

Marine mammal hearing and acoustic trauma: Basic mechanisms, marine adaptations, and beaked whale anomalies

Darlene R. Ketten

Dept. of Biology, Woods Hole Oceanographic Institution, Woods Hole, Mass. 02543, U.S.A. and  
Dept. of Otology and Laryngology, Harvard Medical School, Boston, Mass. 02114 U.S.A.

## ABSTRACT

Concomitant with increasing concern over the impact of anthropogenic sounds in the oceans, there has been a dramatic increase recently in the research efforts on marine mammal hearing. The resulting data suggest marine mammals ears are more diverse and complex than previously appreciated, with acoustic capabilities spanning infra to ultrasonic ranges. Whales in particular have strikingly different adaptations from those of land mammals, with specialized soft tissue sound conduction paths, 50% greater octave spans than most land mammals, and two to three-fold the auditory neural densities of any other mammal known. Recent data also show that despite physical adaptations that could diminish acoustic impacts, whales are not impervious to acoustic trauma and, like land mammals, their susceptibility to auditory damage varies among species.

Beaked whales, because of their rarity and short surface intervals are amongst the least understood of all marine mammals, particularly in terms of hearing. Current anatomical data show that their ears are predominantly ultrasonic adapted and should therefore have relatively poor sensitivities to lower frequencies. However, these data also show that beaked whales have unusually well-developed vestibular structures which may anomalously enhance beaked whale sensitivities to intense, low frequency sounds.

## INTRODUCTION

Before discussing currently available data on marine mammal hearing, much less the implications for determining acoustic trauma sources for beaked whales, it is important to consider the scope of the problem that phrase implies. "Marine mammal" is a broad categorization for over 150 species from four orders. Extant groups include the Pinnipedia (true seals, sea lions, and walrus); marine Fissipedia (sea otters); Sirenia (manatees and dugongs); and Cetacea, which include the baleen or "moustached" (mysticete) whales and echolocating, toothed (odontocete) whales, porpoises, and dolphins. The degree of aquatic adaptation varies for each group. Some, like the pinnipeds, are amphibious, but all cetaceans and sirenians are fully aquatic, unable to move, reproduce, or feed on land.

Until very recently, our knowledge of marine mammal hearing was driven primarily by an interest in replicating the exceptional sonar abilities of dolphins. Consequently, for nearly 50 years, the majority of "marine mammal" hearing studies focused on measuring and modeling dolphin sonar and therefore on the sonic to ultrasonic abilities of remarkably few captive, odontocete species (see Au, 1993). In the last decade, increasing public and scientific concerns about the deployment of man-made acoustic devices in the oceans led to a realization of our lack of basic information on the hearing and sound use of most marine species. Because marine mammals have a high public profile, are arguably highly dependent upon hearing for survival, and, in many cases, are endangered, the concern over noise impacts for these animals became particularly acute. Therefore, in the last five years, there has been a substantial increase in the breadth of species investigated and in the scope of techniques directed at obtaining both direct and indirect measures of hearing in marine mammals

One very important reason for multiple techniques to be used is that the diversity of size and rarity of some marine mammal species demands more creative approaches to obtaining hearing measurements. Given the physical and habitat variations of marine mammals, it is reasonable to expect that their hearing capabilities are diverse, that their ears will have significant adaptations related to both hearing and diving, and that the most extreme, water related adaptations may be found in cetaceans, particularly in the deep-diving species. While behavioural audiograms remain the gold standard for hearing measures, they are clearly not applicable for a wide range of marine species, particularly for the larger, rarer whales and pinnipeds which are expected to be more readily affected by lower frequency sounds.

To get a grasp of the full spectrum of marine mammal hearing, we must rely in part on modeling techniques, which depend in turn on anatomy coupled with behavioural and electrophysiologic data that provide controls and benchmarks for each model's accuracy. Methods that have been employed recently have ranged from conventional audiometry to structurally derived functional models to three-dimensional FEM modeling. By combining results from all these methods, there has indeed been a considerable increase in our data base and understanding of how marine mammal ears operate so that we now have at least some understanding of hearing in 3 balaenid, 16 odontocete, and 7 pinniped species (see Richardson, 1995; Ketten 1997; Wartzok and Ketten 1998 for reviews).

The consensus of recent data on marine mammal hearing, ear anatomy, and vocalizations is that marine mammal ears are more diverse and complex than previously expected. Equally important, they have two unique and intriguing features: 1) they are the only mammalian ears that are successfully adapted for acute underwater sound reception and localization; and 2) as a group they have the widest known range of auditory capacities, spanning very low infrasonic (~10 Hz) to high ultrasonic (200 kHz) frequencies. Although the current data on marine mammal hearing are now substantially greater than one decade ago, they are not encyclopedic, and many species are still largely undocumented. The Ziphiidae, or beaked whales, are in this category. At present, we have no concrete information on their vocalization repertoire nor on their hearing sensitivities. Nevertheless some new information about their ear anatomy and its relation to that of other species can be brought to bear on the question of what and how beaked whales hear. Therefore, this overview will first provide a brief summary of what is currently known about hearing abilities of the most relevant marine mammal group; i.e., the cetaceans, describe how those abilities correlate with auditory structures, and, finally, because of the lack of direct physiologic measures, discuss the implications of those data for both the hearing abilities and the potential for inner ear trauma from low frequency sound in beaked whales.

#### **FUNDAMENTALS OF HEARING IN AIR vs. WATER**

Hearing is a relatively simple chain of mechano-electrical events in which acoustic signals are transformed in neural signals that are sent to the brain, providing a percept of sound. The structural elements performing these actions vary according to species and, therefore hearing ranges and the sensitivities also vary widely by species (see Fay, 1988 for overview). "Functional" hearing refers to the range of frequencies a species hears without entraining non-acoustic mechanisms (Fig. 1). In land mammals, the functional range is generally considered to be those frequencies that can be heard at a threshold (minimum intensity required to hear a given signal) of 60 dB SPL. The basis for this measure and how it differs in air and water are discussed in detail in succeeding paragraphs. By example, a healthy human ear has a potential maximum frequency range of 0.02 to 20 kHz, but the normal functional hearing range in an adult is closer to 0.040 to 16 kHz. In humans, best sensitivities (lowest thresholds) occur between 500 Hz and 4 kHz, which is also where most acoustic energy of speech occurs (Schuknecht 1993, Yost 1994). Sounds that are within the functional range but at high intensities will generally first induce threshold shifts (near 80 dB SPL above threshold at best frequencies of hearing) and then produce discomfort and ultimately pain (above 120 dB SPL for most frequencies). To hear frequencies at the extreme ends of any animal's total range generally requires intensities that are near discomfort, and frequencies outside or beyond the hearing range are undetectable auditorially because of transduction limitations in the ear's middle and inner ear elements. Exceptionally loud sounds that are outside the functional range of the normal ear can sometimes be perceived through bone conduction or direct motion of the inner ear fluids, but this is not truly an auditory sensation (Corso, 1963).

“Sonic” is an arbitrary term derived from the maximal human hearing range. Frequencies outside this range are deemed infrasonic (below 20 Hz) or ultrasonic (above 20 kHz) sonic. Clearly, many animals hear sounds inaudible to humans. Most mammals have some ultrasonic hearing (i.e., can hear well at frequencies >20 kHz) and a few, like the Asian elephant, *Elephas maximus*, hear infrasonic signals (<20 Hz) (Heffner and Heffner, 1980; Payne *et al.* 1983; 1986). Hearing ranges are both animal size and niche related. Mammalian ears scale with body size (Manley 1972; Ketten 1992; West 1985), and the highest frequency an animal hears is generally inversely related to body mass. Smaller animals typically have good high frequency hearing while larger animals tend to have lower overall ranges (Greenwood 1962). In addition, hearing characteristics correlate with habitat. Crepuscular and nocturnal species typically have ultrasonic hearing while subterranean species often have infrasonic ability and, in some cases, can detect seismic vibrations (Fay 1988)

Marine mammals share many of the basic structural and mass/habitat auditory relationships with land mammals, in part because they have common ancestry. All marine mammals, including whales, evolved from land-based animals with air-adapted ears (Barnes *et al.*, 1985). There are, of course, also substantial differences between land and aquatic ears that are related to how the physical differences of air vs. water impact the parameters of hearing. Over 50 million years, as the bodies of whales evolved to withstand enormous pressures, preserve heat, and move efficiently in the comparatively dense, cold environment of the seas, their ears evolved in tandem to effectively process underwater sound by developing mechanisms for handling the substantially greater sound speed and acoustic pressures that are inherent in water vs. air. Water, with a density nearly 800-fold that of air (1.03 g/cc vs. 0.0013 g/cc), has a sonic velocity that is on average 4.5 times faster than in air (1530m/sec vs. 340m/sec). To examine the sensory implications of these values, consider a hypothetical mammal, that hears equally well in water and in air. An animal with an intensity based ear would require the same acoustic power/unit area in water as in air to have an equal sound percept, or ( $I_{\text{air}} = I_{\text{water}}$ ):

$$I_{\text{air}} = p_{\text{air}}^2 / (0.442 \text{ g-m/sec-cc}) = p_{\text{water}}^2 / (1575 \text{ g-m/sec-cc}) = I_{\text{water}} \quad (1)$$

This means the sound pressure in water must be 59.7 times that in air to produce the same intensity and therefore the same sensation in a hypothetically perfectly air-water matched ear. Although the units of intensity are watts/m<sup>2</sup>, conventional hearing studies report hearing thresholds in effective sound pressure level (SPL), expressed in decibels (dB), which in turn are complicated by arbitrary reference pressures. For air-borne sound measures, the reference is generally dB SPL or dB re 20 µPa rms; for underwater sound measures, the reference pressure is dB re 1 µPa. Thus, taking into consideration conventional reference pressures, for an equal intensity, underwater sound pressure levels should be ~61.5 dB greater than the sound pressure levels reported in air. It is particularly important to consider these numerical differences for assessing relative acuity across mammals, across media, and, in the context of this panel, for addressing trauma frontiers extrapolated from air-borne stimuli.

## CETACEAN HEARING

Underwater audiograms are available for eight odontocetes (Fig. 2). Most odontocetes tested to date are delphinids, with the bottlenosed dolphin being the best investigated. There are no published audiograms for larger, deep diving odontocetes, like the sperm and beaked whales. The current data suggest odontocetes commonly have a >10 octave functional hearing ranges, compared with 8 octaves in most mammals. Best sensitivities range from 12 kHz in the killer whale (*Orcinus orca*) to over 100 kHz in bottu (*Inia geoffrensis*) and the harbour porpoise (*Phocoena phocoena*). While very acute ultrasonic hearing is common in odontocetes, the species tested to date appear to have relatively poor sensitivity to frequencies below 200 Hz.

Echolocation performances in bottlenosed dolphins (*Tursiops truncatus*) are similar to that microchiropteran bats and 6 to 8 dB lower than that expected from an ideal receiver (Au, 1993). Angular resolution is generally 1° to 4°. Intensity discrimination is equal to human (1 dB); temporal discrimination (~8% of signal duration) is superior to human. Frequency discrimination varies from 0.28 to 1.4% rdl for frequencies between 1-140 kHz; best values are found between 5 and 60 kHz (Popper, 1980). Odontocetes have more critical bands and the critical ratios are generally smaller than in humans, although they are relatively constant at ~0.25 to 0.35 octaves/mm of basilar membrane (Ketten, 1997).

Odontocete critical bandwidths approach 0 and are not a constant factor of the ratio at different frequencies. The best critical ratios to date (8 to 40 dB) are for the false killer whale, *Pseudorca crassidens*, which is also the species that has performed best in echolocation discrimination tasks (Thomas *et al.*, 1990., Nachtigall *et al.*, 1996)

#### ANATOMICAL CORRELATES AND MODELS OF HEARING

A fundamental assumption in hearing models is that hearing capacities are the output of the integrated components of the whole ear. All mammalian ears, including those of marine mammals, have three basic divisions: 1) an outer ear, 2) an air-filled middle ear with bony levers and membranes, and 3) a fluid-filled inner ear with mechanical resonators and sensory cells. In terms of the common models used to analyse mammalian hearing, the outer ear acts as a sound collector; the middle ear transforms acoustic components into mechanical ones detectable by the inner ear, and the inner ear acts a band-pass filter and mechanochemical transducer of sound into neural impulses. Hearing models are generally anatomically derived but use electrophysiologic and behavioural data as controls. Modeling of land mammal ears has a long and well-established pedigree (Fay, 1992). One strength of models is that they emphasize species-specific structural differences and, given that there are sufficient anatomical data, models can provide an extraordinarily accurate estimate of the hearing characteristics for virtually any species (Fay, 1992). Clearly an important issue is model accuracy, and this is where the interface of behavioral or electrophysiologic data plays an important role, particularly for marine mammals.

As marine mammal ear anatomy data becomes more comprehensive, and as we gain more information on the comparative aspects of marine vs. land species, anatomically derived models become more sophisticated and more reliable and therefore more important as an approach to species that are essentially inaccessible at this time, like the rarer large whales. In addition to providing hearing range estimates for individual species, fundamental issues for which anatomically based modeling is providing some useful indicators are what are the paths to the ear, how is localization accomplished, and what is the function of the middle ear. At present, the principal model data available for marine species are for inner ear response characteristics of odontocetes (Ketten, 1994). Model data for species that also have behavioral audiograms show close agreement between actual and modeled functional hearing ranges. The model data also demonstrate that while some aspects of land based inner ear models are valid for marine mammals, there is an important difference in the frequency to ear morphometric relationship of the inner ear in marine mammals compared to conventional land mammal models (Ketten, 1992); i.e., there is a distinct, underwater auditory bauplan. Hearing range estimates have also been generated for some mysticetes using these techniques which have good agreement with vocalization data, but at this point there no audiometric data available to definitively test baleen models.

An important difference in whale auditory systems that may directly affect acoustic trauma mechanisms in these animals is the possibility of soft tissue sound conduction paths to the middle and inner ears. Whales have no external ear and the canal is blocked by debris and wax. Currently, the lower jaw is considered the primary reception path for ultrasonic signals in odontocetes. Norris (1968, 1969) speculated that fat filling the lower jaw was a preferential low impedance path to the ear and that the pan bone as an acoustic window to the middle ear region. Brill *et al.* (1988) confirmed this role, but some studies also found best thresholds for low to sonic frequencies near the external meatus (Popov and Supin, 1990). Recent CT and MRI data (Ketten, 1994, 1997), suggest there are multi-directional fat channels that may conduct sound to the inner ear. The presence of more than one channel may first explain reported discrepancies among sensitivity measures, but equally important it suggests relatively complex dual channel processing that may be unique in mammals.

Logically, it would seem that whales, with the possibility of fluid to fluid coupling have little need for the classic amplification role of the middle ear. Land mammal middle ears are commonly described as impedance-matching devices or transformers that counteract the ~36 dB loss between air and a fluid-filled inner ear. This gain is achieved by the mechanical advantages provided by area differences of the middle ear membranes (large tympanic vs. small oval window) and by the lever ratio of the bony chain of ear ossicles which create a pressure gain and a reduction in particle velocity at the inner ear. CT data indicate the middle ear of dolphins is air-filled *in vivo* (Ketten, 1994, 1997); therefore, impedance matching may still be important for cetaceans. Further, improving the efficiency of power transfer to the inner ear may not be the only important middle ear function. Recent studies suggest a "tuning" role (see Yost 1994 for overview). Each species has a characteristic middle ear resonance based on the combined chain of impedances. The sum of impedances is lowest; i. e., middle ear admittance is greatest and energy transmission

most efficient, at a species-specific middle ear resonant frequency which generally corresponds to the frequency of best sensitivity for that species (Fay 1992). Although middle ear function in cetaceans is still debated, the anatomy also points to a functional role. Mass and stiffness of the ossicles and the size and shape of the eardrum vary widely among marine mammals; none have overtly degenerate or vestigial middle ear anatomies and some incorporate highly derived structures; e.g., the large, fibrous, everted eardrum (“glove finger”) common in baleen whales.

While middle and outer ear functions in cetaceans remain unclear, inner ears of whales and dolphins are undoubtedly among the most highly developed of any mammal. The inner ear consists of the cochlea (hearing) and the vestibular system (orientation and balance). Key components of mammalian cochleae are the basilar membrane, which is a tonotopically ordered resonator, and the Organ of Corti that rests atop the membrane. When the basilar membrane moves, cilia on the hair cells of the Organ of Corti are deflected eliciting chemical changes that release neurotransmitters. Damage to the hair cells is the primary mechanism underlying most hearing loss. Cetacean inner ears have the same general format as land mammal ears, but particularly in the odontocetes, the structural elements are more robust and represent extreme patterns of specialization. The stria vascularis and spiral ligament are hypercellular, both of which suggest relatively rapid metabolic or repair processes consistent with the importance of hearing to these animals and with moderately high background noise in many ocean regions. Spiral ganglion cell densities are significantly greater in whales than in land mammals, averaging between 2000-4000 cells/mm in most cetaceans (Ketten, 1992, 1997). Greatest densities are found in the highest frequency odontocetes, but all whales have densities and fiber diameters that are significantly greater than those of land mammals. The fact that mysticetes have comparably high auditory nerve to hair cell innervation ratios, suggests that both infrasonic mysticetes and ultrasonic odontocetes are capable of equivalent complexity in acoustic processing or that they may be high ambient adaptations (Ketten, 1997).

Differences in mammalian hearing ranges are dictated largely by differences in the inner ear, specifically in the thickness and width of the basilar membrane. From the base of the inner ear spiral to its apex, this membrane becomes progressively thinner and broader. Consequently, the highest frequency an animal hears depends upon the membrane's resonant frequency at the base where the membrane is generally stiffest (narrow and thick). Moving towards the apex, the lowest frequency region, the membrane becomes broader and more pliant. Key features in the functional frequency range for each species are the thickness to width ratios and gradients along the basilar membrane as well as the presence or extent of auxiliary stiffening agents (Ketten, 1992; Roitblat *et al.* 1996). Auxiliary outer osseous laminae are a distinctive element of all odontocete cochlea and are strong functional correlates of their ultrasonic hearing capacities.

Anatomically, acoustically, and functionally, cetacean inner ears divide into three formats (fig. 3). Type I ears, found in the highest frequency animals (functional upper bound >160 kHz), have basal membrane ratios ( $t/w$ ) >0.8 and outer bony laminar support or support 60% of the basilar membrane length. Type II ears (functional upper bound <160 kHz), have less acute basal membranes (ratio ~0.6) and slightly wider apices as well as <35% of basilar membrane length with outer bony laminar support, consistent with their broader hearing range. Type M ears, common to baleen whales, have unremarkable basal ratios but exceptionally broad apical membranes (up to 2200  $\mu$ ) and apical ratios near 0.002 and no outer laminar support elements, consistent with infrasonic resonances as low as 10 Hz.

Preliminary data from inner ear analyses of five specimens from three species of *Mesoplodon* and one specimen from *Ziphius cavirostris* (Ketten, in prep. 1998) show that structurally these ziphiid species have classic odontocete cochleae with strongly developed inner laminae, implying good ultrasonic sensitivities. No cochlear specializations for lower frequency hearing were found. There were, however non-auditory inner ear developments that were notable, and to some extent anomalous in comparison to other cetaceans. In the majority of cetaceans, the vestibular elements, including the semi-circular canals, related sensory patches, and the vestibular nerve, are exceptionally small in comparison to other mammals. One possible explanation is that vestibular diminution is secondary to cervical fusion and therefore to reduced azimuthal cues from limited head rotations typical in most whales, and there appears to be a statistical correlation between the level of vestibular macular development and head flexibility (Ketten, 1992). Ziphiids are notable exceptions to this cetacean character in that they have vestibular elements closer in size to those of land mammals. Neural data are not yet available on Ziphiid vestibular maculae and therefore no speculation on the sensitivity of the vestibular apparatus in beaked whales is possible at

this time nor on their susceptibility to low frequency-induced vestibular excitation. However, the presence of well-defined semi-circular canals does raise the question of an unusual, for a cetacean, auxiliary, vestibular sensitivity to lower frequencies in an otherwise ultrasonic dominated ear. Such a response could be compounded by an enlarged Eustachian sinus and cochlear aqueduct that were noted also in the preliminary report on these specimens.

### ACOUSTIC TRAUMA AND UNDERWATER ADAPTATIONS

Acoustic trauma is simply the production of a decrease in hearing ability, or worsening of threshold, by exposure to sound. Hearing losses are classified as temporary threshold shifts (TTS) if recoverable or permanent (PTS). For narrow band, high frequency signals, losses typically occur in or near the incident signal band, but intensity and duration can act synergistically to broaden the loss. Long or repeated exposures to TTS level stimuli without adequate recovery periods can induce permanent threshold shifts. In general, if the duration to intense noise is short, and the noise is narrow band and not impulsive, hearing is recoverable and the loss centers near the signal's peak frequency. If exposure is long or the signal is broadband with a sudden onset, some hearing, particularly in the higher frequencies, can be permanently lost. Damage location and severity of TTS and PTS are correlated also with the power spectrum of the signal in relation to the sensitivity of the receiving ear.

PTS results typically from protracted, repeated, intense exposures (*e.g.*, occupational auditory hazards from background noise) or sudden onset, intense, impulsive sounds (*e.g.*, rapid, repeat gun fire). Hearing loss with aging (presbycusis) is the accumulation of acoustic insults to the ear. Typically, high frequencies are lost first with the loss gradually spreading to lower frequencies over time. Repeated TTS events can induce PTS. Acoustic trauma induced by sudden onset, loud noise (a "blast" of sound) is not synonymous with blast trauma, nor are noise and blast effects of the same magnitude. Blast injuries result from exposure to a shock wave which has an initial compressive phase in which a massive pressure increase over ambient is achieved with a few microseconds rise-time followed by a rarefactive wave in which pressure drops well below ambient. Blast damage may be repairable or permanent according to the severity of the single blast exposure.

TTS has been produced in submerged humans with underwater sound sources for frequencies between 0.7 and 5.6 kHz when received levels were 150-180 dB re 1  $\mu$ Pa (Smith and Wojtowicz 1985, Smith *et al.* 1988). Taking into account differences in measurements of sound pressure in air vs. water, these underwater levels are consistent with the 80-90 dB exposure levels that induce TTS in humans at similar frequencies in air. These studies also found sharp rise-time signals produce broad spectrum PTS at lower intensities than slow onset signals in water, which is also consistent with in-air studies and suggests, at least for these ears, the fundamental mechanisms were primarily dynamic range dependent.

Currently, there are insufficient data to accurately determine TTS or PTS exposure guidelines for any marine mammal. Why is the probability of acoustic trauma even debatable in marine mammals and why can we not simply co-opt TTS and PTS findings from land mammals? As the preceding paragraphs outlined, there are significant structural and functional auditory differences between aquatic and land mammal ears which preclude simple extrapolation of trauma mechanisms and damage criteria between groups. At present, there are no studies that provide reliable threshold shift data for any marine mammal species, and there continue to be a wide range of arguments presented about acoustic trauma susceptibilities for all marine mammals.

Vocalization data in marine mammals are frequently cited as indicating high tolerance for intense sounds. Some whales and dolphins have been noted to produce sounds with source levels as high as 180 to 220 dB re 1  $\mu$ Pa (Au, 1993; Richardson *et al.*, 1995). These data must be viewed with caution. Although vocalizations are reasonable indicators for mid-range hearing characteristics because peak spectra of vocalizations are generally near the best frequency of hearing in each species, it is important to recall that recorded outputs from an animal may have little to do with ear tolerances. Animals, including humans, commonly produce sounds which would produce discomfort if they were received at the ear at levels equal to the emitted level. Mammal ears are commonly protected from self-generated sounds passively by intervening tissues (head shadow and impedance mismatches) as well as by active mechanisms (eardrum and ossicular tensors). Marine mammals have analogous structures, and they are likely to be functional.

Further, there are no data that show that such intense source levels are not exceptional or intentionally aggressive stimuli. Arguments that marine mammals can tolerate higher intensities simply because of their size and tissue densities are also not persuasive. The large head size of a whale is not acoustically exceptional when the differences in pressure and sound speed in water vs. air are taken into account.

While there is the possibility that inner ear hypertrophy and dive-related adaptations ameliorate acoustic trauma, recent studies show cetaceans are not immune to either acute or long-term physiologic damage from noise (Ketten et al., 1995, 1997, 1998). CT, MRI, and histologic comparisons of inner ears from juvenile dolphins vs. ears of an older male dolphin with a documented hearing loss found that the older dolphin ears had marked cell loss and laminar demineralization. This structural loss was consistent with a substantial, progressive, hearing loss beginning in the high frequencies and paralleled the noise-induced pattern of progressive hearing loss commonly observed in aged humans. The conclusion was that significant hearing loss had occurred attributable only to age-related changes in the inner ear. Very recently, a behavioural audiogram from another older male dolphin showed a similar loss (Brill et al. 1997; Ketten et al. 1997). Significant decrements in the hearing thresholds of an older sea lion were reported also by Kastak and Schusterman (1995). The reasonable conclusion from these data is that regardless of any speculated resistance to acoustic trauma, marine mammals are not immune to the long term degenerative effects of noise exposure and are likely to be subject to noise induced trauma at some level, even for short-term stimuli.

Unfortunately, the present data are far from definitive, and in some ways, only beg the primary question of what are the most sensitive species and what noises cause significant impacts. Natural loss should be considered in any animal for which there is little or no history, therefore the finding of a single animal with some hearing decrement in the vicinity of a loud source cannot be taken as a clear indicator of a population level hazard from that source. On the other hand, because of the importance of hearing to these animals, it is also unlikely that a high incidence of loss will be normally found in any wild population, and a finding of substantial or common hearing loss in a mass-stranding coincident with a long-term exposure to an intense source would be an appropriate indicator for significant concern. In such cases, ear samples and where possible physiologic tests of hearing should be a prime objective, since in the absence of any ear or physiologic data no specific acoustic tie can be responsibly, scientifically proven.

In summary, not all marine mammal ears are equal, but all species continue to be of equal concern. Marine mammals are acoustically diverse with wide variations in ear anatomy that are consistent with equally diverse hearing characteristics. All ear components are heavily modified from those of land mammals, but the essential plan is the same. Therefore, we expect that damage at the hair cell level proceeds by the same mechanisms as in land mammals in most if not all marine mammals. Data from older dolphins is consistent with this expectation. Underwater acuity, and the level of structural adaptation that underlie these abilities, vary among marine mammals. Cetaceans are now known to have exceptionally wide ranging ears that are structurally more derived than land mammal ears and are probably incapable of hearing in air in any normal functional sense. Whale and dolphin middle and outer ear elements are adapted exclusively to hearing underwater and specialized fatty tissue elements that have acoustic impedances comparable to water may be unique soft tissue analogues to the external canals of other mammals. Given the combination of odontocete sensitivities with their hair cell and aging data, this group should be among the most liable to acoustic impacts from sources within their hearing ranges. Alternatively, it is possible that inner ear hypertrophy in odontocetes provides protective mechanisms from high intensity noise. *Ziphius* may represent a particularly quixotic ear, considering its high frequency auditory adaptations vs. enhanced vestibular and dive-related adaptations.

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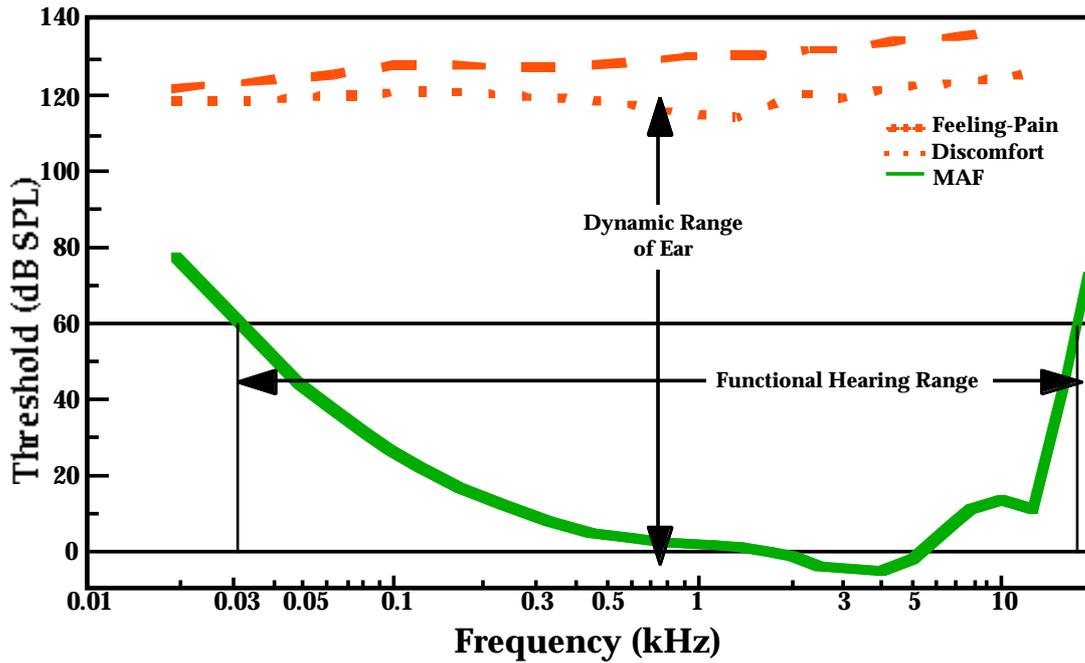


Figure 1 Human audiogram. MAF represents the average minimum audible field threshold response curve for adults. (After Fay, 1988; Schuknecht, 1993; Yost, 1994)

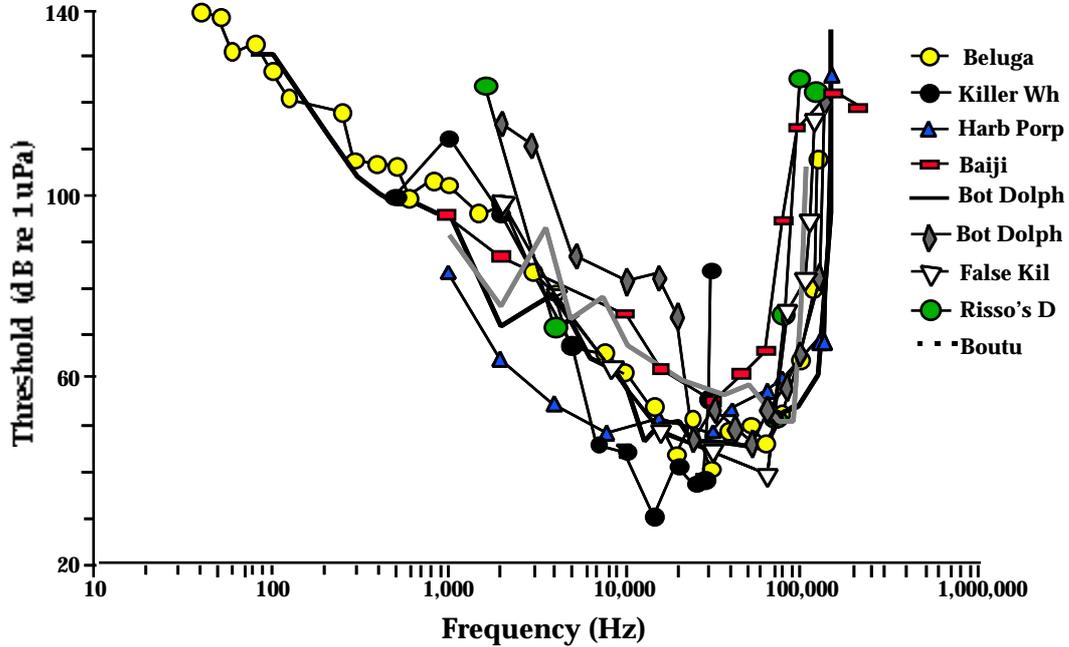


Figure 2 Odontocete behavioural audiograms. (Data compiled from Au, 1993; Richardson et al., 1995; Thomas et al., 1990)

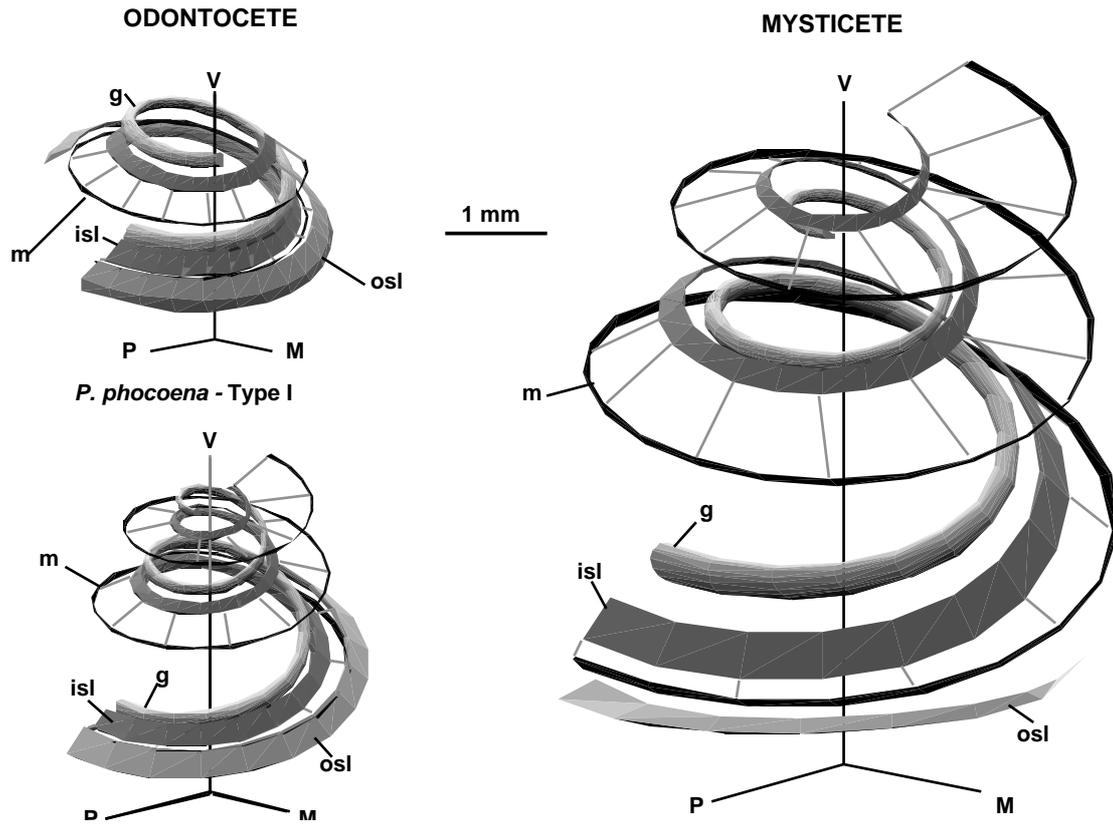


Figure 3 Basilar membrane and spiral laminae distributions in Cetacea. Three-dimensional schematics summarize major cochlear duct components in Type I, Type II, and Type M inner ears. The cochlea are shown inverted from in vivo orientations. (g) spiral ganglion; (isl) inner osseous spiral lamina; (m) basilar membrane; (osl) outer osseous spiral lamina; (M) medial; (P) posterior; (V) ventral.