora</i> , <i>Erignathus</i> , <i>Halichoerus</i> , <i>Histriophoca</i> , <i>Hydrurga</i> , <i>Leptonychotes</i> , <i>Lobodon</i> , <i>Mirounga</i> spp., <i>Monachus</i> , <i>Neomonachus</i> , <i>Ommatophoca</i> , <i>Pagophilus</i> , <i>Phoca</i> spp., <i>Pusa</i> spp.)	5
Phocid carnivores in air	PCA		
Other marine carnivores in water	OCW	Odobenidae (<i>Odobenus</i>); Otariidae (<i>Arctocephalus</i> spp., <i>Callorhinus</i> , <i>Eumetopias</i> , <i>Neophoca</i> , <i>Otaria</i> , <i>Phocarcos</i> , <i>Zalophus</i> spp.); Ursidae (<i>Ursus maritimus</i>); Mustelidae (<i>Enhydra</i> , <i>Lontra felina</i>)	6
Other marine carnivores in air	OCA		

Mountain (2014) and discussed further by Ketten et al. (2016). At present, there is insufficient direct information—notably, no direct measurements of hearing sensitivity or TTS for any species—to make an explicit distinction between VLF and LF cetaceans or to propose separate auditory weighting functions and TTS/PTS onset. It is unlikely that such direct hearing measurements will be obtained in the near future given the substantial logistical challenges of working with these species, which include the largest animals on Earth.

While neurophysiological, AEP methods are a possible alternative that has been considered, they will be challenging to use for several reasons, including the large body size of animals and the expected limitations at low frequencies. Thus, despite acknowledging differences among the mysticetes and possible differences in susceptibility to VLF sounds, these species are assigned a single common weighting function (LF cetaceans). However, subsequent research on comparative auditory anatomy integrating

knowledge of other LF species (e.g., Ketten et al., 2016) and controlled measurements of behavioral responses to sound in free-ranging animals to evaluate certain aspects of hearing, such as frequency ranges of detection, should be promoted and could guide future noise exposure criteria regarding the potential VLF/LF divisions suggested for consideration here.

High-Frequency (HF) Cetacean Hearing Group

The HF cetacean group contains most delphinid species (e.g., bottlenose dolphin, common dolphin, and pilot whale), beaked whales, sperm whales, and killer whales (see Appendix 2). Hearing sensitivity has been directly measured for approximately one-third of the species within this group using either behavioral audiometry or neurophysiological, AEP measurements. Given best hearing sensitivity at frequencies of several tens of kHz or higher for many of the species in this hearing group, they are described as HF species here; it should be noted that this represents most

of the same species identified as MF cetaceans by Southall et al. (2007), Finneran (2016), NMFS (2016, 2018), and Houser et al. (2017).

All odontocetes lack pinnae and a functional auditory meatus and, instead, use a unique auditory pathway of acoustic fats aligned with the lower jaw to direct sound to the ears (Wartzok & Ketten, 1999). Two middle ear types are present within the HF cetaceans (Fleischer, 1978; Nummela, 2008). The odontocete ear type is present in most species (and all delphinids) studied to date and is designed to acoustically isolate ear structures from the rest of the skull. The physeteroid ear type is present within Physeteridae and Ziphiidae families in the HF group, as well as Kogiidae within the VHF cetaceans (below); this ear type features a tightly fused tympanic and periotic bone and several distinct cochlear characteristics (see Wartzok & Ketten, 1999).

Predictions of hearing frequency ranges derived from anatomical modeling are available currently for relatively few species (notably the harbor porpoise and bottlenose dolphin). Sound production (including both social and echolocation signals) is complex, diverse, and generally well-described across most HF cetacean species (for a detailed review, see Appendix 2). Echolocation click type distinctions based on Fenton et al. (2014) provide additional insight into the distinction of HF cetaceans from other hearing groups and support a possible further segregation among them (see below). Three click types have been described among the HF cetaceans: (1) broadband high-frequency clicks (BBHF), (2) frequency-modulated (FM) upsweeps, and (3) multi-pulsed (MP) click types. Most HF cetacean species produce BBHF clicks while searching for prey. Sperm whales are unique in producing extremely loud, relatively low-frequency MP clicks with multiple pulses caused by reverberation of the signal within the head. All beaked whales studied produce an FM click while searching for prey, and some species have been shown to produce a more broadband click in the terminal phases of prey capture. No HF cetacean species produce narrow-band high-frequency (NBHF) clicks, which are exclusive to the VHF cetaceans (below). The distinction between the HF cetaceans described in Appendix 2 vs the LF cetaceans and the specialized VHF cetaceans is thus supported by combined scientific evidence, including phylogeny, direct measurements of frequency ranges of hearing, anatomical distinctions, frequency ranges of acoustic signals, and echolocation click type distinctions.

Within the HF cetaceans, a potential further segregation is proposed here for species that may be relatively more sensitive to lower frequencies than other odontocetes in this group, specifically

sperm whales, killer whales, and beaked whales. Several lines of evidence support such a distinction. First, these species are generally larger than other odontocetes. While there is not a clearly linear relationship between body size and hearing sensitivity, a general trend of lower HF limits and better LF sensitivity with increasing body mass has been documented (e.g., see Heffner & Heffner, 2008). In terms of direct hearing measurements, limited AEP data for a stranded sperm whale (Ridgway et al., 2001) suggest best hearing sensitivity between 5 and 20 kHz. Limited AEP data for beaked whales (Cook et al., 2006; Finneran et al., 2009; Pacini et al., 2011) indicate relatively broad ranges of good sensitivity extending below at least 5 kHz. Earlier behavioral hearing data for killer whales (Szymanski et al., 1999) have recently been augmented by complete audiograms for six killer whales (Branstetter et al., 2017). These results do not necessarily suggest major differences in HF hearing cut-offs from other HF cetacean species but do indicate relatively good hearing at low frequencies compared with other species. Finally, as mentioned above, both the sperm whales and beaked whales have categorically distinct echolocation click signal types from all other HF cetaceans. While they also differ from one another, they are similar in having a lower center frequency of the predominant click energy than clicks of other HF cetaceans. However, these biosonar signal distinctions of sperm and beaked whales do not apply to killer whales, which are much more similar to the other HF cetaceans in this regard. Given these several lines of evidence, subsequent criteria should consider, based on additional research results, whether sperm, beaked, and killer whales should be considered as a separate (MF cetacean) hearing group. This issue is by no means resolved, however, and there are presently insufficient supporting data on hearing and (particularly) TTS/PTS-onset thresholds to establish discrete noise exposure criteria for these species from those derived for the HF cetaceans.

Very High-Frequency (VHF) Cetacean Hearing Group

The VHF cetacean group (see Appendix 3) comprises the true porpoises, most river dolphin species, pygmy/dwarf sperm whales, as well as a number of oceanic dolphins (Commerson's, Chilean, Heaviside's, Hector's, Hourglass, and Peale's dolphins). Direct measurements of hearing using behavioral and/or AEP methods are available for three species within this group, each indicating substantially higher upper-frequency hearing limits than HF cetaceans, with best sensitivity in some species exceeding 100 kHz. The

VHF cetaceans lack a functional auditory meatus but possess an auditory pathway of acoustic fats in the lower jaw. They have an odontocete middle ear type (Nummela, 2008) and temporal bones (the tympanoperiotic complex) that are acoustically isolated from the rest of the skull with dense ossicles, as well as cavernous tissue in the middle ear cavity (e.g., Ketten, 1994, 2000). The inner ear features hypertrophied cochlear duct structures, dense ganglion cell distributions, and several distinguishing cochlear parameters (see Appendix 3). It should be noted that these features are common to essentially all odontocetes and not specific to this group, but these features are particularly prominent within the VHF species.

The VHF cetaceans show some differences in sound production compared to the other hearing groups. Several parameters of search-phase echolocation signals distinguish the VHF cetaceans. Center frequencies exceed 100 kHz in almost all species and 150 kHz in several, representing the highest such values in marine mammals. The NBHF echolocation click type (as defined by Fenton et al., 2014) is exclusively present in all VHF cetacean species and does not occur within any other cetaceans; this includes the six delphinid species categorized as VHF cetaceans, including the *Cephalorhynchus* spp. and two species of the genus *Lagenorhynchus* (hourglass and Peale's dolphin). Thus, direct hearing measurements, anatomy-based predictions of hearing range (see Racicot et al., 2016), and multiple characteristics of biosonar signals are all generally consistent in distinguishing the VHF from the HF cetaceans (see Appendix 3 for more details).

Sirenian (SI) Hearing Group

The SI group includes the manatees and dugongs (see Appendix 4). These species differ from cetaceans and marine carnivores both phylogenetically and in their natural history. Some behavioral and electrophysiological hearing data are available for manatees, indicating some similarities to HF cetaceans and phocid pinnipeds. But based on their taxonomic differences, auditory anatomical distinctions, and apparent differences in aspects of sound production, they are considered here as a separate group. The pinnae are absent, the auditory meatus is thin and apparently occluded, the tympanic membrane is enlarged and bulges outward, and the ossicles are massive with unique features, including oil-filled bony structures (Ketten et al., 1993). They are characterized as having the sirenian ear type, with a U-shaped tympanic bone fused to a much larger periotic bone (Nummela, 2008), which, unlike most other mammals, does not surround the middle ear cavity. Earlier anatomical predictions of auditory range for West Indian manatees suggested they would

be sensitive from the infrasound range to less than 20 kHz, with peak sensitivity around 8 kHz, but direct measurements indicate that hearing can extend from low frequencies to above 60 kHz (see Appendix 4). Only underwater auditory weighting and exposure functions and TTS/PTS-onset levels are derived given that these species, like cetaceans, are functionally obligate aquatic.

Phocid Carnivores in Air (PCA) and Water (PCW) Hearing Groups

This group contains all the true seals, including harbor, gray, and freshwater seals; elephant and monk seals; and both Antarctic and Arctic ice seals (see Appendix 5). Southall et al. (2007) noted the significant differences in hearing between the phocid and otariid pinnipeds, particularly the much higher, upper-frequency hearing limits of phocids measured in water, but concluded there were insufficient data on unmasked amphibious hearing and especially the effects of noise on hearing to consider separate groups, weighting functions, and TTS/PTS-onset levels. A number of subsequent audiometric studies have been published which confirm the extremely broad (7 to 8 octaves in some species) range of best hearing sensitivity among phocid seals (which for this family is the widest among any mammalian taxa), with upper-frequency cut-offs exceeding 60 kHz in almost all species (see Reichmuth et al., 2013; Finneran, 2016). These, along with a number of anatomical characteristics, unequivocally distinguish phocid seals from other pinnipeds and related marine carnivores. These true seal species lack outer pinnae and have cavernous tissue lining the auditory meatus and middle ear cavity (Möhl, 1968; Reppening, 1972; Wartzok & Ketten, 1999). They possess a phocid middle ear type (Nummela, 2008), with features including an enlarged tympanic membrane, ossicles, and middle ear cavity. Given their amphibious nature and fundamental differences in hearing, and the effects of noise between the two media, discrete aerial and underwater auditory weighting and exposure functions and TTS/PTS-onset thresholds are presented here.

Other Marine Carnivores in Air (OCA) and Water (OCW) Hearing Groups

This group contains all non-phocid marine carnivores, including the otariid seals (sea lions and fur seals), walruses, sea otters, and polar bears (see Appendix 6). Recent studies have been published on key species representing each of the main taxa in this group. The combined audiometric, anatomical, and sound production data indicate a clear segregation between the phocid seals and other marine carnivores which have less sensitive HF hearing. Nearly all species included in this group share a common *freely mobile* ear type, which features a loose connection

between the ossicles and the skull (Fleischer, 1978; Nummela, 2008). The one exception is the walrus, which has an ear that is somewhat intermediate to a freely mobile ear and the ear type characteristic of phocids. The walrus has enlarged ossicles, a large tympanic membrane, and, like phocids, lacks pinnae, but the shape and form of the ossicles and other morphological features are distinctively otariid in form (Repenning, 1972). Subsequent research on walrus audiometry, including TTS measurements, and auditory anatomy would support further evaluation of their characterization within the marine carnivores either within phocid or non-phocid hearing groups or, potentially, as a distinct hearing group. Here, they are included with the other marine carnivores both in air and water.

Across these non-phocid marine carnivore species, there are relatively large differences in natural history and the proportion of time spent in and out of water. However, all are amphibious mammals and are known or likely to have amphibious differences in hearing and the effects of noise on underwater hearing. Consequently, separate aerial and underwater auditory weighting and exposure functions and TTS/PTS-onset thresholds are included for this marine mammal hearing group as well.

Estimated Group Audiograms for Marine Mammals

Substantial uncertainties and data gaps remain in understanding marine mammal hearing, but considerably more information exists for some species than was available to Southall et al. (2007). As a result, a more quantitative approach to characterizing group-specific hearing is now possible, the relative support for which depends on the amount and quality of the underlying direct measurements of hearing. The objective is to apply systematic methods and the best available scientific information in describing group-specific hearing for each of the marine mammal hearing groups described in the previous section. The approach is described below, followed by its application in estimating group audiograms. For the LF cetaceans for which no audiograms or direct measurements of hearing at any frequency for any species exist, we estimated hearing parameters relying upon extensive assumptions and extrapolation, including mathematical modeling using anatomical parameters, characteristics of sound production, and assumptions based on other species). This group (LF cetaceans) is thus described separately (last) within this section, with considerable associated caveats, given the extent to which it differs from the median-based method used to interpret direct hearing data in other groups.

The approach in estimating group audiograms to represent many species within each marine

mammal group is to use median values among available data across individuals of different species. Clearly, there is substantial individual variability (both documented and expected) within and among species in the hearing groups identified herein. A comprehensive, quantitative description of this variability within and between all species would be desirable to more fully understand the validity of the hearing groups proposed and potential species-specific deviation from the median-based estimated group audiograms. However, the existing marine mammal hearing data are at present inadequate (with the exception of a very few species) to support such an analysis of variance. This is an acknowledged limitation of the quantitative approach taken and an area where subsequent criteria will benefit from additional data. Given these constraints, the use of a median-derived interpretation of the available data was deemed the most appropriate given the need to consider all species within a reasonable number of hearing groups rather than failing to consider some taxa at all.

Estimated group audiograms derived with median values from available direct measurements of hearing are used to establish several important metrics related to hearing—namely, auditory weighting and exposure functions for estimating the effects of noise on hearing (see the “Marine Mammal Auditory Weighting and TTS Exposure Functions” section). Estimated group audiograms are derived using both absolute and normalized (to the frequency of best sensitivity) thresholds from behavioral hearing studies, following the methodology of Finneran (2016). Such data are available for at least three individuals (and, in some cases, many more) within all but one marine mammal hearing group. Differences in hearing sensitivity have been measured between well-established behavioral audiometric methods (based on animal responses to experimental stimuli using the complete auditory and perceptual systems) and AEP measurements (based on electrophysiological responses within a portion of the auditory system). The AEP method is not capable of testing the full range of hearing as described, so AEP thresholds are not quantitatively applied in deriving estimated group audiograms. However, they were considered directly in hearing group designations for some species (along with other indirect methods of evaluating hearing capabilities as discussed above). Furthermore, some existing behavioral hearing data were considered but excluded from the estimated group audiograms. The excluded data were from individuals with obvious HF hearing loss or other evident aberrations from the normal species audiograms (e.g., obvious notches or thresholds known to be elevated for that species for a clear or likely reason such as auditory masking in the testing

enclosure or frequency-specific hearing loss). For individuals tested in multiple studies, data at overlapping frequencies were averaged such that only one value for any individual was used at any frequency tested. However, multiple measurements from the same individual at different frequencies were treated as independent measurements. As a simplifying assumption deemed reasonable based on a general understanding of normal hearing in marine and other mammals, linear interpolation was used to generate a threshold estimate for every unique frequency tested for any individual in the marine mammal hearing group. This was done so that the results from all individuals contained threshold estimates at all frequencies, which could be considered.

Estimated group audiograms were determined based on the median threshold value at each test frequency among all individuals of any species within a hearing group for which behavioral hearing data were available. This approach incorporated all available data but minimized the influence of outlier values relative to the use of averages. The group audiograms were determined in two ways. First, the original (absolute) threshold values from every individual included among each group (in dB re 1 μ Pa [underwater thresholds] or dB re 20 μ Pa [aerial thresholds]) were used to determine group-wide median threshold values at each test frequency. These median thresholds were then used to derive estimated group audiograms (see below). Second, *normalized* thresholds were determined for each individual. This process involved subtracting thresholds at each frequency from the lowest threshold value obtained at any frequency. For example, if the lowest threshold measured within an individual for any frequency was 68 dB re 1 μ Pa at 10 kHz and a threshold of 88 dB re 1 μ Pa was measured at 1 kHz, the normalized threshold for 1 kHz would be 20 dB, whereas the normalized threshold for 10 kHz would be 0 dB.

Median threshold values were then fit by the following equation derived by Finneran (2016), which was modified from an equation used by Popov et al. (2007) to describe audiograms in dolphins. Finneran (2016) included additional frequency parameters to produce a shallower slope in the region of best sensitivity given the intended broader application across multiple species within groups and acknowledged data limitations for many species being represented:

$$\text{Equation (1)} \quad T(f) = T_0 + A \log_{10} \left(1 + \frac{F_1}{f} \right) + \left(\frac{f}{F_2} \right)^B$$

where $T(f)$ is the threshold at frequency f . Other variables are curve fitting parameters determined from the available group-specific behavioral hearing data:

T_0 fits the overall vertical position of the curve such that the lowest value occurs at the frequency at which the lowest threshold was measured.

F_1 is the inflection point of the LF rolloff.

A is a fitting parameter related to the slope of the LF rolloff.

F_2 is the inflection point and slope of the HF rolloff.

B is a fitting parameter related to the slope of the HF rolloff.

The resulting equation provides a standardized means of estimating a representative absolute and normalized audiogram function for all species within the group. It should be recognized that for all groups, these are estimated functions based on data from a few species and individuals. These curves represent the best fit to the limited existing data based on the assumptions and procedures described herein, but it should be clearly recognized that most species within each group have not been directly tested.

The resulting estimated group audiograms have features typical of mammalian hearing: linear-log threshold decrease with variable slope at low frequencies and a rapid increase in threshold at high frequencies that can be fit with an exponential function. Equation (1) was fit to the available median threshold data using nonlinear regression for each marine mammal group except LF cetaceans.

The original and normalized behavioral hearing threshold data used for most marine mammal hearing groups are discussed below, followed by the different approach taken in proposing a preliminary estimated group audiogram for LF cetaceans given the absence of direct hearing measurements. The resulting estimated group audiograms (using the absolute and normalized threshold data, respectively) based on the fitted curves are given for the odontocete (HF and VHF) cetaceans (Figures 1 & 2), sirenians (Figures 3 & 4), marine carnivores in water (Figures 5 & 6), and marine carnivores in air (Figures 7 & 8). The associated curve fitting parameters for all groups are given subsequently (Tables 2 & 3). Audiometric data that were available but not directly applied are specified, along with the reason for exclusion, within the respective group-specific appendix in which all audiometric and auditory anatomy data are presented. The curve fits based on a different estimation procedure of all fitting parameters for the LF cetaceans are presented separately (Figures 9 & 10).

Estimated Group Audiograms for Odontocete Cetaceans (HF & VHF)

For HF cetaceans, audiometric data were used for the following species and individuals tested: bottlenose dolphin (Johnson, 1967 [$n = 1$]; Ljungblad et al., 1982 [$n = 1$]; Lemonds, 1999 [$n = 1$]; Brill et al., 2001 [$n = 1$]; Schlundt et al., 2007 [$n = 1$]; Finneran et al., 2010 [$n = 1$]), beluga whale (White, 1978 [$n = 1$]; Awbrey et al., 1988 [$n = 3$]; Johnson et al., 1989 [$n = 1$]; Ridgway et al., 2001 [$n = 2$]; Finneran et al., 2005b [$n = 1$]), killer whale (Szymanski et al., 1999 [$n = 2$]), Risso's dolphin (Nachtigall et al., 1995 [$n = 1$]), striped dolphin (Kastelein et al., 2003 [$n = 1$]), tucuxi dolphin (Sauerland & Dehnhardt, 1998 [$n = 1$]), false killer whale (Thomas et al., 1988) [$n = 1$]), and Pacific white-sided dolphin (Tremel et al., 1998 [$n = 1$]). These combined data were applied to derive the HF cetacean estimated group audiograms for the original (absolute sensitivity) threshold data (Figure 1, left) and normalized values (Figure 2, left).

For VHF cetaceans, audiometric data were used for the following species and individuals tested: harbor porpoise (Kastelein et al., 2002a [$n = 1$]; Kastelein et al., 2010 [$n = 1$]; Kastelein et al., 2015 [$n = 1$]) and Amazon river dolphin (Jacobs & Hall, 1972 [$n = 1$]). These combined data were used to derive the VHF cetacean estimated group audiograms for the original threshold data (Figure 1, right) and normalized values (Figure 2, right).

Estimated Group Audiograms for Sirenians (SI)

Behavioral hearing data were used for the following species and individuals tested: West Indian manatee (Gerstein et al., 1999 [$n = 2$]; Mann et al.,

2005 [$n = 2$]). The secondary decrease in thresholds at below 0.3 kHz evident in Gerstein et al. (1999) may have been the result of non-auditory (tactile) sensitivity to vibration; these values were consequently excluded from the determination of the estimated group audiogram. These combined data were applied to derive SI estimated group audiograms for the original threshold data (Figure 3) and normalized values (Figure 4).

Estimated Group Audiograms for Phocids and Other Marine Carnivores in Water (PCW & OCW)

For PCW, audiometric data were used for the following species and individuals tested: northern elephant seal (Kastak & Schusterman, 1999 [$n = 1$]), harbor seal (Terhune, 1988 [$n = 1$]; Kastelein et al., 2009 [$n = 1$]; Reichmuth et al., 2013 [$n = 1$]), spotted seal (Sills et al., 2014 [$n = 2$]), and ringed seal (Sills et al., 2015 [$n = 1$]). These combined data were applied to estimate the PCW group audiograms for the original threshold data (Figure 5, left) and normalized values (Figure 6, left).

For OCW, audiometric data were used for the following species and individuals tested: northern fur seal (Moore & Schusterman, 1987 [$n = 2$]; Babushina et al., 1991 [$n = 1$]), California sea lion (Mulsow et al., 2012 [$n = 1$]; Reichmuth & Southall, 2012 [$n = 2$]; Reichmuth et al., 2013 [$n = 1$]), Steller sea lion (Kastelein et al., 2005 [$n = 2$]), walrus (Kastelein et al., 2002b [$n = 1$]), and sea otter (Ghoul & Reichmuth, 2014 [$n = 1$]). These combined data were applied to derive OCW estimated group audiograms for the original threshold data (Figure 5, right) and normalized values (Figure 6, right).

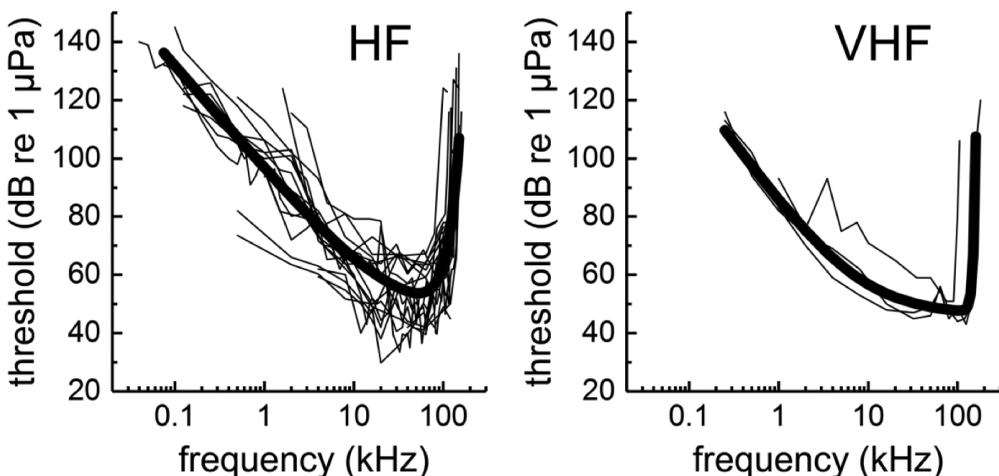


Figure 1. Estimated group audiograms based on original behavioral threshold data for high-frequency (HF) cetaceans (left) and very high-frequency (VHF) cetaceans (right)

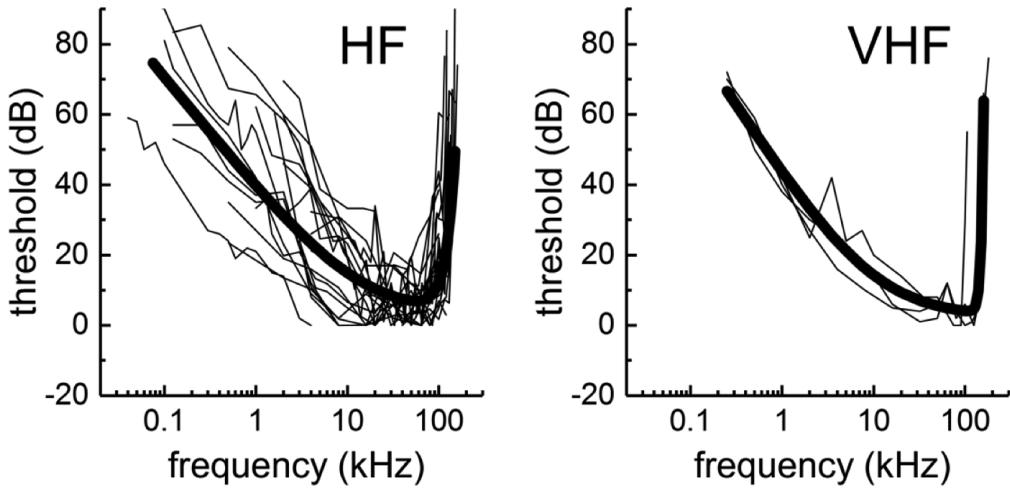


Figure 2. Normalized estimated group audiograms for HF cetaceans (left) and VHF cetaceans (right)

Estimated Group Audiograms for Phocids and Other Marine Carnivores in Air (PCA, OCA)

For PCA, audiometric data were used for the following species and individuals tested: harbor seal (Reichmuth et al., 2013 [$n = 1$]), spotted seal (Sills et al., 2014 [$n = 2$]), and ringed seal (Sills et al., 2015 [$n = 1$]). These combined data were applied to derive estimated group audiograms for the original PCA threshold data (Figure 7, left) and normalized values (Figure 8, left).

For OCA, audiometric data were used for the following species and individuals tested: northern fur seal (Moore & Schusterman, 1987 [$n = 3$]; Babushina et al., 1991 [$n = 1$]), California sea lion (Mulsow et al., 2011 [$n = 1$]; Reichmuth et al., 2013 [$n = 1$]), Steller sea lion (Mulsow & Reichmuth, 2010 [$n = 1$]), polar bear (Owen & Bowles, 2011 [$n = 1$]), and sea otter (Ghoul & Reichmuth, 2014 [$n = 1$]). These combined data were applied to derive OCA estimated group audiograms for the original (absolute) threshold data (Figure 7, right) and normalized values (Figure 8, right).

Estimated Audiogram Parameter Values for Marine Mammal Groups Based on Direct Measurements of Hearing

From the available data, median (50th percentile) threshold values were determined or estimated at each frequency and then fit by Equation (1) using fitting parameters specified. The resulting parameters and goodness of fit values (R^2) to the group-specific estimated group audiograms are given for all absolute (Table 2) and normalized (Table 3) threshold data. While these parameters are related to different aspects of estimated hearing across species, including best absolute sensitivity and respective differences at frequencies

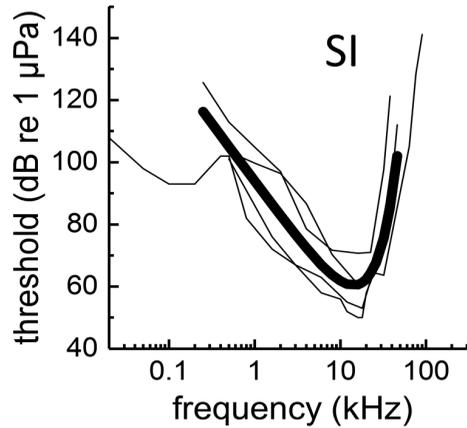


Figure 3. Estimated group audiogram based on original behavioral threshold data for sirenians (SI)

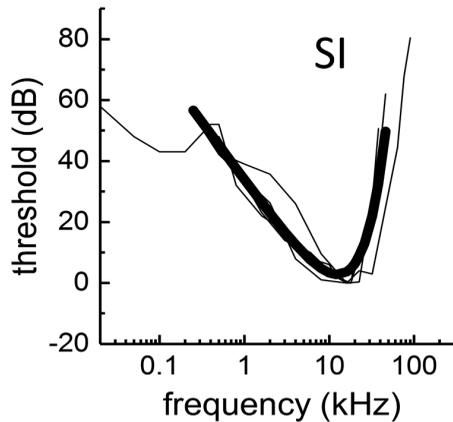


Figure 4. Normalized estimated group audiogram for SI

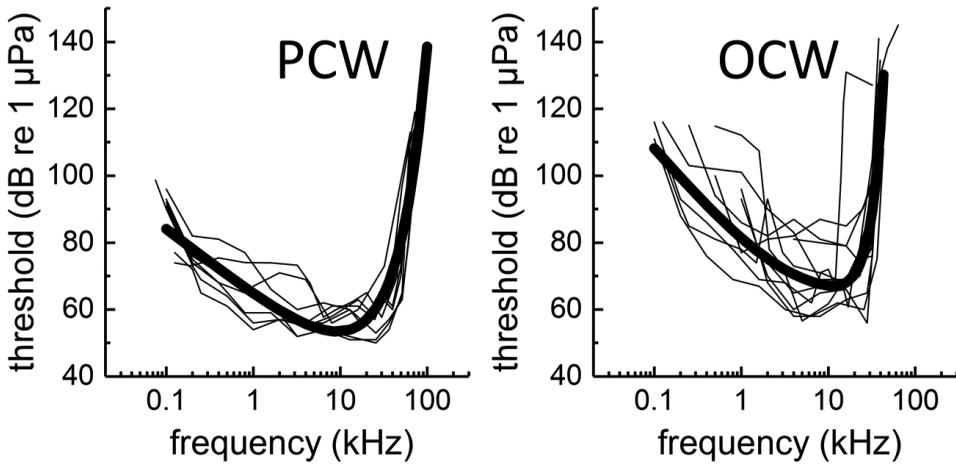


Figure 5. Estimated group audiograms based on original behavioral threshold data for marine carnivores in water (left: phocid carnivores in water [PCW]; right: other carnivores in water [OCW])

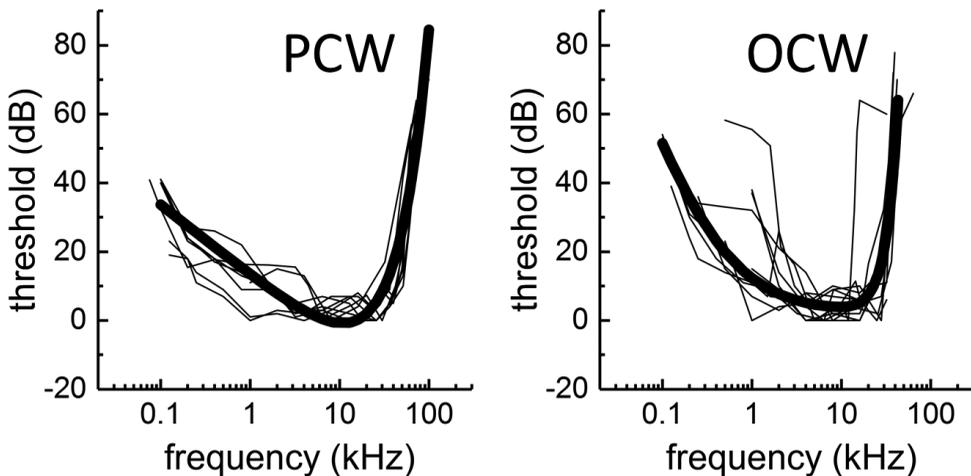


Figure 6. Normalized estimated group audiograms for marine carnivores in water (left: PCW; right: OCW)

below and above the region of best sensitivity, they should be recognized as simply equation fitting parameters and not interpreted as estimates of specific features of the estimated audiograms. The extent to which they differ from certain features is dependent on the overall shape of the resulting curves. For instance, T_0 fits the vertical position of the curve and is comparable to the estimated absolute threshold at best hearing sensitivity for some species groups (e.g., HF cetaceans) but is very different for other groups (e.g., PCA) based simply on the shape of the function and the fit required.

Preliminary Estimated Hearing Parameters for Mysticete Cetaceans (LF)

For LF cetaceans, no direct hearing data (behavioral or electrophysiological) were available at any frequency for any species. That is, there are no comprehensive, directly measured audiograms for any baleen whale from which we can estimate an LF cetacean group audiogram as was done for all other species groups. To avoid simply not providing criteria for these species and to provide some consistency in the overall approach with the other hearing groups, an alternative approach was used to estimate hearing parameters for the LF cetaceans. While determination of these curve fitting

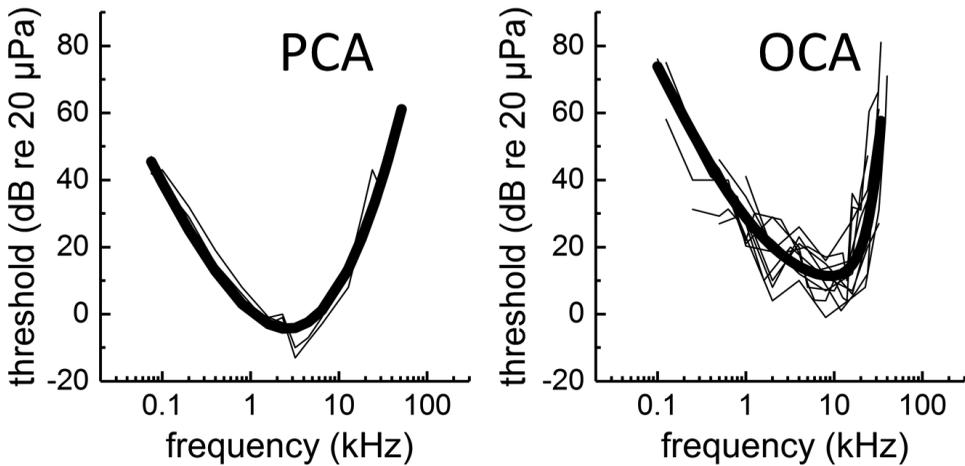


Figure 7. Estimated group audiograms based on original behavioral threshold data for marine carnivores in air (left: phocid carnivores in air [PCA]; right: other carnivores in air [OCA])

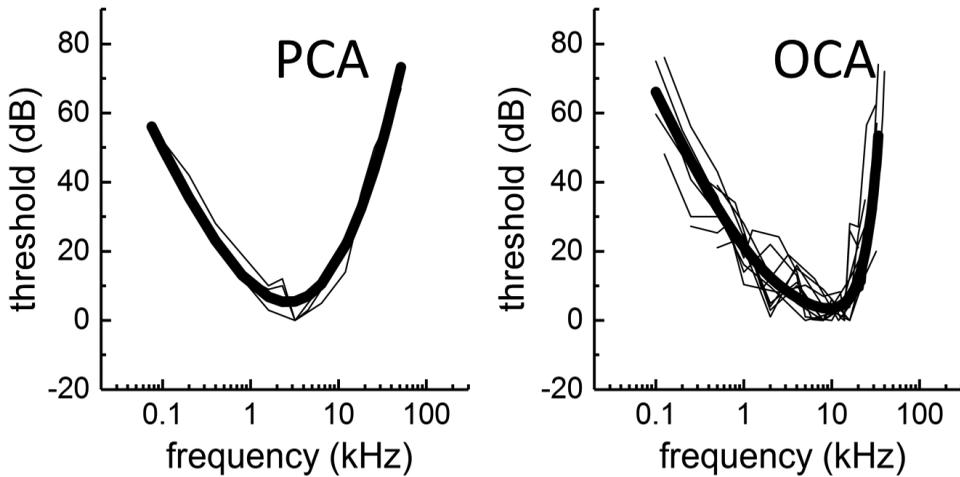


Figure 8. Normalized estimated group audiograms for marine carnivores in air (left: PCA; right: OCA)

parameters is based on limited data for all groups, this process is fundamentally different for the LF cetaceans in that every parameter was estimated without direct data from *in vivo* hearing studies to inform the estimate. Consequently, the underlying assumptions of this alternative methodology are discussed separately. The resulting estimated hearing parameters are given here and should be interpreted with full acknowledgment of the absence of direct data and the extensive requisite extrapolation.

A diverse range of studies were considered in estimating LF cetacean hearing parameters. These included basilar membrane dimensions (e.g., Ketten, 1994, 2014; Parks et al., 2007b; Ketten & Mountain, 2014), scaling relationships between inter-aural

time differences and upper-frequency limits of hearing (see Ketten, 2000), an extrapolation of cat and human threshold data based on earlier frequency-place maps for the humpback whale (Houser et al., 2001), and finite element models of head-related and middle-ear transfer functions. Finite element models of middle ear functions (Tubelli et al., 2012a, 2012b) and skull vibrational bone force curve models (Cranford & Krysl, 2015) informed the determination of the LF slope of the functions ($A = 20$ dB/decade). Estimates of the audible range of hearing and frequencies of best sensitivity were made based on an integration of results from Houser et al. (2001), Tubelli et al. (2012b), and Cranford & Krysl (2015), which suggest that peak sensitivity

Table 2. Estimated group audiogram parameter values determined by the best fit of Equation (1) for marine mammal groups based on directly measured behavioral hearing thresholds

Marine mammal hearing group	T_0 (dB)	F_1 (kHz)	F_2 (kHz)	A	B	R^2
HF	46.2	25.9	47.8	35.5	3.56	0.977
VHF	46.4	7.57	126	42.3	17.1	0.968
SI	-40.4	3,990	3.8	37.3	1.7	0.982
PCW	43.7	10.2	3.97	20.1	1.41	0.907
OCW	63.1	3.06	11.8	30.1	3.23	0.939
PCA	-110	5.56	1.02×10^{-6}	69.1	0.289	0.973
OCA	6.24	1.54	8.24	55.6	2.76	0.978

Table 3. Normalized estimated group audiogram parameters values determined by the best fit of Equation (1) for marine mammal groups based on directly measured behavioral hearing thresholds

Marine mammal hearing group	T_0 (dB)	F_1 (kHz)	F_2 (kHz)	A	B	R^2
HF	3.61	12.7	64.4	31.8	4.5	0.960
VHF	2.48	9.68	126	40.1	17	0.969
SI	-109	5,590	2.62	38.1	1.53	0.963
PCW	-39.6	368	2.21	20.5	1.23	0.907
OCW	2.36	0.366	12.8	73.5	3.4	0.958
PCA	-71.3	4.8	6.33×10^{-5}	63	0.364	0.975
OCA	-1.55	1.6	8.66	54.9	2.91	0.968

occurs between ~1 to 8 kHz for the species modeled, with best sensitivity range of hearing (defined as occurring within ~40 dB of peak sensitivity) ranging from ~30 Hz to ~30 kHz depending on species. The F_1 (LF inflection point) parameter was selected such that thresholds in the 1 to 8 kHz range were within 3 dB of the lowest threshold. Note that this implies considerably reduced sensitivity for some LF species at frequencies emphasized in their vocal repertoire (e.g., the narrowband 20-Hz tonal signals of fin whales; Watkins, 1981; Edds-Walton, 1997). However, it is important not to overlook that the fundamental frequency of a vocalization is not necessarily the key feature for communication or perception but, rather, as has been demonstrated in other species, components, such as the envelope and/or harmonics, may be of equal or greater significance.

The LF high-frequency hearing parameters were determined using hearing data from other marine mammals. Specifically, the median value of the B fitting parameter (related to the slope of HF component) for all other marine mammal groups measured in water (HF, VHF, SI, PCW, and OCW). Given this slope ($B = 3.2$), the F_2 parameter (HF inflection point) was determined as 9.4 kHz such that the estimated threshold at 30 kHz was within 40 dB of the lowest threshold.

Given the absence of any direct measurements of hearing sensitivity, the vertical position of the estimated audiogram was determined based on available behavioral audiometric measurements in other marine mammals. The T_0 fitting parameter was estimated as 53.2 dB based on the median of the lowest hearing thresholds for all other marine mammal groups in water (HF, VHF, SI, PCW, and OCW).

An estimated audiogram for the LF cetaceans was then derived (Figure 9) using these fitting parameter values in Equation (1). No goodness of fit (R^2) value was determined given the lack of direct hearing data with which to compare the curve, underscoring the necessary caveats regarding the estimated audiogram. As with other groups, an estimated normalized audiogram was then derived using identical values for F_1 , F_2 , A , and B and value of T_0 (0.8 dB) that resulted in the lowest point of the curve (frequency of best sensitivity) equaling 0 dB (Figure 10).

These estimated curves suggest better sensitivity and a broader audible frequency range than anatomically based indirect estimates of hearing for humpback (Houser et al., 2001) and fin (Cranford & Krysl, 2015) whales and are in closer agreement with earlier publications of inner ear frequency maps noted above. The hearing parameters estimated for LF cetaceans are generally consistent

with broad predictions of LF sensitivity in mysticetes based on vocal behavior (Parks et al., 2007a) and the predictions of Clark & Ellison (2004) who estimated best hearing sensitivities of 60 to 70 dB re 1 μ Pa for baleen whales. This estimate was based upon the assumption that hearing sensitivity evolves to be 16 to 24 dB above typical ocean ambient noise spectrum levels given a critical ratio of 16 to 24 dB.

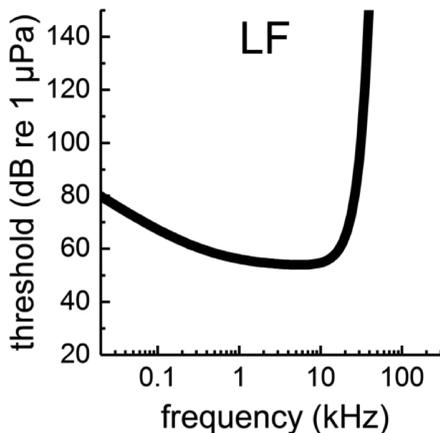


Figure 9. Estimated group audiogram for low-frequency (LF) cetaceans proposed with extensive assumptions, extrapolations, and caveats (see text for details)

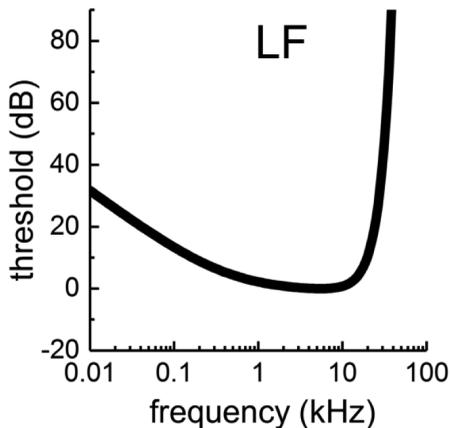


Figure 10. Normalized estimated group audiogram for LF cetaceans proposed with extensive assumptions, extrapolations, and caveats (see text for details)

Marine Mammal Auditory Weighting and TTS Exposure Functions

Weighting Functions and Exposure Functions

Marine mammal hearing groups were identified, and hearing parameters were estimated in the absence of complete data on many individuals of all species to provide what is believed to be a best estimate of hearing among the group as a function of frequency as described above.

At frequencies where an animal has sensitive hearing (lower thresholds), it is more likely to be more susceptible to auditory effects of noise exposure (i.e., lower TTS-onset thresholds) because the relative difference between noise and hearing threshold (often called *sensation level*) is greater for the same exposure level than for frequencies for which the animal has less sensitive hearing (higher thresholds). That is, while effects can occur for frequencies outside an animal's range of best hearing sensitivity, there is a general relationship between hearing sensitivity and susceptibility to noise exposure, allowing conclusions related to frequency-dependence of hearing capabilities to roughly inform assessments of susceptibility to potential auditory effects (see Yost, 2006). This approach has been validated for a range of terrestrial animals (Kerr et al., 2017) and supported by research on marine mammals in the last decade (see Finneran, 2015). The available hearing data used to derive estimated group audiograms were used in combination with other audiometric data (i.e., equal loudness, equal latency, and TTS measurements) to derive *auditory weighting functions* and corresponding *noise exposure functions*. These complementary functions provide different ways to visualize the frequency-specific effects of noise on different species with different hearing characteristics. *Auditory weighting functions* serve as frequency-specific filters that quantify how noise may affect an animal given its spectral content and how it relates to the spectral characteristics of an individual's potential susceptibility to noise. Weighting functions are used to de-emphasize noise at frequencies where susceptibility is lower. *Noise exposure functions* represent exposure levels for the onset of TTS or PTS as a function of noise frequency. Weighting functions and noise exposure functions have identical shapes but are inversely related, in a similar fashion as auditory sensitivity and hearing threshold. For both functions, identical values are determined for lower- and upper-frequency values at which either relative sensitivity or a threshold for a defined exposure begins to change. Similarly, slope parameters describing the rate of this change at both low and high frequencies are identical, although with inverse signs (negative for

weighting functions; positive for exposure functions). However, the *anchor* values determining the vertical positions of each function are different. Whereas weighting functions are grounded at a nominal amplitude of 0 dB (at best hearing sensitivity) with negative weighting at relatively lower and higher frequencies, exposure functions have a minimum value at the lowest threshold for a known or estimated effect level (e.g., TTS) and show higher onset thresholds for different frequencies at values determined by the shape of the function. Methods used to determine these functions within different marine mammal groups are described herein.

Weighting functions have been primarily developed and evaluated systematically in humans, with limited efforts to develop them for non-human animals. Weighting functions are similar to “band-pass” filters—they include a central region corresponding to greatest susceptibility to noise along with lower- and higher-frequency regions where the relative susceptibility is lower (reflected as negative values on these curves). Weighting functions provide a group-specific means of calculating how a specific noise exposure would potentially affect the hearing of an animal given the extent to which the frequency spectra match frequency-specific hearing sensitivity. For noise exposures that occur at frequencies where animals are less susceptible, the effective exposure is reduced according to the weighting function (see Figure 1 in Houser et al., 2017). Effects of noise on an animal are determined by first weighting the noise exposure by filtering the noise using the weighting function. This is analogous to adding the weighting function amplitude (in dB) to the noise spectral amplitude (in dB) at each frequency, then integrating the weighted noise spectra across frequency to obtain the *weighted noise exposure level*, which describes exposure for the entire frequency range with a single metric. The weighted exposure level is then compared to the *weighted threshold* for TTS or PTS. The weighted threshold represents the exposure level required for the onset of TTS/PTS at frequencies where the weighting function has an amplitude of 0 dB (the peak of the weighting function). If the weighted exposure level is greater than or equal to the weighted threshold, TTS or PTS is assumed to occur. Predicting the effects of a noise exposure, therefore, requires both the weighting function and the weighted thresholds for TTS/PTS.

As described above, Southall et al. (2007) proposed frequency-specific auditory M-weighting functions for five marine mammal hearing groups utilizing the underlying format of C-weighting functions in humans, an idealized version of the

human 100-phon equal-loudness curve. Due to the disproportional growth in loudness with increases in relative intensity (loudness recruitment) with increasing level (Yost, 2006), equal loudness functions tend to flatten at higher received levels. The M-weighting functions only estimated upper- and lower-frequency cut-off values defined very conservatively—just 6 dB down from estimated best sensitivity. This was deliberate given the extreme data limitations on hearing and the effects of noise on hearing for most marine mammal species at the time, and the resulting weighting functions were quite broad and flat across most of the audible range. Auditory weighting functions for each hearing group here are defined to better describe relative hearing sensitivity within the audible range using the more data-derived, systematic approach of Finneran (2016), based on the following equation for a generic band-pass filter:

$$\text{Equation (2)} \quad W(f) = C + 10 \log_{10} \left\{ \frac{(f/f_1)^{2a}}{[1+(f/f_1)^2]^a [1+(f/f_2)^2]^b} \right\}$$

where $W(f)$ is the weighting function amplitude (in dB) at frequency f (in kHz). LF transition values (f_1 in kHz) represent the lower frequency at which the function amplitude begins to change from the flat, central portion of the curve. These have been described as *cut-offs* (Finneran, 2016), but it is important to note that they do not represent the lowest sound frequencies at which animals can hear. Some of the values are in fact unreasonable or illogical if interpreted in that manner. The specific amplitude of the weighting and exposure functions at f_1 depends on the value of the LF slope of each curve, which are defined below. HF transition values (f_2 in kHz) represent the upper frequency at which the function amplitude begins to change from the flat, central portion of the curve. Again, the specific amplitude of either function at f_2 depends on the upper-frequency slope of the curves. The LF exponent value (a – dimensionless) defines the rate of decline of the weighting function amplitude at low frequencies. The change in weighting function amplitude with frequency at low frequencies (the LF slope) is $20a$ dB/decade. The HF exponent value (b – dimensionless) defines the rate of decline of weighting function amplitude at high frequencies, becoming linear with the logarithm of frequency. The change in weighting function amplitude with frequency at high frequencies (the HF slope) is $-20b$ dB/decade. The constant C defines the vertical position of the curve. It is defined so that the maximum amplitude of the weighting function equals 0 dB (with all other values being negative).

Noise exposure functions combine the frequency-dependent weighting function with the weighted threshold value to represent exposure levels for the onset of TTS or PTS as a function of noise frequency. Exposure functions provide a group-specific function that characterizes and visualizes how noise exposure would induce a defined effect at different sound frequencies. Exposures equal to the group-specific TTS exposure function curve at a specific frequency would be predicted to result in TTS onset (typically defined as 6 dB TTS), with exposures exceeding these values resulting in some greater magnitude of TTS depending on the value above the curve and TTS growth relationships (see the following section). The exposure function minimum value equals the weighted threshold for TTS (or PTS onset). This value occurs at the frequency where the weighting function has a peak; this is typically similar to, but not necessarily identical to, the frequency of best hearing sensitivity (lowest threshold). Onset TTS levels increase for frequencies below and above this lowest point in the exposure function.

Exposure functions are complementary to weighting functions and are, therefore, defined using a similar equation:

$$\text{Equation (3)} \quad E(f) = K - 10 \log_{10} \left\{ \frac{(f/f_1)^{2a}}{[1+(f/f_1)^2]^a [1+(f/f_2)^2]^b} \right\}$$

where $E(f)$ is the exposure function amplitude (in dB) at frequency f (in kHz). The parameters f_1 , f_2 , a , and b are identical to those for the weighting function (Equation [2]). The parameter K determines the vertical position of the curve (as described in greater detail below). It is defined so that the minimum amplitude of the function equals the weighted TTS or PTS threshold estimated for each marine mammal hearing group.

In addition to the general similarities between Equations (2) and (3), several additional points are worth noting: (1) the second term in each equation is identical and defines the shape of each curve; (2) the change in sign before the second term (positive in Equation [2]; negative in Equation [3]) indicates that the functions are vertically inverted forms of each other; and (3) the parameters K , C , and the weighted threshold for TTS/PTS (T_w) are not independent. Since C is defined such that the peak of Equation (2) is zero and K is defined such that the minimum of Equation (3) equals T_w , Equations (2) and (3) can be manipulated to show that $T_w = C + K$. Additional details regarding these parameters and the relationships between their use in weighting and exposure functions are provided in Figure 1 of Finneran (2016).

Derivation of Function Parameters

Group-specific parameters for the non-impulsive TTS exposure functions and auditory weighting functions were derived following Finneran (2016). This involves both the application of function parameters described above for the weighting and exposure functions as well as a method of using available TTS data within groups where available or extrapolated from other groups where unavailable.

First, the values of a and b were defined for each group. Next, an iterative process was used whereby f_1 and f_2 were varied to minimize the differences between the exposure function and available, non-impulsive TTS-onset data for the HF and VHF groups. While TTS studies have been conducted for at least one species of most of the marine mammal groups, these are the only groups within which sufficient TTS data has been obtained in at least (but in many cases) one individual at multiple frequencies (see Finneran, 2015). That is, direct measurements of TTS that were available at enough frequencies to evaluate frequency differences were used to inform the shape of the weighting and exposure functions by manipulating the f_1 and f_2 parameters. These limited available TTS data were used directly for most hearing groups (an alternate approach was used for LF cetaceans) to inform the shape of the weighting and exposure functions rather than, for instance, simply inverting the estimated group audiograms. The results of the iterative process allowed f_1 and f_2 to be estimated for the remaining groups, albeit with acknowledgment of the greater underlying uncertainty in these estimations given this extrapolation. With f_1 , f_2 , a , and b defined for all groups, the parameter K for the TTS exposure function was defined to provide the best fit between the exposure functions and the available TTS-onset data (HF, VHF, PCW, OCW, PCA, and OCA) or estimated TTS onset (SI and LF). The weighted TTS threshold was then determined from the minimum of the exposure function. Finally, the parameter C was defined for each group by setting the maximum value of Equation (2) to zero. These steps are described in detail next.

The LF exponent (a) was determined for each group using the smaller (shallower) slope of either the LF slope from the estimated group audiogram or the LF slope of equal latency contours, where available. Audiogram slopes were calculated (using this slope) across a frequency range of one decade, beginning with the lowest frequency present for each group, except for the LF cetaceans for which this value was defined in the assumptions for the estimated group audiogram. Additionally, LF slopes based on equal latency measurements,

which are the basis for such functions in humans (see Houser et al., 2017), were determined. This was done for those species for which sufficient data were available, which included HF cetaceans (bottlenose dolphin; Mulsow et al., 2015), VHF cetaceans (harbor porpoise; Wensveen et al., 2014), PCA (harbor seal; Reichmuth, 2013), and OCA (California sea lion; Mulsow et al., 2015). The group-specific slopes at lower frequencies (s_0) were determined for other species groups using the LF slope from estimated group audiograms. The resulting s_0 values and the group-specific frequency of best hearing sensitivity (f_0) based on direct hearing measurements are shown for most marine mammal groups below (Table 4). For the LF cetaceans, given the lack of direct data, a different approach was taken to estimate these values. The f_0 parameter for LF cetaceans derived from the estimated audiogram is predicted to occur at 5.6 kHz based on an integrated interpretation of Houser et al. (2001) and Cranford & Krysl (2015) as described above. Given the lack of equal latency data, the s_0 value for LF cetaceans was estimated as 20 dB/decade based on the A fitting parameter used to derive the estimated group audiogram.

Because of the extreme lack of HF data (e.g., equal loudness or latency contours) with which to estimate this parameter, the HF exponent (b) for all hearing groups was defined as $b = 2$, based on prior weighting functions (Southall et al., 2007; Finneran, 2016), including the upper-frequency slope of human C-weighting functions. This is an area of specific needed research given the influence of this parameter on the overall shape of the function.

Group-specific values for frequencies f_1 and f_2 were defined as the frequencies at which the estimated group audiogram threshold values exceed the lowest threshold value (e.g., threshold at f_0 ; see Table 5) by a difference threshold (DT). The purpose of identifying this parameter was to establish a common relative relationship across all groups between the shape of the weighting function and the estimated group audiogram by using the limited available TTS data. The value of DT was determined in an iterative fashion by minimizing the mean-squared error between the exposure functions and available non-impulsive TTS data for the HF and VHF groups (the only groups with sufficient TTS-onset data at multiple frequencies). This value for DT was then extrapolated for use with all other hearing groups. If the value of DT were set to zero, the weighting function shape would be similar to the inverse shape of the estimated group audiogram. Increasing DT values progressively “compresses” the weighting function, making it broader compared to the audiogram near the frequency region of best sensitivity (see Finneran, 2016, for specific comparisons). This compression process has some of the same effects as loudness recruitment in equal loudness curves, which become flatter with increasing level (Yost, 2006). Compression accounts for available TTS data, which show smaller differences in TTS onset across frequencies than would be predicted by the shape of the inverse audiogram in the region near best sensitivity (Houser et al., 2017). Differences between the exposure functions calculated here using both auditory and TTS data, and simple predictions from an inverse audiogram

Table 4. Frequency of best hearing (f_0) and the magnitude of the low-frequency slope (s_0) derived from estimated group audiograms (from either original and normalized data) and/or equal latency contours. Where both estimates exist, the lowest respective slope values (in bold) were used to determine the low-frequency exponent value (a). The lack of direct hearing data for LF cetaceans forced an estimate of these parameters (see text).

Marine mammal hearing group	Original data estimated group audiogram		Normalized data estimated group audiogram		Equal latency curves
	f_0 (kHz)	s_0 (dB/decade)	f_0 (kHz)	s_0 (dB/decade)	s_0 (dB/decade)
HF	55	35	58	31	31
VHF	105	37	105	36	50
SI	16	36	12	37	--
PCW	8.6	19	13	20	--
OCW	12	27	10	39	--
PCA	2.3	41	2.3	42	41
OCA	10	45	10	45	27

Table 5. Marine mammal group-specific auditory weighting function and TTS exposure function parameters. Note that function parameter K for the LF and SI groups was estimated using TTS-onset data extrapolated from individuals in other marine mammal groups tested in water.

Marine mammal hearing group	f_1 (kHz)	f_2 (kHz)	a	B	K (dB)	R^2	C (dB)
LF	0.20	19	1	2	179	--	0.13
HF	8.8	110	1.6	2	177	0.825	1.20
VHF	12	140	1.8	2	152	0.864	1.36
SI	4.3	25	1.8	2	183	--	2.62
PCW	1.9	30	1	2	180	--	0.75
OCW	0.94	25	2	2	198	0.557	0.64
PCA	0.75	8.3	2	2	132	--	1.50
OCA	2.0	20	1.4	2	156	--	1.39

method are shown in the exposure function figures below. These comparisons illustrate both the differences in predicted sensitivity and the fact that experimental measurements of TTS onset at different frequencies are better predicted using the empirically based weighting functions than a simple inverse audiogram method.

The value of K was determined to minimize the mean squared error between the exposure function and measured or estimated TTS onset. A unique value of K was determined for each group. For hearing groups for which no TTS onset data exist (LF cetaceans and SI), TTS onset at the frequency of best hearing (f_0 from Table 4) was estimated based on the assumption that the differences between hearing threshold and TTS onset at f_0 would be similar across groups. Specifically, the median numeric difference between the non-impulsive TTS onset (in dB re 1 $\mu\text{Pa}^2\text{s}$) for species groups tested in water (HF, VHF, PCW, and OCW) and their respective estimated group audiogram thresholds at f_0 (in dB re 1 μPa) was determined to be 126 dB. This value was added to the estimated threshold at f_0 for LF cetaceans (54 dB re 1 μPa) to produce an estimated TTS-onset value at f_0 of 180 dB re 1 $\mu\text{Pa}^2\text{s}$. For sireni-ans (SI), using the f_0 hearing threshold of 61 dB re 1 μPa and the median numeric difference of 126 dB produced a TTS-onset estimate at f_0 of 187 dB re 1 $\mu\text{Pa}^2\text{s}$. These extrapolated values were then used to determine K and derive associated exposure functions. The weighted TTS threshold was determined from the minimum of the exposure function. The parameter C was determined for each group by setting the maximum value of Equation (2) to zero.

Auditory weighting and exposure functions for all marine mammal hearing groups

were determined using these parameters and Equations (2) and (3) for weighting and exposure functions, respectively. The weighting functions show relative differences in the predicted magnitude of noise effect relative to the predicted most sensitive frequency (e.g., where $W(f) = 0$ dB), and the exposure functions show the estimated TTS-onset levels for different noise exposure frequencies. For the LF, HF, and VHF cetacean hearing groups, auditory weighting functions (Figure 11) and auditory exposure functions (Figure 12) are shown below. Similarly, auditory weighting and exposure functions are given for the SI hearing group (Figures 13 & 14, respectively), PCW and OCW hearing groups (Figures 15 & 16), and PCA and OCA hearing groups (Figures 17 & 18).

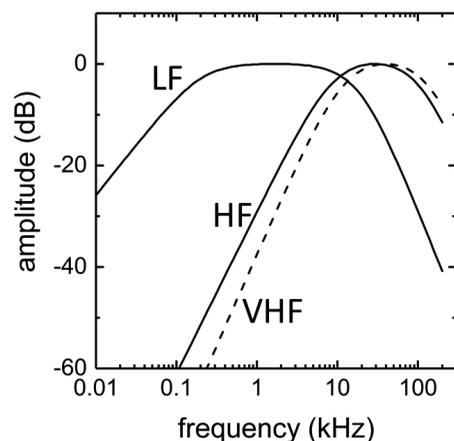


Figure 11. Derived auditory weighting functions for LF, HF, and VHF (dashed line) cetaceans generated with Equation (2) using parameters given in Table 5

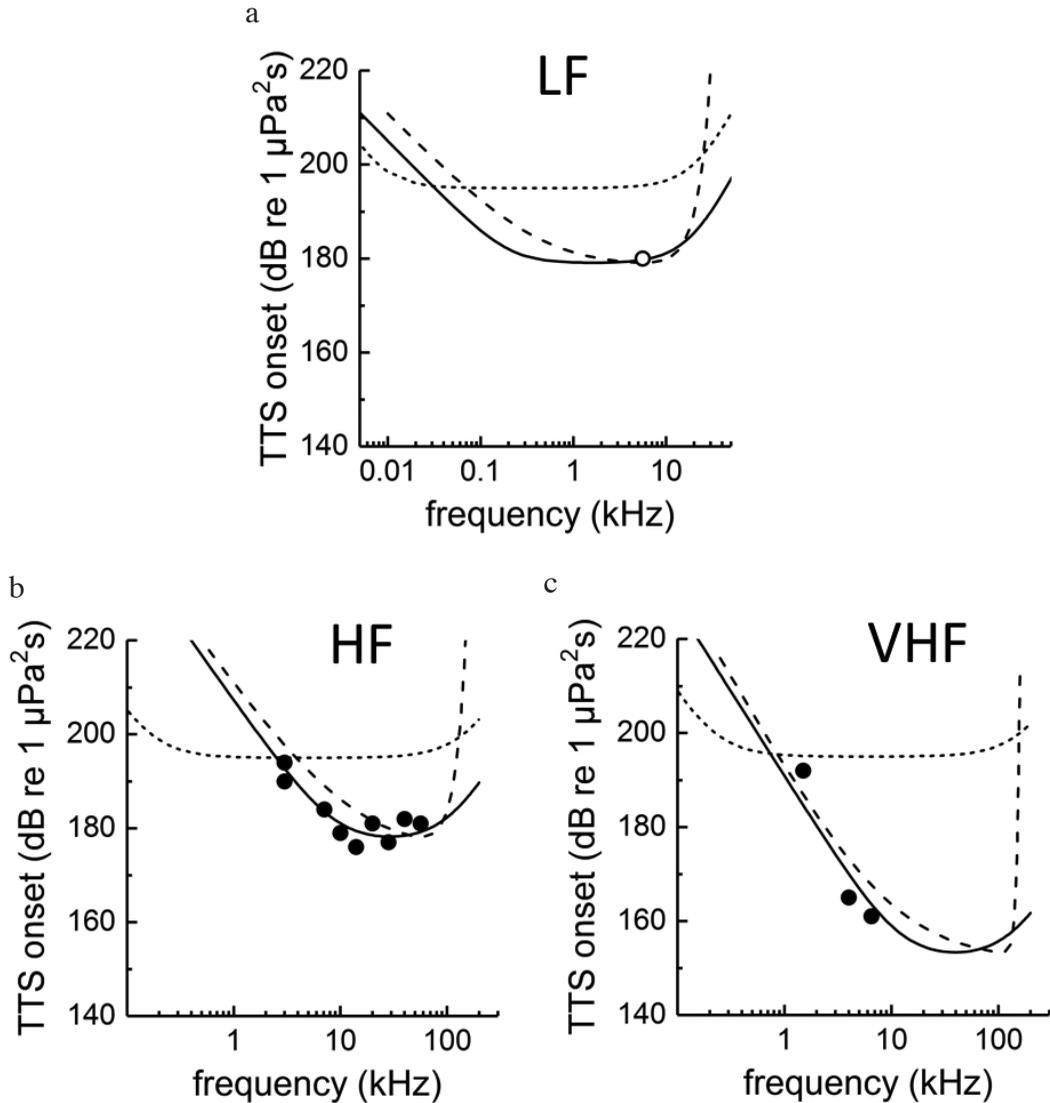


Figure 12. Exposure functions (solid lines) for LF (top), HF (bottom left), and VHF (bottom right) cetaceans generated with Equation (3) using parameters from Table 6. Open symbol for LF cetaceans indicates the estimated TTS onset at f_0 based on TTS data from other groups given that no direct empirical data exist for any LF species. Filled symbols indicate empirical onset TTS exposure data used to determine exposure functions for HF and VHF cetaceans. Normalized estimated group audiograms (dashed lines) are shown for comparison with a minimum value identical to that of the associated exposure functions. Estimated exposure functions derived from M-weighting filters each respective group with a minimum value set at the estimated TTS-onset value (dotted lines) are also shown for comparison (derived from Southall et al., 2007).

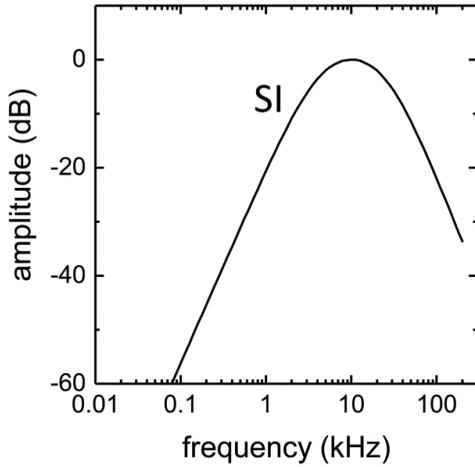


Figure 13. Derived auditory weighting function for SI generated with Equation (2) using parameters given in Table 5

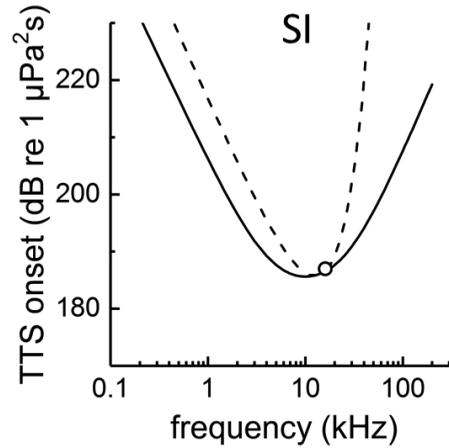


Figure 14. Exposure function (solid line) for sirenians generated with Equation (3) using parameters given in Table 6. The normalized SI estimated group audiogram (dashed line) is shown for comparison with a minimum value identical to that of the exposure function. The open symbol indicates the estimated TTS onset given that no TTS data of any kind exist for sirenians. The SI normalized estimated group audiogram (dashed line) is shown for comparison with a minimum value identical to that of the associated exposure functions.

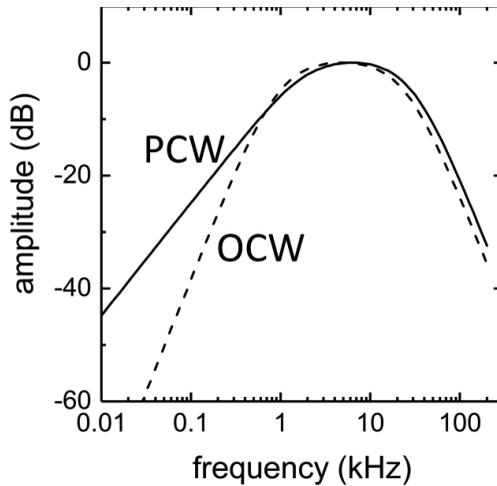


Figure 15. Derived auditory weighting functions for marine carnivores in water (PCW and OCW) generated with Equation (2) using parameters given in Table 5

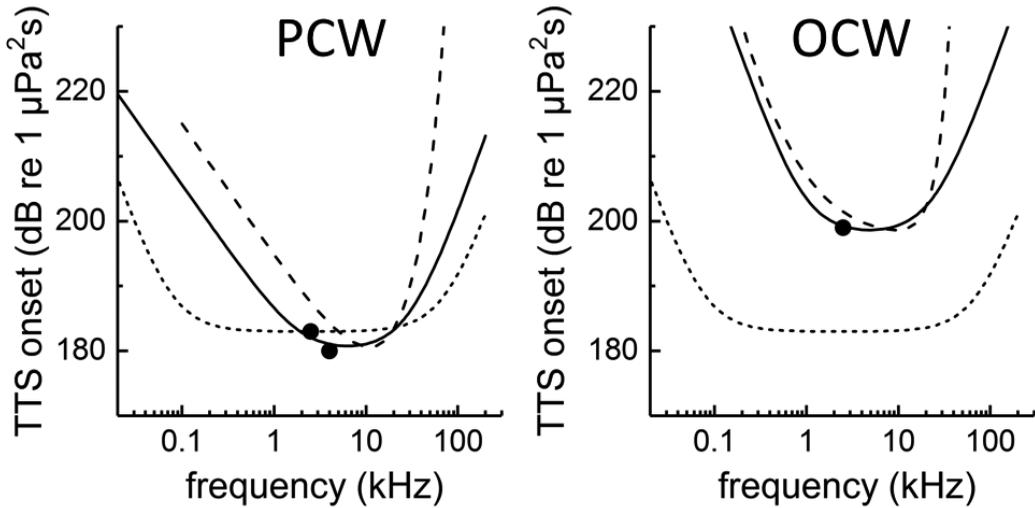


Figure 16. Exposure functions (solid lines) for marine carnivores in water (PCW and OCW) generated with Equation (3) using parameters given in Table 6. Filled symbols indicate empirical onset TTS exposure data used to determine the exposure function. Normalized estimated group audiograms for PCW and OCW (dashed lines) are shown for comparison with a minimum value identical to that of the associated exposure functions. Estimated exposure functions derived from M-weighting filters for pinnipeds in water with a minimum value set at the estimated TTS-onset value (dotted lines) are also shown for comparison on both plots; this was a single function for all pinnipeds in Southall et al. (2007).

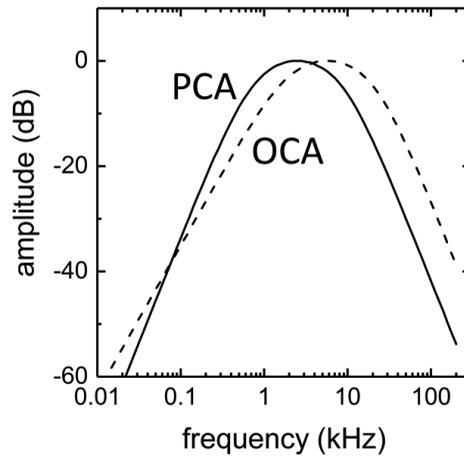


Figure 17. Derived auditory weighting functions for marine carnivores in air (PCA and OCA) generated with Equation (2) using parameters given in Table 5

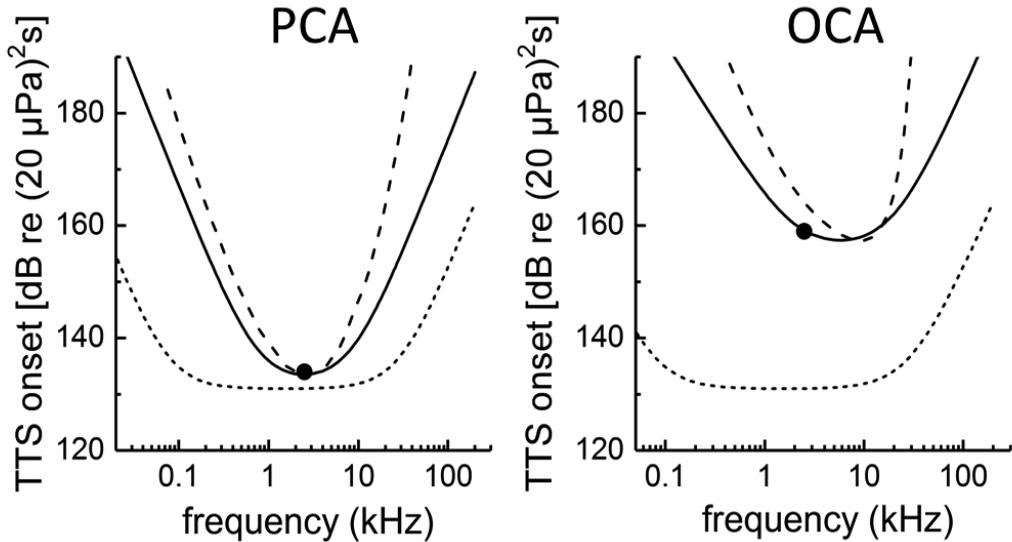


Figure 18. Exposure functions (solid lines) for marine carnivores in air (PCA and OCA) generated with Equation (3) using parameters given in Table 6. Filled symbols indicate empirical onset TTS exposure data used to determine the exposure function. Normalized estimated group audiograms for PCA and OCA (dashed lines) are shown for comparison with a minimum value identical to that of the associated exposure functions. Estimated exposure functions derived from M-weighting filters for pinnipeds in air with a minimum value set at the estimated TTS-onset value (dotted lines) are also shown for comparison on both plots; this was a single function for all pinnipeds in Southall et al. (2007).

Marine Mammal TTS- and PTS-Onset Thresholds

Finneran (2016) proposed systematic modeling procedures to improve on the general approach developed by Southall et al. (2007) to define onset thresholds. These procedures are applied here to generate modified noise exposure criteria for TTS and PTS onset. Frequency-weighted exposure levels for TTS onset were determined from exposure functions (above) in units of weighted SEL. Extrapolation procedures for estimating impulsive noise TTS onset were then applied using results of studies with non-impulsive noise (described in more detail in the “TTS and PTS Criteria for Impulsive Noise Exposure” section).

Dual metric criteria (frequency-weighted SEL and unweighted peak SPL) are proposed for impulsive signals for all marine mammal groups, with the effect (TTS or PTS) being assumed to occur if an exposure exceeds the criterion for either metric. For non-impulsive sounds, only weighted SEL metrics are presented (i.e., no peak SPL criterion). For multiple exposures of either type, SEL provides a means of integrating cumulative exposures. There are insufficient direct measures of TTS from different exposure intermittency patterns in marine mammals to define an explicit

duration of intermittency between exposures following which they should be considered discrete exposures and, thus, no longer accumulated using a single SEL value. While Southall et al. (2007) suggested a 24-h period for this interval, some of the basis for that distinction was related to behavioral issues rather than explicitly hearing effects. Limited available data on exposure intermittency and recovery from a hearing perspective would suggest that a shorter than 24-h exposure intermittency would be appropriate to reset the cumulative SEL calculations for multiple exposures (see Finneran, 2015). It is unlikely that a simple and uniform relationship exists across all species and exposure scenarios and that case-specific evaluations will likely be required to evaluate an appropriate reset duration. We simply note that in many realistic exposure conditions, the 24-h rule for SEL “reset” may be inappropriately long and that further scientific investigation of these issues, especially for species with some existing TTS data, is clearly needed.

For both impulsive and non-impulsive sounds, TTS onset was defined as the exposure required to produce 6 dB of TTS from either direct measurements or extrapolation of available data (as in Southall et al., 2007). Modified extrapolation methods were used to estimate TTS growth and

predict exposures for which 40 dB of TTS would occur. This is identical to the value Southall et al. (2007) used as an estimate of PTS onset, although here this is not presumed to represent the onset of physical injury as there are no available empirical data to test this assumption.

TTS and PTS Criteria for Non-Impulsive Noise Exposure

Weighted exposure thresholds for non-impulsive TTS onset are based on the minimum of the non-impulsive TTS exposure functions (Figures 12, 14, 16 & 18; Table 6). Note that the exposure function minimum is not necessarily equal to the TTS threshold at the frequency of best hearing sensitivity (f_0). As described above, for marine mammal groups for which direct TTS data were available, they were applied directly in the derivation of exposure functions. For marine mammal groups with no direct measurements (LF cetaceans and sirenians), marine mammal TTS data from other groups were applied, with the assumptions and caveats described.

To estimate PTS-onset criteria for non-impulsive noise in terms of SEL, an exposure level of 20 dB above the TTS-onset level (6 dB TTS) was used for each marine mammal group. This assumes the same growth rate (1.6 dB TTS/dB noise) from the point of TTS onset (6 dB TTS) to estimated PTS onset (40 dB TTS) used in Southall et al. (2007); this growth rate is now supported with limited empirical data on TTS growth for a few marine mammal species (reviewed in Finneran, 2015). The associated non-impulsive SEL TTS- and PTS-onset criteria for all marine mammal hearing groups are given in Table 6.

TTS and PTS Criteria for Impulsive Noise Exposure

The TTS and PTS exposure SEL functions for impulsive sources are assumed to be identical in shape to the group-specific non-impulsive functions, with the values for the constant K being the only parameter derived explicitly for impulsive sources. There is currently extremely limited data on impulsive noise TTS onset for marine mammals across a range of exposure frequency conditions with which to evaluate this (Finneran, 2015; Houser et al., 2017), although the existing data are not inconsistent with this assumption. For species groups for which impulsive TTS data are available (HF and VHF cetaceans), impulsive noise SEL TTS thresholds were determined by applying group-specific weighting functions to the exposure waveforms that produced TTS and then calculating the associated weighted SELs. For species groups for which no impulsive TTS-onset data exist, weighted SEL thresholds were estimated using the relationship between the median non-impulsive noise weighted TTS-onset threshold and the median impulsive weighted TTS threshold for the HF and VHF cetacean groups (as in Southall et al., 2007).

For the HF and VHF cetaceans, non-impulsive noise TTS-onset thresholds are 178 and 153 dB re $1 \mu\text{Pa}^2\text{s}$, respectively, while impulsive noise TTS-onset thresholds (derived using Equation [3]) are 170 and 140 dB re $1 \mu\text{Pa}^2\text{s}$, and the median difference is 11 dB. Thus, for each of the remaining groups for which impulsive noise TTS data are not available, the SEL-based impulsive noise TTS-onset threshold is estimated to occur 11 dB below the non-impulsive noise TTS-onset thresholds (from Table 6).

Table 6. TTS- and PTS-onset thresholds for marine mammals exposed to non-impulsive noise: SEL thresholds in dB re $1 \mu\text{Pa}^2\text{s}$ under water and dB re $(20 \mu\text{Pa})^2\text{s}$ in air (groups PCA and OCA only)

Marine mammal hearing group	TTS onset: SEL (weighted)	PTS onset: SEL (weighted)
LF	179	199
HF	178	198
VHF	153	173
SI	186	206
PCW	181	201
OCW	199	219
PCA	134	154
OCA	157	177

As in Southall et al. (2007), a dual metric approach is retained for impulsive stimuli, and the weighted SEL threshold is used in conjunction with an unweighted peak SPL threshold. Few TTS studies have been conducted in marine mammals using representative impulsive noise sources such as pile driving and airgun signals (see Finneran, 2015), in part given the extensive challenges in successfully generating impulsive stimuli in laboratory conditions that approximate exposure conditions for such sources with free-ranging animals. This limits the available information upon which to base peak SPL onset criteria; at present, impulsive TTS data are available for just the HF and VHF species. For these species groups, peak SPL thresholds for TTS were directly based on empirical data. For other species groups for which no TTS data exist, peak SPL thresholds were determined as the difference (in dB) between the impulsive noise peak SPL TTS onset (in dB re 1 μ Pa) and the hearing threshold at the frequency of best sensitivity (f_0) (in dB re 1 μ Pa; see Tables 3 & 4) for the HF and VHF cetaceans. For the HF cetacean group, the hearing threshold at f_0 is 54 dB re 1 μ Pa, and the peak SPL TTS-onset threshold is 224 dB re 1 μ Pa, a difference of 170 dB. For the VHF cetaceans, the hearing threshold at f_0 is 48 dB re 1 μ Pa, and the peak SPL-based TTS-onset threshold is 196 dB re 1 μ Pa, a difference of 148 dB.

The above calculations make clear the substantial deviation in relative exposure sensation level required to induce TTS for the VHF relative to HF groups and raises the issue of how to extrapolate the results to other species for which data do not exist. The VHF cetaceans are clearly more sensitive than other hearing groups in a number of ways discussed throughout this article—notably, lower hearing thresholds and lower TTS-onset thresholds for different noise types. Thus, applying the much smaller difference between hearing and TTS thresholds for VHF species to other hearing groups could be seen as unrepresentative, and a case could be made for applying the difference between these values for HF cetaceans exclusively. However, a precautionary argument could also be made in the absence of direct data to apply the lower dynamic range of VHF cetaceans to all other groups. The approach taken here, in keeping with the overall central tendency philosophy, was to use the median value of the two differences (as in Finneran, 2016). Given the greater overall sensitivity of the VHF cetaceans, their inclusion in this median value is somewhat conservative, but this avoids going to the extreme of applying data from a hearing group that appears fundamentally different from other marine mammals.

The median difference between hearing threshold and TTS onset for HF and VHF cetaceans based on empirical TTS data using impulsive signals is thus 159 dB. For other species groups in water (LF, SI, PCW, and OCW), 159 dB was added to the value of the hearing threshold at f_0 to estimate the impulsive noise peak SPL TTS-onset thresholds. For all marine carnivores in air, there are no published TTS data for impulsive noise exposures. Given the lack of data, a nominal 15 dB offset is used (as in Southall et al., 2007) between the SEL-based TTS threshold and the peak SPL-based threshold. As in Southall et al. (2007) and Finneran (2015), no frequency-weighting is applied to any of the proposed peak SPL criteria.

For impulsive exposure, dual metric PTS-onset thresholds were estimated using an identical approach in terms of TTS growth rates to that proposed by Southall et al. (2007). For SEL-based TTS thresholds, this approach prescribes adding 15 dB to the TTS-onset threshold to estimate PTS onset based on a 2.3 dB TTS/dB noise relationship using the results of studies in chinchillas (Henderson & Hamernik, 1986). For peak SPL criteria, 6 dB is added to TTS-onset threshold to estimate PTS onset based on a ~6 dB TTS/dB noise relationship using the results of the same study.

Using the methods and assumptions described above for each marine mammal group, the associated impulsive SEL and peak SPL TTS- and PTS-onset criteria were calculated, and the resulting exposure criteria are presented in Table 7. Two selected examples are given to illustrate this approach—one in which direct empirical data were available (VHF cetaceans) and one in which extrapolation methods were applied (PCW).

For the VHF cetaceans, the empirically based SEL TTS-onset criterion for impulsive noise is 140 dB re 1 μ Pa²s, and the associated SEL PTS-onset criteria is 155 dB re 1 μ Pa²s. The peak SPL TTS criterion is 196 dB re 1 μ Pa, and the associated peak SPL PTS-onset criteria is 202 dB re 1 μ Pa (i.e., $PTS_{pk} = TTS_{pk} + 6$ dB).

For the PCW group for which direct impulsive TTS data are unavailable, onset criteria were derived using the assumptions described above as follows. The SEL TTS-onset criterion for impulsive noise was estimated as 170 dB re 1 μ Pa²s (181 dB re 1 μ Pa²s for non-impulsive TTS onset -11 dB), and the associated SEL PTS-onset threshold was estimated as 185 dB re 1 μ Pa²s. Peak SPL TTS onset was estimated as 212 dB re 1 μ Pa (53 dB at $f_0 + 159$ dB), and the associated peak SPL PTS-onset criteria threshold was estimated as 218 dB re 1 μ Pa.

Table 7. TTS- and PTS-onset thresholds for marine mammals exposed to impulsive noise: SEL thresholds in dB re 1 $\mu\text{Pa}^2\text{s}$ under water and dB re (20 μPa)²s in air (groups PCA and OCA only); and peak SPL thresholds in dB re 1 μPa under water and dB re 20 μPa in air (groups PCA and OCA only).

Marine mammal hearing group	TTS onset: SEL (weighted)	TTS onset: Peak SPL (unweighted)	PTS onset: SEL (weighted)	PTS onset: Peak SPL (unweighted)
LF	168	213	183	219
HF	170	224	185	230
VHF	140	196	155	202
SI	175	220	190	226
PCW	170	212	185	218
OCW	188	226	203	232
PCA	123	138	138	144
OCA	146	161	161	167

Considerations of Variability and Uncertainty in Regulatory Applications of TTS and PTS Criteria

The exposure criteria proposed here for TTS and PTS onset for non-impulsive and impulsive noise exposures are derived using median values of available data in several areas. We believe that this provides a reasonable best estimate of these effects across many species within hearing groups in light of the limited data in many areas and requisite extrapolation measures. However, there are relevant considerations related to individual variability in susceptibility to noise exposure and context-dependent aspects of exposure scenarios that should be noted. The single threshold-level exposure criteria given here will, almost by definition, underestimate potential effects for some scenarios and overestimate effects for others, the extent of each potential outcome depending on the degree of individual variability as well as key contextual aspects of exposure.

Nowacek et al. (2007) highlighted concerns regarding the use of single threshold-level exposure criteria for predicting the effects of noise on populations of marine mammals given known and expected variability. Subsequent authors have attempted to model regulatory implications of step-function thresholds in terms of predicting impacts within populations for both auditory (Gedamke et al., 2011) and behavioral (National Academies of Sciences, Engineering, and Medicine, 2017) effects. For example, Gedamke et al. (2011) modeled the impact of variability and uncertainty on estimates of TTS in baleen whales exposed to seismic surveys and concluded that, given their underlying assumptions,

a step-function threshold would substantially underestimate ranges for potential effects for the most sensitive one-third of the population. Their approach began with single threshold estimates like those provided here (Tables 6 & 7), albeit with more limited supporting data, and then developed probabilistic risk functions for specific applications in which variability was estimated for TTS onset, variation in received level as a function of sound propagation, and behavior of the animals such as avoidance of the sound source. Herein, we provide a simple assessment of the available TTS-onset data to illustrate some of these considerations as they relate to the application of step-function thresholds. The available data are admittedly limited, but this example is simply intended to illustrate the relative implications of variability that do exist based on the type of effect being evaluated and the overall physical ranges over which effects may occur depending upon species- or group-specific sensitivity.

Just as individual differences exist within and between species in terms of absolute hearing sensitivity relative to estimated group audiograms, variability also exists in terms of individual TTS and PTS onset relative to exposure function predictions. At present, it is difficult to quantify variability in TTS onset among marine mammals given how little data exist on TTS onset for multiple individual subjects from multiple species within each hearing group to sound exposures at the same frequency. The only such marine mammal data currently available are from two bottlenose dolphins tested at 3 kHz for which onset of TTS occurred at SEL of 190 and 194 dB re 1 $\mu\text{Pa}^2\text{s}$, respectively. In an effort to address

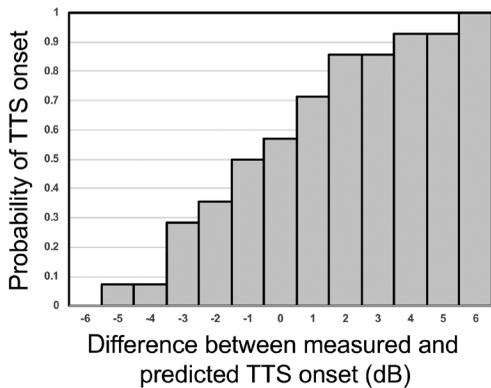


Figure 19. Cumulative distribution function (CDF) for the deviation of frequency-specific TTS-onset measurements from levels predicted by the group-specific TTS exposure function

this issue, Gedamke et al. (2011) estimated variability by taking the standard deviation (SD) of the limited available TTS-onset data they used (5.2 dB) across the range of individuals and frequencies tested by Schlundt et al. (2000) and Finneran et al. (2005a). However, as evident in the estimated audiograms relative to exposure functions here, TTS-onset levels vary as a function of frequency. This means that some of the variation in TTS onset estimated using data available at the time by Gedamke et al. (2011) included variation by frequency, which is explicitly considered within the exposure functions derived herein.

While limited, the available TTS-onset data for individuals at different frequencies relative to group-specific exposure functions does provide insight in terms of variability around predicted effects. The available marine mammal TTS data used here include nine frequency-specific TTS-onset measurements from two HF cetacean subjects (including the values for each subject at 3 kHz mentioned above), three from one VHF cetacean subject, and two values from two different PCW subjects measured under water. By calculating the deviation of measured TTS onset from the value predicted by the exposure function for their hearing group at each test frequency, the variation among these five marine mammal subjects for which frequency-specific TTS-onset data exist may be evaluated. The cumulative distribution function (CDF) in the residual lack of fit of the TTS-onset thresholds to the exposure functions across all subjects is shown in Figure 19. This distribution has a considerably lower SD (2.8 dB) than the 5.2 dB

value estimated by Gedamke et al. (2011) as would be expected given efforts to account for variation by frequency.

If this CDF is taken as a generalized representation of variability in the onset of an effect among a population of animals in the wild, a simplistic illustrative example may be used to compare the respective area over which TTS might be predicted to occur using either the single number threshold or a probability distribution based on the CDF. This example assumes a generic sound source with a source level of 220 dB re 1 μ Pa at 1 m and duration of 1 s, operating at a frequency for which the hearing group is most sensitive and with $20 \log_{10}(\text{range})$ propagation loss. Using the proposed TTS-onset thresholds of 178 dB re 1 μ Pa 2 s for HF cetaceans, the predicted range for TTS onset is 126 m, and the area affected is 0.05 km 2 . Using the proposed TTS-onset threshold of 153 dB re 1 μ Pa 2 s for VHF cetaceans, the predicted range is 2,240 m, and the area affected is 15.7 km 2 . Assuming that exposed animals are evenly distributed with one/km 2 , which could be a reasonable assumption for some species but a poor one for others, this results in an estimated 0.05 HF cetaceans and 15.7 VHF cetaceans experiencing TTS.

Conversely, if the CDF is used to estimate variability, the total number of individuals potentially affected would be determined by sequentially estimating the areas within which individuals with differential sensitivity would be exposed. The CDF here has 14 values (residual differences of measured to predicted TTS onset), ranging from -5 dB to +6 dB. For the HF cetaceans, this corresponds to TTS-onset estimates ranging from $178 - 5 = 173$ dB re 1 μ Pa 2 s to $178 + 6 = 184$ dB re 1 μ Pa 2 s. For VHF cetaceans, this corresponds to TTS-onset estimates ranging from $153 - 5 = 148$ dB re 1 μ Pa 2 s to $153 + 6 = 159$ dB re 1 μ Pa 2 s. Each observation can be taken to represent the estimated TTS-onset threshold for 1/14th of the population or 0.071. In this simple example, the number of individuals that would experience TTS is estimated given the simple assumptions here for individuals with differential sensitivity based upon the variability in the CDF. The estimated number of the most sensitive individuals in the population equals the area corresponding to received levels (for the HF cetaceans) out to 173 dB re 1 μ Pa 2 s (estimated range: 224 m; area: 0.157 km 2) times 0.071, resulting in 0.011 individuals with the greatest sensitivity within that area. This process is repeated for each step in the CDF corresponding to increasingly nearer areas multiplied by a probability of 0.071. The resulting values for each area are then summed. The result of this process for this example yields total estimates of 0.06 HF

cetaceans and 20 VHF cetaceans experiencing TTS, which are 20 and 27% higher relative to the single threshold estimates of 0.05 (HF) and 15.7 (VHF), respectively. Even though there is an equally small proportion of animals assumed to be in the relatively more sensitive subset of individuals for both HF and VHF, there is a larger difference between the methods for the VHF cetaceans because the larger ranges yield larger areas within which more sensitive animals might be exposed at levels predicted to result in TTS.

This example, using limited available data, is not intended to serve as the basis for empirical risk functions for TTS or PTS onset. Rather, they are given primarily to highlight some valid concerns relating to the use of step-function thresholds, the limited data available regarding variability in the onset of auditory effects used to derive exposure criteria, and the need to consider underlying variability in regulatory applications in some manner. The amount of variation shown in the CDF (Figure 19) is derived from measurements from a few individuals from a single species within each of three marine mammal hearing groups. Better estimates of variability in TTS onset within and among species of each hearing group are needed to evaluate whether this level of observed variability is broadly representative, particularly within groups for which no such data exist. Regulatory processes evaluating predicted effects and/or establishing safety mitigation zones should occur within a broader decision framework than simply calculating predicted effects from exposure criteria. Such a framework should integrate information regarding the source of interest, transmission loss in the location, movement patterns of animals with respect to the source (e.g., behavioral avoidance that may reduce higher-level exposures), and features of typical group structure (solitary vs highly social), and should provide at least some means of estimating the variation and uncertainty related to these key factors.

Research Recommendations

The past decade has seen substantial advances in published scientific data on marine mammal hearing and the effects of noise on hearing. Combined with existing data on these issues, these new results have provided a more robust basis for the revised noise exposure criteria presented herein for predicting the fatiguing effects of noise on marine mammal hearing. However, as has been the case in human noise standards for many decades, this will continue to be an iterative, self-correcting process as subsequent scientific results become available (see “Discussion” section).

While noting some of the extensive research recommendations regarding marine mammal hearing, auditory weighting functions, and the effects of noise made in several additional recent reviews (e.g., Finneran, 2015; Erbe et al., 2016; Houser et al., 2017), several key research areas are identified and specific topics for which additional studies are needed to improve and evolve marine mammal noise exposure criteria are highlighted. We also identify several important considerations regarding the derivation of noise exposure criteria and provide some concluding emergent observations based on the current state of this field.

Absolute Hearing Capabilities and Auditory Weighting Functions

While progress has been made in many areas, it is important to recognize that we lack any measurements of hearing in most marine mammal species (see Appendices). Some untested species fall within taxa for which numerous audiometric measurements have been made for related species, which permits some reasonable level of extrapolation within “functional” hearing groups (e.g., Reichmuth et al., 2013). Clearly, additional hearing data for any untested species will be useful to inform subsequent estimations of group-specific audiograms. However, given limited access to study many species in traditional research settings, a strategic approach could be to prioritize efforts for species within less well-represented taxa. Alternatively, testing could focus on species that may be more distantly related to other members of hearing groups (e.g., Antarctic ice seals, other otariids, bearded seals, walrus, and polar bears) for which hearing data are available. This approach should enable a more effective use and extrapolation of the data available to evaluate the marine mammal species groups proposed here given that direct measurements of hearing are unlikely for all species. Taxa for which affinities are unclear, such as within the white-sided dolphins (Appendices 2 & 3), should also be prioritized, particularly for studies relating anatomy to audiometric measurements. Additional data on equal loudness and equal latency are also needed, with a specific need for data at high frequencies given the complete lack of available information with which to inform the HF slope of auditory weighting and exposure functions for all groups.

The most notable example of needed data in terms of hearing sensitivity is within the baleen whales (LF cetaceans) for which there are no direct measurements of hearing for any species. Progress has been made in anatomical modeling methods to describe how certain aspects

of auditory systems respond to sound and may influence how whales hear. However, the capacity of these approaches to predict hearing with any confidence and to reliably inform the derivation of exposure or weighting functions has not yet been validated within other well-studied species for which hearing is well-known. Studies demonstrating the predictive efficacy of these methods in other marine mammals in terms of their ability to accurately predict both frequency ranges of hearing and absolute hearing sensitivity are clearly needed. Similar comparative data from terrestrial mammal taxa that are sensitive to LF sound in air would also be very useful. The models described above treat LF sensitivity as comparable to HF sensitivity, but the available data suggest that animals are prone to lose HF hearing preferentially as a function of age (Clark, 1991). The limited data available on cetaceans are consistent with this finding (Ridgway & Carder, 1997), and this may be a particularly important consideration with regard to estimating HF hearing in baleen whales, which are generally quite long-lived.

As discussed, future approaches to studying the hearing of LF cetaceans will almost certainly rely on comparative anatomical modeling in other LF species given the challenges in obtaining direct hearing measurements. Direct measurements of hearing in LF cetaceans using electrophysiological methods could continue to be pursued (e.g., within stranding scenarios) as this is among the most likely methods for obtaining direct hearing data for mysticetes. However, it should be recognized that while such data may prove useful for some frequencies, they will likely not be useful for the lowest frequencies of most interest (< 5 kHz) given limitations of AEP methods. Further, they may prove feasible only in the youngest and smallest members of the group. Behavioral methods for free-ranging animals using orienting response methods (e.g., measuring behavioral changes in animals exposed to experimental sounds of different frequency content) could be applied in baleen whales (Frankel et al., 1995) as demonstrated in other marine mammals (see Ghoul & Reichmuth, 2014). While such approaches will be unlikely to measure absolute hearing at many frequencies because of masking noise in the environment and the movement of free-ranging animals, they could provide useful insights into some hearing capabilities for baleen whales, notably upper hearing limits. There has been some feasibility work using spontaneous responses of this type (Dahlheim & Ljungblad, 1990) but so far not under controlled or semi-controlled conditions (e.g., with an animal entrapped in a weir; Lien et al., 1990). Finally, the potential distinction among VLF and

LF cetaceans considered above (see “Marine Mammal Hearing Groups & Estimated Group Audiograms” section) is noted as an area of additional evaluation. Characteristics of vocal behavior and auditory anatomy suggest a potential segregation of the baleen whales into two or even more groups. To explore this potential distinction, specific research attention using combinations of anatomical, electrophysiological, and behavioral methods should be applied to species for which at least some underlying data and proven capabilities to study free-ranging animals exist within each of the respective groups (e.g., VLF: blue whales; LF: minke whales). Given the endangered status and LF sensitivity of these species, acquiring additional data remains a priority, but, realistically, our ability to quantitatively describe hearing and the effects of noise on hearing in baleen whales is likely to remain limited for the foreseeable future.

Another area of research interest in terms of potential additional division of marine mammal hearing groups relates to hearing in sperm and beaked whales. As discussed above, their large body size, echolocation click characteristics, and relatively lower-frequency content of species-typical echolocation clicks suggest a possible distinction of these species, along with killer whales, from other odontocetes (HF and VHF cetaceans). Recently obtained behavioral hearing data for killer whales in a study with a relatively large sample size ($n = 8$) (Branstetter et al., 2017) were not included within the estimated group audiograms here (discussed further below), but they clearly expand our understanding of hearing in this species. The upper-frequency cut-off for killer whales in this study (114 kHz) occurs at comparable frequencies (within an octave) of the HF composite audiogram and most individual species audiograms. However, relatively better hearing for killer whales at low frequencies observed by Branstetter et al. (2017) relative to some other odontocetes, and especially the distinctions in some anatomical and echolocation signal parameters (see Appendix 2), are consistent with the species’ potential separation from the HF cetaceans along with sperm and beaked whales.

The challenges of collecting behavioral audiometric measurements on sperm whales are similar to those for mysticetes, but research building on earlier efforts to use AEP methods on live-stranded animals (e.g., Ridgway et al., 2001) would provide unique opportunities as has more recently been accomplished with several beaked whales (Cook et al., 2006; Finneran et al., 2009; Pacini et al., 2010). However, the same caveats regarding AEP testing at low frequencies and the elevated estimates of absolute hearing sensitivity

relative to behavioral hearing thresholds may limit data for the same reasons discussed above. Further anatomical and behavioral evaluations could also provide some insight into the potential segregation of these species as with MF cetaceans.

Finally, a better understanding of relationships between AEP and behavioral threshold data are needed across species. Both methods have provided great insight into the hearing of marine mammals, and each has strengths and limitations. Behavioral methods, with sufficient training and experimental and noise controls, have provided the most consistently reliable and robust measurements of hearing sensitivity across wide ranges of frequencies. However, they are time-consuming and expensive to conduct properly, usually involve small sample sizes, and are unlikely to be applicable for many species that are not maintained in captive settings. Conversely, AEP methods do not require trained subjects, have been conducted in field settings with stranded and/or anesthetized animals, and may be used to generate larger sample sizes on uncommon species. However, as discussed, these methods are limited in their ability to test hearing at relatively low frequencies. Furthermore, across most marine mammal species tested, AEP methods typically result in less consistent predictions of absolute sensitivity compared to behavioral studies; results generally suggest less sensitive hearing than behavioral methods, with increasing divergence at lower frequencies. Some frequencies at the low and high ends of the behaviorally determined hearing range do not elicit detectable AEPs. While AEP data were excluded in deriving estimated group audiograms and weighting and exposure functions, the value and importance of AEP methods are clearly recognized, particularly given the ability to test less common species (e.g., during attempts to rehabilitate them after a stranding).

Results from a number of AEP studies were an important part of the evaluation and species assignments within hearing groups herein (see Appendices). Such studies will likely provide the only means of obtaining additional data for many species to evaluate and refine the hearing groups distinguished here. Subsequent effort should be made to systematically evaluate the relationships between AEP and behavioral methods across frequencies in species for which hearing is relatively well-known, including within terrestrial mammals, to evaluate how AEP results could be integrated, perhaps with associated correction factors, into the estimation of group audiograms and, ultimately, weighting and exposure functions.

Temporary Threshold Shift (TTS) and Permanent Threshold Shift (PTS)

Major strides have been made in understanding TTS onset and growth in marine mammals (Finneran, 2015), with many findings since Southall et al. (2007) that enable a much more informed derivation of criteria here. However, additional studies are still needed to address key questions.

The issue of better understanding relationships between AEP and behavioral hearing data is also relevant to quantifying TTS. AEP methods could be used to test TTS for some species and contexts for which traditional behavioral methods are impractical or impossible. AEP methods also provide additional information in terms of neural signal about auditory response at levels above hearing thresholds that can provide additional insight into the effects of noise. Furthermore, data suggest that some electrophysiological methods (including AEP) may be more sensitive indicators of auditory system dysfunction compared to behavioral threshold measures—for example, by providing information on potential changes in specific auditory structures that contribute to the AEP waveform.

For non-impulsive noise sources, additional studies are also needed, particularly for certain marine mammal taxa (e.g., marine carnivores and sirenians), to build on observations in some odontocetes of major differences in TTS as a function of exposure frequency spectra—that is, explicit evaluation of auditory exposure function predictions of TTS onset in several species from each marine mammal taxa would ideally be collected. This is especially important within the VHF cetaceans given that TTS-onset levels to date are so different than in other taxa, and studies are almost exclusively limited to measures from a single species, the harbor porpoise. Of additional interest are additional TTS measurements for relatively low-exposure frequencies (below several kHz). Across taxa, the LF hearing range appears to be less susceptible to PTS, but it is unclear whether low frequencies are less susceptible generally. It should be recognized that while postmortem analyses of hearing structures may provide some insight into potential auditory injury related to noise exposure, direct TTS studies will almost certainly not be possible in the near future for LF cetaceans. Not only is access a matter of chance in acquiring potential research subjects (e.g., live stranding), but technical developments are also still needed to collect useful AEPs (Ridgway et al., 2001). Recognizing this, subsequent TTS studies of the effects of LF noise within hearing groups that are also more sensitive at low frequencies and for which

increasingly more data exist (e.g., phocid seals) should be evaluated in terms of their potential extrapolation to the LF cetaceans.

While more recent marine mammal results suggest that the TTS growth rates predicted by Southall et al. (2007) appear to be reasonable approximations, more studies in taxa other than odontocete cetaceans would ideally be collected. Additional studies are clearly needed regarding how noise exposure intermittency and recovery time in relatively quiet conditions influence TTS growth and recovery patterns within selected species, ideally in a manner that provides support for comparative assessment within and across hearing groups. Such studies should quantify exposure using a number of different metrics, including, but not limited to, SPL, duration, variable frequency, and SEL for each exposure and accumulated across exposures to evaluate dual criteria predictions, the assumptions underlying SEL as an integrative exposure metric, and the appropriate exposure intermittency for which cumulative SEL values should be reset.

Additional studies of impulsive noise TTS are needed for almost all species. Of particular importance are studies in which systematic variation of peak SPL, SEL, signal duration (especially shorter or longer than temporal integration time), and frequency content are performed to test the weighting function and validity of the dual criteria for peak SPL and SEL. Furthermore, studies with more realistic exposure to real-world impulsive noise sources are needed. This is clearly challenging in laboratory contexts, but recent studies have made some progress in using and characterizing exposure parameters for operational impulsive noise sources (e.g., Kastelein et al., 2013b; Finneran et al., 2015; Reichmuth et al., 2016). Subsequent studies should continue to try to replicate exposure waveforms from impulsive sources, including propagation effects for distances at which received levels may occur. Almost no data exist on TTS growth rates for impulsive noise in marine mammals, including for moderate levels of TTS (20 dB) and higher. This is a key research need as are issues related to multiple impulse noise exposure and patterns of intermittency and recovery as well. Further impulsive noise TTS data will support a more informed and taxon-specific estimation of differences between impulsive and non-impulsive noise and, thus, the most appropriate means of utilizing non-impulsive noise in extrapolating or interpreting more limited impulsive noise TTS data.

Finally, recent data indicate that some marine mammals have reduced hearing sensitivity when warned of an impending noise exposure,

suggesting a potential for self-protection from noise exposures and raising important questions regarding the uncertainties in determining any absolute effects of external noise on hearing (Nachtigall & Supin, 2013, 2014, 2015; Nachtigall et al., 2016a, 2016b). The extent to which such mechanisms could reduce susceptibility to noise exposure is unknown but should be investigated. Of particular importance is testing whether this mechanism is a specialization associated with echolocation or is also present in non-echolocators. This would help inform the extent to which TTS data from echolocators can be appropriately extrapolated to non-echolocators and vice versa. Also unknown is the extent to which existing TTS data have been affected by potential self-mitigation (i.e., could experimental subjects predict impending noise exposures or adapt to ongoing noise to protect their hearing?) and the likelihood of wild marine mammals performing similar actions when exposed to man-made noise. As an example, there is considerable literature on humans showing that initial moderate exposures are protective against exposures to high amplitude noise (e.g., Campo et al., 1991; Niu et al., 2007).

Discussion

Advances in the scientific understanding of how marine mammal hearing is affected by noise have allowed refinement of methods originally proposed by Southall et al. (2007) to predict effects of noise. To do so, a comprehensive evaluation of all hearing, auditory anatomy, and sound production data available for every marine mammal species was reviewed and evaluated. Using these data and the systematic, quantitative methods developed by Finneran (2016), estimated audiograms were derived for seven of eight identified marine mammal hearing groups for which direct hearing data were available based on median values of behavioral audiograms from animals with normal hearing. A modified approach involving additional assumptions, extrapolations, and associated caveats was developed for the baleen whales (LF cetaceans). Ultimately, all marine mammal species were evaluated for the purposes of developing auditory weighting functions and proposing revised exposure criteria.

Available literature on direct and indirect measurements of hearing, auditory morphology, and aspects of sound communication was evaluated using specific criteria to inform categorization of different species into hearing groups (see Appendices). Using published scientific data (with several exceptions regarding LF cetaceans) available through the end of 2016, estimated

group audiograms, auditory weighting functions, and TTS/PTS exposure functions were derived for each group, including both underwater and aerial criteria for all amphibious species.

One of the most important conclusions to emerge from the rapidly evolving science in this field is the critical importance of noise spectrum, in addition to SPL and duration, in determining potential effects on marine mammal hearing. While this was addressed to some degree in the derivation of M-weighting (Southall et al., 2007), the substantially more quantitative approach to weighting functions possible with considerably more available data derived by Finneran (2016) and applied here more appropriately emphasizes potential effects of exposure within frequency regions of relative better hearing sensitivity and greater susceptibility to noise exposure. Interestingly, the derivation of both estimated group audiograms and weighting and exposure functions that integrate aspects of TTS data provide support for slightly more flattened functions than a simple inverse audiogram approach as suggested in slightly different forms for marine mammals by Verboom & Kastelein (2005) and Nedwell et al. (2007) and for some terrestrial mammals (see Bjork et al., 2000; Lauer et al., 2012). These previous approaches have not incorporated aspects of hearing loss into the derivation of weighting functions. The approach herein derives best-fit functions that integrate both aspects of absolute hearing and auditory fatigue into functions that are somewhat flattened relative to auditory thresholds, at least at the low end of the range. This is generally consistent with the use of equal-loudness-based functions that have formed the basis for weighting functions in humans (Houser et al., 2017).

It should be recognized that the proposed criteria simply reflect another step forward in what will remain an iterative, self-correcting process expected to evolve for many decades. This has clearly been the case in the ongoing evolution of human noise exposure criteria of many kinds over the past half century (see Suter, 2009; Kerr et al., 2017). In fact, challenges in deriving broadly applicable quantitative noise exposure criteria for humans are much more straightforward than related efforts for marine mammals given that they consider a single species and have the benefit of many hundreds of direct studies on many thousands of subjects. Marine mammals include > 125 different species inhabiting every kind of marine habitat on the planet and are exceedingly diverse in their taxonomy, anatomy, and natural history. Furthermore, major gaps in scientific understanding of basic hearing abilities and direct measurements of key aspects of how

noise affects hearing persist for most species, notably among the mysticete cetaceans. While strategic research approaches (see “Research Recommendations” section) will better inform subsequent evolutions in these criteria, many data gaps will remain for the foreseeable future. Given these profound challenges, the derivation of quantitative criteria and their application within regulatory applications come with associated and acknowledged cautions and caveats.

Since there continue to be no direct measurements of hearing or the effects of noise on hearing for any mysticete, one could debate a more prescriptive and narrower auditory weighting function than the M-weighting function proposed for LF cetaceans by Southall et al. (2007). However, readers should recognize that simply because the M-weighting function is much broader and flatter than the LF cetacean function derived herein, neither is necessarily more “protective” in all scenarios. The benefit of weighting is to quantify the stimulus as received by the auditory system; therefore, if the proposed function is not a good fit, it will not improve predictions. In addition, both the weighting functions and TTS/PTS exposure functions are required to evaluate the potential effect of noise exposure. While the LF group weighting function derived here is much narrower than M-weighting and effectively excludes less noise at frequencies outside the expected region of estimated best sensitivity, it conversely predicts greater potential auditory effects for noise within the region of best sensitivity by virtue of the lower associated TTS-onset threshold (see Tougaard et al., 2015). Furthermore, the weighting function and TTS-onset thresholds are derived in tandem and cannot simply be interchanged (e.g., retaining M-weighting and applying the current TTS-onset threshold, which is considerably lower than that used in Southall et al., 2007). The quantitative approach presented here represents a new option, using methods comparable to those used for other hearing groups that have direct supporting data. The M-weighting function remains an option that is less prescriptive in its assumptions and broader in terms of frequency but with caveats concerning onset thresholds and potentially much less predictive power. Progress made in indirect methods of evaluating hearing in mysticetes (e.g., modeling and sound production) allowed the proposed criteria to be developed with the best available data even though they were not directly applicable in deriving exposure criteria. Finding ways to improve predictions for LF cetaceans will remain a challenging issue for the foreseeable future. However, this reality cannot preclude efforts to use the best available

information to make requisite decisions and assessments regarding potential noise impacts for these species.

The approach taken regarding categorization of species into hearing groups for the current criteria builds upon the Finneran (2016) expansion of the original Southall et al. (2007) groups, an approach that was adopted by NMFS (2016). However, here, both direct measurements of hearing and a more detailed evaluation of multiple types of indirect supporting information across all species were conducted to inform these categorizations and to propose several further modifications. This evaluation, which included assessments of middle ear and cochlear types as well as vocalization ranges and signal types, revealed a number of potential segregations within the existing groups and highlighted several species of interest that require additional investigation. The potential future subdivisions within the LF cetaceans (to include possible subsequent VLF and LF hearing groups) and within the HF cetaceans (to possibly include MF and HF hearing groups) are supported from various lines of evidence in anatomical features and sound production characteristics. However, at present, there are insufficient direct data on hearing and TTS onset to explicitly derive discrete estimated group audiograms. The broader LF and HF cetacean categories (with associated weighting and exposure functions) are thus retained here, but the likely need for additional VLF and MF is expressly identified for specific subsequent research and consideration.

The evaluation of hearing, anatomical, and sound production parameters also revealed several interesting species (and groups of species) in terms of hearing group categorization. For instance, the walrus has anatomical features intermediate between the phocid and other marine carnivores but is retained in the latter group based on available audiometric data (Appendix 2). There appears to be a clear distinction within the white-sided dolphins, based not only on the presence of VHF energy in echolocation signals in Peale's and hourglass dolphins (as in Finneran, 2016) but also (and perhaps more compelling) considering echolocation click type based on Fenton et al. (2014) relative to other odontocetes, including species within this genus (see Appendix 3). Finally, based on a similar assessment (Appendix 2), some of the river dolphins (family Platanistidae) are assigned here to the HF cetaceans as opposed to the categorical distinction of all river dolphins within the equivalent of the VHF cetacean group by Finneran (2016).

The approach taken here, which is consistent with almost all noise assessment and protective

criteria for humans around the world (e.g., Kerr et al., 2017), was to use median values of available data in several areas (deriving estimated group audiograms and extrapolating TTS data among groups) as the best general predictive value of normal hearing and a reasonable best interpretation of the limited data on the effects of noise on hearing across species within the hearing groups proposed herein. However, it should be recognized that single, discrete threshold values for specified effects (TTS/PTS) do not capture all of the relevant information needed for some important regulatory considerations. For example, in establishing safety zones and estimating the total number of animals that might experience an effect within a population, failure to incorporate some estimates of variation and uncertainty can yield incorrect estimates. Substantial individual variability in hearing is known to exist both among different species in the same hearing groups relative to the predicted average value (see Figures 1, 3, 5 & 7) and between individuals in the same species (e.g., Houser & Finneran, 2006; Popov et al., 2007; Branstetter et al., 2017).

Although it may be reasonable to assume a symmetric distribution for TTS onset about a median value, the logarithmic nature of sound attenuation resulting from geometric spreading loss means that the actual area where animals are exposed to sound levels above thresholds will be smaller than the area where animals are exposed to levels below thresholds. Therefore, by ignoring individual variability, use of a single-value threshold (i.e., a step function) will underestimate the total number of affected animals in most scenarios, but increasingly so as the range to a particular effect increases. Thus, for effects such as TTS or (especially) PTS onset that require quite high levels for most hearing groups and, consequently, occur over smaller ranges, differences may be relatively small; whereas for more sensitive groups (e.g., VHF cetaceans in terms of hearing) or for behavioral effects that are more likely to occur at lower received levels and longer ranges, the differences between a step function and a probabilistic function may be much greater (see Box 2.2, National Academies of Sciences, Engineering, and Medicine, 2017). The extent to which step function thresholds may be problematic in terms of underestimating effects for some individuals depends on the exposure scenario in terms of sound sources, environmental parameters, and species-specific hearing and behaviors factors that affect the likelihood of TTS or PTS. To the extent possible given the available data, future exposure criteria should strive to generate exposure risk functions in addition to or instead of step function thresholds. Unfortunately, the requisite data

are not presently available with which to derive probabilistic approaches that quantitatively characterize individual variance in hearing capabilities, TTS onset, and TTS growth to express exposure criteria within exposure-response probability functions. Fewer than half of all marine mammal species have direct hearing data of sufficient quality to represent normal hearing (almost all being from one or a few individuals), fewer than 10% of species have TTS measurements, and there are zero direct measurements of one of the primary effects evaluated here (PTS onset).

Simulations (e.g., Gedamke et al., 2011) can be used to assess the effects of uncertainty and individual variation on the risk of hearing loss as a function of distance from the sound source. Equally important for this kind of simulation is information specific to each application such as the source levels of sounds produced, transmission loss in the proposed site, life history and behavioral traits of the species in question, and conservation status of each population under review. However, this kind of simulation requires careful consideration of the underlying assumptions (e.g., behavioral avoidance) and judicious estimation of variation and uncertainty specific to the application and its site, with careful attention that decisions are appropriate for the specific regulatory setting.

Future scenarios could occur wherein the assumptions and extrapolations made here result in criteria being either overly or insufficiently protective in light of subsequent data. The latter occurred regarding the Southall et al. (2007) criteria for HF cetaceans (herein VHF cetaceans) for which additional data on harbor porpoises clearly supported the conclusion that much lower exposure criteria should be applied for this species (see Tougaard et al., 2015) and arguably for other species with similar hearing capabilities. Accordingly, revised (much lower) criteria were derived here for the VHF cetacean group using data reviewed in Tougaard et al. (2015) and using subsequent available data for species within this hearing group. Where direct information exists for a single species that is being evaluated within a regulatory context or where subsequent data suggest substantial deviation from the proposed criteria within hearing groups, decisionmakers should consider alternative interpretations of the proposed criteria.

The integrated nature of the quantitative methods applied herein should be recognized in any such alternative application. The approach used here is admittedly complex and, for many species, relies on inter-related extrapolations within and across marine mammal groups and, as in Southall et al. (2007), from terrestrial mammals. It may be tempting to recalculate and revise quantitative

criteria with each new study that fills in key information gaps, especially given that this quantitative method allows such recalculation. However, in a practical sense, caution should be taken in doing so too frequently to avoid creating an ever-evolving set of criteria that are difficult or impossible for regulatory guidelines based upon them to follow.

An example of both the inter-related nature of the criteria and how new and important data may influence the quantitative results is the recent publication from a well-controlled, large sample size study of hearing in killer whales (Branstetter et al., 2017). These results substantially expand on the available data for a species of interest given considerations of their possible inclusion within an MF cetacean hearing group (see Appendix 2) and their potential contribution to the MF/HF estimated group audiogram. These results were unavailable when applicable data used for the current quantitative criteria were truncated, although they were known as this article was prepared. Just as Southall et al. (2007) acknowledged the existence of data on the initial impulse noise TTS studies on harbor porpoise (ultimately published by Lucke et al., 2009), the Branstetter et al. (2017) results are acknowledged here as important contributions to subsequent criteria (and recognized within the consideration of a potential MF cetacean hearing group) but not directly applied within the calculation of weighting and exposure functions. The perspective taken is that evolutions of the exposure criteria should occur at reasonably spaced intervals (a decade from Southall et al., 2007, was chosen) with a specified point for inclusion of data (end of 2016). However, given the awareness of the authors of these forthcoming data, an initial assessment of the implications of including the Branstetter et al. (2017) data was conducted. This revealed that their inclusion would not only result in slight changes in the shape and parameters of the HF cetacean estimated group audiogram and weighting function but, perhaps counter-intuitively, would also have small to moderate impacts on the exposure functions for other hearing groups (e.g., VHF cetaceans and marine carnivores) given the limited available data in some groups as well as the inter-related extrapolation methods applied across groups. This illustrates both the complex nature of the integrated assumptions and extrapolations inherent in the quantitative methods used herein as well as the potential pitfalls in incremental evolution in the criteria based on one or a few studies.

Finally, it is noted that the current criteria remain focused on the derivation of auditory weighting and exposure functions for the purpose of evaluating the potential fatiguing effects

of discrete noise exposure (e.g., TTS/PTS). These approaches are not applicable in evaluating potential auditory effects of chronic noise exposure over periods of weeks, months, or years. As in human noise exposure criteria, this problem will require different methods and metrics other than the SPL or SEL metrics used here. Separate criteria are needed to evaluate behavioral responses and broader-scale auditory effects (e.g., auditory masking) and physiological effects (e.g., stress responses). These will necessarily involve different approaches but should consider integrating some aspects of the current criteria (e.g., weighting functions).

Note

¹Members from the Southall et al. (2007) panel participating here included Brandon Southall, Ann Bowles, William Ellison, James Finneran, Roger Gentry, Charles Greene, Jr., Darlene Ketten, James Miller, Paul Nachtigall, and Peter Tyack. Colleen Reichmuth, Doug Nowacek, and Lars Bejder were added to the panel. Each of these individuals contributed to some degree to the current effort, with a majority contributing as co-authors to this article. Two companion efforts involving different subgroups of the panel worked in parallel on issues related to sound source characterization and the behavioral effects of noise exposure.

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Appendix 1. Low-Frequency Cetaceans

There are four cetacean families represented in the weighting function for low-frequency (LF) cetaceans: (1) Balaenidae (*Balaena* spp. and *Eubalaena* spp.), (2) Neobalenidae (*Caperea*), (3) Eschrichtiidae (*Eschrichtius*), and (4) Balaenopteridae (*Balaenoptera* spp. and *Megaptera*). Species data are consistent with the Society for Marine Mammalogy Committee on Taxonomy (2016). The baleen whales are considered with respect to available evidence from anatomical descriptions, predictions from anatomical models, and analyses of emitted sounds to validate the grouping of these 14 species to the assigned weighting function. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016. Considering the absence of data on audiometry for this group, the appendix also includes models and predictions of hearing based on anatomy from recent grey literature. Data are expressed as frequency ranges for each species where possible.

Audiometry data providing informative frequency data (from behavioral studies or neurophysiological studies) are not available for any mysticete species.

With respect to anatomy, the mammalian middle ear type for all species included in this group is the *mysticete type* (Nummela, 2008). This ear type has similarities to other cetaceans but with tympanic and periotic bones that are fused anteriorly and posteriorly to form a tympanoperiotic complex that is very large and heavy, and positioned close to the midline of the skull rather than laterally. Species in this group have disproportionately large periotic bones that are firmly coupled to the skull and very large corresponding middle ear cavities; within the middle ear cavity, the massive ossicles are loosely joined. In mysticetes, the pinna is absent; the auditory meatus is thin and partially occluded; and there is a conical, large wax plug, or “glove finger,” on the lateral side of the tubular tympanic membrane. The auditory pathway may involve specialized fats associated with the ears (Yamato et al., 2012). The cochlea has notable features, including a basilar membrane that is extremely broad, especially

at the apical (low-frequency) end; this cochlea has been termed Type M (mysticete) by Ketten (1994). Species for which cochlear morphometric data are available are noted in the appendix by the designation of the Type M cochlea. For summary reviews describing anatomy and species differences in mysticetes, see, for example, Ketten (1992, 2000) and Ketten et al. (2016).

Anatomy-based predictions of hearing range are reported for six species (predicted low-frequency hearing limit, predicted high-frequency hearing limit, or both). Note that anatomy-based models or measurements used to predict hearing limits are annotated by superscript by the method used: cochlear shape (radii ratios)^a; inner ear frequency place maps^b; basilar membrane thickness-to-width ratios^c; and composite model estimates, including middle ear transform functions^d or transform functions derived from finite element modeling either of head structures (combining pressure loading and skull vibration loading)^e or middle ear structures.^f

At least some **sound production data** are available for the 14 mysticete species that are presently recognized. Frequency ranges for sound production are cited as the broadest range of frequencies reported across all available cited studies for each species and are referenced to call types at the extremes of this range.

It is notable that the right whales (*Eubalaena glacialis*, *E. australis*, and *E. japonica*), bow-head whale (*Balaena mysticetus*), blue whale (*Balaenoptera musculus*), and fin whale (*Balaenoptera physalus*) are included in the LF cetacean weighting function; however, there is evidence to suggest that these species should be treated separately as very low-frequency (VLF) cetaceans that have better sensitivity to infrasonic sounds of even lower frequencies than other mysticetes. This distinction is based on several factors, including very large body size, exceptionally lower-frequency limits of sound production, high radii ratios based on cochlear morphology, and corresponding relatively long basilar membranes with small apical thickness-to-width ratios (Ketten et al., 2016).

Appendix 1, Table 1. Weighting functions: Low-frequency (LF) cetaceans

Taxon	Ear type	Auditory modeling	Sound production	References
<i>Balaena mysticetus</i> Bowhead whale	Mysticete middle ear, Type M cochlea	0.6 ^b to 32 ^b kHz	0.02 (moan) to 6 kHz (warble)	Audiometry: No data Anatomical modeling: Ketten, 1994 ^b ; Ketten et al., 2014 ^a Acoustic: Ljungblad et al., 1980, 1982; Clark & Johnson, 1984; Cummings & Holliday, 1987; Würsig & Clark, 1993; Blackwell et al., 2007; Stafford et al., 2008; Delarue et al., 2009; Tervo et al., 2009, 2011, 2012
<i>Eubalaena australis</i> Southern right whale	Mysticete middle ear	--	0.02 (pulse) to 2.2 kHz (pulse, belch)	Audiometry: No data Anatomical modeling: No data Acoustic: Cummings et al., 1971, 1972, 1974; Payne & Payne, 1971; Saayman & Tayler, 1973; Clark, 1982; Parks et al., 2007a
<i>Eubalaena glacialis</i> North Atlantic right whale	Mysticete middle ear, Type M cochlea	0.016 ^{a,b} to 25 ^b kHz	0.02 to 22 kHz (gunshot)	Audiometry: No data Anatomical modeling: Ketten, 1994 ^b ; Parks et al., 2007b ^c ; Ketten et al., 2014 ^a Acoustic: Matthews et al., 2001; McDonald & Moore, 2002; Vanderlaan et al., 2003; Parks & Tyack, 2005; Parks et al., 2007a; Trygonis et al., 2013
<i>Eubalaena japonica</i> North Pacific right whale	Mysticete middle ear	--	0.07 to 0.2 kHz (up calls) ¹	Audiometry: No data Anatomical modeling: No data Acoustic: McDonald & Moore, 2002; Mellinger et al., 2004; Mtunger et al., 2008, 2011
<i>Balaenoptera acutorostrata</i> Common minke whale	Mysticete middle ear, Type M cochlea	0.010 ^{d,e,f} to 34 ^f kHz	0.09 to 9 kHz (star wars, boing)	Audiometry: No data Anatomical modeling: Tubelli et al., 2012a ^d , 2012b ^f ; Ketten et al., 2014 ^{a,c} Acoustic: Beamish & Mitchell, 1973; Edds-Walton, 2000; Mellinger et al., 2000; Gedamke et al., 2001; Rankin & Barlow, 2005; Oswald et al., 2011; Risch et al., 2014a
<i>Balaenoptera bonaerensis</i> Antarctic minke whale	Mysticete middle ear	--	0.05 (downsweep, bio-duck) to 1 kHz (bio-duck)	Audiometry: No data Anatomical modeling: No data Acoustic: Schevill & Watkins, 1972; Risch et al., 2014b
<i>Balaenoptera borealis</i> Sei whale	Mysticete middle ear	--	0.02 (LF sweep) to 4 kHz (FM sweep)	Audiometry: No data Anatomical modeling: No data Acoustic: Knowlton et al., 1991; Rankin & Barlow, 2007; Baumgartner et al., 2008; Calderan et al., 2014; Romagosa et al., 2015
<i>Balaenoptera edeni</i> Bryde's whale	Mysticete middle ear	--	0.1 (LF tonal) to 0.9 kHz (pulsed moan)	Audiometry: No data Anatomical modeling: No data Acoustic: Edds et al., 1993; Oleson et al., 2003; Heimlich et al., 2005; Figueiredo, 2014; Rice et al., 2014; Sirović et al., 2014; Vilorio-Gómora et al., 2015

<i>Balaenoptera omurai</i> Omura's whale	Mysticete middle ear	--	0.01 to 0.05 kHz (AM call)	Audiometry: No data Anatomical modeling: No data Acoustic: Cerchio et al., 2015
<i>Balaenoptera physalus</i> Fin whale	Mysticete middle ear, Type M cochlea	0.02° to 20° kHz	0.01 (rumble, thud, 20-Hz signal) to 1 kHz (slam)	Audiometry: No data Anatomical modeling: Cranford & Krysl, 2015 Acoustic: Watkins et al., 1987; Edds, 1988; Thompson et al., 1992; McDonald et al., 1995a; Charif et al., 2002; Širović et al., 2007, 2013; Weirathmueller et al., 2013
<i>Megaptera novaeangliae</i> Humpback whale	Mysticete middle ear	0.018° to 15° kHz	0.02 (moan, grunt, creak, pulse train) to 24 kHz (mid-frequency tonal wail)	Audiometry: No data Anatomical modeling: Ketten, 1994 ^b ; Ketten et al., 2014 ^a Acoustic: Hafner et al., 1979; Payne & Payne, 1985; Thompson et al., 1986; Simão & Moreira, 2005; Au et al., 2006; Dunlop et al., 2007; Stimpert et al., 2007, 2011; Zoidis et al., 2008
<i>Caperea marginata</i> Pygmy right whale	Mysticete middle ear	--	0.06 to 0.1 kHz (thump)	Audiometry: No data Anatomical modeling: No data Acoustic: Dawbin & Cato, 1992
<i>Eschrichtius robustus</i> Gray whale	Mysticete middle ear	--	0.01 (moan) to 20 kHz (clack)	Audiometry: No data Anatomical modeling: No data Acoustic: Cummings et al., 1968; Poulter, 1968; Fish et al., 1974; Norris et al., 1977; Crane & Lashkari, 1996; Stafford et al., 2007; Dahlheim & Castellote, 2016

^aSee Beamish & Mitchell (1971) for suggestion of clicks extending to 31 kHz.

^bNote that Crance et al. (2017) recently added gunshot calls to the species' repertoire. While not reporting frequency range, their figures show that these gunshots have energy exceeding 2 kHz and are consistent with data from the North Atlantic and southern right whale showing that at close range, these gunshots are broadband-pulsed calls with energy extending to substantially higher frequencies.

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Appendix 2. High-Frequency Cetaceans

Four odontocete families are represented in the high-frequency (HF) cetacean weighting function: Delphinidae (*Orcinus*, *Steno*, *Sousa* spp., *Sotalia* spp., *Tursiops* spp., *Stenella* spp., *Delphinus*, *Lagenodelphis*, *Lissodelphis* spp., *Grampus*, *Peponocephala*, *Feresa*, *Pseudorca*, *Globicephala* spp., *Orcaella* spp., *Lagenorhynchus acutus*, *L. obliquidens*, and *L. obscurus*), Physteridae (*Physeter*), Montodontidae (*Delphinapterus* and *Monodon*), and Ziphiidae (*Berardius* spp., *Hyperoodon* spp., *Indopacetus*, *Mesoplodon* spp., *Tasmacetus*, and *Ziphius*). Note that the family Delphinidae is divided between the HF cetacean weighting function and the very low-frequency (VHF) cetacean weighting function, with species from the genus *Lagenorhynchus* additionally divided between these two weighting functions, with *L. acutus*, *L. albirostris*, *L. obliquidens*, and *L. obscurus* assigned to the HF cetacean group. Species listings are consistent with the Society for Marine Mammalogy Committee on Taxonomy (2016).

The HF cetaceans are considered with respect to available evidence from audiometric studies, anatomical descriptions, predictions from anatomical models, and analyses of emitted sounds to validate the grouping of these 57 odontocete species to the assigned HF cetacean weighting function. Data are expressed as frequency ranges for each species where possible. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016. In some cases, behavioral measurements of hearing and predictions of hearing based on anatomy from more recent sources or grey literature are included.

Audiometry data from behavioral (BEH) and neurophysiological (auditory evoked potential, [AEP]) studies are shown separately as the +60 dB frequency bandwidth from best measured sensitivity; sample sizes (number of different individuals [*n*]) are provided with the references. BEH hearing data are available for eight species. Note that due to their importance in the proposed weighting functions, only behavioral hearing studies meeting specific criteria are shown in the table; excluded studies are identified.¹ AEP measures are available for 12 of 57 species; note that all AEP studies reporting frequency-specific thresholds are included.

With respect to anatomy, two middle ear types are present within this grouping: (1) the *odontocete ear type* and (2) the *physeteroid ear type* (Nummela, 2008; see also Fleischer, 1978). Most odontocetes have an odontocete ear type which is uniquely designed to acoustically isolate the structures of the ear from the rest of the skull. The

tympanic and periotic bones form a tympanoperiotic complex that is surrounded by air sinuses, and the middle ear cavity within is lined with distensible (cavernous) tissue to protect the ear from pressure during diving; the density of the tympanoperiotic complex and ossicles is very high relative to the skull, and the temporal bone is suspended by ligaments in a sinus filled with spongy mucosa to limit sound conduction from the skull (e.g., Ketten, 1994, 2000). Two families in the HF cetacean grouping, Physteridae (*Physeter macrocephalus*) and Ziphiidae (*Berardius* spp., *Hyperoodon* spp., *Indopacetus*, *Mesoplodon* spp., *Tasmacetus*, and *Ziphius*), as well as Kogiidae (*Kogia* spp.) in the VHF cetacean grouping, have a physeteroid ear type. This ear type features tympanic and periotic bones that are tightly fused through a lateral synostosis. All odontocetes lack a pinna and functional auditory meatus and, instead, use a unique auditory pathway of acoustic fats aligned with the lower jaw to direct sound to the ears. Their inner ear features hypertrophied cochlear duct structures, extremely dense ganglion cell distribution, and unique basilar membrane dimensions (for summary, see Wartzok & Ketten, 1999). Odontocetes are differentiated into at least two types by the spiral parameters of the cochlea and characteristic thickness-to-width ratios along the length of the basilar membrane (Ketten & Wartzok, 1990). Type II cochleas have been described for at least five HF cetaceans (noted by species in this appendix); no HF cetaceans evaluated thus far have the morphology of a Type I cochlea seen in some VHF cetaceans (see Appendix 3). Type II cochleas have spiral geometry with logarithmically increasing interturn radii that resemble a “chambered nautilus” (Ketten & Wartzok, 1990).

Anatomy-based predictions of hearing range (predicted LF hearing limit, HF hearing limit, or both) are reported for only one species in the HF cetacean group, *Tursiops truncatus*. This species has been evaluated with multiple auditory models since the hearing abilities of this species is well documented. The anatomy-based models or measurements used to predict hearing limits in *T. truncatus* are annotated by superscript in the appendix by the method used: cochlear shape (radii ratios),^a inner ear frequency place maps,^b basilar membrane thickness-to-width width ratios,^c or transform functions derived from finite element modeling of middle ear structures.^f Auditory models of hearing in marine mammals are further informed by postmortem measures of stiffness

of the middle ear (Miller et al., 2006) or basilar membrane (Zosuls et al., 2012) with known correlates to functional hearing in *T. truncatus*.

At least some **sound production data** are available for 42 of 57 species classified here as HF cetaceans. Frequency ranges for sound production are shown separately for social (SOC) and echoic (ECH) signals where applicable. The broadest range of frequencies reported across all referenced studies for each species are provided for SOC signals (i.e., total bandwidth). For ECH signals, the range of center (median) frequencies are provided where possible (denoted by †); where these data are unavailable, the range of peak (dominant) frequencies are shown (denoted by ‡). ECH (click) signals are additionally classified by **click type** as suggested by Fenton et al. (2014). Among the HF cetaceans, three click types are evident: (1) *broadband high-frequency clicks* (BBHF), (2) *frequency-modulated* (FM) upsweeps, and (3) *multi-pulsed* (MP) signals (Fenton et al., 2014). Most HF cetacean species exhibit BBHF clicks while searching for prey, which are brief, high-intensity, broadband signals. Sperm whales (*Physeter macrocephalus*) are unique among all odontocetes in producing an extremely loud, relatively lower-frequency ECH signal with multiple pulses, caused by structured reverberation of the signal within the head. Beaked whales produce a steep FM click while searching for prey and a more broadband click in the terminal phases of prey capture. No odontocetes classified as HF cetaceans are reported to produce *narrow-band high-frequency* (NBHF) clicks, which are exclusive to the VHF cetacean grouping.

While the sperm whale, beaked whales (Family Ziphiidae: *Berardius* spp., *Hyperoodon* spp., *Indopacetus*, *Mesoplodon* spp., *Tasmacetus*, and *Ziphius*), and the killer whale (*Orcinus orca*) are included in the HF cetacean weighting function at this time, there is some suggestion that these species should be treated separately as “mid-frequency” cetaceans, with better sensitivity to sounds of lower frequencies than other HF cetaceans. These species are outliers to the rest of the HF group for several reasons. *Physeter* and the beaked whales have a physeteroid middle ear type in contrast to the odontocete type ear exhibited by other HF species. While all other HF cetaceans

emit BBHF clicks, sperm and beaked whales produce lower-frequency, alternative ECH signals. In addition, killer whales produce relatively lower-frequency broadband clicks. Interestingly, hearing data for *Orcinus* and two beaked whales confirms an upper range of hearing extending above 90 kHz. More data will be required to better understand possible differences in how hearing is related to sound production between these species and other HF cetaceans.

Nearly all delphinids are HF cetaceans that emit BBHF clicks while searching for prey. The exception is the genus *Cephalorhynchus* and the species presently identified as *Lagenorhynchus australis* and *L. cruicger*. These species produce NBHF clicks and are classified as VHF cetaceans (see Appendix 3). The phylogenetic split among species of the genus *Lagenorhynchus* will likely be resolved by the pending reclassification of the two NBHF species (*L. australis* and *L. cruicger*) to a new or different genus (see Tougaard & Kyhn, 2010). *L. albirostris* is an interesting case with ambiguous classification at the high-frequency end of the HF cetacean grouping. The species produces BBHF clicks but with evidence of unusually HF spectral energy (Rasmussen & Miller, 2002),³ and it has an extreme upper-frequency limit of hearing of 160 kHz (Nachtigall et al., 2008); however, *L. albirostris* remains classified as HF for the time being based on echolocation signal type and phylogenetic parsimony.

Most odontocetes that inhabit shallow-water, cluttered environments produce NBHF clicks and have presumed exceptional ultrasonic hearing; these include the porpoises and most of the river dolphins that are classified as VHF cetaceans. One exception is *Platanista gangetica*. This species has been shown to emit a broadband transient click with relatively low-frequency energy (Jensen et al., 2013). *Platanista* is the sole living species of the family Platanistidae. As this species has no close relatives, and no available data related to hearing, it has been classified with the HF cetaceans based only upon these features of sound production. Other inshore or nearshore species in the HF cetacean group include *Sotalia fluviatilis*, *S. guianensis*, and *Orcaella brevirostris*, which all emit BBHF clicks while searching for prey.

Appendix 2, Table 1. Weighting function: High-frequency (HF) cetaceans

Taxon	Audiometry	Ear type	Auditory modeling	Sound production	Click type	References
<i>Physeter macrocephalus</i> Sperm whale	--	Physeteroid middle ear, Type I cochlea	--	SOC: 0.4 (squeal) to 9 kHz (coda) ECH: 3 to 26 kHz [†]	MP	Audiometry: No data Anatomical models: No data Acoustic: Backus & Schevill, 1966; Levenson, 1974; Watkins & Schevill, 1977, 1980; Watkins, 1980; Weilgart & Whitehead, 1988; Goold & Jones, 1995; Madsen et al., 2002a, 2002b; Möhl et al., 2003; Weir et al., 2007
<i>Berardius arnuxii</i> Arnoux' beaked whale	--	Physeteroid middle ear	--	SOC: 5 kHz (whistle)	--	Audiometry: No data Anatomical models: No data Acoustic: Rogers & Brown, 1999
<i>Berardius bairdii</i> Baird's beaked whale	--	Physeteroid middle ear	--	ECH: 12 to 46 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Dawson et al., 1998; Baumann-Pickering et al., 2013a, 2013b; Stimpert et al., 2014
<i>Hyperoodon ampullatus</i> Northern bottlenose whale	--	Physeteroid middle ear	--	SOC: 3 (whistle) to 16 kHz (whistle) ECH: 32 to 51 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Hooker, 2002; Wahlberg et al., 2011a; Moors-Murphy, 2015
<i>Hyperoodon planifrons</i> Southern bottlenose whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Indopacetus pacificus</i> Tropical bottlenose whale	--	Physeteroid middle ear	--	ECH: 12 to 38 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Rankin et al., 2011; Baumann-Pickering et al., 2013b
<i>Mesoplodon bidens</i> Sowerby's beaked whale	--	Physeteroid middle ear	--	ECH: 32 to 51 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Cholewiak et al., 2013
<i>Mesoplodon bowdoini</i> Andrews' beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon carlhubbsi</i> Hubb's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data

<i>Mesoplodon densirostris</i> Blainville's beaked whale	AEP: < 6 to 117 kHz	Physeteroid middle ear	--	SOC: 1 (whistle) to 12 kHz (whistle) ECH: 30 to 57 kHz [†]	FM	Audiometry: AEP: Pacini et al., 2011 — $n = 1$ Anatomical models: No data Acoustic: Johnson et al., 2004, 2006; Rankin & Barlow, 2007; McDonald et al., 2009; Ward et al., 2011; Baumann-Pickering et al., 2013a; Ward Shaffner et al., 2013
<i>Mesoplodon europaeus</i> Gervais' beaked whale	AEP: < 5 to > 90 kHz	Physeteroid middle ear	--	ECH: 37 to 55 kHz [†]	FM	Audiometry: AEP: Cook et al., 2006; Finneran et al., 2009 — $n = 2$ Anatomical models: No data Acoustic: Gillespie et al., 2009; Baumann-Pickering et al., 2013b
<i>Mesoplodon ginkgodens</i> Ginkgo-toothed beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon grayi</i> Gray's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon hectori</i> Hector's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon hotautla</i> Deraniyagala's beaked whale	--	Physeteroid middle ear	--	ECH: 30 to 66 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Baumann-Pickering et al., 2013a, 2013b
<i>Mesoplodon layardii</i> Strap-toothed beaked whale Layard's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon mirus</i> True's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon perrini</i> Perrin's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon peruvianus</i> Pygmy beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mesoplodon stejnegeri</i> Stejneger's beaked whale	--	Physeteroid middle ear	--	ECH: 46 to 76 kHz [†]	FM	Audiometry: No data Anatomical models: No data Acoustic: Baumann-Pickering et al., 2013b
<i>Mesoplodon traversii</i> Spade-toothed whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data

<i>Tasmacetus shepherdi</i> Tasman beaked whale Shepherd's beaked whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Ziphius cavirostris</i> Cuvier's beaked whale goose-beaked whale	--	Physeteroid middle ear	--	ECH: 28 to 47 kHz*	FM	Audiometry: No data Anatomical models: No data Acoustic: Frantzis et al., 2002; Zimmer et al., 2005; Baumann-Pickering et al., 2013b
<i>Orcinus orca</i> Killer whale	BEH: 0.2 to 140 kHz AEP: < 1 to 90 kHz	Odontocete middle ear	--	SOC: 0.1 (click burst) to 75 kHz (ultrasonic whistles) ECH: 22 to 80 kHz*	BBHF	Audiometry: BEH: Szymanski et al., 1999— $n = 2$; exclude Hall, 1972; AEP: Szymanski et al., 1999— $n = 2$; see also recent paper from Branstetter et al., 2017— $n = 6$, with individuals "A" and "B" excluded Anatomical models: No data Acoustic: Schevill & Watkins, 1966; Diercks et al., 1971; Steiner et al., 1979; Dahlheim & Awbrey, 1982; Ford & Fisher, 1983; Hoelzel & Osborne, 1986; Morton et al., 1986; Moore et al., 1988; Ford, 1989; Barrett-Lennard et al., 1996; Thomsen et al., 2001; Au et al., 2004; Van Opzeeland et al., 2005; Miller, 2006; Riesch et al., 2006, 2008; Simon & Ugarte, 2006; Simon et al., 2007; Samarra et al., 2010; Riesch & Deecke, 2011; Simonis et al., 2012
<i>Delphinapterus leucas</i> Beluga	BEH: 0.04 to 130 kHz AEP: < 4 to 150 kHz	Odontocete middle ear	--	SOC: 0.1 (whistle, pulsed calls) to 21 kHz (whistle, pulsed calls) ECH: 40 to 120 kHz*	BBHF	Audiometry: BEH: White et al., 1978; Awbrey, 1988; Johnson et al., 1989; Ridgway et al., 2001; Fineran et al., 2005b— $n = 8$; exclude Fineran et al., 2005b (individual <i>Turner</i>); AEP: Popov & Supin, 1990; Klishin et al., 2000; Mooney et al., 2008; Popov et al., 2013; Castellote et al., 2014— $n = 12$ Anatomical models: No data Acoustic: Kamminga & Wiersma, 1981; Sjare & Smith, 1986; Au et al., 1987; Turl et al., 1991; Belikov & Bel'kovich, 2001, 2005, 2006, 2007; Karlsen et al., 2001; Rutenko & Vishnyakov, 2006; Lammers & Castellote, 2009; Chmelitsky & Ferguson, 2012
<i>Monodon monoceros</i> Narwhal	--	Odontocete middle ear	--	SOC: 0.3 (whistle, pulsed calls) to 24 kHz (pulsed calls) ECH: 53 kHz* (mean)	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Watkins et al., 1971; Ford & Fisher, 1978; Møhl et al., 1990; Miller et al., 1995; Shapiro, 2006; Marcoux et al., 2012; Stafford et al., 2012; Rasmussen et al., 2015; Kobitz et al., 2016
<i>Delphinus delphis</i> Short- and long-beaked common dolphins	--	Odontocete middle ear	--	SOC: 0.3 (whistle) to 44 kHz (whistles) ECH: 25 to 35 kHz*	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Busnel & Dziedziec, 1966; Fish & Turl, 1976; Moore & Ridgway, 1995; Oswald et al., 2003; Ansmann et al., 2007; Petrella et al., 2012; Azzolin et al., 2014
<i>Feresa attenuata</i> Pygmy killer whale	AEP: 5 to 106 kHz	Odontocete middle ear	--	ECH: 70 to 85 kHz*	BBHF	Audiometry: AEP: Montie et al., 2011— $n = 2$ Anatomical models: No data Acoustic: Madsen et al., 2004

<i>Globicephala macrorhynchus</i> Short-finned pilot whale	AEP: < 10 to 105 kHz	Odontocete middle ear	--	SOC: 2 (whistle) to 40 kHz (whistle) ECH: 3 to 13 kHz [†]	BBHF	Audiometry: AEP: Schlundt et al., 2011; Greenhow et al., 2014— <i>n</i> = 5 Anatomical models: No data Acoustic: Fish & Turl, 1976; Rendell et al., 1999; Oswald et al., 2003; Baron et al., 2008; Jensen et al., 2011
<i>Globicephala melas</i> Long-finned pilot whale	AEP: < 4 to 89 kHz	Odontocete middle ear	--	SOC: 0.1 (chirp, squeal) to 24 kHz (whistle)	--	Audiometry: AEP: Pacini et al., 2010— <i>n</i> = 1 Anatomical models: No data Acoustic: Steiner, 1981; Rendell et al., 1999; Nemiroff, 2009; Azzolin et al., 2014
<i>Grampus griseus</i> Risso's dolphin	BEH: 1.6 to 100 kHz [‡] AEP: < 4 to 142 kHz	Odontocete middle ear, Type II cochlea	--	SOC: 0.1 (grunt) to 29 kHz (whistle) ECH: 24 to 131 kHz [†]	BBHF	Audiometry: BEH: Nachtigall et al., 1995— <i>n</i> = 1; AEP: Nachtigall et al., 2005— <i>n</i> = 1 Anatomical models: Wartzok & Ketten, 1999; Nummela, 2008 Acoustic: Au, 1993; Rendell et al., 1999; Corkeron et al., 2001; Philips et al., 2003; Madsen, 2004; Soldevilla et al., 2008; Smith et al., 2016
<i>Lagenodelphis hosei</i> Fraser's dolphin	--	Odontocete middle ear	--	SOC: 4.3 (whistle) to 24 kHz (whistle)	--	Audiometry: No data Anatomical models: No data Acoustic: Leatherwood et al., 1993; Watkins et al., 1994; Oswald et al., 2007
<i>Lagenorhynchus acutus</i> Atlantic white-sided dolphin	--	Odontocete middle ear	--	SOC: 0.1 (squeak) to 20 kHz (whistle) ECH: 44 to 86 kHz [†]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Ding et al., 1995; Herzog, 1996; Au & Herzog, 2003; Hamran, 2014
<i>Lagenorhynchus albirostris</i> White-beaked dolphin	AEP: < 16 to 160 kHz	Odontocete middle ear, Type II cochlea	--	SOC: 1 to 47 kHz (pulses) ECH: 82 to 98 kHz ^{†,3}	BBHF ³	Audiometry: AEP: Nachtigall et al., 2008— <i>n</i> = 2 Anatomical models: No data Acoustic: Watkins & Shevill, 1972; Mitson, 1990; Rendell et al., 1999; Rasmussen & Miller, 2002, 2004; Simard et al., 2008; Atem et al., 2009
<i>Lagenorhynchus obliquidens</i> Pacific white-sided dolphin	BEH: 0.3 to 139 kHz	Odontocete middle ear	--	SOC: 2 (whistle) to 20 kHz (whistle) ECH: 22 to 38 kHz [†]	BBHF	Audiometry: BEH: Tremel et al., 1998— <i>n</i> = 1 Anatomical models: No data Acoustic: Caldwell & Caldwell, 1970b; Soldevilla et al., 2008
<i>Lagenorhynchus obscurus</i> Dusky dolphin	--	Odontocete middle ear	--	SOC: 1 (whistle) to 28 kHz (whistle) ECH: 90 to 100 kHz [†]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Ding et al., 1995; Matthews et al., 1999; Au & Würsig, 2004; Au et al., 2010; Vaughn-Hirshorn et al., 2012

<i>Lissodelphis borealis</i> Northern right whale dolphin	--	Odontocete middle ear	--	SOC: 1 (whistle) to 49 kHz (burst pulse) ECH: 23 to 41 kHz [‡]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Leatherwood & Walker, 1979; Rankin et al., 2007
<i>Lissodelphis peronii</i> Southern right whale dolphin	--	Odontocete middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Orcaella brevirostris</i> Irrawaddy dolphin	--	Odontocete middle ear	--	SOC: 1 (whistle) to 22 kHz (creak, buzz, squeak) ECH: 70 to 109 kHz [‡]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Van Parijs et al., 2000; Jensen et al., 2013; Ingale & Lokhande, 2015
<i>Orcaella heinsohni</i> Australian snubfin dolphin	--	Odontocete middle ear	--	SOC: 6 (whistle) to 13 kHz (whistle)	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Berg Soto et al., 2014
<i>Peponocephala electra</i> Melon-headed whale	--	Odontocete middle ear	--	SOC: 1 (whistle) to 25 kHz (whistle) ECH: 21 to 38 kHz [‡]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Baumann-Pickering et al., 2010, 2015a; Frankel & Yin, 2010; Kaplan et al., 2014
<i>Pseudorca crassidens</i> False killer whale	BEH: 2 to 111 kHz AEP: < 4 to > 45 kHz	Odontocete middle ear	--	SOC: 3 (whistle) to 9 kHz (whistle) ECH: 25 to 87 kHz [‡]	BBHF	Audiometry: BEH: Thomas et al., 1988 — $n = 1$; exclude Yuen et al., 2005; AEP: Yuen et al., 2005 — $n = 1$ Anatomical models: No data Acoustic: Mizue et al., 1969; Kamminga & van Velden, 1987; Thomas et al., 1988; Thomas & Turl, 1990; Brill et al., 1992; Au et al., 1995; Murray et al., 1998; Rendell et al., 1999; Oswald et al., 2003; Madsen, 2004; Kloepper et al., 2012; Madsen et al., 2013; Baumann-Pickering et al., 2015b
<i>Sousa chinensis</i> Indo-Pacific humpback dolphin	AEP: < 5.6 to 135 kHz	Odontocete middle ear	--	SOC: 0.5 (grunt) to 28 kHz (whistle) ECH: 57 to 134 kHz [‡]	BBHF	Audiometry: AEP: Li et al., 2012 — $n = 1$ Anatomical models: No data Acoustic: Schultz & Corkeron, 1994; Van Parijs & Corkeron, 2001a, 2001b; Goold & Jefferson, 2004; Sims et al., 2012; Xu et al., 2012; Li et al., 2013; Wang et al., 2013; Berg Soto et al., 2014; Fang et al., 2015; Hoffman et al., 2015; Kimura et al., 2016
<i>Sousa plumbea</i> Indian Ocean humpback dolphin	--	Odontocete middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Sousa sahulensis</i> Australian humpback dolphin	--	Odontocete middle ear	--	ECH: 86 to 125 kHz [‡]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: de Freitas et al., 2015

<i>Sousa teuszii</i> Atlantic humpback dolphin	--	Odontocete middle ear	--	SOC: 1 (whistle) to 24 kHz (whistle)	--	Audiometry: No data Anatomical models: No data Acoustic: Weir, 2010
<i>Sotalia fluviatilis</i> Tucuxi	BEH: < 4 to > 135 kHz AEP: < 5 to 140 kHz	Odontocete middle ear	--	SOC: 0.2 (whistle) to 29 kHz (whistle) ECH: 60 to 148 kHz ⁺	BBHF	Audiometry: BEH; Sauerland & Dehnhardt, 1998— <i>n</i> = 1; AEP; Popov & Supin, 1990— <i>n</i> = 2 Anatomical models: No data Acoustic: Caldwell & Caldwell, 1970a; Norris et al., 1972; Nakasai & Takemura, 1975; Kamminga et al., 1993; Ding et al., 1995; Monteiro-Filho & Monteiro, 2001; Wang et al., 2001; Azevedo & Simão, 2002; Erber & Simão, 2004; Azevedo & Van Sluys, 2005; Pivari & Rosso, 2005; May-Collado & Wartzok, 2010; Yamamoto et al., 2015
<i>Sotalia guianensis</i> Guiana dolphin	--	Odontocete middle ear	--	SOC: 0.3 (gargle) to 40 kHz (whistle)	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Wiersma, 1982; Monteiro-Filho & Monteiro, 2001; Duarte de Figueiredo & Simão, 2009; May-Collado & Wartzok, 2009; May-Collado, 2010, 2013; Deconto & Monteiro-Filho, 2013, 2016; de Andrade et al., 2014, 2015; Lima & Le Pendu, 2014; Barrios-Garrido et al., 2016; Leão et al., 2016
<i>Stenella attenuata</i> Pantropical spotted dolphin	--	Odontocete middle ear, Type II cochlea	--	SOC: 3 (whistle) to 22 kHz (whistle) ECH: 83 kHz ⁺ (mean)	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Ding et al., 1995; Oswald et al., 2003; Schotten et al., 2004
<i>Stenella clymene</i> Clymene dolphin	--	Odontocete middle ear	--	--	--	Audiometry: No data Anatomy: No data Acoustic: No data
<i>Stenella coeruleoalba</i> Striped dolphin	BEH: 2 to 154 kHz	Odontocete middle ear	--	SOC: 1 (whistle) to 34 kHz (whistle)	--	Audiometry: BEH; Kastelein et al., 2003— <i>n</i> = 1 Anatomical models: No data Acoustic: Oswald et al., 2003; Azzolin et al., 2013; Papale et al., 2013
<i>Stenella frontalis</i> Atlantic spotted dolphin	--	Odontocete middle ear	--	SOC: 1 (whistle) to 32 kHz (whistle) ECH: 44 to 86 kHz ⁺	--	Audiometry: No data Anatomical models: No data Acoustic: Caldwell & Caldwell, 1971; Caldwell et al., 1973; Steiner, 1981; Ding et al., 1995; Lammers et al., 2003; Baron et al., 2008; Azevedo et al., 2010; Frankel et al., 2014; Jensen et al., 2015
<i>Stenella longirostris</i> Spinner dolphin	--	Odontocete middle ear	--	SOC: 0.8 (whistle) to 26 kHz (whistle) ECH: 33 to 81 kHz ⁺	--	Audiometry: No data Anatomical models: No data Acoustic: Watkins & Schevill, 1974; Steiner, 1981; Brownlee & Norris, 1994; Bazúa-Durán & Au, 2002, 2004; Lammers et al., 2003, 2004; Oswald et al., 2003; Schotten et al., 2004; Baumann-Pickering et al., 2010

<i>Steno bredanensis</i> Rough-toothed dolphin	AEP: < 10 to > 120 kHz	Odontocete middle ear	--	SOC: 3 (whistle) to 29 kHz (whistle) ECH: 16 to 29 kHz [†]	BBHF	Audiometry: AEP: Mann et al., 2010 — $n = 1$ Anatomical models: No data Acoustic: Norris & Evans, 1967; Oswald et al., 2003; Seabra de Lima et al., 2012; Rankin et al., 2015
<i>Tursiops aduncus</i> Indo-Pacific bottlenose dolphin	--	Odontocete middle ear	--	SOC: 0.5 (whistle) to 28 kHz (whistle) ECH: 85 to 114 kHz [†]	BBHF	Audiometry: No data Anatomical models: No data Acoustic: Morisaka et al., 2005; Hawkins & Gartside, 2009; Hawkins, 2010; Wahlberg et al., 2011a, 2011b; Gridley et al., 2012; de Freitas et al., 2015; Lubis et al., 2016; Wård et al., 2016; Wulandari et al., 2016
<i>Tursiops truncatus</i> Common bottlenose dolphin	BEH: 0.4 to 146 kHz AEP: < 5 to 169 kHz	Odontocete middle ear, Type II cochlea	0.15 ^a to 163 ^b kHz	SOC: 0.1 (thunk) to 165 kHz (creak) ECH: 23 to 102 kHz [†]	BBHF	Audiometry: BEH: Johnson, 1967; Ljungblad et al., 1982; Lemonds, 1999; Brill et al., 2001; Schlundt et al., 2008; Finneran et al., 2010 — $n = 6$; exclude Finneran et al., 2005a, 2007; AEP: Popov & Supin, 1990; Houser & Finneran, 2006; Popov et al., 2007; Finneran et al., 2008, 2011; Houser et al., 2008; Mann et al., 2010 — $n > 39$ Anatomical models: Ketten, 1994 ^b ; Tubelli et al., 2012 [†] ; Ketten et al., 2014 ^{a, b} ; Racicot et al., 2016 [§] Acoustic: Lilly & Miller, 1961; Evans & Prescott, 1962; Lilly, 1963; Caldwell & Caldwell, 1968, 1979; Diercks et al., 1971; Evans, 1973; Au et al., 1974; Fish & Turl, 1976; Kamminga, 1979; Au & Penner, 1981; Steiner, 1981; Au et al., 1982; Wiersma, 1982; dos Santos et al., 1990; Au, 1993, 2004; Jacobs et al., 1993; Ding et al., 1995; McCowan & Reiss, 1995; Schulz et al., 1995; Connor & Smolker, 1996; Blomqvist & Amundin, 2004; Boisseau, 2005; Azevedo et al., 2007; van der Woude, 2009; Hawkins, 2010; Simard et al., 2011; Wahlberg et al., 2011b; Branstetter et al., 2012; Azzolin et al., 2014; Frankel et al., 2014; Buscaino et al., 2015; Gridley et al., 2015
<i>Platanista gangetica</i> South Asian river dolphin Indian river dolphin Ganges river dolphin	--	Odontocete middle ear	--	ECH: 54 to 72 kHz	BBT	Audiometry: No data Anatomical models: No data Acoustic: Herald et al., 1969; Andersen & Pilleri, 1970; Kamminga, 1979; Jensen et al., 2013

[†]Due to the primary role of behavioral audiometric data in determining the shape of the weighting function, only psychophysical studies meeting certain criteria were used to determine group-specific audiograms (see “Estimated Group Audiograms for Marine Mammals” section); citations for individuals were excluded if data for the same individual were reported elsewhere, if hearing loss was suspected, if audiograms appeared aberrant (e.g., obvious notches or flattened shape), or if masking or other environmental or procedural factors likely influenced reported data. While these data were excluded from the group audiograms, the excluded citations may still provide useful information about the sounds that can be detected by a given species.

[‡]Note that the BEH (Nachtigall et al., 1995) and AEP (Nachtigall et al., 2005) audiograms for *Grampus griseus* are incongruous. The difference in high-frequency hearing limit for a young stranded individual suggests that the behavioral audiogram for the trained adult subject was not representative. However, as Finneran (2016) and National Marine Fisheries Service (2016) do not exclude this behavioral audiogram, we note this anomaly but do not exclude these data from the composite audiogram in the “Estimated Group Audiograms for Marine Mammals” section.

[§]Note that for *Lagenorhynchus albirostris*, some BBHF echolocation signals contain a secondary peak in the spectrum, with energy above 200 kHz (Rasmussen & Miller, 2002).

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Appendix 3. Very High-Frequency Cetaceans

There are six odontocete families represented in the very high-frequency (VHF) weighting function: Phocoenidae (*Neophocaena* spp., *Phocoena* spp., and *Phocoenoides*), Iniidae (*Inia*), Kogiidae (*Kogia*), Lipotidae (*Lipotes*), Pontoporiidae (*Pontoporia*), and Delphinidae (*Cephalorhynchus* spp., *Lagenorhynchus australis*, and *L. cruciger*). Note that the family Delphinidae is divided between the high-frequency (HF) cetacean weighting function and the VHF cetacean weighting function, with species from the genus *Lagenorhynchus* additionally split between these two weighting functions. The species listings provided here are consistent with the Society for Marine Mammalogy Committee on Taxonomy (2016). With respect to the mixed phylogeny of delphinids between the HF and VHF weighting functions, it is notable that both *L. australis* and *L. cruciger* are now thought to belong to a phylogenetic group aligned with the *Cephalorhynchus* genus, which is also assigned to the VHF group. These two *Lagenorhynchus* species are likely to be reassigned to the *Cephalorhynchus* genus or a new genus (for review, see Tougaard & Kyhn, 2010), which would be consistent with the assignment of *L. australis* and *L. cruciger* to the VHF weighting function.

The VHF odontocetes are considered with respect to available evidence from audiometric studies, anatomical descriptions, predictions from anatomical models, and analyses of emitted sounds to validate the grouping of these 18 species to the assigned VHF cetacean weighting function. Data are expressed as frequency ranges for each species where possible. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016; this appendix also includes models and predictions of hearing based on anatomy from recent grey literature.

Audiometry data from behavioral (BEH) and neurophysiological (auditory evoked potential [AEP]) studies of hearing are shown separately as the +60 dB frequency bandwidth from best measured sensitivity; sample sizes (number of different individuals [*n*]) are provided with the references. BEH hearing data are available for two VHF odontocete species. Note that due to their importance in the proposed weighting functions, only BEH hearing studies meeting specific criteria are shown in the table; excluded studies are identified.¹ AEP measures are available for three species; note that all AEP studies reporting frequency-specific thresholds are included.

With respect to **anatomy**, the mammalian middle ear type for most species in this group is the *odontocete ear type* (Nummela, 2008), which

is uniquely designed to acoustically isolate the structures of the ear from the rest of the skull. The tympanic and periotic bones form a tympanoperiotic complex that is surrounded by air sinuses, and the middle ear cavity within is lined with distensible (cavernous) tissue to protect the ear from pressure during diving; the density of the ossicles is very high relative to the skull, and the temporal bone is suspended by ligaments in a sinus filled with spongy mucosa to limit sound conduction from the skull (e.g., Ketten, 1994, 2000). One genus, *Kogia*, has a *physeteroid ear type* (Nummela, 2008; see also Fleischer, 1978) which features tympanic and periotic bones that are tightly fused through a lateral synostosis, and a bony plate (the tympanic plate) in place of a more compliant tympanic membrane. All odontocetes lack a pinna and functional auditory meatus, and, instead, use a unique auditory pathway of acoustic fats in the lower jaw to direct sound to the ears. Their inner ear features hypertrophied cochlear duct structures, extremely dense ganglion cell distribution, and unique basilar membrane dimensions (for summary, see Wartzok & Ketten, 1999). Odontocetes are differentiated into at least two types by the spiral parameters of the cochlea and characteristic thickness-to-width ratios along the length of the basilar membrane (Ketten & Wartzok, 1990). Type I cochleas have been described for at least two VHF cetaceans; no VHF cetaceans evaluated thus far have the morphology of a Type II cochlea. Type I cochleas, as seen in *Phocoena phocoena* and *Inia geoffrensis*, have spiral geometry with a relatively constant interturn radius curve like that of a “tightly coiled rope” (Ketten & Wartzok, 1990, p. 95).

Anatomy-based predictions of hearing range (predicted low-frequency hearing limit, high-frequency hearing limit, or both when available) are reported for seven species. Data for six of these species are reported by Racicot et al. (2016) and include estimates of the low-frequency hearing limit derived from cochlear shape (radii ratios)^a based on the method of Manoussaki et al. (2008). The final species, *P. phocoena*, is best studied in terms of anatomy. Data are reported by Racicot et al. (2016), as are similar radii ratio data from Ketten et al. (2014). There are also independent low- and high-frequency limits for this species predicted by inner ear frequency place maps^b (Ketten et al., 2014). Note that predictions of hearing limits from auditory modeling obtained from different models are not analogous; therefore, the hearing limits provided in the appendix are annotated by the method used.

At least some **sound production data** are available for 15 of 18 species classified as VHF cetaceans. Frequency ranges for sound production are shown separately for social (SOC) and echoic (ECH) signals where applicable. The broadest range of frequencies reported across all referenced studies for each species are provided for SOC signals (total bandwidth). For ECH signals, the range of center (median) frequencies are provided where possible (denoted by ⁺); where these data are unavailable, the range of peak (dominant) frequencies are shown (denoted by [‡]). ECH (click) signals are additionally classified by **click type** as suggested by Fenton et al. (2014). Cetaceans categorized as VHF all produce narrow-band high-frequency (NBHF) clicks while searching for prey. This is a derived signal that has arisen independently in several phylogenetic groups (e.g., porpoises, some non-whistling dolphins, some river dolphins, and the genus *Kogia*). While best studied in harbor porpoises (*P. phocoena*), this NBHF click type is also present in six delphinids (*Cephalorhynchus* spp., *L. australis*, and *L. cruciger*), as well as in inshore or near-shore species (*I. geoffrensis*, *Pontoporia blainvillei*, and the [now likely extinct] *Lipotes vexillifer*). The NBHF click type is thought to be related to foraging in shallow or cluttered environments, although it is also observed in at least one open water species (*Kogia breviceps*; Madsen et al., 2005).

It is notable that *Platanista gangetica* was originally classified as VHF, along with other river dolphins. However, this species has been shown to emit a broadband transient click with relatively low-frequency energy (Jensen et al., 2013). *Platanista* is the sole living species of the family Platanistidae. As this species has no close relatives, and no audiometric or auditory anatomy data are available, it has been classified with the HF odontocetes rather than the VHF odontocetes based solely upon features of sound production.

Appendix 3, Table 1. Weighting function: Very high-frequency (VHF) cetaceans

Taxon	Audiometry	Ear type	Auditory modeling	Sound production	Click type	References
<i>Lagenorhynchus australis</i> Peale's dolphin	--	Odontocete middle ear	--	SOC: 0.3 to 5 kHz (buzz) ECH: 123 to 138 kHz ⁺	NBHF	Audiometry: No data Anatomical models: No data Acoustic: Schevill & Watkins, 1970; Kyhn et al., 2010
<i>Lagenorhynchus cruciger</i> Hourglass dolphin	--	Odontocete middle ear	--	ECH: 124 to 132 kHz ⁺	NBHF	Audiometry: No data Anatomical models: No data Acoustic: Kyhn et al., 2009; Tougaard & Kyhn, 2010
<i>Cephalorhynchus commersonii</i> Commerson's dolphin	--	Odontocete middle ear	0.3 ⁺ to -- kHz	SOC: 0.2 (cry) to 16 kHz (whistle) ECH: 120 to 171 kHz ⁺	NBHF	Audiometry: No data Anatomical models: Racicot et al., 2016 ^a Acoustic: Watkins & Schevill, 1980; Kamminga & Wiersma, 1981, 1982; Yeh et al., 1981; Evans et al., 1988; Dziedzić & de Buffrenil, 1989; Kyhn et al., 2010; Yoshida et al., 2014; Reyes Reyes et al., 2015, 2016
<i>Cephalorhynchus eutropia</i> Chilean dolphin	--	Odontocete middle ear	--	ECH: 126 kHz ⁺	NBHF	Audiometry: No data Anatomical models: No data Acoustic: Götz et al., 2010
<i>Cephalorhynchus heavisidii</i> Heaviside's dolphin	--	Odontocete middle ear	--	SOC: 0.8 to 4.5 kHz (cries) ECH: 121 to 130 kHz ⁺	NBHF ²	Audiometry: No data Anatomical models: No data Acoustic: Watkins et al., 1977; Morisaka et al., 2011
<i>Cephalorhynchus hectori</i> Hector's dolphin	--	Odontocete middle ear	--	SOC: squeals and cries ECH: 125 to 132 kHz ⁺	NBHF ³	Audiometry: No data Anatomical models: No data Acoustic: Dawson & Thorpe, 1990; Thorpe & Dawson, 1991; Thorpe et al., 1991; Kyhn et al., 2009
<i>Neophocaena asiatorientalis</i> Narrow-ridged finless porpoise	--	Odontocete middle ear	--	ECH: 100 to 135 kHz [±]	NBHF	Audiometry: No data Anatomical models: No data Acoustic: Li et al., 2005, 2007 ^a
<i>Neophocaena phocaenoides</i> Indo-Pacific finless porpoise	AEP: < 8 to > 152 kHz	Odontocete middle ear	0.3 ⁺ to -- kHz	ECH: 142 kHz [±] (mean)	NBHF	Audiometry: AEP: Popov et al., 2005, 2011 — $n = 4$ Anatomical models: Racicot et al., 2016 ^a Acoustic: Pilleri et al., 1980; Kamminga et al., 1986; Akamatsu et al., 1998; Goold & Jefferson, 2002

<i>Phocoena dtioptrica</i> Spectacled porpoise	--	Odontocete middle ear	0.2 ^a to – kHz	--	--	Audiometry: No data Anatomical models: Racicot et al., 2016 ^a Acoustic: No data
<i>Phocoena phocoena</i> Harbor porpoise	BEH: 0.3 to 160 kHz AEP: < 10 to 160 kHz	Odontocete middle ear, Type I cochlea	0.2 ^{5a} to 220 ^b kHz	SOC: see endnote 5 ECH: 125 to 200 kHz [†]	NBHF	Audiometry: BEH: Kastelein et al., 2002, as updated by Kastelein, 2010; Kastelein et al., 2010, 2015— <i>n</i> = 3; exclude Andersen, 1970; AEP: Popov et al., 1986; Popov & Supin, 1990; Ruser et al., 2016— <i>n</i> = 28 Anatomical models: Ketten, 1994 ^a ; Ketten et al., 2014 ^b ; Racicot et al., 2016 ^a Acoustic: Busnel & Dziedzic, 1966; Schevill et al., 1969; Dubrovskii et al., 1971; Møhl & Andersen, 1973; Kamminga & Wiersma, 1981; Wiersma, 1982; Verboom & Kastelein, 1995; Au et al., 1999; Kastelein et al., 1999; Teilmann et al., 2002; Villadsgaard et al., 2007; Hansen et al., 2008; Madsen et al., 2010; Clausen et al., 2011; Kyhn et al., 2013
<i>Phocoena sinus</i> Vaquita	--	Odontocete middle ear	0.2 ^a to – kHz	ECH: 128 to 139 kHz [‡]	NBHF	Audiometry: No data Anatomical models: Racicot et al., 2016 ^a Acoustic: Silber, 1991
<i>Phocoena spinipinnis</i> Burmeister's porpoise	--	Odontocete middle ear	0.4 ^a to – kHz	--	--	Audiometry: No data Anatomical models: Racicot et al., 2016 Acoustic: No data
<i>Phocoenoides dalli</i> Dall's porpoise	--	Odontocete middle ear	0.2 ^a to – kHz	ECH: 121 to 147 kHz [†]	NBHF	Audiometry: No data Anatomical models: Racicot et al., 2016 ^a Acoustic: Bassett et al., 2009; Kyhn et al., 2013
<i>Inia geoffrensis</i> Amazon river dolphin Boto	BEH: < 1 to > 105 kHz AEP: < 8 to > 130 kHz	Odontocete middle ear, Type I cochlea	--	SOC: 0.06 (pulse) to 48 kHz (whistle) ECH: 55 to 138 kHz [†]	NBHF	Audiometry: BEH: Jacobs & Hall, 1972— <i>n</i> = 1; AEP: Popov & Supin, 1990— <i>n</i> = 4 Anatomical models: No data Acoustic: Caldwell & Caldwell, 1970; Penner & Murchison, 1970; Diercks et al., 1971; Norris et al., 1972; Evans, 1973; Kamminga, 1979; Wiersma, 1982; Kamminga et al., 1993; Ding et al., 1995; Wang et al., 2001; Podos et al., 2002; May-Collado & Wartzk, 2007; Ladegaard et al., 2015; Yamamoto et al., 2015; Amorim et al., 2016
<i>Lipotes vexillifer</i> ⁶ Yangtze river dolphin Chinese river dolphin Baiji	--	Odontocete middle ear	--	SOC: 3 (whistle) to 19 kHz (whistle) ECH: 92 kHz [†]	NBHF ⁷	Audiometry: BEH: exclude Wang et al., 1992— <i>n</i> = 1 Anatomical models: No data Acoustic: Jing et al., 1981; Wang et al., 1989, 2006; Xiao & Jing, 1989; Akamatsu et al., 1998

<i>Pontoporia blainvillei</i> Franciscana	--	Odontocete middle ear	--	ECH: 139 kHz [‡] (mean)	NBHF [§]	Audiometry: No data Anatomical models: No data Acoustic: Melcón et al., 2012; Tellechea & Norbis, 2014
<i>Kogia breviceps</i> Pygmy sperm whale	--	Physeteroid middle ear	--	SOC: 1.4 to 1.5kHz ECH: 125 to 130 kHz [‡]	NBHF	Audiometry: No data Anatomical models: No data Acoustic: Thomas et al., 1990; Marten, 2000; Ridgway & Carder, 2001; Madsen et al., 2005
<i>Kogia sima</i> Dwarf sperm whale	--	Physeteroid middle ear	--	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data

¹Due to the primary role of behavioral audiometric data in determining the shape of the weighting function, only psychophysical studies meeting certain criteria were used to determine group-specific audiograms (see “Estimated Group Audiograms for Marine Mammals” section); citations for individuals were excluded if data for the same individual were reported elsewhere, if hearing loss was suspected, if audiograms appeared aberrant (e.g., obvious notches or flattened shape), or if masking or other environmental or procedural factors likely influenced reported data. While these data were excluded from the group audiograms, the excluded citations still provide useful information about the sounds that can be detected by a given species.

²Note that Watkins et al. (1977) also report lower-frequency buzz clicks (below 5 kHz) for *Cephalorhynchus heavisidii*; a recent report from Martin et al. (2018) confirms a broadband click type produced by this species with energy < 100 kHz in addition to NBHF clicks.

³Note that Götz et al. (2010) also report lower-frequency buzz clicks (with center frequency of 100 kHz) for *Cephalorhynchus eutropia*.

⁴Note that Li et al. (2005, 2007) use the species listing *Neophocaena phocaenoides asiatorientalis*.

⁵Note that Verboom & Kastelein (1995) describe whistles for *Phocoena phocaena* with a frequency range of 0.04 to 0.6 kHz and clicks of 1,800 Hz; further, Busnel & Dziedzic (1966) also describe signals with a frequency range up to 8 kHz. However, the production of low-frequency clicks has been explained as insignificant components of high-frequency clicks or acoustic artifacts by Hansen et al. (2008), and there is no substantive updated evidence that harbor porpoises produce whistles.

⁶*Lipotes vexillifer* is included here as listed by the Society for Marine Mammalogy Committee on Taxonomy (2016); however, we note that this species is almost certainly now extinct.

⁷Note that Xiao & Jing (1989) report the centroid frequency of a high-frequency click at 92 kHz for *Lipotes vexillifer* but also report the centroid frequency of a lower-frequency pulse at 5.6 kHz.

⁸Note that Tellechea & Norbis (2014) describe lower-frequency click production for *Pontoporia blainvillei* by neonates.

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Appendix 4. Sirenians

There are two sirenian families represented in the sirenian (SI) weighting function: Trichechidae (*Trichechus* spp.) and Dugongidae (*Dugong*). Species listings are consistent with the Society for Marine Mammalogy Committee on Taxonomy (2016). Manatees and dugongs are considered with respect to available evidence from audiometric studies, anatomical descriptions, and analyses of emitted sounds to validate the grouping of these four species to the assigned weighting function for acoustic exposure: SI. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016. Data are expressed as frequency ranges for each species where possible.

Audiometry data from behavioral (BEH) and neurophysiological (auditory evoked potential [AEP]) studies are shown separately as the +60 dB bandwidth from best measured sensitivity in water; sample sizes (number of different individuals [*n*]) are provided with the references. BEH hearing data are available for one species, *Trichechus manatus*. Note that only BEH hearing studies meeting specific criteria are shown in the audiometry column of the table; excluded studies are identified.¹ AEP data providing frequency-specific thresholds are available for one species, *Trichechus inunguis*.

With respect to **anatomy**, the mammalian middle ear type for the four species included in this group is the *sirenian ear type*, which features a U-shaped tympanic bone that is fused to a much larger periotic bone (Nummela, 2008); in contrast

to other mammals, this tympanoperiotic complex is attached to the inner wall of the cranium and does not entirely surround the middle ear cavity with bone (Ketten et al., 1992; Nummela, 2008). In sirenians, the pinnae are absent, the auditory meatus is thin and apparently occluded, the tympanic membrane is enlarged and bulges outward, and the ossicles are massive with unusual features (Ketten et al., 1992). Significantly, the zygomatic process contains spongy bone that is oil filled; this unique feature, which is directly associated with bony structures connected to the tympanoperiotic complex, may be involved in selectively ducting sound to the ear (Ketten et al., 1992). While formal anatomy-based predictions of hearing range are presently unavailable for any sirenian species, early predictions of auditory range for *T. manatus* (based on review of middle and inner ear structures) suggested the species would be sensitive to “infrasound,” or sounds less than 20 kHz, with peak sensitivity around 8 kHz. Audiometry data shows that the hearing range in sirenians extends from low frequencies to above 60 kHz, with the perception of sounds below 0.02 kHz likely mediated by vibrotactile rather than acoustic cues (Gerstein et al., 1999; Gaspard et al., 2013).

Sound production data are available for three of four sirenian species. Frequency ranges for underwater sound production are cited as the broadest range of frequencies reported across all available studies for each species and are referenced to call types at the extremes of this range.

Appendix 4, Table 1. Weighting function: Sirenians (SI)

Taxon	Audiometry	Ear type	Auditory modeling	Sound production	References
<i>Trichechus inunguis</i> Amazonian manatee	AEP: < 5 to 60 kHz	Sirenian type	--	0.7 to 17 kHz (vocalization/harmonic vocalization)	Audiometry: AEP: Klishin et al., 1990; Popov & Supin, 1990— <i>n</i> = 1 Anatomical models: No data Acoustic: Evans & Herald, 1970; Sousa-Lima et al., 2002; Sousa-Lima, 2006; Landrau-Giovanetti et al., 2014 ²
<i>Trichechus manatus</i> West Indian manatee Antillean manatee	BEH: < 0.25 to 72 kHz	Sirenian type	“Infrasound” to < 20 kHz	0.4 to 22 kHz (tonal harmonic vocalization)	Audiometry: Gerstein et al., 1999; Gaspard et al., 2012— <i>n</i> = 4; excluded Mann et al., 2005 Anatomical models: Ketten et al., 1992 Acoustic: Schevill & Watkins, 1965; Nowacek et al., 2003; O’Shea & Poché, 2006; Sousa-Lima et al., 2008; Miksis-Olds & Tyack, 2009; Grossman et al., 2014; Landrau-Giovanetti et al., 2014 ² ; Rivera Chavarria et al., 2015
<i>Trichechus senegalensis</i> West African manatee	--	Sirenian type	--	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Dugong dugon</i> Dugong	--	Sirenian type	--	0.15 (squeak) to 18 kHz (trills, chirp-squeak)	Audiometry: No data Anatomical models: No data Acoustic: Nair & Lal Mohan, 1975; Marsh et al., 1978; Anderson & Barclay, 1995; Ichikawa et al., 2003; Hishimoto et al., 2005; Parsons et al., 2013

¹Due to the primary role of behavioral audiometric data in determining the shape of the weighting function, only psychophysical studies meeting certain criteria were used to determine group-specific audiograms (see “Estimated Group Audiograms for Marine Mammals” section); citations for individuals were excluded if data for the same individual were reported elsewhere, if hearing loss was suspected, if audiograms appeared aberrant (e.g., obvious notches or flattened shape), or if masking or other environmental or procedural factors likely influenced reported data. While these data were excluded from the group audiograms, the excluded citations may still provide useful information about the sounds that can be detected by a given species.

²Vocalization emitted in air and recorded with a hydrophone coupled to the skin

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Appendix 5. Phocid Carnivores

There is a single Carnivore family represented in the weighting functions for phocid carnivores in water (PCW) and phocid carnivores in air (PCA): Phocidae (*Cystophora*, *Erignathus*, *Halichoerus*, *Histriophoca*, *Hydrurga*, *Leptonychotes*, *Lobodon*, *Mirounga* spp., *Monachus*, *Neomonachus*, *Ommatophoca*, *Pagophilus*, *Phoca* spp., and *Pusa* spp.). Species listings provided are consistent with those of the Society for Marine Mammalogy Committee on Taxonomy (2016). True seals are considered with respect to available evidence from audiometric studies, anatomical descriptions, and analyses of emitted sounds to validate the grouping of these 18 species to the assigned weighting functions. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016. Data are expressed as frequency ranges for each species where possible and are considered separately for water (Table 1) and air (Table 2), as these species are amphibious.

Audiometry data from behavioral (BEH) and neurophysiological (auditory evoked potential [AEP]) studies are shown separately here as the +60 dB frequency bandwidth from best measured sensitivity; sample sizes (number of different individuals [n]) are provided with the references. BEH data are available for four species in water and three species in air. Note that only BEH hearing studies meeting specific criteria are shown in

the tables; excluded studies are identified.¹ AEP measures are available for one species in water and three species in air. Note that all AEP studies reporting frequency-specific thresholds are included.

With respect to **anatomy**, the mammalian middle ear type for all species included in this group is the *phocid ear type* (Nummela, 2008), which features an enlarged tympanic membrane, ossicles, and middle ear cavity. Species in this group lack an outer pinna and have cavernous tissue lining the auditory meatus and middle ear cavity as an apparent adaptation for pressure regulation during diving (Møhl, 1968b; Repenning, 1972; Wartzok & Ketten, 1999). Some species have a spiral cartilage and musculature along the lateral portion of the external auditory canal that may function to close the canal under water. Anatomy-based predictions of hearing range are presently unavailable for any phocid carnivore.

Underwater sound production data are available for 12 of 18 species; in-air sound production data are available for 12 of 18 species. Frequency ranges for sound production are provided as the broadest range of frequencies reported across all available studies for each species and in each medium, and they are referenced to call types at the extremes of this range.

Appendix 5, Table 1. Weighting function: Phocid carnivores in water (PCW)

Taxon	Audiometry	Ear type	Sound production	References
<i>Cystophora cristata</i> Hooded seal	--	Phocid type	0.1 (snort, click) to 16 kHz (click)	Audiometry: No data Anatomical models: No data Acoustic: Schevill et al., 1963; Terhune & Ronald, 1973; Ballard & Kovacs, 1995
<i>Erignathus barbatus</i> Bearded seal	--	Phocid type	0.08 (groan) to 22 kHz (moan)	Audiometry: No data Anatomical models: No data Acoustic: Poulter, 1968; Ray et al., 1969; Stirling et al., 1983; Cleator et al., 1989; Terhune, 1999; Van Parijs et al., 2001; Van Parijs & Clark, 2006; Risch et al., 2007; Charrier et al., 2013; MacIntyre et al., 2013; Jones et al., 2014
<i>Halichoerus grypus</i> Gray seal	AEP: < 1.4 to 100 kHz	Phocid type	< 0.1 (click, hiss) to 40 kHz (hiss)	Audiometry: AEP: Ridgway & Joyce, 1975 — $n = 2$ Anatomical models: No data Acoustic: Schevill et al., 1963; Schusterman et al., 1970; Oliver, 1978; Asselin et al., 1993
<i>Histriophoca fasciata</i> Ribbon seal	--	Phocid type	0.01 (downsweep) to 12 kHz (downsweep)	Audiometry: No data Anatomical models: No data Acoustic: Watkins & Ray, 1977; Miksis-Olds & Parks, 2011; Denes et al., 2013; Jones et al., 2014; Mizuguchi et al., 2016a
<i>Hydrurga leptonyx</i> Leopard seal	--	Phocid type	0.04 (growl, thump pulse) to 164 kHz (FM buzz)	Audiometry: No data Anatomical models: No data Acoustic: Poulter, 1968; Stirling & Siniff, 1979a; Thomas et al., 1983; Rogers et al., 1995, 1996; Thomas & Golladay, 1995; Rogers & Cato, 2002; Kreiss et al., 2014; Rogers, 2014
<i>Leptonychotes weddelli</i> Weddell seal	--	Phocid type	0.1 (short duration calls) to 15 kHz (unspecified)	Audiometry: No data Anatomical models: No data Acoustic: Thomas & Kuechle, 1982; Thomas & Stirling, 1983; Green & Burton, 1988; Morrice et al., 1994; Pahl et al., 1997; Evans et al., 2004; Moors & Terhune, 2004, 2005; Terhune, 2004; Terhune & Dell'Apa, 2006; Terhune et al., 2008; Doiron et al., 2012
<i>Lobodon carcinophaga</i> Crabeater seal	--	Phocid type	0.25 (low moan) to 5 kHz (high moan)	Audiometry: No data Anatomical models: No data Acoustic: Stirling & Siniff, 1979b; McCreery & Thomas, 2009; Klinck et al., 2010
<i>Mirounga angustirostris</i> Northern elephant seal	BEH: < 0.075 to > 60 kHz	Phocid type	--	Audiometry: BEH: Kastak & Schusterman, 1999 — $n = 1$; excluded Kastak & Schusterman, 1998 Anatomical models: No data Acoustic: No data

<i>Mirounga leonina</i> Southern elephant seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Monachus monachus</i> Mediterranean monk seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Neomonachus schauinslandi</i> Hawaiian monk seal	--	Phocid type	--	Audiometry: BEH: excluded Thomas et al., 1990— $n = 1$ Anatomical models: No data Acoustic: No data
<i>Ommatophoca rossii</i> Ross seal	--	Phocid type	0.6 (siren) to 4.5 kHz (siren)	Audiometry: No data Anatomical models: No data Acoustic: Watkins & Ray, 1985
<i>Pagophilus groenlandicus</i> Harp seal	--	Phocid type	0.1 (adult call) to 10 kHz (adult call)	Audiometry: BEH: excluded Terhune & Ronald, 1972— $n = 1$ Anatomical models: No data Acoustic: Schevill et al., 1963; Watkins & Schevill, 1979; Terhune & Ronald, 1986; Miller & Murray, 1995; Serrano, 2001; Serrano & Terhune, 2001; Moors & Terhune, 2003, 2005; Van Opzeeland & Van Parijs, 2004; Rossong & Terhune, 2009; Van Opzeeland et al., 2009
<i>Phoca largha</i> Spotted seal Largha seal	BEH: < 0.1 to 87 kHz	Phocid type	0.2 (knock, drum, growl, sweep) to 3.5 kHz (drum)	Audiometry: Sills et al., 2014; Cunningham & Reichmuth, 2016— $n = 2$ Anatomical models: No data Acoustic: Beier & Wartzok, 1979; Yang et al., 2017
<i>Phoca vitulina</i> Harbor seal	BEH: < 0.1 to 79 kHz	Phocid type	0.02 (roar) to 24 kHz (roar)	Audiometry: BEH: Terhune, 1988; Kastelein et al., 2009; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016— $n = 4$; excluded Möhl, 1968a; Kasiak & Schusterman, 1998; Southall et al., 2005 Anatomical models: No data Acoustic: Schevill et al., 1963; Schusterman et al., 1970; Perry & Renouf, 1988; Hanggi & Schusterman, 1994; Van Parijs et al., 1997, 1999, 2003; Van Parijs & Kovacs, 2002; Bjørgesaeter et al., 2004; Sauvé et al., 2015; Nikolich et al., 2016; Casey et al., 2017; Sabinsky et al., 2017
<i>Pusa caspica</i> Caspian seal	--	Phocid type	--	Audiometry: excluded Babushina, 1997— $n = 1$ Anatomical models: No data Acoustic: No data
<i>Pusa hispida</i> Ringed seal	BEH: < 0.1 to > 72.4 kHz	Phocid type	0.02 (woof, click) to 30 kHz (click)	Audiometry: Sills et al., 2015— $n = 1$; excluded Terhune & Ronald, 1975; Sills et al., 2015 (individual "Natchek") Anatomical models: No data Acoustic: Schevill et al., 1963; Stirling, 1973; Stirling et al., 1983; Hyvärinen, 1989; Kunnasranta, 1996; Kautio et al., 2009; Jones et al., 2014; Mizuguchi et al., 2016b
<i>Pusa sibirica</i> Baikal seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data

Appendix 5, Table 2. Weighting function: Phocid carnivores in air (PCA)

Taxon	Audiometry	Ear type	Sound production	References
<i>Cystophora cristata</i> Hooded seal	--	Phocid type	0.1 (pup calls, male calls) to 6 kHz (growl, roar)	Audiometry: No data Anatomical models: No data Acoustic: Terhune & Ronald, 1973; Ballard & Kovacs, 1995
<i>Erignathus barbatus</i> Bearded seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Halichoerus grypus</i> Gray seal	AEP: <0.2 to > 29.7 kHz	Phocid type	0.25 (pup call) to 6 kHz (pup call)	Audiometry: AEP: Ridgway & Joyce, 1975; Ruser et al., 2014 — $n = 8$ Anatomical models: No data Acoustic: Caudron et al., 1998; McCulloch et al., 1999
<i>Histriophoca fasciata</i> Ribbon seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Hydrurga leptonyx</i> Leopard seal	AEP: < 1 to > 4 kHz	Phocid type	--	Audiometry: AEP: Tripovich et al., 2011 — $n = 1$ Anatomical models: No data Acoustic: No data
<i>Leptonychotes weddellii</i> Weddell seal	--	Phocid type	0.09 (grunt) to 10 kHz (call)	Audiometry: No data Anatomical models: No data Acoustic: Terhune et al., 1993, 1994; Oetelaar et al., 2003; Collins et al., 2005, 2006; Collins & Terhune, 2007
<i>Lobodon carcinophaga</i> Crabeater seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Mirounga angustirostris</i> Northern elephant seal	AEP: < 4 to > 4 kHz	Phocid type	Phocid type	Audiometry: BEH: excluded Kastak & Schusterman, 1998, 1999; Reichmuth et al., 2013 — $n = 1$; AEP: Houser et al., 2007 — $n = 1$ Anatomical models: No data Acoustic: Bartholomew & Collias, 1962; Le Boeuf & Peterson, 1969; Le Boeuf et al., 1972; Sandegren, 1976; Shipley et al., 1986; Southall et al., 2003; Holt et al., 2010; Casey et al., 2015
<i>Mirounga leonina</i> Southern elephant seal	--	Phocid type	0.02 (drumming, call) to 4 kHz (gargling, explosive)	Audiometry: No data Anatomical models: No data Acoustic: Sanvito & Galimberti, 2000; Sanvito et al., 2008

<i>Monachus monachus</i> Mediterranean monk seal	--	Phocid type	0.26 (pup call) to 3 kHz (female call)	Audiometry: No data Anatomical models: No data Acoustic: Muñoz et al., 2011
<i>Neomonachus schauinslandi</i> Hawaiian monk seal	--	Phocid type	0.10 (pup call, huh-huh) to 4 kHz (sneeze/cough)	Audiometry: No data Anatomical models: No data Acoustic: Miller & Job, 1992; Job et al., 1995
<i>Ommatophoca rossii</i> Ross seal	--	Phocid type	0.1 (pulse) to 1 kHz (pulse)	Audiometry: No data Anatomical models: No data Acoustic: Watkins & Ray, 1985
<i>Pagophilus groenlandicus</i> Harp seal	--	Phocid type	0.1 (pup call) to 10 kHz (pup call)	Audiometry: BEH: excluded Terhune & Ronald, 1971 Anatomical models: No data Acoustic: Miller & Murray, 1995; Van Opzeeland & Van Parijs, 2004; Van Opzeeland et al., 2009
<i>Phoca largha</i> Spotted seal Largha seal	BEH: <0.075 to >51.2 kHz	Phocid type	0.1 (grunt) to 3.5 kHz (drum)	Audiometry: Sills et al., 2014— $n = 2$ Anatomical models: No data Acoustic: Beier & Wartzok, 1979; Zhang et al., 2016
<i>Phoca vitulina</i> Harbor seal	BEH: <0.1 to >32.5 kHz AEP: < 1.4 to > 30 kHz	Phocid type	0.1 (pup call) to 9 kHz (pup call)	Audiometry: BEH: Reichmuth et al., 2013— $n = 1$; excluded Møhl, 1968a; Terhune, 1989, 1991; Kastak & Schusterman, 1998; Wolski et al., 2003; AEP: Wolski et al., 2003; Lucke et al., 2016— $n < 25$ Anatomical models: No data Acoustic: Ralls et al., 1985; Renouf, 1985; Perry & Renouf, 1988; Van Parijs & Kovacs, 2002; Khan et al., 2006; Sauvé et al., 2015
<i>Pusa caspica</i> Caspian seal	--	Phocid type	--	Audiometry: excluded Babushima, 1997— $n = 1$ Anatomical models: No data Acoustic: No data
<i>Pusa hispida</i> Ringed seal	BEH: <0.075 to 40 kHz	Phocid type	0.4 (howl) to 0.7 (howl)	Audiometry: Sills et al., 2015— $n = 1$; excluded Sills et al., 2015 (individual "Natchek") Anatomical models: No data Acoustic: Sipilä et al., 1996; Rautio et al., 2009
<i>Pusa sibirica</i> Baikal seal	--	Phocid type	--	Audiometry: No data Anatomical models: No data Acoustic: No data

¹Due to the primary role of behavioral audiometric data in determining the shape of the weighting function, only psychophysical studies meeting certain criteria were used to determine group-specific audiograms (see "Estimated Group Audiograms for Marine Mammals" section); citations for individuals were excluded if data for the same individual were reported elsewhere, if hearing loss was suspected, if audiograms appeared aberrant (e.g., obvious notches or flattened shape), or if masking or other environmental or procedural factors likely influenced reported data. While these data were excluded from the group audiograms, the excluded citations still provide useful information about the sounds that can be detected by a given species.

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Appendix 6. Other Marine Carnivores

There are four Carnivore families represented in the other marine carnivores in water (OCW) and other marine carnivores in air (OCA) weighting functions: Odobenidae (*Odobenus*), Otariidae (*Arctocephalus* spp., *Callorhinus*, *Eumetopias*, *Neophoca*, *Otaria*, *Phocarctos*, and *Zalophus* spp.), Ursidae (*Ursus*), and Mustelidae (*Enhydra* and *Lontra*). Species listings provided are consistent with those of the Society for Marine Mammalogy Committee on Taxonomy (2016). In this appendix, the sea lions, fur seals, walrus, marine otter, sea otter, and polar bear are considered with respect to available evidence from audiometric studies, anatomical descriptions, and analyses of emitted sounds to validate the grouping of these 18 species to the assigned weighting functions for acoustic exposure. Citations used to populate this appendix are generally from peer-reviewed papers published through 2016. Data are expressed as frequency ranges for each species where possible and are considered separately for water (Table 1) and air (Table 2) as these species are amphibious.

Audiometry data from behavioral (BEH) and neurophysiological (auditory evoked potential [AEP]) studies are shown separately here as the +60 dB frequency bandwidth from best measured sensitivity; sample sizes (number of different individuals [*n*]) are provided with the references. BEH data are available for five species in water and six species in air. Note that only BEH hearing studies meeting specific criteria are shown in the table; excluded studies are identified.¹ AEP measures are available for three species in air and unavailable for any species in water. Note that all

AEP studies reporting frequency-specific thresholds are included.

With respect to anatomy, the mammalian middle ear type for the species included in this group is the *freely mobile ear type* (Fleischer, 1978; Nummela, 2008), which features a loose connection between the ossicles and the skull. Species in this group have essentially terrestrial, broad-bore external ear canals, relatively small tympanic membranes, and moderate to distinctive pinnae; inner ear structures appear similar to terrestrial high-frequency generalists (Repenning, 1972; Wartzok & Ketten, 1999). The single exception in terms of anatomy is the walrus, which has an ear that is somewhat intermediate to a freely mobile ear type and a *phocid middle ear type* characterized by an enlarged tympanic membrane, ossicles, and middle ear cavity, and which lacks an external pinna (Repenning, 1972; Nummela, 2008). For example, while the walrus has enlarged ossicles and a large tympanic membrane, and lacks a pinna (like phocid seals), the shape and form of the ossicles and other morphological features are distinctively otariid in form (Repenning, 1972). Anatomy-based predictions of hearing range are presently unavailable for any species classified as other marine carnivores.

Underwater **sound production data** are available for six of 18 species; in-air sound production data are available for 16 of 18 species. Frequency ranges for sound production are provided as the broadest range of frequencies reported across all available studies for each species and in each medium, and they are referenced to call types at the extremes of this range.

Appendix 6, Table 1. Weighting function: Other marine carnivores in water (OCW)

Taxon	Audiometry	Ear type	Sound production	References
<i>Odobenus rosmarus</i> Walrus	BEH: < 0.125 to > 1.5 kHz	Intermediate to freely mobile and phocid type	0.2 (rasp) to 20 kHz (knock)	Audiometry: BEH: Kastelein et al., 2002 — $n = 1$ Anatomical models: No data Acoustic: Schevill et al., 1966; Ray, 1975; Stirling et al., 1983; Schusterman & Reichmuth, 2008
<i>Arctocephalus australis</i> South American fur seal Peruvian fur seal	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Arctocephalus forsteri</i> New Zealand fur seal	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Arctocephalus galapagensis</i> Galapagos fur seal	--	Freely mobile	0.1 (growl) to 2 kHz (snap/ knock)	Audiometry: No data Anatomical models: No data Acoustic: Merlen, 2000
<i>Arctocephalus gazella</i> Antarctic fur seal	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Arctocephalus philippii</i> Juan Fernandez fur seal Guadalupe fur seal	--	Freely mobile	0.12 to 0.2 kHz (LF pulses)	Audiometry: No data Anatomical models: No data Acoustic: Norris & Watkins, 1971
<i>Arctocephalus pusillus</i> Cape fur seal Australian fur seal	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Arctocephalus tropicalis</i> Subantarctic fur seal	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Callorhinus ursinus</i> Northern fur seal	BEH: < 0.5 to 41.1 kHz	Freely mobile	0.1 (click) to 4.5 kHz (click)	Audiometry: BEH: Moore & Schusterman, 1987; Babushina et al., 1991 — $n = 3$ Anatomical models: No data Acoustic: Poulter, 1968
<i>Eumetopias jubatus</i> Steller sea lion	BEH: < 0.5 to > 32 kHz	Freely mobile	0.5 to 2 kHz (belch)	Audiometry: BEH: Kastelein et al., 2005 — $n = 2$ Anatomical models: No data Acoustic: Poulter, 1968; Schusterman et al., 1970
<i>Neophoca cinerea</i> Australian sea lion	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data

<i>Otaria byronia</i> (<i>Otaria flavescens</i>) South American sea lion	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Phocarcus hookeri</i> Hooker's sea lion New Zealand sea lion	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Zalophus californianus</i> California sea lion	BEH: <0.1 to 55 kHz	Freely mobile	<0.08 (sweep) to 8 kHz (bark, bang)	Audiometry: BEH: Mulsow et al., 2012; Reichmuth & Southall, 2012; Reichmuth et al., 2013; Cunningham & Reichmuth, 2016— $n = 4$; excluded Schusterman et al., 1972; Kastak & Schusterman, 1998, 2002 Anatomical models: No data Acoustic: Schevill et al., 1963; Schusterman & Feinstein, 1965; Brauer et al., 1966; Schusterman et al., 1967; Poulter, 1968; Schusterman & Balliet, 1969
<i>Zalophus wolfebaeki</i> Galapagos sea lion	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Ursus maritimus</i> Polar bear	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Enhydra lutris</i> Sea otter	BEH: <0.125 to 36 kHz	Freely mobile	--	Audiometry: BEH: Ghoul & Reichmuth, 2014— $n = 1$ Anatomical models: No data Acoustic: No data
<i>Lontra felina</i> Marine otter	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data

Appendix 6, Table 2. Weighting function: Other marine carnivores in air (OCA)

Taxon	Audiometry	Ear type	Sound production	References
<i>Odobenus rosmarus</i> Walrus	--	Intermediate to freely mobile and phocid type	0.01 (guttural sounds) to 17 kHz (burr)	Audiometry: BEH: excluded Kastelein et al., 1993, 1996 Anatomical models: No data Acoustic: Miller & Boness, 1983; Miller, 1985; Kastelein et al., 1995; Verboom & Kastelein, 1995; Schusterman, 2008; Schusterman & Reichmuth, 2008; Charrier et al., 2010, 2011
<i>Arctocephalus australis</i> South American fur seal Peruvian fur seal	--	Freely mobile	0.4 (pup call) to 7 kHz (male threat)	Audiometry: No data Anatomical models: No data Acoustic: Trillmich & Majluf, 1981; Phillips & Stirling, 2000
<i>Arctocephalus forsteri</i> New Zealand fur seal	--	Freely mobile	0.1 (female pup attraction call) to 8 kHz (male bark)	Audiometry: No data Anatomical models: No data Acoustic: Page et al., 2001, 2002a, 2002b
<i>Arctocephalus galapagoensis</i> Galapagos fur seal	--	Freely mobile	0.2 (pup call) to 6 kHz (pup call)	Audiometry: No data Anatomical models: No data Acoustic: Trillmich, 1981
<i>Arctocephalus gazella</i> Antarctic fur seal	--	Freely mobile	0.1 (male guttural threat) to 9 kHz (pup call)	Audiometry: No data Anatomical models: No data Acoustic: Stirling, 1971; Page et al., 2001, 2002a, 2002b; St Clair Hill et al., 2001
<i>Arctocephalus philippii</i> Juan Fernandez fur seal Guadalupe fur seal	--	Freely mobile	0.5 (roar) to 7 kHz (roar)	Audiometry: No data Anatomical models: No data Acoustic: Peterson et al., 1968
<i>Arctocephalus pusillus</i> Cape fur seal Australian fur seal	--	Freely mobile	0.08 (male guttural threat) to 5.5 kHz (female pup attraction call)	Audiometry: No data Anatomical models: No data Acoustic: Stirling, 1971; Tripovich et al., 2005, 2006, 2008a, 2008b, 2009
<i>Arctocephalus tropicalis</i> Subantarctic fur seal	--	Freely mobile	0.1 (male bark) to 8 kHz (pup call)	Audiometry: No data Anatomical models: No data Acoustic: Page et al., 2001, 2002a, 2002b; St Clair Hill et al., 2001; Charrier et al., 2002, 2003a, 2003b, 2003c; Mathevon et al., 2004
<i>Callorhinus ursinus</i> Northern fur seal	BEH: 0.1 to > 32 kHz	Freely mobile	0.1 (pup call) to 8 kHz (pup call)	Audiometry: BEH: Moore & Schusterman, 1987; Babushina et al., 1991 — $n = 3$ Anatomical models: No data Acoustic: Poulter, 1968; Lisitsyna, 1973; Takemura et al., 1983; Insley, 1992, 2001

<i>Eumetopias jubatus</i> Steller sea lion	BEH: < 0.125 to 32 kHz AEP: < 1 to 30 kHz	Freely mobile	0.03 (female call) to 4 kHz (male wheedling call)	Audiometry: BEH: Mulsow & Reichmuth, 2010 — $n = 1$; AEP: Mulsow & Reichmuth, 2010; Mulsow et al., 2011b — $n = 5$ Anatomical models: No data Acoustic: Poulter, 1968; Campbell et al., 2002; Park et al., 2006
<i>Neophoca cinerea</i> Australian sea lion	--	Freely mobile	0.2 (female call) to 10 kHz (male bark)	Audiometry: No data Anatomical models: No data Acoustic: Charrier & Harcourt, 2006; Gwilliam et al., 2008; Picher et al., 2009; Ahonen et al., 2014
<i>Otaria byronia</i> (<i>Otaria flavescens</i>) South American sea lion	--	Freely mobile	0.2 (male growl) to 6 kHz (pup call)	Audiometry: No data Anatomical models: No data Acoustic: Fernández-Juricic et al., 1999; Trimble & Charrier, 2011
<i>Phocartos hookeri</i> Hooker's sea lion New Zealand sea lion	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data
<i>Zalophus californianus</i> California sea lion	BEH: 0.13 to 37 kHz AEP: < 2 to 30 kHz	Freely mobile	0.1 (male/female bark) to 16 kHz (male/female bark)	Audiometry: BEH: Moore & Schusterman, 1987; Mulsow et al., 2011a; Reichmuth et al., 2013 — $n = 4$; excluded Schusterman, 1974; Moore & Schusterman, 1987; Kastak & Schusterman, 1998; see also recent paper from Reichmuth et al., 2017; AEP: Finneran et al., 2011; Mulsow et al., 2011a, 2011b, 2014 — $n = 23$ Anatomical models: No data Acoustic: Schusterman & Feinstein, 1965; Brauer et al., 1966; Schusterman, 1978; Schusterman et al., 1992
<i>Zalophus wollebaeki</i> Galapagos sea lion	--	Freely mobile	0.3 (female call) to 4 kHz (female call)	Audiometry: No data Anatomical models: No data Acoustic: Trillmich, 1981
<i>Ursus maritimus</i> Polar bear	BEH: < 0.25 to 29 kHz AEP: < 1.4 to > 22.5 kHz	Freely mobile	0.28 to 0.85 kHz (humming)	Audiometry: BEH: Owen & Bowles, 2011 — $n = 2$; AEP: Nachtigall et al., 2007 — $n = 3$ Anatomical models: No data Acoustic: Derocher et al., 2010
<i>Enhydra lutris</i> Sea otter	BEH: 0.23 to 38.2 kHz	Freely mobile	0.3 (coco) to 60 kHz (scream)	Audiometry: BEH: Ghoul & Reichmuth, 2014 — $n = 1$ Anatomical models: No data Acoustic: Sandegren et al., 1973; McShane et al., 1995; Ghoul & Reichmuth, 2012
<i>Lontra felina</i> Marine otter	--	Freely mobile	--	Audiometry: No data Anatomical models: No data Acoustic: No data

¹Due to the primary role of behavioral audiometric data in determining the shape of the weighting function, only psychophysical studies meeting certain criteria were used to determine group-specific audiograms (see "Estimated Group Audiograms for Marine Mammals" section); citations for individuals were excluded if data for the same individual were reported elsewhere, if hearing loss was suspected, if audiograms appeared aberrant (e.g., obvious notches or flattened shape), or if masking or other environmental or procedural factors likely influenced reported data. While these data were excluded from the group audiograms, the excluded citations still provide useful information about the sounds that can be detected by a given species.

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Errata

Marine Mammal Noise Exposure Criteria: Updated Scientific Recommendations for Residual Hearing Effects

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On page 131, Kastelein (2013) was incorrectly identified as a new study of TTS from impulsive noise when it should have been listed as a new study of TTS from non-impulsive noise in the preceding paragraph.

There is a typographical error in Table 5 on page 149. What is indicated as parameter “B” should be parameter “b,” which is consistent with “b” in Eq.(2) W(f) on page 146.

There are four typographical errors in Table 7 on page 156. The corrected table is provided on the following page:

- For PCA, the value in column “TTS onset: Peak SPL” should be 155 (rather than 138) and the value in column “PTS onset: Peak SPL” should be 161 (rather than 144).
- For OCA the value in column “TTS onset: Peak SPL” should be 170 (rather than 161) and the value in column “PTS onset: Peak SPL” should be 176 (rather than 167).

Data for the blue whale (*Balaenoptera musculus*) was inadvertently omitted from Appendix 1, Table 1 during publication. The corrected table for “Low-Frequency Cetaceans” is provided herein with the blue whale data included. All the references associated with the blue whale that are referred to in this table were provided within the appendix as it was published.

We apologize for the errors.

Table 7. TTS- and PTS-onset thresholds for marine mammals exposed to impulsive noise: SEL thresholds in dB re 1 $\mu\text{Pa}^2\text{s}$ under water and dB re (20 μPa)²s in air (groups PCA and OCA only); and peak SPL thresholds in dB re 1 μPa under water and dB re 20 μPa in air (groups PCA and OCA only).

Marine mammal hearing group	TTS onset: SEL (weighted)	TTS onset: Peak SPL (unweighted)	PTS onset: SEL (weighted)	PTS onset: Peak SPL (unweighted)
LF	168	213	183	219
HF	170	224	185	230
VHF	140	196	155	202
SI	175	220	190	226
PCW	170	212	185	218
OCW	188	226	203	232
PCA	123	155	138	161
OCA	146	170	161	176

Appendix 1, Table 1. Weighting functions: Low-frequency (LF) cetaceans

Taxon	Ear type	Auditory modeling	Sound production	References
<i>Balaena mysticetus</i> Bowhead whale	Mysticete middle ear, Type M cochlea	0.6 ^b to 32 ^b kHz	0.02 (moan) to 6 kHz (warble)	Audiometry: No data Anatomical modeling: Ketten, 1994 ^b ; Ketten et al., 2014 ^a Acoustic: Ljungblad et al., 1980, 1982; Clark & Johnson, 1984; Cummings & Holliday, 1987; Würsig & Clark, 1993; Blackwell et al., 2007; Stafford et al., 2008; Delarue et al., 2009; Tervo et al., 2009, 2011, 2012
<i>Eubalaena australis</i> Southern right whale	Mysticete middle ear	--	0.02 (pulse) to 2.2 kHz (pulse, belch)	Audiometry: No data Anatomical modeling: No data Acoustic: Cummings et al., 1971, 1972, 1974; Payne & Payne, 1971; Saayman & Taylor, 1973; Clark, 1982; Parks et al., 2007a
<i>Eubalaena glacialis</i> North Atlantic right whale	Mysticete middle ear, Type M cochlea	0.016 ^{a,b} to 25 ^b kHz	0.02 to 22 kHz (gunshot)	Audiometry: No data Anatomical modeling: Ketten, 1994 ^b ; Parks et al., 2007b ^c ; Ketten et al., 2014 ^a Acoustic: Matthews et al., 2001; McDonald & Moore, 2002; Vanderlaan et al., 2003; Parks & Tyack, 2005; Parks et al., 2007a; Trygonis et al., 2013
<i>Eubalaena japonica</i> North Pacific right whale	Mysticete middle ear	--	0.07 to 0.2 kHz (up calls) ¹	Audiometry: No data Anatomical modeling: No data Acoustic: McDonald & Moore, 2002; Mellinger et al., 2004; Munger et al., 2008, 2011
<i>Balaenoptera acutorostrata</i> Common minke whale	Mysticete middle ear, Type M cochlea	0.010 ^{a,f} to 34 ^f kHz	0.09 to 9 kHz (star wars, boing)	Audiometry: No data Anatomical modeling: Tubelli et al., 2012 ^d , 2012b ^f ; Ketten et al., 2014 ^{a,c} Acoustic: Beamish & Mitchell, 1973; Edds-Walton, 2000; Mellinger et al., 2000; Gedamke et al., 2001; Rankin & Barlow, 2005; Oswald et al., 2011; Risch et al., 2014a
<i>Balaenoptera bonaerensis</i> Antarctic minke whale	Mysticete middle ear	--	0.05 (downsweep, bio-duck) to 1 kHz (bio-duck)	Audiometry: No data Anatomical modeling: No data Acoustic: Schevill & Watkins, 1972; Risch et al., 2014b
<i>Balaenoptera borealis</i> Sei whale	Mysticete middle ear	--	0.02 (LF sweep) to 4 kHz (FM sweep)	Audiometry: No data Anatomical modeling: No data Acoustic: Knowlton et al., 1991; Rankin & Barlow, 2007; Baumgartner et al., 2008; Calderan et al., 2014; Romagosa et al., 2015
<i>Balaenoptera edeni</i> Bryde's whale	Mysticete middle ear	--	0.1 (LF tonal) to 0.9 kHz (pulsed moan)	Audiometry: No data Anatomical modeling: No data Acoustic: Edds et al., 1993; Oleson et al., 2003; Heimlich et al., 2005; Figueiredo, 2014; Rice et al., 2014; Sirović et al., 2014; Vitoria-Gómora et al., 2015

<i>Balaenoptera musculus</i> Blue whale	Mysticete middle ear, Type M cochlea	0.012 ^a to 15 ^b kHz	0.01 (B call) to 0.4 kHz (pulse, HFS) ²	Audiometry: No data Anatomical modeling: Ketten, 1994 ³ ; Ketten et al., 2014 ⁴ Acoustic: Cummings & Thompson, 1971; Edds, 1982; McDonald et al., 1995b; Thompson et al., 1996; Rivers, 1997; Stafford et al., 1998, 2001; Thode et al., 2000; Mellinger & Clark, 2003; Berchok et al., 2006; Oleson et al., 2007; Buchan et al., 2010; Frank & Ferris, 2011
<i>Balaenoptera omurai</i> Omura's whale	Mysticete middle ear	--	0.01 to 0.05 kHz (AM call)	Audiometry: No data Anatomical modeling: No data Acoustic: Cerchio et al., 2015
<i>Balaenoptera physalus</i> Fin whale	Mysticete middle ear, Type M cochlea	0.02 ^c to 20 ^c kHz	0.01 (rumble, thud, 20-Hz signal) to 1 kHz (slam)	Audiometry: No data Anatomical modeling: Cranford & Krysl, 2015 Acoustic: Watkins et al., 1987; Edds, 1988; Thompson et al., 1992; McDonald et al., 1995a; Charif et al., 2002; Širović et al., 2007, 2013; Weirathmueller et al., 2013
<i>Megaptera novaeangliae</i> Humpback whale	Mysticete middle ear	0.018 ^a to 15 ^b kHz	0.02 (moan, grunt, creak, pulse train) to 24 kHz (mid-frequency tonal wail)	Audiometry: No data Anatomical modeling: Ketten, 1994 ³ ; Ketten et al., 2014 ⁴ Acoustic: Hafner et al., 1979; Payne & Payne, 1985; Thompson et al., 1986; Simão & Moreira, 2005; Au et al., 2006; Dunlop et al., 2007; Stumpert et al., 2007, 2011; Zoidis et al., 2008
<i>Caperea marginata</i> Pygmy right whale	Mysticete middle ear	--	0.06 to 0.1 kHz (thump)	Audiometry: No data Anatomical modeling: No data Acoustic: Dawbin & Cato, 1992
<i>Eschrichtius robustus</i> Gray whale	Mysticete middle ear	--	0.01 (moan) to 20 kHz (clack)	Audiometry: No data Anatomical modeling: No data Acoustic: Cummings et al., 1968; Poulter, 1968; Fish et al., 1974; Norris et al., 1977; Crane & Lashkari, 1996; Stafford et al., 2007; Dahlheim & Castellote, 2016

¹See Beamish & Mitchell (1971) for suggestion of clicks extending to 31 kHz.

²Note that Crance et al. (2017) recently added gunshot calls to the species' repertoire. While not reporting frequency range, their figures show that these gunshots have energy exceeding 2 kHz and are consistent with data from the North Atlantic and southern right whale showing that at close range, these gunshots are broadband-pulsed calls with energy extending to substantially higher frequencies.