Assessing the hearing capabilities of mysticete whales

A proposed research strategy for the Joint Industry Programme on Sound and Marine Life

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Colleen Reichmuth, PhD
University of California Santa Cruz
Long Marine Laboratory
100 Shaffer Road
Santa Cruz, CA 95060

colleen.reichmuth@gmail.com

Summary

One of the most difficult problems faced by those charged with protecting animals from anthropogenic noise in marine environments is decision-making in the absence of essential information. The mysticetes, or baleen whales, are species of particular concern with respect to this issue for several reasons, including their dependence on sound for social communication, their global distribution, and their vulnerable conservation status following massive human exploitation over the past several centuries. Presently, there is an immediate need for reliable estimates of hearing sensitivity in mysticetes; however, scientists face numerous challenges in acquiring this information. A coordinated research strategy that identifies possible technical approaches to this problem, evaluates potential benefits and limitations of these approaches, prioritizes technology development and research efforts, and outlines funding and logistical requirements, is the vital first step towards addressing a topic of this scale and significance. This paper suggests such a research strategy for the Joint Industry Programme on Sound and Marine Life, whose interest and action with respect to this problem may significantly advance current understanding of whales and sound in the oceans.

Background

The mysticete whales belong to a suborder of the cetaceans; there are thirteen tentatively recognized species that are classified into four families (see Table 1). Of these living species, all but one have experienced extreme pressure from whaling activities, and about half remain in danger of extinction. All mysticetes are large (6 to 30 meters) and long-lived (40 to 100+ years), with slow attainment of sexual maturity and low fecundity, factors which impede their recovery from depletion. Furthermore, mysticete whales are extremely wide-ranging animals, and their presence and movements throughout the world's oceans make their protection a complicated international concern. As a consequence of their unique life-history and distribution patterns, whales are vulnerable to a variety of stressors that may be qualitatively, temporally, and geographically distributed. These stressors may act independently, cumulatively, or synergistically to negatively influence the health of individuals and populations (National Research Council, 2005).

A stressor of particular concern for mysticete whales is anthropogenic noise in marine habitats. While virtually nothing is known about the hearing of whales, it is a widely held belief that these animals depend on sound for their survival. All mysticetes are known to produce vocalizations in communicative contexts, and some of these sounds are detectable across hundreds and perhaps thousands of kilometers (e.g., Payne & Webb, 1971; Sears, 2002). Especially significant is the frequency bandwidth of whale sound emissions, which, while ranging from pulsed infrasonics (<30 Hz) to shrieks and clicks (>5 kHz), tend to have dominant frequencies below 200 Hz (Wartzok & Ketten, 1999). The intense, low-frequency sound emissions of mysticetes implies hearing sensitivity to similar frequency bandwidths, placing them into potential conflict with industry noise sources that also produce intense, sometimes pulsed, long-distance, low-frequency sounds. Like the sounds emitted by whales, these anthropogenic noises are transmitted efficiently through water and may radiate significant distances from their sources.

The known and potential effects of seismic exploration and other oil and gas production activities on whales and other marine mammals have been the subject of debate and study for at least 30 years (see review in Richardson et al., 1995), and concern surrounding this issue continues to grow as industry operations in marine environments expand and change. Exploration and production activities are now encroaching into deeper offshore waters, where noise sources are likely to be louder and where sounds propagate over greater distances. As a result, greater numbers of mysticetes may be exposed during foraging, breeding, and migration (see National Research Council, 2003). Anticipated future industry activities at higher latitudes will bring about increased acoustic interactions with whales in areas with little prior history of anthropogenic disturbance. Currently, mysticetes are protected by law in the exclusive economic zones of many of the countries through which they travel, as well as by international treaties (for review, see Scott, 2004). Industry presently faces national permitting requirements to regulate the incidental exposure of mysticetes to noise generated by exploration and production activities, and, as the issues surrounding the impact of anthropogenic noise on marine life gain increasing attention in the conservation community, it is likely that regulatory oversight over these activities will continue to expand.

In the absence of reliable information about mysticete hearing, regulators issue permits with uncertainty and caution. To resolve delays caused by uncertainty, regulators require quantitative information about mysticete hearing so that accurate zones of audibility, masking, and susceptibility to acoustic injury with respect to industry noise sources can be estimated. The aim of this report is to identify, evaluate, and prioritize research approaches capable of providing critically needed data to regulators charged with protecting whales from anthropogenic noise. Decision-making based on best available science will reduce uncertainty and should improve protection for mysticete whales in contact with industry sounds.

Table 1. Present common and taxonomic identification, general distribution, and conservation status of mysticete whales.

Balaenidae (bowhead and right whales)			
Bowhead whale	*Balaena mysticetus*	Circum-Arctic Oceans	LR/CD*
North Atlantic right whale	*Eubalaena glacialis*	Northern Atlantic Ocean	EN
North Pacific right whale	*Eubalaena japonica*	Northern Pacific Ocean	EN
Southern right whale	*Eubalaena australis*	All Southern Oceans	LR/CD
Neobalaenidae (pygmy right whale)			
Pygmy right whale	*Caperea marginata*	Circum-Antarctic Oceans	LR/LC
Balaenopteridae (fin whales or rorquals)			
Minke whale	*Balaenoptera acutorostrata sp.*	All Northern Oceans	LR/NT
Dwarf minke whale	*Balaenoptera acutorostrata sp.*	All Southern Oceans	DD
Antarctic minke whale	*Balaenoptera bonaerensis*	All Southern Oceans	LR/CD
Sei whale	*Balaenoptera borealis*	All Major Oceans	EN
Bryde's whale	*Balaenoptera edeni*	All Tropical to Temperate Oceans	DD
Blue whale	*Balaenoptera musculus*	All Major Oceans	EN
Fin whale	*Balaenoptera physalus*	All Major Oceans	EN
Humpback whale	*Megaptera novaeangliae*	All Major Oceans	VU*
Eschrichtiidae (gray whale)			
Gray whale	*Eschrichtius robustus*	Northern Pacific Ocean	LR/CD*

Note: The phylogenetic and taxonomic relationships of the mysticete whales are still poorly understood and considered tentative pending additional research. The minke and dwarf minke whale are currently considered two subspecies of the same genus but are listed separately here. Present conservation status is reported from the IUCN (International Union for the Conservation of Nature and Natural Resources) Red List of Threatened Species, which identifies all baleen whales as species of conservation concern. Abbreviations are defined as follows: EN: endangered, VU: vulnerable, DD: data deficient (no reliable population estimates exist), LR/NT: lower risk, near threatened, LR/CD: lower risk but conservation dependent, LR/LC: lower risk, least concern. *In addition to those species listed as endangered by the ICUN, the United States National Marine Fisheries Service also lists bowhead whales, humpback whales, and the western population of gray whales as endangered/depleted.

The research problem

Interest in whale hearing arises from theoretical as well as practical concerns. Accurate descriptions of mysticete hearing pathways, anatomical adaptations, acoustic perception, and specializations for low-frequency sound detection have significant implications in the scientific community as well as for informing mitigation measures. Therefore, both scientists and regulators are motivated to advance knowledge of this topic. However, acquiring useful information about hearing in mysticetes is difficult, and there are a variety of intellectual, technical, financial, legal, and logistical hurdles to overcome so that significant research progress can be achieved.

Traditional approaches commonly used to examine sensory systems in animals include direct methods such as psychoacoustic and electrophysiological measurements, and indirect methods such as examination of communicative signals, natural and controlled exposure experiments, anatomical investigation, and anatomy-based modeling. Of these, psychophysical assessment is considered the most practical and accurate means of evaluating sensory capabilities. With respect to sound reception by mysticete whales, it is generally assumed that this approach, which depends upon subjects that are conditioned to produce reliable behavioral responses to the presentation of specific auditory cues, will not be possible as the size and feeding characteristics of whales preclude extended periods in captivity (e.g., see Gordon et al., 2003). Electrophysiological studies, which directly measure neural responses transmitted from the peripheral auditory system in response to acoustic stimulation, may provide a more promising means by which to investigate hearing in whales. However, such methods require direct access to living whales, and the technical difficulties associated with gathering and detecting the extremely low-voltage neural responses scale with increasing body size and decreasing frequency and bandwidth of the stimulus to be tested. While electrophysiological techniques are presently available for the audiometric testing of odontocete cetaceans and some other marine mammals (e.g., Supin et al., 2001, André & Nachtigall, 2007), they have not yet been developed for large animals that produce and presumably hear low-frequencies; therefore, a good deal of experimentation and effort will be required to adapt this approach before it can be applied to obtain useful audiometric data from mysticete whales.

Less direct but more accessible methods that can be applied to the study of whale hearing have already yielded some useful information. In field studies, controlled and natural sound exposure experiments have confirmed behavioral reactions to certain acoustic cues, and studies of sound production and communicative interactions show that conspecifics can detect and respond to one another's calls at a variety of distances (see reviews in Richardson, 1995; Tyack et al., 2003). Therefore, behavioral techniques show some promise for determining response thresholds for synthetic and biologically relevant sounds, suggesting that field studies may provide gross estimates of hearing sensitivity within certain frequency bands. Likewise, anatomical techniques provide clues into mysticete hearing. Available descriptions of auditory structures indicate hypertrophy of the nerves, bones, and soft tissues comprising mysticete ears—highlighting the apparent evolutionary importance of sound to these animals—and analyses of inner ear structures suggest substantial specialization for low-frequency function (Wartzok & Ketten, 1999). It is possible that anatomical research combining fine-scale measurements of auditory structures with their corresponding biophysical properties may be used to establish and refine theoretical models of auditory function and to describe probable sound conduction pathways (e.g., Hemilä et al., 2001; Ketten, 1994).

At present, very little is known about how sounds are received and perceived by mysticete whales, and no one approach is likely to provide the answers to the most pressing questions. What is currently known about hearing in mysticetes is inferred from an assortment of studies and observations conducted to address various objectives. To support the development of a cohesive JIP research program with clearly defined goals, the following sections of this paper briefly summarize current knowledge regarding hearing in mysticetes, identify significant knowledge gaps, describe and evaluate possible approaches that may be used to address these knowledge gaps, prioritize technology development and research collaborations to support these research efforts, and outline the general funding and logistical requirements for implementation of this research strategy. The information provided in the following sections is drawn from the scientific literature, government and technical reports, interviews with specialists, and topical pre-proposals submitted to the JIP by potential investigators.

Current knowledge

The hearing characteristics of baleen whales are virtually unknown. At present, we do not know how they receive sounds, their frequency range of hearing, or their hearing sensitivity at any frequency (see Au, 2000). This is not in itself surprising as there is a great deal of basic knowledge about mysticetes that remains unknown, including fundamental aspects of their life history, physiology, ecology, and behavior. Much of what is generally known about hearing in the mysticetes has been broadly summarized in scientific reviews including those by Richardson and colleagues (1995), Au and colleagues (2000), Wartzok and Ketten (1999), and in a series of reports by the National Research Council (NRC) of the United States (1994, 2000, 2003b, 2005). The auditory data that are presently available can be roughly broken down into four topical areas: sound production and communication, responses of free-ranging whales to sound, neuro-physiological responses to sound, and anatomy and anatomy-based modeling. The following subsections of this report briefly summarize important concepts and highlight key and recent studies within each of these subject areas.

Sound production and communication

In the absence of direct information about hearing sensitivity, an understanding of species-typical features of sound production can inform inferences about species-typical features of sound reception. In particular, the frequency range of vocalizations is correlated with regions of best hearing sensitivity in some species of fish, amphibians, reptiles, and mammals (e.g., Ladich & Yan, 1988; Marcellini, 1977; Ryan & Wilczynski, 1988; Esser & Daucher, 1996, respectively), and it is probably reasonable to assume that hearing sensitivity in mysticetes will similarly be tuned to their frequency ranges of sound emissions (see Endler, 1992). However, knowledge of acoustic behavior is not sufficient to predict the frequency sensitivity profile, or audiogram, for a given species because regions of best hearing in animals often extend to or also occur in bandwidths well below or above frequency ranges of vocalizations (e.g., Ketten, 2002). Selective pressures acting upon hearing sensitivity, in addition to those related to communication among conspecifics, include those related to prey detection, predator avoidance, and the physical and acoustic environment in which signals are produced and received. Furthermore, evolutionary changes in hearing sensitivity may occur, not only as primary adaptations for enhanced signal detection, but also as byproducts of other adaptations; for example, those changes to auditory structures that may be related to withstanding pressure effects in deep-diving mammals (Repenning, 1976). Despite the restricted value of using vocalizations as means of accessing hearing sensitivity, this approach is still essential to the investigation of hearing in mysticetes, as other clues to their auditory function are lacking. Additionally, measurements of vocalizations and associated individual and conspecific behavior are required to determine the behavioral significance of communicative signals and to establish accurate estimates of communicative ranges within which noise may interfere with social behavior.

Vocalizations can be described along several acoustic and behavioral dimensions. Mysticete vocalizations are often reported with respect to call type, frequency range, frequency range near maximum energy, and source level. Other acoustic parameters include the temporal and complex spectral characteristics of calls and call components, and the transmission or “beam” patterns of emitted sounds. Sound production repertoires for mysticetes range from simple, stereotyped calls in some species such as blue and fin whales, to complex songs comprising discrete sounds that are arranged into units, phrases, and themes, as found in humpback and bowhead whales (e.g., Clark, 1990). This range can be subdivided into four general vocal categories as reviewed by the NRC (2003b): low-frequency moans (fundamental frequency below 200 Hz), simple calls (impulsive, narrowband, with peak frequency <1 kHz), complex calls (broadband, pulsatile, with amplitude-modulations or frequency-modulations), or songs (sequences of sounds in a regular sequence and patterned in time).

While sound emissions would appear to be some of the most accessible characteristics of mysticetes, there are still significant knowledge gaps for many species. In a recent review, Clark and Ellison (2003) noted that representations of sound repertoires are fairly complete for only five to six species of mysticetes: the bowhead, gray, humpback, southern right whale, and the northern right whales (not differentiated by Atlantic and Pacific right whale species). Reasonably good data exist for blue and fin whales, but available data for the remaining mysticetes are inadequate to evaluate hypotheses regarding communication and auditory sensitivity (S. Parks, personal communication). As an example, Clark and Ellison (2003) predicted that whales might fall into two natural groupings on the basis of vocalizations shaped by different acoustic environments, with those spending significant time in shallow-bottom environments favoring sound emissions in different bandwidths from those typically residing in deeper water, due to features of ambient noise and transmission loss in these environments. Such typological differences in sound production, if substantiated, may help to identify potential functional hearing groups among whales; however, more complete descriptions of vocal characteristics for mysticete species are required in order to make such comparisons.

There are several reviews of sound production in mysticetes (Richardson et al., 1995; Edds-Walton, 1997; Wartzok & Ketten, 1999; Clark & Ellison, 2003); however, none of these are comprehensive with respect to current knowledge. These surveys do indicate that the present understanding of mysticete sound repertoires and acoustic functions is uneven (Clark, 1990). Several biases in the available data are apparent. First, acoustic observations have been skewed toward species that are more accessible; in effect, those species that spend a significant portion of time in coastal waters, particularly during calving and breeding activities (Clark & Ellison, 2003). Such mainly coastal species include all those for which reasonably complete acoustic repertoires have been described. Less is known about the acoustic behavior of whales that tend to be more pelagic. Additionally, fewer acoustic studies have been conducted with whales in the southern hemisphere, and as a result, the sound emissions of species such as the Bryde’s whale, the Antarctic minke whale, and the dwarf subspecies of the common minke whale are not well known. Research efforts have often focused on whales engaged in breeding and feeding activities, resulting in a poorer understanding of acoustic communication during seasonal periods associated with migration and traveling (Edds-Walton, 1997). The distribution of research effort has primarily been a product of researcher motivation and logistical considerations, and does not reflect species abundance, as evidenced by the few acoustic studies of common and Antarctic minke whales, despite their large population sizes relative to other mysticete species.

From the review literature, it is striking that so many of the reports concerning basic features of sound production and acoustic repertoires in whales were published in the 1970s and 1980s, prior to the availability of new technologies and methodologies that have vastly improved sound recording quality, caller localization, source level determination, and archiving of data. Most of these older reports provide descriptions, measurements, and spectrographic representations of the recorded sounds; however, recordings of the sounds themselves have not typically been accessible. Presently, the Macauley Library of Natural Sounds at Cornell University is making a significant effort to compile, digitally archive, and make publicly accessible recordings from key scientific collections (see http://www.birds.cornell.edu/macaulaylibrary/). The mysticete recordings presently available in this database include some of those that were obtained by early investigators using analog recording devices. Therefore, this project provides public access to some of the original acoustic data from which species repertoires have been described and a direct basis of comparison for new data sets. Significantly, the sound quality on these early recordings is typically of relatively low quality, a point that underscores the caution with which some of this often-cited data should be used, and emphasizes the continuing need for the type of high-quality recordings and accurate acoustic measurements that can be obtained using newer tools and archived using databases that are broadly accessible.

In addition to advances in recording technology and equipment, analysis techniques have also been improved since much of the original data was reported. As a result, many of the estimates and comparisons of acoustic variables reported in the primary and review literature need to be carefully reconsidered. In particular, due to the difficulties associated with obtaining calibrated recordings and in estimating transmission loss in complex environments, source level measurements reported for many mysticete species may be questionable (see e.g., Charif et al., 2002). Presently, the vocalization source level estimates reported in the review literature on mysticetes cover a 60 dB range between about 130 and 190 dB re 1uPa (see e.g., Wartzok & Ketten, 1999); reliable estimates of the mean and maximum source levels and the true extent of variability in mysticete sound emissions by species and sound type requires further investigation in most, if not all, species. Source-level data, along with spectral data, provide critical information to sound-propagation models, including those that are used to establish estimates of sound levels received by conspecifics and to estimate potential boundaries beyond which calls may be masked by ambient or anthropogenic noise. Thus, it is essential that investigators of whale bioacoustics continue to report basic characteristics of vocalizations, even for species with fairly well established vocal repertoires.

The behavioral and social contexts associated with sound production in vocalizing whales are generally not well understood, as much of the behavior associated with vocalizations occurs beneath the ocean's surface and out of sight of investigators. Often, the age, sex, and behavior (and sometimes the species) of the signaler are unknown in recordings obtained from hydrophones suspended from boats or from fixed bottom-mounted arrays or surface buoys. The importance of gaining insight into the behavioral relevance of sound production in mysticetes has been pointed out in several review articles (Edds-Walton, 1997; Popper, Hawkins & Gisiner, 1997; Clark & Ellison, 2003) that converge on the view that relating sound structure to potential function is critical in assessing what whales "need" to hear. This type of approach allows questions relating to behavioral and biological significance to be addressed, which in turn are essential for management of populations (National Research Council, 2005). While much remains to be learned about the function of mysticete calls, the best behavioral data presently available are for relatively accessible species that engage in reproductive activities in clear, coastal waters, such as gray and humpback whales (for review, see Ellison & Clark, 2003).

In addition to standard bioacoustic approaches, a variety of different research tools, and sometimes a combination of tools, can be applied to improve understanding of the acoustic behavior of whales across demographic, geographic, and seasonal/temporal scales. For example, Croll and colleagues (2002) used behavioral and acoustic observations combined with genetic analyses to show that, among fin whales, only males produce loud, repetitive vocalizations, thereby implicating breeding displays, rather than echo-ranging for spatial orientation, as the most likely function of these calls. Clark and Gagnon (1994) used acoustic tracking methods and data obtained from deep ocean hydrophone arrays to relate the acoustic behavior of blue whales to their movement patterns across entire ocean basins. Acoustic recordings may be combined with dive records obtained from tags and prey distribution profiles obtained from echo-sounders to gain perspective into the potential role of vocalizations in feeding behavior (A. Stimpert, personal communication). Clearly, a good deal may be gained from applying new technologies to improve our understanding of the functional relevance of mysticete vocalizations (see Popper et al., 1997).

Two recent studies demonstrate how detailed behavioral observations can be correlated with high quality acoustic data to provide new insights into sound production by mysticetes. Gedamke and colleagues (2001) used shipboard and in-water observers along with time-stamped video to provide behavioral and positional reference to vocalizing dwarf minke whales during the whales' presumed breeding season near the Great Barrier Reef, Australia. The whales were recorded at close range in clear water using a hydrophone array, from which accurate measurements of range, source level, and temporal and acoustic features could be extracted. The study revealed a highly complex and stereotyped sound sequence which spanned an unusually large frequency range (50 Hz to nearly 10 kHz) and provided the first confirmed sound recordings of this poorly known subspecies. Au and colleagues (2004) also used in-water observers who positioned a hydrophone array to record the singing behavior of humpback whales at close range. Their study documented precise source-level measurements for various song components, and also attempted the first description of the acoustic field emitted by a mysticete whale. The study described the vertical azimuth of sound projection, revealing directionality of the sound emissions. It also documented spectral components of song elements that exceeded 20 kHz; such high frequency components were likely lost in earlier recordings obtained from longer distances. Ongoing studies are expanding this work to the horizontal azimuth so that the complete transmission patterns of the emitted sounds can be modeled (A. Pack, personal communication). Such work has implications for modeling propagation of communicative sounds in different habitats.

On a practical level, accurate measurements of call source amplitude, frequency, and directionality may be used to estimate potential communicative ranges of vocalizing mysticetes. Such acoustic information may be used in propagation models considering local ambient noise, water depth, range-dependent ocean acoustic layering, and seafloor geoacoustics. Such prediction models have been developed to estimate the propagation of sonars and other sound sources in marine habitats and at least some of these operational models are commercially available. This approach has been applied to model potential communication ranges of southern right whales in the Great Australian Bight using naval sonar prediction software (C. Jenkins, personal communication). While information on hearing sensitivity is required in order to make appropriate assumptions about the distances at which whales may detect conspecific sounds, such an approach is quite valuable in determining the outer bounded limits at which call detection would be theoretically possible in different background noise conditions (see e.g., Payne and Webb, 1971; Erbe, 2003). The accuracy of such models depends in large part on the quality of the sound source characterizations that serve as input, whether they are military or industry noise sources or biological ones, such as mysticete vocalizations.

Responses of free-ranging whales to sounds

Perhaps the most intuitive means available for estimating hearing sensitivity is to document measurable responses to known sound sources. Sound sources may be natural (such as the calls of conspecifics or predators) or anthropogenic (such as the sounds of tones, ships, sonars, or airguns), and their production may be spontaneous and uncontrolled or intentionally manipulated by investigators. In captive situations, investigators can condition behavioral responses to sounds in order to use psychoacoustic methods to measure hearing range and sensitivity. Such methods have proven to be the most effective way to obtain accurate measurements of hearing in species that can be housed and trained in laboratories, zoos, and aquaria. In wild situations, behavioral changes in response to received sounds may be utilized as metrics of signal detection; however, such studies are challenging for a variety of reasons, a number of which are considered in the following sections.

Among the ~88 living species of cetaceans, about 30 individuals representing 11 different species have had their underwater hearing assessed using psychoacoustic methods in captive situations (see Nedwell et al., 2004; Kastelein et al., 2003). All of the cetacean species for which hearing data are presently available belong to the suborder Odontoceti, which includes 10 family groupings ranging from the relatively large sperm and beaked whales to the much smaller river dolphins and porpoises. In contrast to the mysticete cetaceans that generally use baleen to strain large amounts of small prey such as krill from seawater or mud, all odontocetes have teeth, echolocate using high frequency sounds, and consume fish or squid which they actively pursue. The auditory data obtained from odontocete cetaceans thus far indicate that their hearing capabilities are correlated with both phylogeny (evolutionary relatedness) and ecology (foraging habitat), with dolphins and beluga whales forming one functional hearing group and nearshore and inshore porpoises and river dolphins forming another (Wartzok & Ketten, 1999). The hearing abilities of the largest and deepest-diving odontocetes, the sperm and beaked whales, have not yet been examined using behavioral response audiometry.

Mysticetes are unlikely to have their hearing tested using psychoacoustic methods in captive environments, although some neonatal and juvenile whales have been held successfully in captivity for periods of months, and in the case of one gray whale calf, for over a year (Sumich et al., 2001). Field studies measuring spontaneous behavioral responses to sounds are therefore essential to determining what types and levels of sounds are detectable to mysticetes. Two critical components of such studies are detection and measurement of behavioral responses associated with sound detection, and characterization of sounds received by focal individuals. Reliable orientation, approach, avoidance, or otherwise altered responses to incident sounds can be measured from visual observations or from electronic tags placed on the animal. Additionally, acoustic responses can serve as behavioral indicators of sound detection; these responses may include changes in vocal behavior correlated with sound exposure or changes in movement patterns derived from vocalizations localized in space. The sounds received by free-ranging whales in these studies may be estimated from known source levels using propagation models, calculated from information received by arrays of hydrophones, or measured directly from tags placed on individual animals.

Investigations of mysticete responses to sounds may be conducted for many reasons, ranging from analyses of the social functions of natural sounds (e.g., Edds-Walton, 1997) to identification of behavioral disturbance from anthropogenic sounds (e.g., Miller et al., 2000). In the context of examining sensory capabilities, such studies can theoretically provide valuable, albeit indirect, insight into hearing capabilities including frequency range of hearing, relative hearing sensitivity, and auditory masking parameters derived from received signal-to-noise ratios. The most important caveat to consider when behavioral responses are used to estimate hearing capabilities is that while the presence of reliable behavioral change in response to an acoustic stimulus can confirm audibility, the lack of a detectable behavioral response cannot conclusively demonstrate inaudibility. Animals are constantly exposed to a variety of audible but insignificant acoustic stimuli in their environments that they do not respond to. Learning and motivation are important factors influencing individual behavior and need to be considered in auditory studies that rely on behavioral responses. These factors are sometimes neglected in field studies of marine mammals and will be considered in more detail at the end of this section.

There are several thorough reviews of marine mammal responses to anthropogenic sounds, the most significant of which was published as a book by Richardson, Greene, Malme, and Thomson in 1995. Nowacek and colleagues (2007) recently updated this review by detailing research progress made on this topic since the book's publication. In addition to reports of mysticete responses to anthropogenic sounds, there are an assortment of individual studies that deal with marine mammal responses to natural sounds, such as those produced by conspecifics or predators. Investigations that have involved controlled playback of sounds, including natural sounds, to free-ranging whales are summarized by Deeke (2006).

A variety of different behavioral responses including changes in acoustic behavior have been observed from mysticetes in response to the presence of specific sounds, or to stimuli (such as sea vessels) paired with specific sounds. These include changes in movement patterns and diving behavior; approach or avoidance responses; alterations in respiratory patterns; changes in aerial behaviors such as breeching; and modifications of acoustic behavior including call rate, structure, and duration (see Richardson et al. 1995; Miller et al., 2000). Historically, the behavior of mysticetes has been difficult to observe, and the tools for measuring responses have been somewhat crude, including theodolite tracks measured from shore stations and visual and acoustic observations made by shipboard observers. As a result, while significant behavioral changes to sound sources have been detected, it is nearly certain that more subtle responses to less salient stimuli have been overlooked (see discussion in Tyack et al., 2003/4). While gross measures of behavioral change may be appropriate for identifying strong, suprathreshold responses, inferences about hearing capabilities are improved by assessing the lower limits of responsivity to auditory cues. Despite the constraints imposed by limited response detection capabilities, the reliable responses that have been measured from mysticetes to date have served to identify sound types and levels that are convincingly detectable by individuals of different species. For example, such studies have shown that some mysticetes respond to sounds as low in frequency as 20 Hz, as high in frequency as 28 kHz, and as low in level as ~84 dB re 1 µPa (or ~6 dB above ambient noise) (see reviews in Richardson, 1995; see also Lucifredi & Stein, 2007).

Two studies in particular have intentionally explored features of auditory function in mysticetes. In a pilot study, Dahlheim and Ljungblad (1990) attempted to determine the feasibility of conducting hearing assessments on gray whales swimming through a channel in Laguna San Ignacio, in Baja California. The investigators placed a bottom-mounted transducer in a region of the channel with known physical characteristics of the water column and bottom topography and calibrated the tonal stimuli to be used in the study at various positions surrounding the sound source. As whales moved through the study area, a 1-second signal of pre-determined frequency and level was played from the transducer. Control exposures, in which no sound was presented to focal individuals, were also conducted. Whale behavior was measured from two independent observation stations before, during, and immediately after each exposure. Sound frequencies tested ranged from 200 to 2500 Hz, and startle responses were documented to stimuli between 100 and 1500 Hz at received exposure levels of 100 to 135 dB re 1 µPa. While this was a preliminary study comprising a total of only 24 sound exposures, it provides an innovative approach that may be effective for gauging auditory responsivity in a quantitative, controlled fashion with potentially large sample sizes of individuals. Using a different approach, Frankel, Mobley and Herman (1995) derived response thresholds for playbacks of social and synthetic sounds to humpback whales off the coast of Hawaii. The sound levels received by individual whales during the playbacks were modeled and then verified with empirical transmission loss measurements. The investigators reported behavioral responses measured from shore stations to social sounds as low as 102 dB re 1 µPa and to synthetic sounds as low as 106 dB re 1 µPa. While the relatively overt behavioral responses measured in this study likely underestimate absolute hearing sensitivity to the playback stimuli, this titration of stimulus levels moves closer to revealing true sound detection capabilities in whales.

Technological advancements in telemetry have provided powerful new tools for the examination of mysticete behavior in the context of acoustics (see e.g., Burgess, 2001; Johnson & Tyack, 2003). Benign tags placed temporarily on free-ranging whales have the potential to provide information that may include certain temporal, positional, behavioral, physiological, environmental, and/or acoustic variables recorded directly from the tagged individual. When this data is obtained in conjunction with natural or anthropogenic sound exposure studies, it is possible to measure responses that are both more definitive and more subtle than has previously been possible, as well as allowing direct measurements of signal and ambient noise levels at the position of the focal animal (e.g., see Nowacek et al., 2003). In 1994, the National Research Council predicted that increasingly sophisticated methods for measuring marine mammal responses to sound would result in detectable responses being documented to lower and lower received levels of sound. As tagging efforts and capabilities of data-logging tags expand and this prediction comes closer to reality, there is a growing consensus that field studies of noise impacts on marine mammals should emphasize measurable responses that are not just detectable, but also biologically significant (see Tyack et al., 2003/4). It is worth pointing out that for the purposes of hearing assessment—where response magnitude is likely to decline with stimulus saliency—the observation of subtle, biologically insignificant but reliable responses to low amplitude sounds will be critical in closing the gap between estimation of response thresholds and absolute auditory thresholds.

In addition to their importance in determining subtle behavioral response thresholds, acoustic recording tags can be used to obtain precise measurements of sound levels received by focal individuals. In playback or controlled exposure experiments, this allows accurate, relatively instantaneous measurement of received signal and background noise to be determined. Responses associated with sound detection may therefore provide essential insight into the effect of received sounds on listening individuals; for example, observations of minimum signal-to-noise ratios required for detection of conspecific calls or measurements of levels at which behavioral disturbance may be caused by anthropogenic noise. The availability of acoustic recording tags, as well as hydrophone arrays that can be used for passive acoustic monitoring, also facilitate measurement of sound production characteristics as a function of different noise conditions. Changes in acoustic behavior as a function of different noise conditions may potentially include differences in the level, rate, duration, and frequency bandwidth of vocalizations; these differences can in turn be related to auditory phenomena such as detection, masking, and hearing loss.

Regardless of how the response is measured and whether the auditory stimulus received by an individual is natural or anthropogenic, a controlled sound source or an opportunistic one, studies of free-ranging mysticetes are challenging and difficult to conduct for many reasons. Pitfalls, logistical constraints, technological limitations, and common problems associated with such studies are detailed in several recent review articles (see Tyack et al., 2003/4; Deeke, 2006; Nowacek et al., 2007). Two of the general issues raised in these reviews are worthy of particular consideration here. First, these sorts of studies often require that sufficient background information be available on the habits and normal behavior patterns exhibited by the particular population of animals to be tested. This is important for scientific reasons, such as determining how to define a “response,” and for practical reasons, such as making appropriate logistical decisions with respect to experimental design and execution. This may require work to be conducted in the context of well-established research programs and/or the inclusion of preliminary and pilot studies as components of major research efforts. Further, while most interested parties would agree that population level measures of response are desirable, it is important to consider that acoustic response studies are generally conducted at the level of individual animals, which may vary considerably in terms of their responsivity to sound.

The behavior of individual animals in response to auditory stimuli may vary as a function of physical as well as biological factors (see Richardson, 1995). In particular, individual differences in responsivity under comparable exposure conditions are influenced not just by idiosyncratic perceptual sensitivities, but also by factors related to learning and motivation. For example, while an individual may initially respond to the detection of a stimulus, that response will attenuate with repeated exposures if the stimulus is neither rewarding nor harmful, a non-associative learning process termed habituation. If the stimulus is altered following habituation of the initial response, the response will rebound when the stimulus is changed, as long as the individual is sensitive to the difference between the two stimuli. This process is termed dishabituation. In some cases, sensitization may occur, that is, increased responding to a range of previously neutral sounds following exposure to a particularly intense or salient stimulus. Aspects of motivation also come into play when interpreting behavioral responses to sound, for example, it may be quite difficult to elicit a response from whales that are engaged in active feeding, social interactions, or mating, but much easier to elicit responses from individual whales that are traveling or resting quietly (see Richardson, 1995). The role of associative learning processes may modify responses to stimuli ranging from barely audible to injurious through conditioning or counter-conditioning. All of these psychological phenomena need to be considered in interpreting the responses, and lack of responses, that marine mammals exhibit to sound sources. Many of these non-sensory phenomena can actually be exploited in order to better understand the sensory capabilities of individual subjects (see Werner, 1995, for applications in studies of human hearing). Several of these phenomena, particularly that of habituation, have been identified as high priority research topics to explore in mysticetes (e.g., Nowacek, 2007).

Neuro-physiological responses to sound

Due to the difficulties associated with extracting relevant hearing data from indirect approaches such as studying acoustic communication and monitoring behavioral responses to sound exposures, there is hope in the scientific community that more direct assessment of auditory function by measurement of neuro-physiological responses will prove possible in mysticetes (see National Research Council, 1994). Specifically, the application of electrophysiological methods allows small-voltage neural responses associated with detection of stimuli by the auditory nervous system to be measured in living subjects. These low-amplitude electrical potentials, which are evoked by auditory stimulation, are detected within much greater ambient electrical and physiological background noise through a process of signal averaging. The neural events associated with auditory-evoked potentials involve the transmission of a response through the auditory nervous system, including the auditory nerve, structures in the brainstem, and the cortex. As a result, the earliest portions of the averaged auditory-evoked responses are associated with activity at and below the level of the brainstem (auditory brainstem responses, or ABRs), while the later portions of the responses are associated with activity at the level of the cortex (cortical responses).

Auditory-evoked responses exhibit a variety of characteristics that make them relevant in physiological studies of hearing. Their presence is correlated with stimulus detection by the auditory system, which means they can potentially be used to probe the upper and lower frequency limits of hearing. Their amplitude and latency change as a function of stimulus level, which means they can be used to determine minimum measurable response thresholds in the auditory system. Their waveform composition reflects anatomical loci within the auditory nervous system, which means they can be used to diagnose origins of sensorineural hearing deficits. These features, along with several others that provide insight into temporal and spectral aspects of auditory function, are exploited in studies of human hearing undertaken in both clinical and research settings (for review, see Hall, 2006). The most common application of electrophysiological methods in the study of human hearing is in neonatal screening of hearing sensitivity, where behavioral response audiometry is not typically possible. Although evoked-potential measures of hearing are generally not as definitive as psychoacoustic measures of hearing, these techniques can provide insight into auditory capabilities that are not otherwise accessible.

The study of auditory-evoked potentials is well developed in odontocete cetaceans, the auditory nervous systems of which have been examined using electrophysiological methods for nearly as long as the auditory systems of humans have been (see Supin et al, 2001 for review). Certain adaptive features of odontocete auditory systems related to their echolocation capabilities, including hypertrophy of peripheral auditory structures, refined high-frequency hearing sensitivity, and rapid temporal processing capabilities, make them especially suitable for measurement of auditory-evoked responses. Increasingly sophisticated technology development and testing methodologies have resulted in highly efficient electrophysiological procedures for measuring evoked potentials from odontocetes using benign suction cup electrodes placed on the skin (see e.g., Finneran et al., 2007), and related applications of these methods have extended beyond the measurement of physiological hearing thresholds to other applied aspects of auditory function including auditory masking (see Supin et al., 2001), temporary threshold shift (Nachtigall et al., 2004), and permanent hearing loss (Houser & Finneran, 2006).

Electrophysiological procedures are not likely to be as successfully applied with mysticetes as they have been with odontocetes. While echolocating animals such as dolphins and bats have relatively large auditory evoked responses, the responses of other mammals, including humans, are much smaller and therefore more difficult to detect in background noise. The amplitude of evoked potentials measured from the skin depends primarily on two factors: the amplitude of the response at its sources in the auditory nervous system, and the attenuation of the response between the sources and the position of the recording electrodes. While some data exist on the distribution and density of cells in the auditory nervous system of whales (see Ketten, 1997 and following subsection of this report), neurophysiologists have not yet established what the source amplitudes of auditory-evoked responses are likely to be in mysticetes. With respect to response attenuation, the small relative brain size of mysticetes (a function of a large brain encased in a much larger body) results in a proportionately large distance between the sources of the neural response and the surface of the skin, a distance that is spanned by electrically insulative layers of bone and tissue that limit response transmission. As a result, regardless of source amplitude, detection of auditory evoked responses becomes more difficult as body size increases, a phenomenon that has been clearly demonstrated in different sized species of odontocete cetaceans ranging from porpoises to killer whales (Supin et al., 2001).

Evoked potential measures of hearing in odontocetes provide unusually good correspondence to psychoacoustic measures of hearing sensitivity (see Yuen et al., 2005; Finneran & Houser, 2006). This may be attributable in part to the higher frequencies typically tested in these animals (>10 kHz). In other mammals including humans, behavioral and physiological measures of hearing are not as well matched (Stapells & Oates, 1997). However, in the case of mysticetes, even coarse measures of sound detection capabilities are urgently needed. In order for evoked potential methods to be successfully applied with mysticetes, a series of technical challenges must first be overcome. These include issues related to subject accessibility, type of evoked responses to be measured, characteristics of evoking sounds, modes of delivering low-frequency acoustic stimulation, signal processing capabilities, electrode design and placement, and reduction of extraneous noise. To date, only a single effort has been made to obtain auditory-evoked responses from a mysticete whale. Ridgway and Carder (2001) attempted ABR measurements from a captive gray whale calf housed in captivity for rehabilitation at SeaWorld, in San Diego, California. Although the results of these measurements were equivocal, this effort demonstrates the potential to access mysticetes, at least relatively small mysticetes, for electrophysiological testing. Previous efforts with odontocete cetaceans have already demonstrated the capability of electrophysiological hearing assessment on stranded dolphins (see Nachtigall et al., 2005; Cook et al., 2005) and dolphins that are temporarily captured for testing and then released (Cook et al., 2004; P. Nachtigall, personal communication). Significantly, successful short-term capture and release of gray whales calves has been by reported by Norris and Gentry (1974) and similar methods may prove appropriate for evoked-potential assessment of these and other smaller mysticetes.

It remains to be determined whether electrophysiological methods can be developed and applied so that meaningful information about auditory function can be obtained from mysticetes. While this approach has been repeatedly identified as potentially the most promising for addressing the issue of whale hearing (National Research Council, 1994, 2000, 2003b), the ability to conduct the research necessary to advance such studies has been hampered for a variety of reasons, ranging from difficulties in obtaining necessary permits to collect data from stranded animals to lack of available information on neuro-anatomical characteristics of these animals. However, the rapid advancement of evoked potential methods during the past decade, and especially during the last few years, provides a strong argument that the expertise and technology to do this work exists, and that the time has come to attempt focused feasibility studies and field testing of potential approaches.

Anatomy and anatomy-based modeling

Anatomical studies are critical to the investigation of hearing in mysticetes, providing the most significant clues presently available as to how sounds are received and processed by these animals. While living whales are difficult to access and challenging to observe below the water's surface, post-mortem whales provide investigators with biological materials that can be examined, described, and used to establish practical and theoretical models of auditory function. Samples become available for anatomical studies sporadically through several different sources including museum collections, stranding events, carcasses washing ashore, native harvests, and hunting carried out by whaling nations. Fresh samples of auditory structures including neural tissues are often difficult to obtain due to the time and expertise required to efficiently extract and process fresh, delicate materials from animals of such massive size. Presently, most knowledge of mysticete auditory anatomy comes from a small number of individuals representing a few species.

Given the high priority placed on obtaining auditory data from mysticetes, and the incomplete knowledge presently available about the structural and functional characteristics of their ears, it is somewhat surprising that relatively little new information has become available on the auditory anatomy of extant mysticetes over the last decade. In contrast, substantial research progress has been made with respect to odontocete auditory anatomy. This discrepancy may be due in part to military interest in replicating odontocete biosonar capabilities, and to the emphasis placed on odontocete species that are at apparently high risk to anthropogenic noise impacts. Interestingly, some progress has been made in the study of archaic cetaceans in the context of describing the evolution of aquatic hearing capabilities (e.g., Thewissen & Hussein, 1993; Geisler & Luo, 1996; Nummela et al., 2007). Findings from studies of fossil species suggest that modern mysticetes are adapted for low-frequency sound detection and that bony characteristics associated with low-frequency hearing had substantially emerged at least 10 million years ago (Geisler & Luo, 1996). The evolutionary changes that have occurred in the mysticete ear that appear to be related to the detection and localization of underwater low-frequency sounds underscore the probable significance of low-frequency sound detection to mysticetes. Despite this, the ear structures presumed to play a role in low-frequency hearing in mysticetes have not thus far been studied in great detail (Ketten, 2000).

Available knowledge of auditory anatomy in living cetaceans including mysticetes has been described in detail by Ketten (1994, 1999, 2000, 2004) and is only superficially summarized here. Cetaceans evolved from terrestrial ancestors whose ears presumably functioned in a manner similar to that of modern mammals. The air-adapted ear of mammals operates by converting aerial sound into fluid-borne vibrations of inner ear structures. This conversion is necessary because of the vastly different physical properties of air and water—for a given average intensity, airborne sound comprises relatively smaller amplitude pressure fluctuations and larger magnitudes of particle velocity than waterborne sound. The air-filled outer and middle ear of mammals, which includes the pinna, ear canal, tympanic membrane, ossicles, and oval window membrane, compensate for these differences by amplifying the acoustic pressure of the airborne sound that is transmitted to the inner ear, resulting in better hearing sensitivity than would be expected by simple direct transmission of airborne sound through the bones of the skull and associated tissues into the inner ear. Modern cetaceans are fully aquatic and their auditory systems are highly derived from those of their land-living ancestors. The typical mammalian sound-amplification pathway of the air-filled outer and middle ear, so helpful for the detection of airborne sounds, impedes sound conduction in water, as acoustic pressure is greatly attenuated when crossing air-water boundaries. Therefore, the auditory structures of cetaceans evolved to efficiently receive sound in water. The contemporary auditory anatomy of whales and dolphins reflects both adaptations for aquatic living and structural characteristics common to their terrestrial ancestors.

The detailed examination of auditory anatomy—including bony structures; soft tissues such as muscle, cartilage and ligaments; fatty deposits; membranes and mucosa; neural fibers and tissues; fluid- and air-filled spaces; and cellular architecture—provides descriptive and morphometric information that can provide insight into hearing capabilities. Comparative studies of auditory anatomy (for example, between living and fossil species, between modern terrestrial and marine mammals, between odontocete and mysticete cetacean lineages, and amongst different mysticete species) reveal relationships between structure and function that can address practical as well as theoretical questions regarding hearing. For example, over the past few decades, focused anatomical investigations of odontocete cetaceans have been used to identify sound transmission paths to the inner ear, explain the basis of exquisite high frequency hearing capabilities, reveal evidence of hearing losses and acoustic trauma, and develop predictive models of hearing sensitivity in poorly studied species. Success in these efforts has been helped along by complementary data provided from behavioral and physiological studies. For mysticetes, far less progress has been made in anatomical studies, and there is little in the way of complementary research to guide anatomical investigations.

While fine-scale anatomical investigations of auditory structures have rarely been conducted in mysticetes, the data that are presently available are informative when considered in a comparative context. Mysticetes share several derived features in common with odontocetes, the most notable of which are loss of pinnae, closure and reduction of the outer ear canal, extra-cranial placement of auditory structures, distensible tissue lining the middle ear cavity, broad and tough eustachian tubes, hypertrophy of inner ear structures and associated neural tissues, and significant reduction of the vestibular system. These features are probably generally related to aquatic hearing and regulation of pressure in air spaces at depth. In addition to these features, mysticetes have several unique auditory characteristics, including an unusual tympanic membrane covered by a waxy mound that is coupled to bony surfaces in the ear canal. The middle ear is housed in a massive bulla which, despite being positioned extracranially, has well-developed bony articulations to the skull. The cavity of the middle ear is voluminous and has low-frequency resonance. The ossicles suspended in this cavity are large, dense, and loosely-joined. In the inner ear, a large cochlea houses a broad, long, thin and floppy basilar membrane and relatively large cochlear ducts. While sound reception mechanisms in mysticetes are unknown, the presence of some of these features suggests bone and soft tissue pathways of sound conduction to auditory structures and well-developed low to infrasonic hearing capabilities. The wide range of morphometric differences observed thus far in gross auditory structures suggests there may be large acoustic differences amongst mysticete species.

Quantitative morphological data are available for some auditory structures in a few mysticete species, but there is no mysticete species for which a relatively comprehensive assessment of auditory anatomy has been conducted. Such data are also limited for large terrestrial mammals presumed to have good low-frequency hearing, such as elephants. However, neuro-anatomical investigations conducted with mysticetes thus far have revealed some intriguing findings. While the diameters of their individual auditory fibers are not unusually large like those of odontocete cetaceans, mysticetes appear to have auditory nerve densities that rival those of the hyper-developed odontocetes. While odontocetes likely use their enhanced neural capability for echolocation, it is unknown what role such neural development may serve for mysticetes. Auditory nerve densities have been compared to optic nerve densities for only two mysticetes, humpback whales and fin whales. There are no mysticetes for which comparable vestibular nerve densities are reported. The auditory to optic nerve comparison of humpback and fin whales shows disproportional development of the auditory nervous system that is similar to that seen in odontocetes, which greatly exceeds the trend observed in land mammals. The lack of available information on vestibular development of mysticetes is significant, as the vestibular system has been implicated in low-frequency hearing (as cited by Ketten, 1997). Clearly, the data that are available on mysticete neural morphology suggest auditory specializations; however, additional measurements and comparable information from other mysticete species will be required to resolve the extent and probable functional significance of those specializations.

Anatomical information can be described and compared between species in order to gain insight into the evolution and operation of auditory structures. On a more practical level, anatomical information can also be reconstructed, extrapolated, or modeled to gain insight into functional hearing capabilities. Depending on the type of data used and the amount of validating data available, models of hearing may be theoretical, qualitative, or quantitative. Because the ear is such a complex structure, auditory models typically encompass only a subset of features that may be used to predict hearing capabilities.

Auditory models are constructed by looking at the physical properties of different parts of the ear and how they interact to influence hearing capabilities. Mechanical models look at the middle ear and ear complex as mechanical systems which transmit sounds with differential efficiencies. In studies of cetacean hearing, for example, the configuration, morphology, and biophysical properties of structures are precisely measured to obtain parameters that can be used to model the propagation of mechanical vibrations through the system (S. Nummela, personal communication; D. Mountain, personal communication). In odontocetes, where validating audiograms are available for many species, this approach has resulted in quantitative models of auditory function that predict low- and high-frequency hearing limits and audiogram shape reasonably well (e.g., Hemilä et al., 1999, 2001; Miller et al., 2006). For mysticetes, theoretical and qualitative mechanical models of middle ear function remain to be developed, and quantitative models must await complementary data for validation.

In the last decade, an engineering modeling approach called finite element analysis has been increasingly applied to the study of biological systems including auditory systems. This is a computer simulation technique which can create functional multi-dimensional models of auditory structures based on anatomical shapes, biological material properties, and realistic boundary and loading conditions and then test the responsivity of these models to different vibrational input conditions (Elkhouri & Funnell, 2006). This type of mechanical model has been applied to the study of hearing in humans and in terrestrial animals commonly used in hearing studies. In these species, it has been applied at various levels of the auditory system, from outer and middle ear function (Gan et al., 2004) to hair cell micromechanics (Duncan & Grant, 1997). It is especially well-suited to simulation of low-frequency hearing capabilities, and therefore, this method may prove useful to future studies of mysticete hearing.

In addition to mechanical models, correlational models of auditory function can also provide insight into likely hearing capabilities. For example, Ketten (1994) has proposed a predictive model of hearing based on morphometric analyses of cochlear structures that are compared to similar measures obtained in animals with known hearing capabilities. This correlational model has been applied with odontocete cetaceans with good results, and has been used similarly with samples obtained from bowhead and right whales, and more recently, minke whales (Yamato et al., 2007). Houser, Helwig, and Moore (2001) expanded this general approach by combining cochlear morphometric data for humpback whales with mathematical functions established for hearing in other better studied species, and then optimizing the results of the model with the use of evolutionary programming. Obviously, it cannot be known for certain if any anatomy-based model will successfully predict the hearing capabilities of mysticetes. However, if independent models predict similar results, or if integrated models are consistent with other lines of evidence, such as those provided by studies of communicative signals, behavioral responses, or electrophysiological studies, then probable hearing capabilities may be more confidently estimated.

While no mysticete species has been directly tested for any hearing ability, anatomical studies have resulted in some predictions of auditory function. Correlational models based on basilar membrane characteristics suggest that the low-frequency hearing of mysticetes extends to 20 Hz, with some species, including fin whales, predicted to hear at infrasonic frequencies as low as 10-15 Hz. The upper frequency range for some mysticetes has been predicted to extend to 20-30 kHz (see National Research Council, 2003). Absolute and relative sensitivity to sounds within the audible range is unknown (but see Houser et al., 2001 for a prediction of relative sensitivity in humpback whales based on extrapolation from terrestrial species). Finally, at least partially because whale ears are most often studied outside of heads, anatomical studies have not yet succeeded in identifying the hearing pathways that are most likely used to receive and mechanically transfer underwater sounds to the auditory nervous system. The eventual description of hearing pathways in mysticetes will help to determine not just how mysticetes hear, but what sounds they are most likely to hear.

Overarching goals in the assessment of mysticete hearing capabilities

As part of the process in the development of a research strategy for assessing the hearing capabilities of mysticetes, the Joint Industry Programme on Sound and Marine Life released a preliminary request for proposals. The JIP set forth the ambitious goals of obtaining empirically-measured or closely estimated audiograms from mysticetes, and identifying approaches capable of predicting the effects of acoustic exposure on their auditory systems. These high level goals are based on the need to better understand the potential effects of seismic airguns, ships, and other low-frequency sound sources on free-ranging whales.

The JIP's request for proposals was designed to challenge potential investigators to think broadly and creatively about how these goals might best be achieved. In practice, to obtain an audiogram from any animal, two types of information are required: the frequency limits of hearing and the sensitivity to sound frequencies that fall within those limits. The frequency limits of hearing are defined as the frequency cut-offs beyond which an animal can no longer detect a loud stimulus. Because the stimulus levels used to determine the frequency limits of hearing greatly exceed those of background noise levels, these limits can theoretically be obtained in a variety of settings. Hearing sensitivity, however, which dictates the shape of the audiogram, can only be obtained in conditions where the background noise near the frequency range of interest is low enough as to not mask (elevate) the hearing threshold. Ambient noise in marine environments varies as a function of frequency, with the greatest noise occurring in frequency bands below a few hundred hertz (Wenz, 1962). Therefore, unless the hearing sensitivity of whales is much poorer than expected at low frequencies, it will be difficult to obtain unmasked thresholds to low-frequency sounds in field settings. At higher frequencies, greater than a few thousand hertz, the liklihood of obtaining unmasked hearing thresholds improves.

Some hearing-based measures of acoustic exposure can reasonably be estimated in the presence of background noise. For example, the masking effects of noise on hearing can be evaluated by measuring hearing sensitivity in the presence of noise to determine critical ratios, or the levels by which signal amplitude must exceed noise amplitude in order for signal detection to occur. Threshold shifts, or the changes in hearing threshold that may occur following noise exposure, can also be measured in the presence of background noise. However, threshold shifts may be influenced by the amount of masking that occurs during threshold determination. As the issue of high background noise at low frequencies is relevant for both ambient acoustic noise and "ambient" physiological noise, the problems associated with assessing hearing capabilities at lower frequencies are unfortunately common to both behavioral response and neuro-physiologic response procedures.

While it is constructive to look at the research problem of mysticete hearing conceptually from the standpoint of high-level goals such as audiogram determination, another way of looking at the issue is to take a bottom-up approach. From this practical perspective, lower-level knowledge gaps identified from presently available data can be considered within the context of the research approaches best suited to addressing these gaps.

Knowledge gaps and general research needs

Given our present understanding, the most significant knowledge gaps that presently exist with respect to the topic of hearing in mysticete species can be broadly summarized as follows:

- Description of the structural, functional, and propagation characteristics of vocalizations
- Improved understanding of auditory anatomy, including identification of the path or pathways through which sound travels from the underwater environment to the auditory nervous system
- Determination of upper and lower frequency limits of hearing
- Measurement of auditory responsivity in different frequency bands
- Consideration of the simultaneous (masking) and residual (temporary threshold shift, permanent threshold shift, injury) effects of noise on hearing
- Assessment of species-specific and demographic variability within these topical areas, and identification of potential functional groupings

These six knowledge gaps are consistent with those identified in the first National Research Council report issued on marine mammals and noise (1994), and their importance has been restated and re-emphasized in each of the three reports that have been issued since (2000, 2003b, 2005). The study and review boards that contributed to these reports included international experts from a variety of disciplines, and their consensus findings are generally held as the most definitive on this subject. The NRC reports also include specific research priorities for marine mammals in addition to those related directly to hearing, for example, those aimed at determining impacts of particular anthropogenic noise sources. For the purposes of this report, the findings of the NRC are scoped to the levels that most directly inform understanding of mysticete hearing, and specific recommendations are provided to address these issues.

The interaction between the four general research areas previously reviewed and the six knowledge gaps just described is depicted in Table 2. In the following section, each of the columns of this table is expanded upon. Specific research topics within each area are described, and recommendations for actions that are likely to advance understanding of these topics are provided. It is worth mentioning that because so little information on mysticete hearing is available, much of the initial work that is required involves establishing a solid science foundation upon which to build. Unless and until some of the required basic research is completed with mysticetes, as it has been for some other marine mammal groups, it will be difficult to push forward with reasonable higher-level applied studies. For example, there is at present no justifiable basis for lumping mysticetes together in terms of their hearing capabilities or their susceptibility to anthropogenic noise. Comparative research from different research areas is required to determine if functional groupings are appropriate, and if so, to determine the conditions under which it is valid to extrapolate from representative species within these groupings, given that it is unlikely that adequate knowledge of hearing and behavior will become available for all species.

Table 2. Primary knowledge gaps that can be addressed within general research areas.

	General research area			
Knowledge gap	Sound production and communication	Responses of free-ranging whales to sound	Neuro-physiological responses to sound	Anatomy and anatomy-based modeling
Description of the structural, functional, and propagation characteristics of vocalizations	✓	✓		
Improved understanding of auditory anatomy, including identification of hearing path or pathways				✓
Determination of upper and lower frequency limits of hearing		✓	✓	✓
Measurement of auditory responsivity in different frequency bands		✓	✓	
Consideration of the simultaneous and residual effects of noise on hearing			✓	
Assessment of species-specific and demographic variability, identification of potential functional groupings	✓	✓	✓	✓

Research priorities and recommendations grouped by research area

Sound production and communication

- Establish adequate baseline knowledge of mysticete vocalizations, including accurate temporal, spectral, and source characteristics of emitted sounds, characterize signal-to-noise ratios for vocalizations in different acoustic environments, and describe species-typical vocal repertoires
- Assess whether mysticete species can be lumped into different functional groupings based on features of their sound production
- Improve understanding of the functional significance of mysticete vocalizations
- Improve estimation of potential conspecific communication ranges under different propagation and noise conditions

Comments. Sound production by mysticetes has been studied for some time but there is a lack of high quality comparative data for mysticete species. Currently available reviews rely upon pooling studies with little or no consideration for variables such as methodology, sample sizes, recording locations, and caller information such as age, sex and behavioral context. Source level data, critical for determining the potential for masking of signals by noise and for estimating communication ranges, are often be inappropriately reported. Acoustic recordings are not commonly made available with published descriptions of vocalizations. Presently, information on species repertoires are not complete, and although scientists have speculated on possible functional groupings based on characteristics of vocalizations, the data are not sufficient to identify reasonable species groupings at this time. Such groupings that may emerge from statistical treatments can focus future research efforts and facilitate generalization of findings by emphasizing research on “representative” species. Readily available propagation models can be used to determine potential conspecific communication ranges, but these models need to be populated with accurate bioacoustic data. Modeling of communicative ranges can be combined with both tracking/population data and modeling of noise sources so that a better overall understanding of mysticetes’ acoustic environments can be obtained.

Recommendations. (1) Mysticetes need to be characterized as acoustic sources in much the same way as industry sources are characterized. Measurements need to be obtained for multiple individuals and multiple species using standardized methods, so that variability can be assessed and species and demographic differences can be evaluated. Results should be linked to accessible digital waveforms so that high quality acoustic data can be used to inform modeling efforts. It is possible that such an effort could be accomplished by a small, specialist group of physical acousticians who could provide technology or expertise to field biologists and ensure consistency in how data from different sources are obtained and reported. A team of experienced investigators already engaged in field studies of mysticetes could be selected to participate in the present effort. Archival of new data could be accomplished through publications as well as through a centralized database including annotated acoustic measurements and linked sound files which could be augmented as new data become available. Data archival might be established within the framework of an existing program, such as Cornell’s *Macauley Library* or Scripps Institution of Oceanography’s *Voices of Sound in the Sea*, or perhaps through a database which combining whale sighting and movement data with information about the physical and biological environment such as OBIS-SEAMAP (Ocean Biogeographic Information System-Spatial Ecological Analysis of Megavertebrate Populations).

(2) Facilitate the organization of currently available information on mysticete vocalizations into a comprehensive and standardized review format with appropriate supporting documentation. To accomplish this, a contractor active in the field of mysticete bioacoustics could be selected to prepare and publish a comparative review of vocalizations in all studied mysticete species. Data could be mined not only from the literature, but from working investigators who could participate in the effort at the level of co-authors to encourage their participation and release of unpublished data relevant to the present effort. An updated, inclusive review that provided annotations of relevant measurement variables such as those related to sample size, recording methods, source level determination, behavioral context, etc., would provide a resource on mysticete sound production that is more accurate and comprehensive than any presently available. The publication could be linked to the publishing journal's electronic supplementary material or an online acoustic database to provide access to representative sound files. Such a document could include statistical analysis of functional species groupings based on vocal behavior or at the identification of the specific research needs required to conduct this analysis.

(3) Support individual research programs that will provide information on the acoustic, functional, and propagation characteristics of lesser known mysticete species, and support ongoing programs that can provide baseline behavioral and acoustic data for recommendations comparative studies of sound production and for future controlled exposure studies.

(4) Support the development and implementation of acoustic modeling efforts that predict the active acoustic space of mysticetes in different noise conditions.

Responses of free-ranging whales to sound

- Examine how mysticetes respond to the incidence of natural and synthetic sounds using both opportunistic and controlled exposure studies
- Determine the limits of responsivity to loud sounds at upper and lower frequency boundaries, and to progressively attenuated sounds in different frequency bands
- Examine subject- and state-dependent aspects of acoustic responsivity

Comments. Research efforts depending on the reliable identification of behavioral responses will be challenged most by investigators' ability to define, detect, and interpret subtle and variable responses (see subsequent section on Technology for additional comments). Knowledge of baseline behavior is essential to these studies. Because response amplitude is likely to decline with stimulus strength, thresholds measured in free-ranging animals will underestimate actual auditory thresholds. However, carefully measured response thresholds can reveal relative sensitivity in different frequency bands, and repeatable responses to loud sounds at high and low frequencies should reveal the frequency limits of hearing. Differences in responsivity as a function of subject- and state-dependent variables (e.g., age, experience, temporal and behavioral contexts) must be considered in these studies. In all studies, it is essential that received characteristics of the sounds be appropriately measured or modeled and that background levels of noise in relevant frequency bands be characterized.

Recommendations. (5) Exploit opportunities to measure responses of individuals to uncontrolled sounds, such as calls of conspecifics, predators, or human noise sources. A variety of different behavioral responses (e.g., orientation, movement, location, breathing, diving behavior, vocalization) should be evaluated as potential metrics of response. Changes in baseline vocal responses (e.g., level, rate, frequency) in response to received sounds and background noise levels should be considered. Results can be compared between groups sampled at a variety of levels, including subject- or state-dependent levels within populations, between populations in different physical, global, and acoustic environments, and between species. Individually, such studies will provide evidence for audibility of certain stimuli and can also be used to evaluate subject variables such as potential habitation or sensitization to loud noise sources. Measured responses to conspecific calls can improve understanding of their functional significance. These investigations of opportunistic sound exposures can be accomplished in the context of established research efforts with adequate knowledge of baseline behavior. The results of such studies can be used to inform the design of and predict the likelihood of success of controlled exposure experiments.

(6) Conduct controlled exposure experiments on one or two target species to examine frequency range of hearing, auditory response thresholds in different noise bands, and subject- and state-dependent influences on responsivity. These studies have rarely been attempted with the goal of extracting relevant information on hearing capabilities, and experimental design can be optimized for this purpose. For example, studies of frequency range can be conducted with animals individually or in groups resting near or moving past a sound source with known propagation characteristics (see e.g., Dalheim & Ljungblad, 1990; also Malme, 1984). Acoustic startle responses to loud sounds surrounding estimated high- and low-frequency limits can be elicited so that psychometric response functions can be obtained at a population level, and pooled subject-level variability in responsivity can be evaluated. For single animals presented with multiple moderate to low-level sound exposures, habituation can be examined and potentially exploited as a means of determining limits of sensitivity. There are a variety of promising approaches that can combine controlled exposure experiments with new technologies and psychophysical methodologies in order to acquire useful information about hearing capabilities. These approaches should be explored with captive marine mammals with known hearing profiles to demonstrate their predictive capabilities.

Neuro-physiological responses to sound

- Develop and apply neuro-physiological methods to examine the hearing capabilities of mysticetes

Comments. Studies of neuro-physiological responses to sound in mysticetes are the most risky in their likelihood of providing useful results but are potentially the most promising for revealing hearing capabilities if techniques can be successfully adapted for use with large, low-frequency animals. There are a variety of technical problems that must be addressed in order for the technique to be adapted for mysticetes. These include determining how low-frequency sounds can be presented in the testing environments likely to become available for these animals. The science is likely to move forward with some failed attempts which will inform the development of new testing methods. Any evoked potential research activities to be attempted with mysticetes should be coordinated with anatomical studies to inform consideration of variables such as electrode type and placement, stimulus features and projection methods, and estimation of likely response amplitudes.

Recommendations. (7) Conduct methodology, technology, and feasibility studies to determine whether auditory evoked potentials are likely to be obtained from living mysticetes. There are a variety of approaches that can be used to identify and address the types of problems likely to be encountered during evoked potential testing of mysticetes. These will require flexibility on the part of investigators to explore and resolve, should involve interactions with individuals experienced in anatomy, modeling, signal processing, and field studies and stranding responses of mysticetes. Technology development would benefit from applied studies of large, low-frequency terrestrial and marine mammals, such as elephants and elephants seals, who can be more easily accessed for testing and whose hearing has been described though the use of behavioral methodologies. In addition, the testing of odontocete cetaceans at frequencies below 10 kHz, and ideally below 1 kHz, should help to resolve some of the issues involved in working with marine mammals at lower frequencies. Investigators should stay open to the possibility of using non-traditional methods to obtain more easily measured responses, such as the use of cortical evoked potentials and myogenic response indicators. Such non-traditional approaches can be explored with captive marine mammals with known hearing profiles to demonstrate their predictive capabilities.

(8) In concert with recommendation 7, attempts should be made to measure relevant features of auditory function using auditory evoked potentials obtained from stranded or temporarily restrained mysticetes. Even with the best of advance feasibility studies, direct experience with mysticetes will be required for the development of appropriate testing protocols. At least initially, it is likely that greater progress will be made in examining hearing at higher—rather than lower—frequencies. An investigator or team of investigators should be selected (similar to the SWAT—Stranded Whale Auditory Test—team first proposed by the NRC in 1994) to identify and respond to potential opportunities which would provide access to living whales for audiometric testing. These opportunities could be stranding or entanglement events, or planned efforts to examine temporarily restrained or tidally beached young whales. Depending on where the research activities occur, there are significant logistical and permitting constraints to be addressed with respect to this recommendation that exceed those of any other suggested action. The constraints and time required for planning and coordination of activities with government agencies should be included within the scope of such a project.

Anatomy and anatomy-based modeling

- Improve general understanding of mysticete auditory anatomy, including the structures of the outer, middle, and inner ear and auditory nervous system, as well as the surrounding tissues of the head
- Assess whether mysticete species can be lumped into different functional groupings based on features of their auditory anatomy

- Develop predictive models of auditory function that can be evaluated using complementary data obtained with mysticetes and correlational data obtained with non-mysticete species

Comments. A good deal of progress can be made in the field of mysticete auditory anatomy using existing technologies and resources. The lack of basic research in this area appears to be due more to limited attention from a small group of specialists rather than major research constraints. General data gaps are clearly identified in the literature, and existing data sets need to be increased to include more individuals and expanded to include more species. Functional species groupings have been speculated on by investigators but such groupings have been based on a limited number of species and have not been quantitative (see Ketten, 2000). Constraints on progress in the study of mysticete auditory anatomy include the availability of specimens, the ability to examine fresh materials in the context of surrounding tissues, and lack of available expertise to efficiently process specimens. Due to limited expertise in this field, gaps in funding result in loss of trained personnel required to process specimens. Despite these limitations, there are several ongoing projects presently dealing with the topic of mysticete auditory anatomy, mainly from the perspective of bony structures and mechanical models. One ongoing study is examining auditory anatomy, especially cochlear structures, in minke whales in order to predict frequency range of hearing from correlational models.

Recommendations. (9) Conduct basic comparative research on the functional anatomy of mysticete auditory systems. Obtain data from multiple individuals and all possible mysticete species so that intra- and inter-specific differences can be evaluated. Characterizations should be made at a variety of levels, from describing the shape, size, composition, and configuration of gross structures to measuring the distribution and density of nerve fibers in the optic and vestibular, as well as the auditory, tracts. It is important that where possible, ears be studied in the context of surrounding cranial structures so that possible hearing pathways from the environment can be identified and evaluated. A variety of tools, including dissection, histology, radiology, and tissue reconstruction and modeling, should be employed by investigators skilled in examining auditory tissues or collaborating closely with those that are. This should be a broad, multi-year effort aimed at advancing understanding of auditory function in mysticetes. The results of such an effort should include descriptive materials and access to annotated images that will be useful to future investigations and include training for students who may eventually contribute additional expertise to this small field of specialists. This effort should facilitate determination of potential functional groupings based on auditory anatomy that can be compared to those determined from studies of sound production and communication.

(10) Where sufficient understanding of auditory anatomy exists, develop predictive models of auditory function that can be informed by and evaluated against complementary data obtained with mysticetes and correlational data obtained with non-mysticete species. The approaches that can be employed include biophysical/mechanical modeling, correlational modeling, and finite element modeling. Each of these approaches will provide unique results and offer different insights into auditory function. Where they can be independently compared, weight will be lent to efforts predicting similar results. It is important to keep in mind that anatomy-based modeling efforts in mysticetes will remain qualitative until they can be validated with audiometric input from other research areas. At this point, modeling efforts with

mysticetes still require a more complete grounding in basic knowledge of auditory anatomy, so their results should be used cautiously.

Significant challenges

As mentioned throughout this report, there are many challenges in studying mysticetes that make the execution of the best laid research plans problematic. Chief among these is the lengthy and unpredictable permit process faced by American and some other investigators. Delays associated with obtaining necessary permissions must generally be accommodated in research planning stages. The effort inherent in acquiring research permits also precludes many investigators from applying for permits prior to the assurance of research funding. The only way around such delays is to build appropriate lead times into research projects, work with investigators that already hold appropriate or modifiable permits, or to conduct work in areas not requiring lengthy permit application procedures. Another significant constraint on investigators working with living animals is the fact that most mysticetes are accessible to investigators only during limited seasonal periods. That means that research opportunities may be limited, timing of research funding and permitting is critical, and that high-quality research projects generally take multiple years to complete. Research projects would often benefit from linking investigators who could benefit from shared resources, information, or expertise, but such cooperative efforts are often difficult to arrange amongst investigators who are often competing for limited funds. Finally, it is obvious that research involving mysticetes tends to be extremely costly relative to many other types of projects, and the data output in many cases tends to be more limited.

Due to the difficulties in carrying out research with mysticetes, it is important that research dollars are invested wisely in projects that have been carefully thought out in terms of necessary baseline studies, experimental designs, and pilot studies, and that have adequate support for key personnel from different specialty areas. In the present research climate, there is a strong emphasis on applied studies providing rapid and quantitative results for minimum cost. With respect to the study of mysticetes, it is essential that research is conducted from a scientifically sound foundation. Since relatively little relevant background knowledge exists for these animals, higher-level questions may need to await the support and completion of more general research objectives in order for scientifically valid and successful outcomes to be achieved. Research goals need to be logical and realistic. This is especially true in regards to the current effort to develop and implement a research strategy to assess the hearing capabilities of mysticete whales.

Technology requirements

The primary technology requirements identified in the present assessment are the availability of specialist support to investigators and access to appropriate tagging resources. Investigators working in the areas of communication and behavior are often biologists and animal behaviorists without formal training in physical acoustics. Specialist support to investigators appears to be needed primarily in the areas of marine physical acoustics and sound field modeling and is appropriate to consider on a case-by-case basis. Access to tagging resources and passive acoustic monitoring support, however, does appear to be a more dominant factor affecting and limiting the research methods available to and used by many investigators. This issue has been recently addressed in detail during a workshop on the technology requirements needed to support the investigation of the effects of sound on marine wildlife, sponsored by the Joint Industry Programme and held at St. Andrews, Scotland, March 20-22, 2007. An analysis of the tagging technology issue is provided in the report generated by that workshop and the findings of that report are entirely relevant to the assessment of hearing capabilities in mysticetes. In the context of the present research strategy, it is worth mention that the primary issues regarding acoustic and behavioral monitoring that emerged during preparation of this document included those related to limited direct access to specific data logging capabilities, lack of expertise in tag deployment and recovery, and concerns regarding data transparency of tagging technologies.

Summary of recommended actions

(1) Characterize mysticetes as underwater acoustic sources. Measurements should be obtained for multiple individuals and multiple species using standardized methods, so that variability can be assessed and species and demographic differences can be evaluated. Results can help to identify potential functional groupings that can be compared to those identified in recommendation 9, and provide data needed for recommendations 4, 5, and 10.

(2) Facilitate the organization of currently available information on mysticete vocalizations into a comprehensive and standardized review format with appropriate supporting documentation. Results can help to identify potential functional groupings that can be compared to those identified in recommendation 9, and provide data needed for recommendations 4, 5, and 10.

(3) Support individual research programs that will provide information on the acoustic, functional, and propagation characteristics of lesser known mysticete species, and support ongoing programs that can provide needed baseline behavioral and acoustic data for recommendations 1, 2, 5, and 6. Results should also provide data for recommendations 4 and 10.

(4) Support the development and implementation of acoustic modeling efforts that predict the active acoustic space of mysticetes in different noise conditions.

(5) Exploit opportunities to measure responses of individuals to uncontrolled sounds, such as calls of conspecifics, predators, or human-generated noise sources. Results can inform planning efforts for recommendation 6, and provide data needed for recommendation 10.

(6) Conduct controlled exposure experiments on target species to examine frequency range of hearing, auditory response thresholds in different noise bands, and subject- and state-dependent influences on responsivity. Results will provide data needed for recommendation 10.

(7) Conduct methodology, technology, and feasibility studies to determine whether auditory evoked potentials can be measured from living mysticetes. Research efforts should be informed by recommendation 9.

(8) Attempt to measure relevant features of auditory function using auditory evoked potentials obtained from stranded or temporarily restrained mysticetes. Results should provide data needed for recommendation 10.

(9) Conduct basic comparative research on the functional anatomy of mysticete auditory systems so that auditory adaptations and hearing pathways can be identified. Obtain data from multiple individuals and all possible mysticete species so that intra- and inter-specific differences can be evaluated. Results should inform planning for recommendations 7 and 8, and provide independent assessment of functional groupings that can be compared to those identified from recommendations 1 and 2.

(10) Where sufficient understanding of auditory anatomy exists, develop predictive models of auditory function that can be informed by and evaluated against complementary data obtained with mysticetes and correlational data obtained with non-mysticete species.

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