Direct Hearing Measurements in a Small Mysticete Whale, The Common Minke (*Balaenoptera acutorostrata*)

Dorian S. Houser, Petter H. Kvadsheim, Lars Kleivane, Jason Mulsow,
Rolf A. Ølberg, Craig A. Harms, Jonas Teilmann,
and James J. Finneran

Contents

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D. S. Houser (✉)
Department of Conservation Biology, National Marine Mammal Foundation, San Diego, CA, USA
e-mail: dorian.houser@nmmf.org

P. H. Kvadsheim
Sensor and Surveillance Systems, Norwegian Defence Research Establishment (FFI), Horten, Norway
e-mail: Petter-Helgevold.Kvadsheim@ffi.no

L. Kleivane
LKARTS-Norway, Skutvik, Norway
e-mail: lkarts@lkarts.no

J. Mulsow · J. J. Finneran
US Navy Marine Mammal Program, Naval Information Warfare Center Pacific, San Diego, CA, USA
e-mail: jason.l.mulsow.civ@us.navy.mil; james.j.finneran.civ@us.navy.mil

R. A. Ølberg
Kristiansand Dyrepark, Kardemomme By, Norway
e-mail: rolfarne@dyreparken.no

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Abstract

The hearing abilities of baleen whales have long been a mystery that has in recent decades impeded understanding of how anthropogenic noise might affect them. Because of their large size and difficulty maintaining them under human care, the use of behavioral audiometry to test their hearing has been impractical. Knowledge of baleen whale hearing has historically been inferred from the frequency range of their vocalizations, although this is known to be a poor predictor of the full range of hearing in mammals and provides no information on hearing thresholds. Additional information on sound sensitivity in baleen whales has been obtained through behavioral response studies, anatomical modelling, and most recently, the use of electrophysiological methods. Collectively, these approaches demonstrated or predicted that baleen whale hearing ranges exceed the range of vocalization frequencies, which is a common feature of mammalian hearing. Within the last 2 years, a modified behavioral observation audiometry study with free-ranging humpback whales and an electrophysiological study with temporarily held common minke whales suggest higher-frequency sensitivity than previously predicted. These approaches provide information on sound sensitivity, and the approaches may potentially be combined to permit a baleen whale audiogram to be obtained.

Keywords

Anthropogenic noise · Baleen whale · Auditory evoked potential · Behavioral response · Anatomical modelling

Introduction

Baleen whales, or mysticetes, include the largest mammals in the world. These fully aquatic mammals are globally distributed across polar, temperate, and tropical waters and many engage in long-distance migrations on the order of thousands of kilometers. The mass of species within the four baleen whale families (*Balaenidae, Balaenopteridae, Neobalaenidae,* and *Eschrictiidae*) ranges from ~1000 kg to over 100,000 kg, and prey varies significantly across species, from planktonic krill, to benthic amphipods, to fish such as sardines, mackerel, and herring. All baleen whales are known to produce sound, although not all species, such as the pygmy right whale (*Caperea marginata*), are well-studied. With respect to the frequency range, duration and complexity of baleen whale calls, the vocal repertoire observed

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C. A. Harms
College of Veterinary Medicine, North Carolina State University, Morehead City, NC, USA
e-mail: caharms@ncsu.edu

J. Teilmann
Department of Ecoscience, Marine Mammal Research, Aarhus University, Roskilde, Denmark
e-mail: jte@ecos.au.dk

across species is as diverse as the mass of the animals and the types of prey they feed upon. For example, the humpback whale (*Megaptera novaeangliae*) produces complex songs that vary regionally and that can change over time, whereas minke whales (*Balaenoptera acutorostrata*) in the North Pacific produce short (~100–300 ms), stereotypical sound bursts, called "boings" (Erbe et al. 2025b). In addition, many whales make non-vocal sounds (e.g., breaching, tail slaps). It is assumed that both vocal and non-vocal signals support communication.

Baleen whale vocalization frequencies overlap with the frequencies of many anthropogenic sound sources, including seismic exploration, sonar systems, and shipping (Erbe et al. 2025b). Historically, the overlap in frequencies prompted concern about the potential for anthropogenic noise to interfere with whale communication signals, although the impact of anthropogenic noise exposure has grown to include the disruption of other biologically important behaviors (e.g., feeding) and the potential to impact hearing directly (e.g., noise-induced reductions in hearing sensitivity). Unfortunately, little is known about baleen whale hearing, either with respect to the frequency range of hearing or hearing sensitivity, and it is therefore difficult to estimate the potential for anthropogenic noise to affect acoustic communication, disrupt behaviors, or impair auditory physiology.

Many smaller marine mammals, including odontocetes, pinnipeds, and sea otters have had their hearing tested through behavioral audiometry (Houser 2025). In contrast, hearing has not been directly studied using classical behavioral audiometry approaches in baleen whales for practical reasons—they are large and difficult to capture, and they are extremely difficult (if not impossible) to maintain under human care for the duration needed to perform a behavioral hearing test. The few historical efforts that attempted to catch baleen whales for keeping at aquaria ended poorly for the whales, even if the catch effort was deemed "successful" (Vinje 2022). Given the difficulty in gaining access to baleen whales for hearing tests, other options for studying aspects of baleen whale hearing have been pursued. Over the last ~30+ years, the study of baleen whale hearing has been approached in several ways: (1) through assessment of the frequency of vocalizations; (2) through behavioral responses to sound exposures; (3) through mathematical models based upon auditory anatomy; and (4) through electrophysiological testing. Each of these approaches has provided insight into baleen whale hearing, but each also has its own limitations.

Methods of Studying Baleen Whale Hearing

Extrapolation from Vocalization Frequencies

It is generally accepted that mammals hear at frequencies at which they produce vocalizations since communication signals, receptor systems, and the coordinated behavior resulting from the interaction of the signaler and receiver are functionally related and influence the evolution of one another, a process called "sensory drive" (Endler 1993). Since vocalizations are often associated with social and breeding activities, it is generally assumed that vocalization frequencies overlap with the range of hearing. However, empirically measured hearing ranges typically extend above and below the frequencies at which a species vocalizes, indicating that the use of vocalization frequencies for predicting the frequency range of hearing are probably limited to a smaller frequency band within the total hearing range. Additionally, no information about hearing sensitivity can be derived from the source level of vocalizations without an understanding of the responsiveness of intended receivers and the level of sound they receive (see section "Behavioral Responses to Sound," below).

Table 1 provides the frequency range of the dominant frequency band of various call types produced by mysticetes, mainly tones, pulses (single stereotypical sound type), pulse trains, noisy narrowband signals, impulses, and clicks. It can reasonably be assumed that these species are capable of hearing within these reported frequency ranges. However, some signals have harmonics at much higher frequencies (e.g., "gunshots" in right whales). It is possible that these harmonics include both audible and inaudible frequencies, depending on the upper-frequency limit of hearing of the species. For some of the species listed, a limited number of recordings likely underrepresent the full breadth of vocalization frequencies (e.g., southern minke whale). Additionally, it should be noted that in some cases vocalization recordings could not be attributed to a sighted whale, but were rather assumed because of the presence of the species in the area at the time of the recording.

Table 1 Reported vocalization frequency ranges for some mysticete whales. Vocalization ranges are mean minimum of all reported lower frequencies and mean maximum of all reported higher frequencies in the dominant frequency band of the collective call types, as derived from Table 3.1 in Erbe et al. (2025b)

Scientific name	Common name	Vocalization frequency range (Hz)
Balaenoptera musculus	Blue whale	19–158
Balaena mysticetus	Bowhead whale	288–2031
Balaenoptera acutorostrata	Common minke whale	50–9400
Balaenoptera borealis	Sei whale	30–273
Balaenoptera brydei/edeni	Bryde's whale	67–701
Balaenoptera musculus brevicauda	Pygmy blue whale	10–750
Balaenoptera physalus	Fin whale	18–62
Balaenoptera bonaerensis	Southern minke whale	79–201
Caperea marginata	Pygmy right whale	60–135
Eschrichtius robustus	Gray whale	114–6000
Eubalaena australis	Southern right whale	61–3042
Eubalaena glacialis	North Atlantic right whale	52–8132
Eubalaena japonica	North Pacific right whale	50–5500
Megaptera novaeangliae	Humpback whale	80–2156

Behavioral Responses to Sound

Determining whether an animal can hear a sound can be assessed by exposing it to the sound and observing whether a behavioral reaction occurs. This approach assumes that there are no other factors during the sound exposure that might also inhibit or produce a behavioral reaction (e.g., the presence of humans). The method can inform the frequency range of hearing, but it has drawbacks. For example, an animal may not respond to a sound, even if it hears it. This could be due to the animal's motivational state, prior experience with the sound, whether it has a risk-averse or risk-tolerant personality, the age of the animal, etc. For similar reasons, the approach cannot reliably determine the threshold of audibility for an individual because the animal might not be responsive until some critical level of audibility is reached, i.e., even if the animal can hear the sound, it might only respond if the sound exceeds a certain received level.

Numerous behavioral response studies and observations of baleen whale responses to sound from conspecifics and anthropogenic sources support hearing sensitivity at frequencies within the vocal range (Erbe et al. 2025a). However, responses to incidental and intentional anthropogenic sound exposures have demonstrated that at least some mysticetes likely hear at frequencies above their vocal frequency range. For example, blue, minke, and humpback whales, have all been shown to respond to anthropogenic sounds at frequencies higher than those at which they vocalize (Erbe et al. 2025a). Such observations give credence to anatomical models that suggest high-frequency hearing in some species (see below). Unfortunately, few behavioral response studies have been constructed for the purpose of estimating the frequency range of hearing and thresholds of hearing sensitivity (see Houser 2025). Most behavioral response studies have been designed to address the concerns of agencies responsible for managing marine mammal stocks and regulating and/or mitigating potential impacts to marine mammals from anthropogenic noise exposure. These studies typically seek to determine response thresholds to a specific type of sound source (e.g., vessel, drilling, seismic survey, military sonar, acoustic deterrents), as well as determining how context affects the potential of a behavioral response. For example, they might address how the behavior state of the animal at the time of the exposure affects the response, or how the distance between the sound source and the whale affects the response given similar received levels of sound.

Recently, Dunlop et al. (this volume) modified behavioral observation audiometry methods to specifically address the hearing sensitivity and frequency range of hearing in humpback whales. The approach relied on exposing many animals to the same acoustic stimulus and controlling for context by testing whales during the migration and focusing on females and mother/calf pairs. The latter were assumed to be the most sensitive subjects with respect to responsiveness to novel sounds in their environment. By assessing the distribution of received levels at which responses to a particular frequency of sound exposure were observed, a minimum response level was obtained for that frequency. The study, conducted over multiple years, assessed behavioral responses to 1/3-octave frequency upsweeps beginning at 0.08, 0.25, 1, 4, 16, and 22 kHz. The results showed that humpback whales can hear at frequencies from as low as 0.08 kHz and up to at least 22 kHz. The signal to noise ratio (SNR) calculated at the minimum response level suggested masked hearing at frequencies where the animals were expected to hear, as well as potentially unmasked thresholds at frequencies at the upper and lower end of the frequency range of hearing. In addition, the SNRs at the minimum response level suggested that humpback whales probably have critical ratios similar to other marine mammals. The study further demonstrated how a field experiment can be designed to estimate hearing sensitivity within a population of wild animals and established an approach that might be applicable to other mysticete species.

Anatomical Predictions of Baleen Whale Hearing

A handful of efforts to model aspects of mysticete hearing based on anatomy and tissue properties of the auditory system have been made. These include the use of finite element modeling to predict the response of anatomical structures to acoustic excitation, and measurements of basilar membrane dimensions to estimate the frequency range of hearing. Collectively, these modeling efforts have provided anatomically based predictions of hearing that can be related to behavioral response studies. However, no direct validation of any model (e.g., comparison of model predictions to an empirical audiogram) has yet been made. The anatomical modeling efforts conducted to date are described below. Because there are relatively few efforts and they make specific predictions about the hearing range and sensitivity of baleen whales, the studies are discussed in more detail than publications related to behavioral responses and vocalization frequencies.

One method of predicting an audiogram can be accomplished by modeling of the outer, middle, and inner ear. Tubelli et al. (2012) modelled the middle ear component of the auditory pathway as a transfer function. The transfer function parameters were determined following a finite element model of computed tomographic data of a minke whale tympanoperiotic bulla. Material properties (bone and soft tissue elastic modulus) were determined either empirically or were derived from other studies. The model included assumptions about ossicular and tympanic bone density, damping, and boundary conditions reflective of constraints on ossicular chain motion. The resultant middle-ear transfer function predicted variations in hearing sensitivity as a function of the location of the acoustic input to the ear. The “best hearing range” was defined as the frequency response within −40 dB of the peak transfer function magnitude. Mechanical (acoustic) stimulation at the “glove finger,” which is homologous to the tympanic membrane in terrestrial mammals, resulted in best hearing sensitivity predictions from 30 Hz to 7.5 kHz. Stimulation of the tympanic bone suggested best hearing sensitivity ranged from 100 Hz to 25 kHz. Although an audiogram could not be predicted from the model (as it lacked other component representation, e.g., the inner ear), the predicted range of sensitivity did overlap with observed vocalization frequencies of this species.

Although not published in the peer-reviewed literature, Ketten (2012) used cochlear morphology and ratios of the basilar membrane thickness to width (T/W) to predict the frequency range of hearing in the minke. The T/W measurements correspond to inner ear resonances and can thus be used as predictors of hearing bandwidth in a healthy ear. Based on the assessment of multiple minke ears, the team predicted that minke whales had a potential hearing range of 18 Hz–32 kHz, but with a likely functional range of 25 Hz–24 kHz. The latter prediction was similar to the predictions of Tubelli et al. (2012) with their model of tympanic bone stimulation (100 Hz–25 kHz).

Tubelli et al. (2018) later performed a similar finite element modeling effort to predict a middle ear transfer function for the humpback whale. As with the minke, the predicted range of hearing sensitivity varied as a function of the anatomical location where primary mechanical stimulation occurred. Mechanical stimulation at the "glove finger" resulted in best hearing range predictions from 15 Hz to 3 kHz, whereas stimulation of the tympanic bone suggested a best hearing range from 200 Hz to 9 kHz. Again, the predictions overlapped observed vocalization frequencies of the humpback whale, but the authors acknowledged considerable limitations in the model due to unknowns about other tissue properties (e.g., waxes, lipids), the primary mode by which acoustic energy is transferred to the inner ear (ossicular chain motion vs. bone conduction), and the impact of post-mortem handling on tissue properties.

Prior to the work of Tubelli et al. (2018), Houser et al. (2001) predicted the hearing range of the humpback whale based upon a frequency-place map of the basilar membrane. To predict relative sensitivity across the bandwidth of hearing, they assumed that the dynamic range of hearing sensitivity was distributed in a manner similar to that observed across the bandwidth of hearing in cats and humans. The model output predicted that humpback whales would have most sensitive hearing from 700 Hz to 10 kHz, and a full range of hearing from ~100 Hz to 18 kHz. No prediction of absolute sensitivity was made utilizing this method.

Parks et al. (2007) estimated the frequency range of hearing for the North Atlantic right whale (*Eubalaena glacialis*) using measurements of basilar membrane T/W, pitch, and turn ratio, similar to work conducted by Ketten for the minke whale (see above). Using a previously developed anatomical model for cetaceans, and incorporating data from 18 ears and 13 different whales, the researchers estimated that North Atlantic right whale functional hearing ranged from 10 Hz to 22 kHz.

Cranford and Krysl (2015) applied finite element modeling to computed tomography data to predict an audiogram for the fin whale (*Balaenoptera physalus*). The approach supposed both a bone conduction and a pressure mechanism analogous to the sound conduction pathway of delphinids. Cranford and Krysl proposed that the mechanism of sound conduction would affect the velocity at the stapes footplate and that the stapes-velocity transfer function could be used to predict an audiogram based on the bone conduction mechanism, the pressure mechanism, and the combination of the two mechanisms. An audiogram was predicted from the combined effects of the pressure and bone conduction mechanisms and suggested a hearing bandwidth of ~10 Hz to 20 kHz, like that predicted for the North Atlantic right whale. Thresholds were referenced to a minimum threshold of 70 dB re 1 μPa based on hearing threshold data from a bottlenose dolphin (*Tursiops truncatus*) and two killer whales (*Orcinus orca*), as no inner ear component was included in the model. The model predicted an audiogram with a jagged shape that is atypical of audiograms for mammals obtained to date.

The anatomical model predictions of hearing range in fin, humpback, and right whales are relatively consistent. They include the frequencies where the whales vocalize, but predict sensitivity to frequencies higher than the fundamental frequencies of their calls. This prediction is consistent with those seen in other mammals in which the hearing range is substantially broader than vocal frequency range. Nevertheless, the predicted frequency range for the humpback, particularly the upper frequency limit of hearing, might be underestimated from anatomical models given recent results using modified behavioral observation audiometry approaches (Dunlop et al., this volume). Similarly, anatomical model estimates of the frequency range of hearing in the common minke might also underestimate the upper frequency limit of hearing given recent results of electrophysiological hearing tests conducted in that species.

Electrophysiological Hearing Tests

Behavioral audiometry, which does not include behavioral observation audiometry, is the “gold standard” for measuring hearing sensitivity and hearing range because it represents an integrated animal response (i.e., from sensory reception to perception) under tightly controlled experimental conditions. Classical behavioral audiometry tests have not been performed on any baleen whale due to the previously mentioned challenges of holding and maintaining such large animals for training. An alternative approach is the use of auditory evoked potentials (AEPs) to test hearing, which is an approach that measures voltages produced by the auditory system in response to an animal hearing a sound. This approach is also limited by access to baleen whale subjects and few efforts have been made to apply it. The first attempt to measure AEPs in a baleen whale was made on a juvenile grey whale that underwent rehabilitation at SeaWorld of San Diego (USA) after stranding (Ridgway and Carder 2001). Little detail was provided by the authors about the procedure, but tone pips (short tone bursts) and clicks (broadband transients) were both used as acoustic stimuli. The authors had difficulty replicating measured evoked responses to various tone-pip frequencies, but suggested that the limited data obtained indicated the whale might have been more sensitive to 3, 6, and 9 kHz than at higher and lower frequencies.

A recent effort caught and restrained adolescent common minke whales for the purpose of performing AEP tests (Kleivane et al. 2024). At less than 5 m length and with a mass less than 1000 kg, the small size of the adolescent minke whales made them more amenable to catching and increased the likelihood that AEP testing would succeed; i.e., the approach becomes less effective as the brain to body mass ratio decreases, suggesting the method will have limited utility in the largest whale species. The whales were temporarily caught in a large trap built along the Norwegian coastline that consisted of both barrier and guide nets (Kleivane et al. 2024). The guide nets directed the whale into a basin between two small islands; one end of the basin was blocked off with a barrier net, while the entry to the basin had a net drawn across it to contain the whale. Once contained, the whale was corralled into a modified aquaculture farm and the nets of the farm were drawn up to strand the whale in a net hammock. AEP tests were conducted with the whale in the hammock, and the whales were released following the tests.

Initial tests with the first two whales caught focused on determining optimal acoustic stimuli for AEP tests in this species, and an assessment of the upper frequency limit of hearing (Houser et al. 2024). Chirps, which are short-duration frequency up-sweeps meant to compensate for temporal dispersion along the cochlear partition, were found to better elicit an auditory brainstem response than were clicks. Suprathreshold (i.e., presumed clearly audible) tone pips of increasing frequency were subsequently used to estimate an upper frequency limit of hearing of 45 kHz or higher, suggesting some degree of ultrasonic sensitivity. The ultrasonic sensitivity was hypothesized to support detection of echolocation clicks from the minke's primary predator, the killer whale (Houser et al. 2024). In the last year of the study, two additional whales were tested with the goal of determining the thresholds of sensitivity (unpublished data). The collective data from the four whales confirmed an upper frequency limit of hearing near 45 kHz, possibly between 45 and 64 kHz, and a relatively flat region of sensitivity (thresholds within 10 dB of one another) that extended from 5.6 to 32 kHz.

The evoked response thresholds reported by Houser et al. (2024) are the first directly measured in a baleen whale, but it is important to note that AEP thresholds are not equivalent to behavioral hearing thresholds. For this reason, some correction factor will need to be applied to the thresholds to make them useful for interpreting in a biological or regulatory context. Additional opportunities for baselining the AEP thresholds could be achieved through behavioral observation audiometry studies designed like the recent study on humpback whales performed by Dunlop et al. (this volume). Provided sufficient numbers of individual minke whales were exposed to previously tested AEP frequencies, and a distribution of level-dependent behavioral responses could be obtained, a minimum response level could be determined. If the minimum response level were unmasked, it could be used to correct (or baseline) the AEP threshold obtained at the same frequency, thus providing an anchor for extrapolating to thresholds at other frequencies.

Summary

No direct measure of baleen whale hearing has yet been made using classical behavioral methods. However, a combination of approaches used over decades has shed light on the question of what baleen whales might hear. Historically, estimating hearing ranges based on vocalization frequencies provided only limited insight into mysticete hearing abilities. The implementation of behavioral response studies, anatomical model predictions, and AEP methods to assess baleen whale hearing (or aspects of auditory processing) have substantially advanced our understanding of the likely frequency range of hearing in a handful of species. Behavioral response studies have shown that many baleen whales will respond to frequencies that are higher than those covered by the range of dominant frequencies in their vocalizations. Anatomical models have predicted similar hearing ranges for several large mysticetes (humpback, fin, and North Atlantic right whale), with the highest upper frequency limit of hearing estimated for the smallest species modelled (common minke). In all cases, the anatomical model predictions exceed predictions based on vocalization frequencies. However, recent discoveries using modified behavioral observation audiometry studies and AEP methods suggest that the upper frequency limit of hearing for the minke and humpback whale are likely even higher than anatomical model predictions. The thresholds of hearing in baleen whales remain elusive. Creative modifications to behavioral response methods in combination with the continued application of AEP methods nevertheless have the potential to get estimates closer to behavioral hearing thresholds.

Cross-References

► Humpback Whale Frequency-Dependent Hearing Using Modified Behavioral Observation Audiometry

Competing Interest Declaration The author(s) has no competing interests to declare that are relevant to the content of this manuscript.

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