

in mysticetes can be as great as in odontocetes with membranes in some species ranging from 100 μm at the base (similar to the base in humans) to 1600 μm at the apex. The apical widths in mysticetes are 3X that of human, 3-5X those of most odontocetes, and 1.2X that of elephants, which are known to perceive infrasonics (Payne *et al.* 1986).

Comparing bat, odontocete, and mysticete basilar membrane thickness to width (T:W) ratios is a good exercise in structure-function relationships. T:W ratios are consistent with the maximal high and low frequencies each species hears and with differences in their peak spectra (Ketten and Wartzok, 1990; Ketten, 1992; Ketten, 1997). Echolocators have significantly higher basal ratios than mysticetes, and odontocete ratios are higher than for bats in the basal regions where their ultrasonic echolocation signals are encoded. For example, *Phocoena*, a Type I odontocete, has a basal T:W ratio of 0.9 and a peak frequency of 130 kHz. *Tursiops*, a Type II odontocete, has a T:W ratio of 0.7 and a peak signal of 70 kHz, and *Rhinolophus*, a bat, a 0.3 T:W ratio and a 40 kHz echolocation signal. All three have terminal apical ratios near 0.01. Mysticete T:W ratios range from 0.1 at the base to ~ 0.001 at the apex; i. e., the mysticete basal ratios are equivalent to mid-apical ratios in the three echolocators and decrease steadily to a value one-tenth that of odontocetes at the apex. The exceptionally low apical ratio in Mysticeti is consistent with a broad, flaccid membrane that can encode infrasonics.

A striking feature of odontocete basilar membranes is their association with extensive outer bony laminae. In mammals, ossified outer spiral laminae are hallmarks of ultrasonic ears (Yamada 1953, Reysenbach de Haan 1956, Sales and Pye 1974, Ketten 1984). Thick outer bony laminae are present throughout the basal turn in all odontocetes, and the proportional extent of outer laminae is functionally correlated with odontocete ultrasonic frequency ranges (Ketten and Wartzok 1990). In the basal, high frequency region of the cochlea, odontocete basilar membranes resemble thick girders, stiffened by attachments at both margins to a rigid bony shelf. In Type I echolocators with peak frequencies above 100 kHz an outer lamina is present for 60% of the cochlear duct (Figure 6). Type II echolocators with lower peak frequencies have a bony anchor for $\sim 30\%$ of the duct. The Type I basilar membrane therefore is coupled tightly to a stiff ledge for twice as much of its length as a Type II membrane. If Type I and Type II membranes have similar thickness:width ratios, a Type I cochlea with longer outer laminae would have greater membrane stiffness and higher resonant frequencies than an equivalent position in a Type II membrane without bony support. Both membrane ratios and the extent or proportion of auxiliary bony membrane support are important mechanistic keys to how odontocetes achieve ultrasonic hearing despite ear size.

Both inner and outer laminae are present in mysticete cochleae but they are morphologically and functionally very different from those of odontocetes. Mysticete outer laminae are narrow spicules located on the outer edge of the spiral ligament. They do not attach to the basilar membrane. The broad, thin mysticete basilar membrane attaches only to a flexible spiral ligament. It is likely that the spike-like outer lamina in mysticetes is a remnant of an ancestral condition rather than a functional acoustic structure and that low basilar membrane ratios and large Organ of Corti mass are the principal structural determinants of mysticete hearing ranges. To date, few mysticete species have been analyzed for very low frequency sensitivity, but the inner and middle ear anatomy argues strongly that they are low to infrasonic specialists.

Pinnipeds

Outer Ear

Pinniped ears are less derived than cetacean ears. The external pinnae are reduced or absent. Ear canal diameter and closure mechanisms vary widely in pinnipeds, and the exact role of the canal in submerged hearing has not clearly been determined. Otariids have essentially

terrestrial, broad bore external canals with moderate to distinctive pinnae. Phocids, particularly *M. angustirostris*, spend more time in water than otariids and have only a vestigial cartilaginous meatal ring, no pinnae, and narrow ear canals (Ketten and Schusterman, unpublished). Although the phocids have no external pinna, it is not yet known which species normally have air-filled vs. partial to fully blocked external canals. No specialized soft tissue sound paths for underwater hearing been clearly demonstrated in seals.

An obvious amphibious adaptation in phocid ears is that the external canal is well-developed and has a ring of voluntary muscle that can close the meatus (Møhl 1967, Repenning 1972). It has been suggested that seal middle ears are capable of operating entirely liquid-filled (Repenning 1972) and that various soft tissue attachments to the ossicles are related to the operation of a liquid-filled middle ear or for enhancing high-frequency sensitivity in water (Ramprashad *et al.* 1972, Renouf 1992), but neither of these suggestions is consistent with the level of development of the external canal or the size and development of the Eustachian tube. Whether the external canal remains patent and air-filled, collapses, or becomes flooded during dives remains a heavily debated subject. The ear canal contains a corpus cavernosum (cavernous epithelium) analogous to that in the middle ear, which may close the canal and regulate air pressures during dives (Møhl 1968, Repenning 1972). There are strong theoretical arguments for each position. Flooding the canal would provide a low impedance channel to the tympanic membrane, but then directing sound input to only one window of the cochlea becomes a problem. If the middle ear is fluid-filled, the oval and round windows can receive simultaneous stimulation that would interfere with normal basilar membrane response. However, if the canal remains air-filled, it poses the problem of an impedance mismatch that could make the canal less efficient for sound conduction to the middle and inner ear than surrounding soft tissues when the animal is submerged. To date, there is no clear evidence for specialized soft tissues, like those found in odontocetes, and no direct measures of the shape of the ear canal when submerged.

The position and attachment to the skull of the tympanic and periotic bones in pinnipeds is not significantly different from that of land mammals. The middle ear space is encased in a tympanic bulla, a bulbous bony chamber with one soft-walled opening, the tympanic membrane. The tympanic bulla is fused to the periotic. Both have partially or fully ossified articulations with the skull. These connections are less rigid than those in some land mammals, but the ears are not as clearly detached (and acoustically isolated) as those of cetaceans.

Middle Ear

Pinniped middle ears have a moderate layer of cavernous tissue, but it is less developed than that of cetaceans (Møhl 1968, Ramprashad *et al.* 1972, Repenning 1972, Fleischer 1978). Pinniped ossicular chains are diverse: those in otariids resemble terrestrial carnivores; ossicles of phocids are more massive but with large species variation in shape (Doran 1879, Fleischer 1978), which suggests a wider range of peak frequencies and more emphasis on lower frequency reception than in otariids. Although some authors indicate phocids have small eardrums (Repenning 1972) the size is not significantly different from that of equivalent mass land mammals. The oval and round window areas in terrestrial mammals are of approximately the same size. In pinnipeds, the oval window can be one-half to one-third the size of the round window. Eardrum to oval window ratios have been cited frequently as a factor in middle ear gain, but this association is still being debated (Rosowski, 1994), and depending upon the exact size distributions among these three membranes in each pinniped species, there could be wide differences in middle ear amplification among pinnipeds.

Inner Ear

Relatively few pinniped inner ears have been investigated and published data that are available are largely descriptive (Ramprashad *et al.* 1972; Solntseva 1990). Most pinnipeds have inner ears that resemble terrestrial high frequency generalists; *i.e.*, multiple turn spirals with partial laminar support. Preliminary data on larger species suggest they may have some low frequency adaptations consistent with their size. There is no indication of extensive adaptation for either high ultrasonic or infrasonic hearing. Pinnipeds have one feature in common with cetaceans; *i.e.*, a large cochlear aqueduct. Møhl (1968) suggested that this would facilitate bone conduction, but the mechanism is not clear, nor is it consistent with equally large aqueducts in odontocetes.

Sirenians

Anatomical studies of sirenian ears are largely descriptive (Robineau 1969, Fleischer 1978, Ketten *et al.* 1992). Like Cetacea, they have no pinnae. Also, the tympano-periotics are constructed of exceptionally dense bone, but like pinnipeds (and unlike odontocetes), manatee ear complexes are partly fused to the inner wall of the cranium. Neonate ears vary less than 20% in shape and size from adult specimens; consequently, the ear complex is disproportionately large in young manatees and can constitute 14% of skeletal weight (Domning and de Buffrénil 1991).

Outer Ear

Exact sound reception paths are not known in manatees. The unusual anatomy of the zygomatic arch, combined with its relation to the squamosal and periotic have made it a frequent candidate for a sirenian analogue to the odontocete fat channels. The periotic is tied by a syndesmotic (mixed fibrous tissue and bone) joint to the squamosal which is fused to the zygomatic process which is, in turn, a highly convoluted, cartilaginous labyrinth filled with lipids. The zygomatic is, in effect, an inflated, oil-filled, bony sponge that has substantial mass but less stiffness than an equivalent process of compact bone (Domning and Hayek 1986, Ketten *et al.* 1992). In the Amazonian manatee, the best thresholds in evoked potential recordings were obtained from probes overlying this region (Bullock *et al.* 1980, Klishin *et al.* 1990), but no clear acoustic function has been demonstrated

Middle Ear

The middle ear system of sirenians is large and mass dominated but the extreme density of the ossicles adds stiffness (Fleischer 1978, Ketten *et al.* 1992). The middle ear cavity, as in other marine mammals, is lined with a thick, vascularized fibrous sheet. The ossicles are loosely joined and the stapes is columnar, a shape that is common in reptiles but rare in mammals and possibly unique to manatees. The tympanic membrane is everted and supported by a distinctive keel on the malleus. Deeply bowed, everted tympanic membranes, epitomized by the fibrous "glove finger" in mysticetes, are common in marine mammals but are relatively rare in non-aquatic species. Like eardrum of cats, the manatee tympanic membrane has two distinct regions, implying membrane response patterns are frequency-dependent (Pickles 1982). The tympanic-oval window ratio is approximately 15:1 in *T. manatus*, which places it mid-way between that of humans and elephants (Ketten *et al.* 1992, Rosowski 1994). Chorda tympani, a branch of the facial nerve (cranial nerve VII) which traverses the middle ear cavity, is relatively large in manatees. It crosses the middle ear but has no known auditory function. In humans, chorda tympani is ~10% of the facial nerve, conveys taste from the anterior two-thirds of the tongue, and carries parasympathetic pre-ganglionic fibers to the salivary glands. In *T. manatus*, chorda tympani forms 30% of the facial nerve bundle.

Inner Ear

The sirenian inner ear is a mixture of aquatic and land mammal features. Anatomically, *T. manatus* inner ears are relatively unspecialized. The cochlea has none of the obvious features related to ultra- or infra-sonic hearing found in cetacean ears. Basilar membrane structure and neural distributions are closer to those of pinnipeds or some land mammals than to those of cetaceans (Ketten *et al.* 1992). The outer osseous spiral lamina is small or absent and the basilar membrane has a small base to apex gradient. At the thickest basal point, the membrane is approximately 150 μm wide and 7 μm thick; apically it is 600 μm by 5 μm . The manatee therefore has a relatively small basilar membrane gradient compared to cetaceans, which is consistent with the audiometric profile and 7 octave hearing range recently reported for *T. manatus* (Gerstein *et al.* 1993). Spiral ganglion cell densities are low compared to odontocetes (500/mm), but auditory ganglion cell sizes (20 μm X 10 μm) are larger than those of many land mammals.

Fissipeds

Remarkably little is known about sea otter, *Enhydra lutris*, hearing even in comparison to the sirenians.

E. lutris has a well-defined external ear flap and a canal which is open at the surface. Kenyon (1981) indicated that the pinnae fold downward on dives, which suggests the canal is at least passively closed during dives, but there are no data on whether specialized valves are associated with the ear canal like those found in pinnipeds. Otter auditory bullae are attached to the skull and resemble those of pinnipeds. CT scans of *E. lutris* (Ketten, unpublished) show that their middle and inner ears are grossly configured like ears of similarly sized terrestrial carnivores, with the same orientation and 2.5 turn distribution. Spector (1956) and Gunn (1988) both indicated an upper frequency limit of 35 kHz for common river otters which have similar ear anatomy.

Mechanisms of Acoustic Trauma

Temporary and Permanent Threshold Shifts

Noise trauma is a well-investigated phenomenon for air-adapted ears (see Lehnhardt, 1986; Lipscomb, 1978; and Richardson, *et al.*, 1991 for reviews). For the sake of completeness in the following discussion, noise trauma has been divided into lethal and sublethal impacts. Lethal impacts are those that result in the immediate death or serious debilitation of the majority of animals in or near an intense source; i.e., profound injuries related to shock wave or blast effects which are not, technically, pure acoustic trauma. Lethal impacts are discussed briefly at the end of this section. Sublethal impacts are those in which a hearing loss is caused by exposures to sounds that exceed the ear's tolerance to some acoustic parameter; i.e., auditory damage occurs from metabolic exhaustion or over-extension of one or more inner ear components. Of course, sublethal impacts may ultimately be as devastating as lethal impacts, causing death indirectly through behavioural reactions, such as panic, as well as impaired foraging or predator detection, but the potential for this type of extended or delayed impact from any sound source is not well understood for any mammal.

To determine whether any one animal or species is subject to a sublethal noise impact from a particular sound requires understanding how its hearing abilities interact with that sound. Basically, any noise at some level has the ability to damage hearing by causing decreased

sensitivity. The loss of sensitivity is called a threshold shift. Not all noises will produce equivalent damage at some constant exposure level. The extent and duration of a threshold shift depends upon the synergistic effect of several acoustic features, including how sensitive the subject is to the sound. Most recent research efforts have been directed at understanding the basics of how frequency, intensity, and duration of exposures interact to produce damage rather than interspecific differences: that is, what sounds, at what levels, for how long, or how often will commonly produce recoverable (TTS - Temporary Threshold Shift) vs permanently (PTS) hearing loss.

Three fundamental effects are known at this time:

- 1) the severity of the loss from any one signal may differ among species.
- 2) for pure tones, the loss centers around the incident frequency.
- 3) for all tones, at some balance of noise level and time, the loss is irreversible.

Hearing losses are recoverable (TTS - temporary threshold Shift) or permanent (PTS) primarily based on extent of *inner* ear damage the *received* sound causes (see Lipscomb 1978, Lehnhardt 1986, Richardson *et al.* 1991 for reviews). Temporary threshold shifts (TTS) will be broad or punctate, according to source characteristics. The majority of studies have been conducted with cats and rodents, using relatively long duration stimuli (> 1 hr.) and mid to low frequencies (1-4 kHz) (see Lehnhardt, 1986, for summary). Inner ear damage location and severity are correlated with the power spectrum of the signal in relation to the sensitivity of the animal. Virtually all studies show that losses are centered around the peak spectra of the source and are highly dependent upon the frequency sensitivity of the subject. For narrow band, high frequency signals, losses typically occur in or near the signal band, but intensity and duration can act synergistically to broaden the loss.

It has also been established that repeated exposures to TTS level stimuli without adequate recovery periods can induce permanent, acute threshold shifts. Liberman (1987) showed that losses were directly correlated with graded damage to the outer and inner hair cells, and that the majority of cells recover. With short duration, narrow band stimuli, recovery periods can vary from hours to days. In effect, the duration of a threshold shift, is correlated with both the length of time and the intensity of exposure. In general, if the duration to intense noise is short and the noise is narrow, the loss is limited and recoverable. Based on both the available experimental data and on human data from occupational hearing loss, moderate to protracted exposures to a signal intensity of 80 dB or more over the individual threshold at each frequency for land species is required for significant threshold shifts (see NIH./CDC, 1990; Yost, 1994 for overview). These findings led to the current allowable limit of 80-90 dB re 20 μ Pa for human workplace exposures for broad spectrum signals, as well as an allowance of the 3-5 dB increase in exposure as a trade-off for halving of exposure times (Lehnhardt, 1986). While the commonality of 80 dB suggests that TTS is a dynamic range dependent phenomenon which is probably related to fundamental mammalian inner ear mechanisms, this specific dB criterion for exposure limits cannot be supported nor refuted with current data for marine mammals, particularly since some marine species have inner ear adaptations that could alter these responses (see Marine Mammal Issues section).

Given the complex nature of the interaction of species-specific hearing parameters with each signal feature a simplistic rule for species dependent impacts based on any one acoustic feature or hearing characteristic is not possible, as is shown in a quick review of Table 3. Some broad trends do emerge, however, from inter-species comparisons of sources that induce TTS in air.

At the grossest level, TTS effects from approximately equivalent exposures appear to be inversely related to weight or mass; i.e., effects were less pronounced in humans than in cat or in chinchilla, but this may be a secondary effect of frequency sensitivities differing also with animal

size. The majority of effects appear to be species independent, suggesting that basic cochlear mechanisms may be the dominating factor. Effects that were common to all species were the following:

1. Shifts were strongly dependent on interactions of timing, level, and frequency.
2. Cumulative or compound effects are common.
2. Asymptotic shifts appear to depend on similar metabolic and mechanical fatigue phenomena.
3. Hearing impaired individuals have approximately the same absolute exposure limit for TTS as unimpaired individuals, which is manifested in an apparently smaller exposure window prior to TTS.
4. Effects spread primarily upward in frequency, which is a reflection of the basilar membrane's tonotopic organization and the asymmetric distribution of the traveling wave envelope (Fig. 4).
5. Frequency discrimination is unaffected.
6. Temporal integration is reduced.

Effects that showed strong species dependence were:

1. Loss at a particular frequency are correlated with species sensitivity.
2. Losses at all frequencies are correlated with metabolic, hair cell, and neural differences throughout the cochlea.

The majority of PTS effects are minimally species dependent, but nevertheless equally complex. One important aspect of PTS is that signal rise-time and duration of peak pressure are significant factors. If the exposure is short, hearing is recoverable; if long, or has a sudden, intense onset and is broadband, hearing, particularly in the higher frequencies, can be permanently lost (PTS). Experimentally, PTS is induced with multi-hour exposures to narrow band noise. In humans, PTS results most often from protracted, repeat intense exposures (*e.g.*, occupational auditory hazards from background noise) or sudden onset of intense sounds (*e.g.*, rapid, repeat gun fire). Sharp rise-time signals have been shown also to produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water (Lipscomb, 1978; Lehnhardt, 1986; Liberman, 1987). Hearing loss with aging (presbycusis) is the accumulation of PTS and TTS insults to the ear. Typically, high frequencies are lost first with the loss gradually spreading to lower frequencies over time.

In experiments, multi-hour exposures to narrow band noise are used to induce PTS. As noted above, most mammals with air-adapted ears incur losses when the signal is 80 dB over threshold. TTS has been produced in humans for frequencies between 0.7 and 5.6 kHz (our most sensitive range) from underwater sound sources when received levels were 150-180 dB re 1 μ Pa (Smith and Wojtowicz 1985, Smith *et al.* 1988). Taking into account differences in measurements of sound pressure in air vs. water (equations 4 and 5), these underwater levels are consistent with the 80-90 dB exposure levels that induce TTS in humans at similar frequencies in air. Sharp rise-time signals produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water (Lipscomb 1978, Lehnhardt 1986).

Blast Effects

Simple intensity related loss is not synonymous with blast injury. 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 generally result from a single exposure to an explosive shock wave which has a compressive phase with a few microseconds

initial rise time to a massive pressure increase over ambient followed by a rarefactive wave in which pressure drops well below ambient.

Blast injuries may be reparable or permanent according to the severity of the exposure and are conventionally divided into three groups based on severity of symptoms, which parallel those of barotrauma:

<u>MILD - Recovery</u>	<u>MODERATE - Partial loss</u>	<u>SEVERE - Permanent loss - death</u>
Pain	Otitis media	Ossicular Fracture/Dislocation
Vertigo	Tympanic membrane rupture	Round/Oval window rupture
Tinnitus	Tympanic membrane hematoma	CSF leakage into middle ear
Hearing Loss	Serum-blood in middle ear	Cochlear and saccular damage
Tympanic tear	Dissection of mucosa	

Moderate to severe stages result most often from blasts, extreme intensity shifts, and trauma; i.e., explosions or blunt cranial impacts that cause sudden, massive systemic pressure increases and surges of circulatory or spinal fluid pressures (Schuknecht, 1993). Hearing loss in these cases results from an eruptive injury to the inner ear; i.e., with the rarefactive wave of a nearby explosion, cerebrospinal fluid pressures increase and the inner ear window membranes blow out due to pressure increases in the inner ear fluids. Inner ear damage frequently coincides with fractures to the bony capsule of the ear or middle ear bones and with rupture of the eardrum. Although technically a pressure induced injury, hearing loss and the accompanying gross structural damage to the ear from blasts are more appropriately thought of as the result of the inability of the ear to accommodate the sudden, extreme pressure differentials and over-pressures from the shock wave.

At increasing distance from the blast, the effects of the shock wave lessen and even though there is no overt tissue damage, mild damage with some permanent hearing loss occurs (Burdick, 1981, in Lehnhardt, 1986). This type of loss is generally called an asymptotic threshold shift (ATS) because, as was found with protracted exposures in TTS experiments, ATS derives from a saturation effect. Like TTS, the hair cells are damaged, but as in PTS, recovery is unlikely to take place. Because ATS depends upon complex interactions of rise time and wave form, not simply intensity at peak frequency, hearing losses are typically broader and more profound than simple PTS losses.

There is no well defined single criterion for sublethal ATS from blasts (Roberto, et al., 1989), but eardrum rupture, which is common to all stages of blast injury, has been moderately well investigated. Although rupture *per se* is not synonymous with permanent loss (eardrum ruptures have occurred at as little as 2.5 kPa overpressure and are strongly influenced by the health of the ear), the incidence of tympanic membrane rupture is strongly correlated with distance from the blast (Kerr, & Byrne, 1975). As frequency of rupture increases so does the incidence of permanent hearing loss. In zones where >50% tympanic membrane rupture occurred, 30% of the victims had long term or permanent loss.

Recent experimental work has shown that weighted sound exposure level is a more robust predictor of permanent loss than peak pressure (Patterson, 1991). Data with weighted levels are rare; overpressure data are more common and have been shown to be highly correlated with received levels (Roberto *et al.*, 1989). In general, complex and fast-rise time sounds cause ruptures at lower overpressures than slow-rise time waveforms, and smaller mammals will be injured by lower pressures larger animals. Of the animals tested to date, sheep and pig have ears anatomically closest to those of whales and seals. The air-based data for pigs and sheep imply that overpressures <70 kPa are needed to induce 100% tympanic membrane rupture. However, cross-study/cross-species comparisons and extrapolations are risky because of radically different experimental conditions as well as differences in acoustic energy

transmission in the air and water. The data available for submerged and aquatic animals imply that lower pressures in water than in air induce serious trauma (Myrick et al., 1989; see also summary in Richardson, *et al.* 1991). For submerged terrestrial mammals, lethal injuries have occurred at overpressures >55 kPa (Yelverton, 1973, in Myrick, *et al.*, 1989; Richmond, *et al.*, 1989). In a study of Hydromex blasts in Lake Erie the overpressure limit for 100% mortality for fish was 30 kPa (Chamberlain, 1976). The aquatic studies imply therefore that overpressures between 30 and 50 kPa are sufficient for a high incidence of severe blast injury. Minimal injury limits in both land and fish studies coincided with overpressures of 0.5 to 1 kPa.

Marine Mammal Issues

Major impacts from noise can be divided into direct physiologic effects, such as permanent vs. temporary hearing loss, and those that are largely behavioral, such as masking, aversion, or attraction. Although there is no substantial research accomplished in any of these areas in marine mammals, behavioral effects have been at least preliminarily investigated through playback and audiometric experiments, while marine mammal susceptibility to physiologic hearing loss is virtually unexplored. Despite increasing concern over the effects on marine mammals of man-made sound in the oceans, we still have little direct information about what sound frequency-intensity combinations damage marine mammal ears, and at present there are insufficient data to accurately determine acoustic exposure guidelines for any marine mammal.

Is acoustic trauma even moderately debatable in marine mammals? Recalling the paradox mentioned earlier, there are a variety of reasons to hypothesize that marine mammals may have evolved useful adaptations related to noise trauma. Vocalizations levels in marine mammals are frequently cited as indicating high tolerance for intense sounds. Some whales and dolphins have been documented to produce sounds with source levels as high as 180 to 220 dB re $1 \mu\text{Pa}$ (Richardson *et al.*, 1991; Au, 1993). Vocalizations are accepted indicators for perceptible frequencies because peak spectra of vocalizations are near best frequency of hearing in most species, but it is important to recall that the two are not normally precisely coincident.

It must be borne in mind also that animals, including humans, commonly produce sounds which would produce discomfort if they were received at the ear at levels equal to levels at the production site, and arguments that marine mammals, simply by nature of their size and tissue densities, can tolerate higher intensities are not persuasive. First, mammal ears are protected from self-generated sounds not only by intervening tissues (head shadow and impedance mismatches) but also by active mechanisms (eardrum and ossicular tensors). These mechanisms do not necessarily provide equal protection from externally generated sounds largely because the impact is not anticipated as it is in self-generated sounds. Our active mechanisms are initiated in coordination and in anticipation of our own sound production. Just as the level of a shout is not indicative of normal or tolerable human hearing thresholds, source level calculations for vocalizations recorded in the wild should not be viewed as reliable sensitivity measures. As was indicated earlier, while there is little question of anomalous dysfunction of the middle ear in pinnipeds, middle ear function continues to be debated for cetaceans. However, it is very important to recall also that cetaceans do have very well developed middle ear anatomies, including stapedial ligaments (Ketten, 1984; 1992) which argues that they have the capability for middle ear attenuation responses. Further, 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. As noted earlier, ear separation in a bottle-nosed dolphin is acoustically equivalent to that of a rat when the distances are corrected for the speed of sound in water. Exactly how head size in water affects attenuation of incident sound at the inner ear has not been investigated and remains an important open question.

Data from several pilot studies may, however, provide some useful insights into both facets of the paradox. In one investigation (detailed below, Ketten et al, 1993; Lien et al. 1993), ears from humpbacks that died following underwater explosions had extensive mechanical trauma while animals that were several kilometers distant from the blasts and at the surface showed no significant behavioral effects. These findings indicate adaptations that prevent barotrauma do not provide special protection from severe auditory blast trauma, but it remains unclear whether lower intensity purely acoustic stimuli induce temporary and/or acute threshold shifts in marine mammals.

A second study compared inner ears from one long-term captive dolphin with a documented hearing loss with the ears of one juvenile and two young adult dolphins (Ketten et al., 1995). CT, MRI, and histologic studies of the oldest dolphin ears showed cell loss and laminar demineralization like that found in humans with presbycusis, the progressive sensorineural hearing loss that accompanies old age. The location and degree of neural degeneration in this animal implied a substantial, progressive, hearing loss beginning in the high frequency regions. This too is consistent with the pattern commonly observed in humans. Frequency-position estimates of the elder animal's hearing loss done blind; i.e., without prior knowledge of its audiogram, predicted a profound loss for all frequencies >58 kHz. A review of the animal's behavioral audiogram subsequently showed that over a 12 year period this dolphin's hearing curve shifted from normal threshold responses for all frequencies up to 165 kHz to no functional hearing over 60 kHz prior to his death at age 28. For this animal at least, the conclusion was that significant hearing loss had occurred attributable only to age-related changes in the ear. Similar significant differences in the hearing thresholds of two *Zalophus* have also been reported by Kastak and Schusterman (1995) that are consistent with age-related hearing differences between the animals but which are also consistent with protracted exposures to construction noise.

Micrographs from young adult dolphin ears show several important cochlear duct cellular adaptations that are markedly different from those of conventional land mammals and seals. Transmission electron micrographic studies revealed dolphins have active fibrocytes in the spiral ligament and four times as many cell layers in stria vascularis as any other mammal. The stria is considered to be the principal dictator of mammalian cochlear metabolism. If these results are confirmed in other dolphin ears, these structural differences could mean dolphins have faster hair cell recovery times than air adapted ears and may therefore be less subject to temporary threshold shifts than most land animals or pinnipeds.

Unfortunately, these data only beg the question. The problem of hearing loss has not been realistically considered prior to this point in any systematic way in any marine mammal. In fact, the most studied group, odontocetes, have generally been thought of as ideal underwater receivers. A captive animal's age or history is not normally considered in analyzing its auditory responses, and, in the absence of overt data (e.g., antibiotic therapy), we assume a test animal has a normal ear with representative responses for that species. It is not clear that this is both reasonable and realistic. Particularly when data are obtained from one animal, it is important to question whether that hearing curve is representative of the normal ear for that species. The pilot studies noted clearly suggest age and/or exposure to noise can significantly alter hearing in marine mammals. In fact, in some cases (compare the two curves shown in figure 3a for *Tursiops*), "individual differences" that are seen in "normal" audiograms for two animals from the same species may be the result of undetected hearing loss in one of the animals. The fact that some studies show losses in marine mammals consistent with age-related hearing changes and disease considerably complicates the diagnosis and assessment of hearing loss from anthropogenic sources based on small samplings of populations. 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 hearing loss from, for instance, a mass-stranding or fishery coincident with a long-term exposure to an intense source would be appropriate cause for significant concern.

Given the minimal state of marine mammal data, the only comprehensive database that can be brought to bear at this time for predicting physiologic impacts is from acoustic trauma studies of land mammals and fish.

Few reports exist that detail injuries in marine mammals from blast induced trauma. Bohne et al. (1985) reported on inner ear damage in Weddell seals that survived blasts, but they were unable to determine exposure levels or number of exposures for each animal. There are scattered reports of opportunistic examinations of animals exposed to large blasts, including one on otters with extensive trauma from nuclear explosions (Richardson *et al.*, 1991) that concluded that peak pressures of 100-300 psi were invariably lethal. Recently, several humpbacks exposed to TOVEX blasts were shown to have severe blast injuries (Ketten et al., 1993). TOVEX, like Hydromex, is a TNT clone explosive similar to HBX-1 with a detonation velocity of ~7500 m/sec (Ketten, 1994). Received levels in the humpbacks could not be calculated with confidence; however, the charge weights associated with the injuries ranged from 1700 to 5000 kg. The animals died within three days of the blasts, and the extent of the injuries found implied they were close to the blast site. Mechanical trauma in these ears included round window rupture, ossicular chain disruption, bloody effusion of the peribullar spaces, dissection of the middle ear mucosa with pooled sera, and bilateral periotic fractures. These observations are consistent with classic blast injuries reported in humans, particularly with victims near the source who had massive, precipitous increases in cerebrospinal fluid pressure and brain trauma. There was no evidence of ship collision or prior concussive injury in these humpbacks, and no similar abnormalities were found in ears from humpbacks not exposed to blasts. These findings imply that despite adaptations in whales and seals that minimize barotrauma, marine mammals are not immune to blast trauma. Given the similarities of seal and whale ears to land mammal ears, it is clear that explosions and the shock wave and intense transient sound field that result can produce both blast injury and acoustic trauma in marine animals. More important, even though the whale ear is ostensibly a fluid-to-fluid coupler, marine mammals, having retained an air-filled middle ear (Ketten, 1994), are subject to all ranges of compressive-rarefactive/blast injury.

The level of impact from blast will depend on both an animal's location and, at outer zones, on its sensitivity to the residual noise. Factors that are most important for trauma from explosive sources are the following:

1. Topography
2. Proximity of ear
3. Anatomy and health of ear
4. Charge weight and type
5. Rise time
6. Overpressure
7. Pressure and duration of positive pressure phase

Topographic effects for open ocean are minimal for most boat deployed sources. Surface reflections will have a significant effect on the blast and acoustic wave spread patterns at some depth that is largely dependent on detonation depth. This effect also complicates predictions of received levels for animals at surface or within the air-sea boundary layer.

The health of individual ears that may be impacted cannot be estimated in advance. It is reasonable to assume an average distribution. Many explosives (TNT clones and water-gel explosives; e.g., HBX, Tovex, etc.) currently in use have high detonation velocities and are

therefore effectively an instantaneous onset, high peak pressure, broad spectrum blast. Consequently, effects of the acoustic signature and certainly of the blast wave from these charges are likely to be similar in all species in the target area; i.e., individual hearing ranges are largely irrelevant in assessing TTS/PTS and blast effects in the near field, except for those species that have no discrete air pockets.

Although multiple parameters are associated with both lethal and sublethal effects, virtually all studies agree fairly closely on baseline criteria for lethal or compulsory injury zones for fast-rise time, complex waveforms: ~ 30-50 kPa peak overpressure in water and > 180 dB re 20 μ Pa in air (~240 dB re 1 μ Pa in water), (Chamberlain, 1976; Yelverton and Richmond, 1981; Phillips *et al.*, 1989; Richmond, *et al.*, 1989; Myrick, *et al.*, 1989). If, for comparison, the lowest otter impact estimate were chosen (100 psi), the impact range is substantially greater. Depending upon this range of criteria, a lethal impact zone limit for a 1200 lb source could be placed at 40 m. (absolute minimum, land mammal) or 300 m (conservative estimate of 100 psi based on otter observations). For a 10,000 lb. charge, the equivalent min-max limits for a killing ground are 70 m to 800 m. If a conservative average overpressure of ~30 kPa is used as the criterion, the lethality limit for both large charges is approximately 100 m. in comparison to approximately 10 m. and 50 m. for the 9 and 50 lb. charges.

Criteria for differentiating PTS or ATS zones from TTS are less clear. For this discussion, peak pressures of ~150 psi, which are consistent with 50% incidence of eardrum rupture (30% hearing loss) in larger mammals were chosen to define PTS/ATS limits. For a 9 lb. charge, pressures that result in significant auditory damage can be expected along a long axis radius of nearly 50 m. from the source. For a 50 lb charge, the equivalent PTS/ATS radius is nearly 100 m. For the 1200 and 10,000 lb charges, the transitional lethal zones in which serious sublethal injury will predominate are estimated as 300 m and 750 m, respectively. Beyond these zones, the relative incidence of PTS to TTS will largely depend on individual susceptibility. That is, the variables that will determine TTS vs PTS are highly dependent on both species-specific and individual ear factors.

There is consensus in the literature on the criteria for an outer limit for mild TTS zones. 5-15 psi is accepted as the frontier at which TTS and detectable injury become rare (Yelverton and Richmond, 1981; Smith *et al.*, 1985, 1988; Myrick *et al.*, 1989; Roberto *et al.*, 1989). This is also the zone in which the greatest differences are found in effects among charge weights. For 9 lb. charges, moderate incidence of TTS may be expected up to 700 m from the epicenter; the 50 lb TTS zone could extend to 1600 m in contrast to a 5 and 10 km radius from the heavier charges before the acoustic impact could be expected to drop precipitously.

Acoustic Devices, Fisheries, and Mitigation Measures

Potential impacts

Although the remainder of this discussion is concerned with purely physiologic elements of the effects of sound, it is important first to note that acoustic trauma *per se* is only one side of a significant effect coin.

Acoustic trauma is a very real and appropriate physiologic concern. It is also one for which we can obtain a metric that will allow us to provide a usable limit. That is, given that we know sound level X induces TTS while Y induces PTS, for frequency Z in a specific species, we can apply these data to the estimated exposure curve for that species and determine its risk of hearing loss. As discussed earlier, this is the basic principle behind both the 80 dB/5 dB rule currently in use for workplace exposures. Because of the importance of hearing to marine mammals, understanding how man-made sources may impact that sense is an important and

reasonable step towards minimizing adverse impacts from man-made sound sources in the oceans, but it is imperative that we employ a scientifically valid, marine specific meter-stick for underwater exposures.

Above all, it is equally important to consider that sub-trauma levels of sound can have profound effects on individual fitness that propagate to the population level. These effects can take the form of masking of important signals, including echolocation signals, intra-species communication, and predator-prey cues; of disrupting important behaviors through startle and repellence, or of acting as attractive nuisances, all of which may alter migration patterns or result in abandonment of important habitats. Unfortunately, these issues are beyond the scope of this document as well as the expertise of the author and therefore cannot be productively and responsibly discussed here. Nevertheless, it is important to at least note the concern, and above all to suggest that there is a substantial need for field monitoring of behaviors in wild populations in tandem with controlled studies directed at expanding our audiometric data and understanding of acoustic trauma mechanisms.

As indicated earlier, there are no discrete data at this time that provide a direct measure of acoustic impact from a calibrated, underwater sound source for any marine mammal. Preliminary data from work underway on captive cetaceans and pinnipeds (Ridgway, pers. comm.; Schusterman, pers. comm.) suggest that odontocetes may have asymptotic responses while pinnipeds are more similar to land mammals in their dynamic range for threshold shift effects. This response difference as well as the difference in hearing ranges - *if these data are shown to be robust* - suggest that pinnipeds are the more acoustically fragile group from most anthropogenic sound sources and that odontocetes are relatively immune or require substantially higher sound levels to incur TTS.

In terms of the specifics of tuna-marine mammal-echo-ranging device interactions, the principal acoustic concern is to determine a balance of frequencies vs. level vs. duty cycle that will effectively detect and census commercially viable schools at long ranges but will not repel the target species nor harm marine mammals within that sound field. To accomplish these goals it is necessary to determine and balance the following components:

1. What are the effective frequencies for longer range detection? Presumably this will require a moderately low frequency for maximizing distance of detection balanced against a need to detect relatively small targets.
2. What is the hearing curve of the target species for capture? This feature must be considered in order to avoid startle or repellent effects in the fish schools that are to be detected by the source.
3. What are the hearing curves for non-target species within the sound field? This has the same concern as the second component, with a different end objective; i.e., to avoid impact or harassment but is driven also by an additional desire to prevent long-term, multiple exposure effects that can compound the probability of hearing loss.

Put simply, the device must be able to detect fish without cueing them but at the same time avoid frequency-intensity-sensitivity combinations likely to impact non-targeted, acoustically fragile species. Detection devices proposed recently (see Nero, 1996; Rees, 1996; Denny et al. 1997) commonly employ frequencies in the low to mid-sonic ranges (50-5000 Hz) with a wide set of emission algorithms, including repeat pulsed signals, and, in at least one scenario, explosive/high intensity impulsive source. Source levels proposed vary widely but can range as high as 235 dB re 1 μ Pa at 1 m. These spectra are coincident with virtually all marine mammal hearing ranges, and ironically may be well perceived by at least some fish species. In fact, for clupeids, recent data show a coincident high frequency sensitivity that suggests convergence of

predator and prey auditory systems at both mid-sonic (2-4 kHz) and ultrasonic (20-40 kHz) ranges (Popper, 1997). Rather than complicating the issue, this coincidence may prove beneficial by driving the frequency choice in the same direction; i.e., avoiding these frequencies may maximize the utility of the device for finding fish without disturbance of the school while minimizing the probability of its impact on marine mammals.

Mitigation measures

For all species, the first issue in the proposed devices is signal shape, or rise time and peak spectra. As discussed earlier, impulsive sound has substantial potential for inducing broad spectrum, compounded acoustic trauma; i.e., an impulsive source can produce greater threshold changes than a non-impulsive source with equivalent spectral characteristics. Consequently, impulse is a complicating feature that may exacerbate the impact. Conventional suggestions for minimizing such effects are to ramp the signal, narrow the spectra, lower the pressure, and/or alter the duty cycle to allow recovery and decrease impact. Once again, however, it must be recalled which, if any, of these measures is important to the marine mammal ear has not been determined.

Given that impulsive noise can be avoided, the question devolves largely to the coincidence of signal characteristics with species sensitivities. High intensity, ultrasonic devices of course have enormous potential for serious impact on virtually every odontocete and their deployment in pelagic fisheries raises the greatest concern after impulse or explosive sources. Such devices are relatively unlikely to be employed, however, because they are unsuitable for longer range detection. With high frequency sonic range devices, the possibility of profound impact from disruption or masking of odontocete communication signals must certainly be considered, as well as the possibility of coincident impacts to pinnipeds. Because the majority of devices proposed use frequencies below ultra or high sonic ranges, odontocetes may be the least likely to be impacted species. Most odontocetes have relatively sharp decreases in sensitivity below 2 kHz (see fig. 3). If frequencies below 2 kHz are employed with a non-impulsive wave-form, the potential for impacting odontocetes is likely to be drastically reduced, but it must also be borne in mind that it is non-zero. In every case, the difference between some to little or no significant physiologic impact will depend upon received levels at the individual ear. For the purposes of general discussion, a theoretical comparison is shown in Figure 7 for marine mammals audiograms compared with a human audiogram and with source levels of major anthropogenic underwater noise sources. Because mechanisms and onset levels of TTS and PTS are still unresolved for marine mammals, this curve is presented largely for the purposes of gross comparisons of spectra of different sources with animal hearing ranges and is not intended to suggest mitigation guidelines.

Mysticetes and the majority of pinnipeds have substantially greater potential than odontocetes for direct acoustic impact from low to mid-sonic range devices. However, depending upon the diving and foraging patterns of these animals in comparison to the sound field propagated to detect fish, the risks to mysticetes and the majority of pinnipeds may be substantially less than a simple sound analysis would imply. That is, given that substantial numbers of these marine mammal groups are either not present or are infrequently found in the areas of tuna fisheries, there is little probability of any one animal encountering a signal with an intensity and a period of time that will induce acoustic trauma, despite their better absolute sensitivity to the signal.

Mitigation, like estimation of impact, requires a case by case assessment. At this time we have insufficient data to accurately predetermine the underwater acoustic impact from any anthropogenic source. Consequently, it is not possible to definitively state what measures will ameliorate any one impact.

For the immediate future and in the absence of needed data, a best faith effort at mitigation must be founded on reasoned predictions from land mammal and the minimal marine mammal and fish data available. It is reasonable to expect, based on the similarities in ear architecture and in the shape of behavioral audiograms between marine and land mammals, that marine mammals will have similar threshold shift mechanisms and will sustain acute trauma through similar mechanical loads. Therefore, fast-rise impulse and explosive sources are likely to have greater or more profound impacts than narrow band, ramped sources. Similarly, we can expect that a signal that is shorter than the integration time constant of the odontocete, mysticete or pinniped ear or which has a long interpulse interval has less potential for impact than a protracted signal; however, simply pulsing the signal is not a sufficient strategy without considering adequate interpulse recovery time. Strategies, such as compression, that allow the signal to be near or below the noise floor are certainly worth exploring. Certainly, no single figure can be supplied for these values for all species. Because of the exceptional variety in marine mammals ears and the implications of this variety for diversity of hearing ranges, there is no single frequency or combination of pulse sequences that will prevent any impact. It is however, reasonable, because of species-specificities, to consider minimizing effects by avoiding overlap with the hearing characteristics of species that have the highest probability of encountering the signal for each device deployed.

Research Needs

To that end, substantially better audiometric data are required. This means more species must be tested, with an emphasis on obtaining audiograms on younger, clearly unimpaired animals and repeat measures from multiple animals. Too often our data base has been undermined by a single measure from an animal that may have some impairment. It is equally important to obtain some metric of the hearing impairments present in normal wild populations in order to avoid future over-estimates of impact from man-made sources. To obtain these data requires a three-pronged effort of behavioural audiograms, evoked potentials on live strandings, and post-mortem examination of ears to determination of the level of "natural" disease and to hone predictive models of hearing capacities. It should be noted also that equivalent auditory databases are lacking for most commercially important fish species. Again, all of the recommendations presented are applicable for the fish stocks of interest in this endeavor, and coordinated or tandem research on both the commercially targeted and protected species that may be impacted may be the most productive approach to the problem of determining an effective frequency range for a device that balances effectiveness in fish censusing against minimal impact.

The most pressing research need in terms of marine mammals is data from live animals on sound parameters that induce temporary threshold shift and aversive responses. Indirect benefits of behavioral experiments with live captive animals that address TTS will also test the hypotheses that cellular structure in the inner ear of odontocetes may be related to increased resistance to auditory trauma. Combined data from these two areas could assist in determining whether or to what extent back-projections from land mammal data are valid.

Biomedical techniques, such as ABR and functional MRI, offer considerable potential for rapidly obtaining mysticete and pinniped hearing curves. Evoked potential studies of stranded mysticetes are of considerable value but must also carry the caveat of determining how reliable is a result from a single animal that may be physiologically compromised. Post-mortem studies should be considered on any animal that is euthanized after an ABR with the goal of both providing data about the normality of the ear and supplying feedback to modeling studies of hearing ranges. Otoacoustic emission experiments are not considered to be a viable approach for cetaceans; they may provide basic hearing data in pinnipeds but are technically difficult.

Playback studies are a well-established technique but because of the uncertainties about individually received levels they may not considerably advance our knowledge of acoustic impact *per se* unless tied to dataloggers or very accurate assessments of the animal's sound field. Tagging and telemetry are valuable approaches particularly if linked to field or video documentation of behavior that is coordinated with recordings of incident sound levels at the animal. Telemetric measurement of physiological responses to sound; e.g., heart rate, may be valuable, but little is currently known of how to interpret the data in terms of long term impact.

Permanent threshold shift data may be obtainable by carefully designed experiments that expose post-mortem marine mammal specimens to either intense sound and explosive sources since these effects are largely detectable through physical changes in the inner ear. These studies would also substantially increase the species diversity of the available data base because most marine mammal species will not be testable with conventional live animal audiometric techniques. Lastly, because many impact models depend upon assumptions about received levels at the ear, these projections would clearly be enhanced by basic measures on specimens of the underwater acoustic transmission characteristics of marine mammal heads and ears.

Summary

Marine mammals are acoustically diverse with wide variations not only in ear anatomy, but also in frequency range and amplitude sensitivity. In general their hearing is as acute as that of land mammals, and they have wider ranges. Although marine mammals exhibit habitat and size related hearing trends that parallel those of land mammals in that larger species tend to have lower frequency ranges than smaller species, the majority of species have some ultrasonic capability and there are multiple specialized, auditory adaptations in odontocetes that provide large species exceptional high frequency hearing capabilities. Both mysticetes and odontocetes appear to have soft tissue channels for sound conduction to the ear. Sirenians may have analogous adaptations. It remains unclear whether pinnipeds use soft tissue channels in addition to the air-filled external canal for sound reception. Comparisons of the hearing characteristics of otarids and phocids suggest that there are at least two types of pinniped ears, with phocids being better adapted for underwater hearing. Sea otter ears are the most similar to those of land mammals of all marine mammal ears that have been investigated, but they do have some aquatic-related features, and it is not known how well they hear underwater. No data are available on polar bear hearing.

All marine mammals have middle ears that are heavily modified structurally from those in terrestrial mammals in ways that reduce the probability of barotrauma. The end product is an acoustically sensitive ear that is simultaneously adapted to sustain moderately rapid and extreme pressure changes, and which appears capable of accommodating acoustic power relationships several magnitudes greater than in air. It is possible that these special adaptations may coincidentally provide acoustically protective mechanisms that lessen the risk of injury from high intensity noise, but no behavioral or psychometric studies are yet available that directly address this issue.

One irony of sensory system research is that the more tools we invent to explore animals and their senses the greater the hints we receive that our reach is still too short. How extensive is our research arm currently? We know marine mammals use frequencies we cannot hear but we can technologically detect and transduce their frequency range into something we can analyze. Tools that help us probe and visualize how marine mammal sounds are produced and processed, like fast biomedical imaging, are helpful but still comparatively limited. The anatomical sophistication and the extensive cortical space allotted to temporal divisions of the brain in virtually all cetaceans, including baleen whales, implies a more important role for auditory processing than we have previously expected. Our greatest short-coming is that we cannot yet

measure or observe reliably and frequently in the truly relevant environment for marine mammals: at depth in a free-ranging animal but technology that will make these studies routine are rapidly becoming available - and ironically will certainly have to employ acoustics to obtain definitive answers.

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Table 1. Marine Mammal Sound Production Characteristics
(Data compiled from Popper 1980; Watkins and Wartzok 1985; Richardson *et al.* 1995)

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Maximum Energy (kHz)	Source Level (dB re 1 µPa)	References (Partial references only for some species)
Cetacea						
Odontoceti						
Delphinidae						
<i>Cephalorhynchus commersonii</i>	Commerson's dolphin	pulsed sounds	<10	0.2-5	-	Watkins and Schevill 1980; Dziedzic and De Buffrenil 1989
		clicks	-	6	-	Dziedzic and De Buffrenil 1989
		click	116-134	-	160	Kamminga and Wiersma 1981; Shochi <i>et al.</i> 1982; Evans <i>et al.</i> 1988; Au 1993
		click	0.8-5 ^c	0.8-4.5 ^c	-	Watkins <i>et al.</i> 1977
<i>Cephalorhynchus heavisidii</i>	Heaviside's dolphin	pulsed sounds	0.8-5 ^c	0.8-4.5 ^c	-	Watkins <i>et al.</i> 1977
		click	2-51	-	-	Dawson 1988; Dawson and Thorpe 1990; Au 1993
		click	112-135	-	150-163	Dawson 1988; Dawson and Thorpe 1990; Au 1993
<i>Cephalorhynchus hectori</i>	Hector's dolphin	whistles, chirps, barks	-	2-18	-	Caldwell and Caldwell 1968; Moore and Ridgway 1995
<i>Delphinus delphis</i>	Common dolphin	whistles, chirps, barks	-	2-18	-	Caldwell and Caldwell 1968; Moore and Ridgway 1995
		whistles	4-16	-	-	Gurevick in Evans 1973
		click	0.2-150	30-60	-	Gurevick in Evans 1973
		click	-	4-9	-	Busnel and Dziedzic 1966
		click	23-67	-	-	Dziedzic 1978
<i>Feresa attenuata</i>	Pygmy killer whale	growls, blats	-	-	-	Pryor <i>et al.</i> 1965
<i>Globicephala melana</i>	Long-finned pilot whale	whistles	1-8	1.6-6.7 ^a	-	Busnel and Dziedzic 1966a
		clicks	1-18	-	-	Taruski 1979; Steiner 1981
		click	6-11	-	-	McLeod 1986
		whistles	0.5->20	2-14	180	Caldwell and Caldwell 1969; Fish and Turl 1976
<i>Globicephala macrorhynchus</i>	Short-finned pilot whale	click	30-60	-	180	Evans 1973
		whistles	-	3.5-4.5	-	Caldwell <i>et al.</i> 1969
		rasp/pulse burst	0.1->8	2-5	-	Watkins 1967
<i>Grampus griseus</i>	Risso's dolphin	click	65	-	~120	Au 1993
		whistles	-	6-15 ^a	-	Steiner 1981
<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin	squeals	-	8-12	-	Watkins and Schevill 1972
<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	pulses (buzz)	0.3, 4-5	0.3	-	Schevill and Watkins 1971
<i>Lagenorhynchus australis</i>	Peale's dolphin	clicks	to 12	to 5	low	Schevill and Watkins 1971
		whistles	1->20	4-12	-	Caldwell and Caldwell 1971
<i>Lagenorhynchus obliquidens</i>	Pacific white-sided dolphin	click	0.06-80	60-80	180	Evans 1973
		whistles	1.0-27.3	6.4-19.2 ^a	-	Wang Ding <i>et al.</i> 1995
<i>Lagenorhynchus obscurus</i>	Dusky dolphin	whistles	7.6-13.4	-	-	Leatherwood <i>et al.</i> 1993
<i>Lagenodelphis hosei</i>	Fraser's dolphin	whistles, tones	1-16	1.8, 3	-	Leatherwood and Walker 1979
<i>Lissodelphis borealis</i>	Northern right whale dolphin	whistles, tones	1-16	1.8, 3	-	Leatherwood and Walker 1979

<i>Orcinus orca</i>	Killer whale	whistles	1.5-18	6-12	-	Steiner <i>et al.</i> 1979; Ford and Fisher 1983; Morton <i>et al.</i> 1986
		click	0.25-0.5	-	-	Schevill and Watkins 1966
		scream	2	-	-	Schevill and Watkins 1966
		click	0.1-35	12-25	180	Dierck <i>et al.</i> 1971, Diercks 1972
		pulsed calls	0.5-25	1-6	160	Schevill and Watkins 1966; Awbrey <i>et al.</i> 1982; Ford and Fisher 1983; Moore <i>et al.</i> 1988
<i>Pseudorca crassidens</i>	False killer whale	whistles	-	4-9.5	-	Busnel and Dziedzic 1968; Kamminga and van Velden 1987
		click		25-30; 95-130	220-228	Kamminga and van Velden 1987; Thomas and Turl 1990
<i>Sotalia fluviatilis</i>	Tucuxi	whistles	3.6-23.9	7.1-18.5 ^a	-	Wang Ding <i>et al.</i> 1995
		click	80-100	-	high	Caldwell and Caldwell 1970; Norris <i>et al.</i> 1972; Kamminga <i>et al.</i> 1993
<i>Sousa chinensis</i>	Humpback dolphin	whistles	1.2->16	-	-	Schultz and Corkeron 1994
<i>Stenella attenuata</i>	Spotted dolphin	whistles	3.1-21.4	6.7-17.8 ^a	-	Wang Ding <i>et al.</i> 1995
		whistles	-	-	-	Evans 1967
		pulse	to 150	-	-	Diercks 1972
<i>Stenella clymene</i>	Clymene dolphin	whistles	6.3-19.2	-	-	Mullin <i>et al.</i> 1994a
<i>Stenella coeruleoalba</i>	Spinner dolphin	whistles	1-22.5	6.8-16.9 ^a	109-125	Watkins and Schevill 1974; Steiner 1981; Norris <i>et al.</i> 1994; Wang Ding <i>et al.</i> 1995
		wide band		5-60	108-115	Watkins and Schevill 1974; Norris <i>et al.</i> 1994
		pulse bursts		-	-	Norris <i>et al.</i> 1994
		screams		8-12.5	-	Busnel <i>et al.</i> 1968
		whistles	6->24	6.7-17.9 ^a	-	M. Caldwell <i>et al.</i> 1973b; Steiner 1981; Wang Ding <i>et al.</i> 1995
<i>Stenella frontalis</i>	Atlantic spotted dolphin	whistles	5.0-19.8	-	-	Busnel <i>et al.</i> 1968
		clicks	1-8	-	-	Caldwell and Caldwell 1971a
		squawks, barks, growls, chirps	0.1-3	-	-	Caldwell and Caldwell 1971b
			4-8	-	-	Caldwell <i>et al.</i> 1973
<i>Stenella longirostris</i>	Long-snouted spinner dolphin	pulse	1-160	5-60	-	Brownlee 1983
		whistle	1-20	8-12	-	Brownlee 1983
		click	low->65	-	-	Watkins and Schevill 1974; Norris <i>et al.</i> 1994
		click	1-160	60	-	Ketten 1984
<i>Steno bredanensis</i>	Rough-toothed dolphin	whistles	-	4-7	-	Busnel and Dziedzic 1966b
<i>Tursiops truncatus</i>	Bottlenosed dolphin	click	5-32	-	-	Norris and Evans 1967
		whistles	0.8-24	3.5-14.5 ^a	125-173	Lilly and Miller 1961; Tyack 1985; Caldwell <i>et al.</i> 1990; Schultz and Corkeron 1994; Wang Ding <i>et al.</i> 1995
		low frequency narrowband rasp, grate, mew, bark, yelp	<2	0.3-0.9	-	Schultz <i>et al.</i> in press
		click	-	-	-	Wood 1953
		bark	0.2-150	30-60	-	Diercks <i>et al.</i> 1971
		bark	0.2-16	-	-	Evans 1973
		whistle	4-20	-	-	Evans and Presscott 1962
		whistle	-	-	-	Caldwell and Caldwell 1967
		click ^d	110-130	-	218-228	Au <i>et al.</i> 1974; Au 1993

Monodontidae

<i>Delphinapterus leucas</i>	Beluga	whistles	0.26-20	2-5.9	-	Schevill and Lawrence 1949; Sjare and Smith 1986a,b
		pulsed tones	0.4-12	1-8	-	Schevill and Lawrence 1949; Sjare and Smith 1986a,b
		noisy vocalizations	0.5-16	4.2-8.3	-	Schevill and Lawrence 1949; Sjare and Smith 1986a,b
<i>Monodon monoceros</i>	Narwhal	echolocation click pulsed tones whistles click	0.5-5 0.3-18 40	40-60, 100-120 - 0.3-10	206-225 - -	Au <i>et al.</i> 1985, 1987; Au 1993 Ford and Fisher 1978 Ford and Fisher 1978 Møhl <i>et al.</i> 1990
Phocoenidae						
<i>Neophocaena phocaenoides</i>	Finless porpoise	clicks	1.6-2.2	2	-	Pilleri <i>et al.</i> 1980
<i>Phocoenoides dalli</i>	Dall's porpoise	click clicks click	128 0.04-12 135-149	- - -	- 120-148 165-175	Kamminga <i>et al.</i> 1986; Kamminga 1988 Evans 1973; Evans and Awbrey 1984 Evans and Awbrey 1984; Hatakeyama and Soeda 1990; Hatakeyama <i>et al.</i> 1994
<i>Phocoena phocaena</i>	Harbour porpoise	clicks pulse click	2 100-160 110-150	- 110-150 -	100 - 135-177	Busnel and Dziedzic 1966a; Schevill <i>et al.</i> 1969 Møhl and Anderson 1973 Busnel <i>et al.</i> 1965; Møhl and Anderson 1973; Kamminga and Wiersma 1981; Akamatsu <i>et al.</i> 1994
<i>Phocoena sinus</i>	Vaquita	click	128-139	-	-	Silber 1991
Physeteridae						
<i>Physeter catodon</i>	Sperm whale	clicks	0.1-30	2-4, 10-16	160-180	Backus and Schevill 1966; Levenson 1974; Watkins 1980
<i>Kogia breviceps</i>	Pygmy sperm whale	coda clicks	16-30 60-200	- 120	- -	Watkins 1980 Santoro <i>et al.</i> 1989, Caldwell and Caldwell 1987
Platanistoidae						
Iniidae						
<i>Inia geoffrensis</i>	Boutu	squeals whistle click click	<1->12 0.2-5.2 25-200 85-105	1-2 1.8-3.8 ^a 100 95-105	- - - -	Caldwell and Caldwell 1970 Wang Ding <i>et al.</i> 1995 Norris <i>et al.</i> 1972 Kamminga, Engelsm and Terry 1989 Diercks <i>et al.</i> 1971; Evans 1973; Kamminga <i>et al.</i> 1993
Platanistidae						
<i>Platanista minor</i>	Indus susu	clicks click	0.8-16 15-100	- -	low -	Xiao Youfu and Jing Rongcai 1989 Andersen and Pilleri 1970 Herald <i>et al.</i> 1969; Pilleri <i>et al.</i> 1971
Pontoporiidae						
<i>Pontoporia blainvillei</i>	Franciscana	click	0.3->24	-	-	Busnel <i>et al.</i> 1974
<i>Lipotes vexillifer</i>	Baiji	whistles	3-18.4	6	156	Jing Xianying <i>et al.</i> 1981; Xiao Youfu and Jing Rongcai 1989
Ziphiidae						
<i>Hyperoodon ampullatus</i>	Northern bottle-nose whale	whistles	3-16	-	-	Winn <i>et al.</i> 1970
<i>Hyperoodon spp.</i>	Bottlenose whale	clicks click	0.5->26 8-12	- -	- -	Winn <i>et al.</i> 1970 Winn <i>et al.</i> 1970

<i>Mesoplodon densirostris</i>	Blainville's beaked whale	short whistles	<1-6	-	-	Caldwell and Caldwell 1971
<i>Mesoplodon carlhubbsi</i>	Hubb's beaked whale	pulses	0.3-80	0.3-2	-	Buerki <i>et al.</i> 1989; Lynn and Reiss 1992
		whistles	2.6-10.7	-	-	Buerki <i>et al.</i> 1989; Lynn and Reiss 1992
Mysticeti						
Balaenidae						
<i>Balaena mysticetus</i>	Bowhead	calls	.1-0.580	.14-.16	128-190	Thompson <i>et al.</i> 1979; Ljungblad <i>et al.</i> 1980; Norris and Leatherwood 1981; Würsig and Clark 1993
<i>Eubalaena glacialis</i>	Northern right whale	call	<0.400	<0.200	-	Watkins and Schevill 1972; Clark 1990
Balaenopteridae						
<i>Balaenoptera acutorostrata</i>	Mimke whale	sweeps, moans	0.06-0.140	-	151-175	Winn and Perkins 1976; Schevill and Watkins 1972
<i>Balaenoptera musculus</i>	Blue whale	moans	0.012-0.40	0.012-.018	188	Cummings and Thompson 1971; Edds 1982
<i>Balaenoptera physalus</i>	Fin whale	moans	0.016-0.75	0.020	160-190	Thompson <i>et al.</i> 1979; Edds 1988
<i>Megaptera novaeanglia</i>	Humpback whale	pulse pulse ragged pulse rumble songs	.040-.075 .018-.025 <.030 - 0.03-8	- .020 - <.030 .1-4	- - - - 144-186-	Clark 1990 Watkins 1981 Watkins 1981 Watkins 1981 Thompson <i>et al.</i> 1979; Watkins 1981; Edds 1982, 1988; Payne <i>et al.</i> 1983; Silber 1986; Clark 1990; Dahlheim and Ljungblad 1990
		social	.05-10.0	<3	-	Thompson, Winn and Perkins 1979
Eschrichtiidae						
<i>Eschrichtius robustus</i>	Gray whale	call	0.2-2.5	1-1.5	-	Dahlheim and Ljungblad 1990
Fissipedia						
Mustelidae						
<i>Enhydra lutris</i>	Sea otter	growls ^b whine	3-5	-	-	Kenyon 1981; Richardson <i>et al.</i> 1995
Pinnipedia						
Odobenidae						
<i>Odobenus rosmarus</i>	Walrus	bell tone	-	0.4-1.2	-	Schevill <i>et al.</i> 1966; Ray and Watkins 1975; Stirling <i>et al.</i> 1983
		clicks, taps, knmks	0.1-10	<2	-	Schevill <i>et al.</i> 1966; Ray and Watkins 1975; Stirling <i>et al.</i> 1983
		rasps grunts	0.2-0.6 <1	0.4-0.6 <1	- -	Schevill <i>et al.</i> 1966 Stirling <i>et al.</i> 1983
Otariidae						
<i>Arctocephalus philippii</i>	Juan Fernandez fur seal	clicks	0.1-0.2	0.1-0.2	-	Norris and Watkins 1971
<i>Callorhinus ursinus</i>	Northern fur seal	clicks, bleats	-	-	-	Poulter 1968
<i>Eumetopias jubatus</i>	Northern sea lion	clicks, growls	-	-	-	Poulter 1968
<i>Zalophus californianus</i>	California sea lion	barks	<8	<3.5	-	Schusterman <i>et al.</i> 1967
		whinny	<1-3	-	-	Schusterman <i>et al.</i> 1967

Table 1 - p. 4

Phocidae						
<i>Cystophora cristata</i>	Hooded seal	grunt	-	0.2-0.4	-	Terhune and Ronald 1973
<i>Erignathus barbatus</i>	Bearded seal	snort buzz(click) song	- to 6 0.02-6	0.1-1 1.2 1-2	- - 178	Terhune and Ronald 1973 Terhune and Ronald 1973 Ray <i>et al.</i> 1969; Stirling <i>et al.</i> 1983; Cummings <i>et al.</i> 1983
<i>Halichoerus grypus</i>	Gray seal	clicks, hiss 6 call types knocks	0-30, 0-40 0.1-5 to 16	- 0.1-3 to 10	- -	Schevill <i>et al.</i> 1963; Oliver 1978 Asselin <i>et al.</i> 1993 Asselin <i>et al.</i> 1993
<i>Hydrurga leptonyx</i>	Leopard seal	pulses and trills	0.1-5.9	-	-	Ray 1970; Stirling and Simiff 1979; Rogers <i>et al.</i> 1995
<i>Leptonychotes weddellii</i>	Weddell seal	thump,blast ultrasonic >34 call types	0.04-7 up to 164 0.1-12.8	- 50-60 -	- low 153-193	Rogers <i>et al.</i> 1995 Thomas <i>et al.</i> 1983a Thomas and Kuechle 1982; Thomas <i>et al.</i> 1983b; Thomas and Stirling 1983
<i>Ommatophoca rossii</i>	Crabeater seal	groan	<0.1->8	0.1-1.5	high	Stirling and Simiff 1979
<i>Phoca fasciata</i>	Ross seal	pulses	0.25-1 4-14	-	-	Watkins and Ray 1985 Watkins and Ray 1985
<i>Phoca hispida</i>	Ribbon seal	frequency sweeps	0.1-7.1	-	160	Watkins and Ray 1977
<i>Phoca largha</i>	Ringed seal Spotted seal	barks, clicks, yelps clicks	0.4-16 8-150	<5 1240	95-130 -	Stirling 1973; Cummings <i>et al.</i> 1984 Schevill <i>et al.</i> 1963; Cummings and Fish 1971; Renouf <i>et al.</i> 1980; Noseworthy <i>et al.</i> 1989
<i>Phoca (Pagophilus) groenlandica</i>	Harp seal	roar bubbly growl grunt, groan creak	0.4-4 <0.1-0.4 <0.1-4 0.7-4	0.4-0.8 <0.1-0.25 -	- -	Hanggi and Schusterman 1992, 1994 Hanggi and Schusterman 1992, 1994 Hanggi and Schusterman 1992, 1994 Hanggi and Schusterman 1992, 1994
<i>Phoca vitulina</i>	Harbor seal	15 sound types clicks social sounds	<0.1->16 -	0.1-3 30	130-140 131-164	Möhl <i>et al.</i> 1975; Watkins and Schevill 1979; Terhune and Ronald 1986; Terhune 1994 Möhl <i>et al.</i> 1975 Beier and Wartzkow 1979
Sirenia						
Dugongidae						
<i>Dugong dugon</i>	Dugong	chirp-squeak ^b sound 1 ^b chirp ^b all sounds	3-8 1-2 2-4 0.5-18	- - - 1-8	low -	Nair and Mohan 1975 Marsh <i>et al.</i> 1978 Marsh <i>et al.</i> 1978 Nishiwaki and Marsh 1985; Anderson and Barclay 195
Trichechidae						
<i>Trichechus inunguis</i>	Amazon manatee	squeaks,pulses	6-16	6-16	-	Evans and Herald 1970
<i>Trichechus manatus</i>	West Indian manatee	squeaks	0.6-16	0.6-5	low	Schevill and Watkins 1965

^a Frequency determined as "mean minimum frequency minus 1 s.d...to...mean maximum frequency plus 1 s.d." (*sensu* Richardson *et al.* 1995).

^b Recorded in air.

^cEquipment capable of recording to 10 kHz only.
^dPerformance in high background noise (Au, 1993)

Table 2. Auditory, Vestibular, and Optic Nerve Distributions

(Data compiled from Yamada 1953; Gacek and Rasmussen 1961; Jansen and Jansen 1969; Firbas 1972; Morgane and Jacobs 1972; Bruns and Schmieszek 1980; Dawson 1980; Ketten 1984, 1992; Vater 1988; Nadol 1988; Gao and Zhou 1991, 1992, 1995; Kössl and Vater 1995).

Species	Common Name	Cochlear Type	Membrane Length (mm)	Auditory Ganglion Cells	Density (cells/mm cochlea)	Vestibular Ganglion Cells	Vestibular-Auditory Ratio	Optic Nerve Fibers	Optic-Auditory Ratio	Optic-Vestibular Ratio
<i>Inia geoffrensis</i>	Boutu	I	38.2	104,832	2744			15,500	0.15	
<i>Lipotes vexillifer</i>	Baiji			82,512		3,605	0.04	23,800	0.29	6.60
<i>Neophocoena phocoenoides</i>	Finless porpoise			68,198		3,455	0.05	88,900	1.30	25.73
<i>Sousa chinensis</i>	Humpbacked dolphin			70,226		3,213	0.05	149,800	2.13	46.62
<i>Phocoena phocoena</i>	Harbour porpoise	I	22.5	70,137	3117	3,200		81,700	1.16	25.53
<i>Delphinapterus leucas</i>	Beluga		42	149,386	3557			110,500	0.74	
<i>Delphinus delphis</i>	Common dolphin	II	34.9	84,175	2412	4,091	0.05	165,600	1.97	40.48
<i>Lagenorhynchus obliquidens</i>	White-sided dolphin	II	34.9	70,000	2006			77,500	1.11	
<i>Stenella attenuata</i>	Spotted dolphin	II	36.9	82,506	2236					
<i>Tursiops truncatus</i>	Bottlenosed dolphin	II	38.9	96,716	2486	3,489	0.04	162,700	1.68	46.63
<i>Physeter catodon</i>	Sperm Whale		54.3	161,878	2981			172,000	1.06	
<i>Balaenoptera physalus</i>	Fin Whale	M	64.7	134,098	2073			252,000	1.88	
<i>Megaptera novaeangliae</i>	Humpback Whale	M	58	156,374	2696			347,000	2.22	
<i>Rhinolophus ferrumequinum</i>	Horseshoe bat	I	16.1	15,953	991/1750*					
<i>Pteronotus parnellii</i>	Mustached bat	T	14.0	12,800	900/1900*					
<i>Cavia porcella</i>	Guinea Pig	T	19.0	24,011	1264	8,231	0.34			0.00
<i>Felis domesticus</i>	Cat	T	28.0	51,755	1848	12,376	0.24	193,000	3.73	15.59
<i>Homo sapiens</i>	Human	T	32.1	30,500	950	15,590	0.51	1,159,000	38.00	74.34

*Densities at auditory fovea as described by Bruns and Schmieszek (1980)

Table 3.
 (Data compiled from Lipscomb 1978; Lehnhardt 1986; Liberman 1987; Patterson 1991)

SOURCE	LEVEL (dB)	EXPOSURE TIME	TTS₃₀ (dB)	BAND
HUMAN				
narrowband (<10 kHz)	(occupational)	10 yrs	(20-60)	CF + 1/2 octave
500 Hz	81.5	48 hours	10.5	(3 day recovery)
500 Hz	92.5	29.5 hours	27.5	(asymptotic loss at 12 hrs.)
500 Hz	90	48 hours	27.5	(4 day recovery)
CAT				
broadband noise	105	15 min.	20-40	2-8 kHz
broadband noise	115	7.5 min.	20-50	2-8 kHz
broadband noise, repeat	115	7.5 min. on 24 hrs off	20-30	3.5 kHz
broadband noise, repeat	115	7.5 min. on 1-6 hrs off	30-50 (some PTS)	2-8 kHz
500 Hz CF 1 octave band	105	8-48 hours	20-30 (no PTS)	2-8 kHz
CHINCHILLA				
500 Hz CF/1 octave band	(100)	48 Hrs	40-45	2-8 kHz
500 Hz CF/1 octave band	100	7 days	60	0.75 kHz
500 Hz CF/1 octave band	75	7-21 days	30-35	0.15 - 8 kHz
4 KHz CF/1 octave band	86-98	9 days	20-35	3 - 8 kHz (15 day recovery)
SQUIRREL MONKEY				
500 Hz CF/1 octave band	100	2 Hrs	30-40	0.5-2 kHz (2 day recovery)
2 kHz CF/1 octave band	100	2 Hrs	40-50	2-6 kHz
pure tones	120	9-15 mins.	16-23	CF+1/2 octave

CF - Center Frequency of exposure band

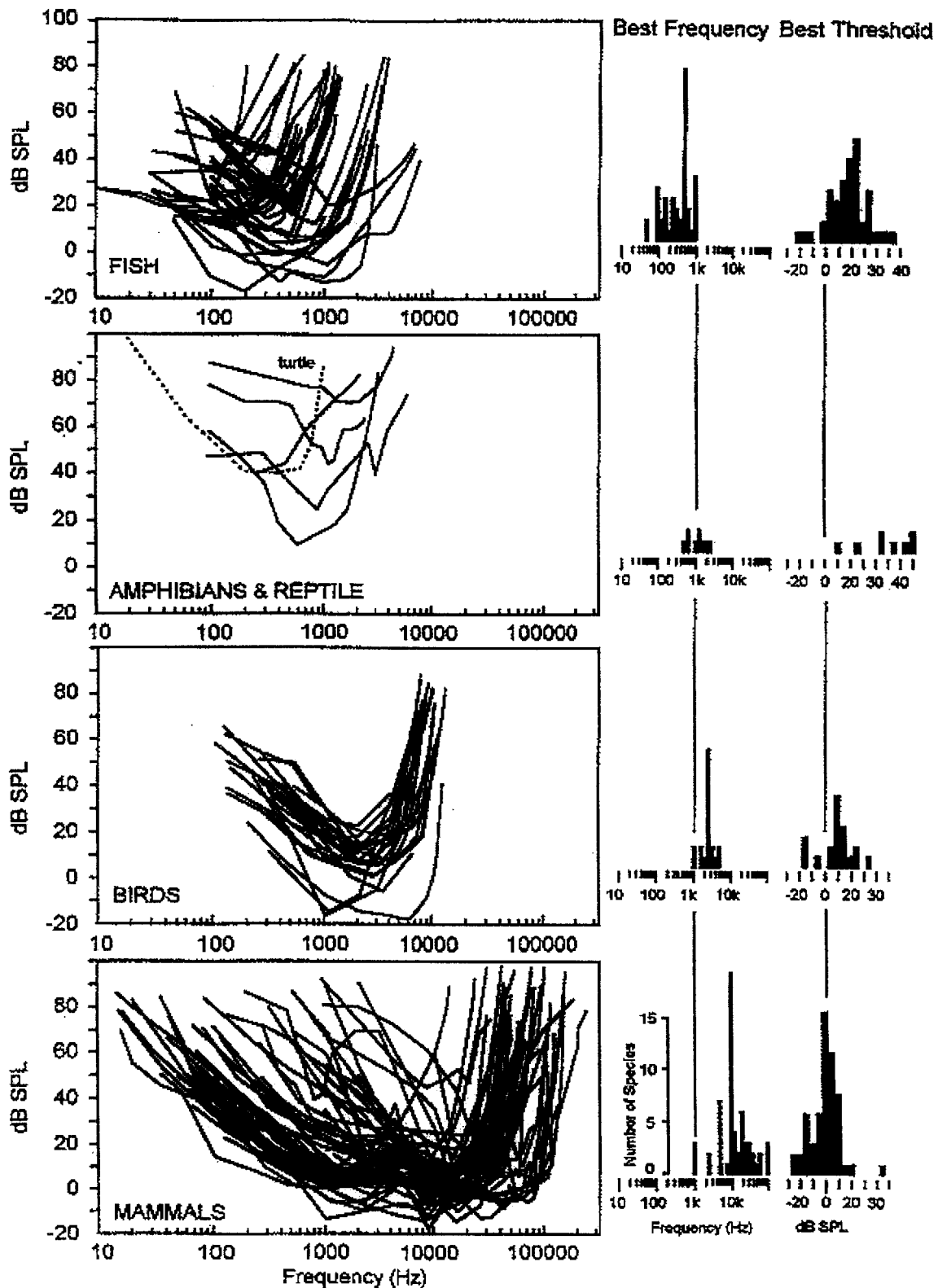


Figure 1. Audiograms of representative terrestrial mammals. Note that the ordinate is labeled dB SPL and that thresholds are therefore at or near 0 dB in the regions of best sensitivity for most species. The histograms to the right of the audiograms show the distribution of peak sensitivities and level at peak for each group. (Data compiled from Fay 1988, Yost, 1994, Yost, ASA Bioacoustic Workshop Materials, MMS Biennial Conf., 1995).

Human Hearing Thresholds

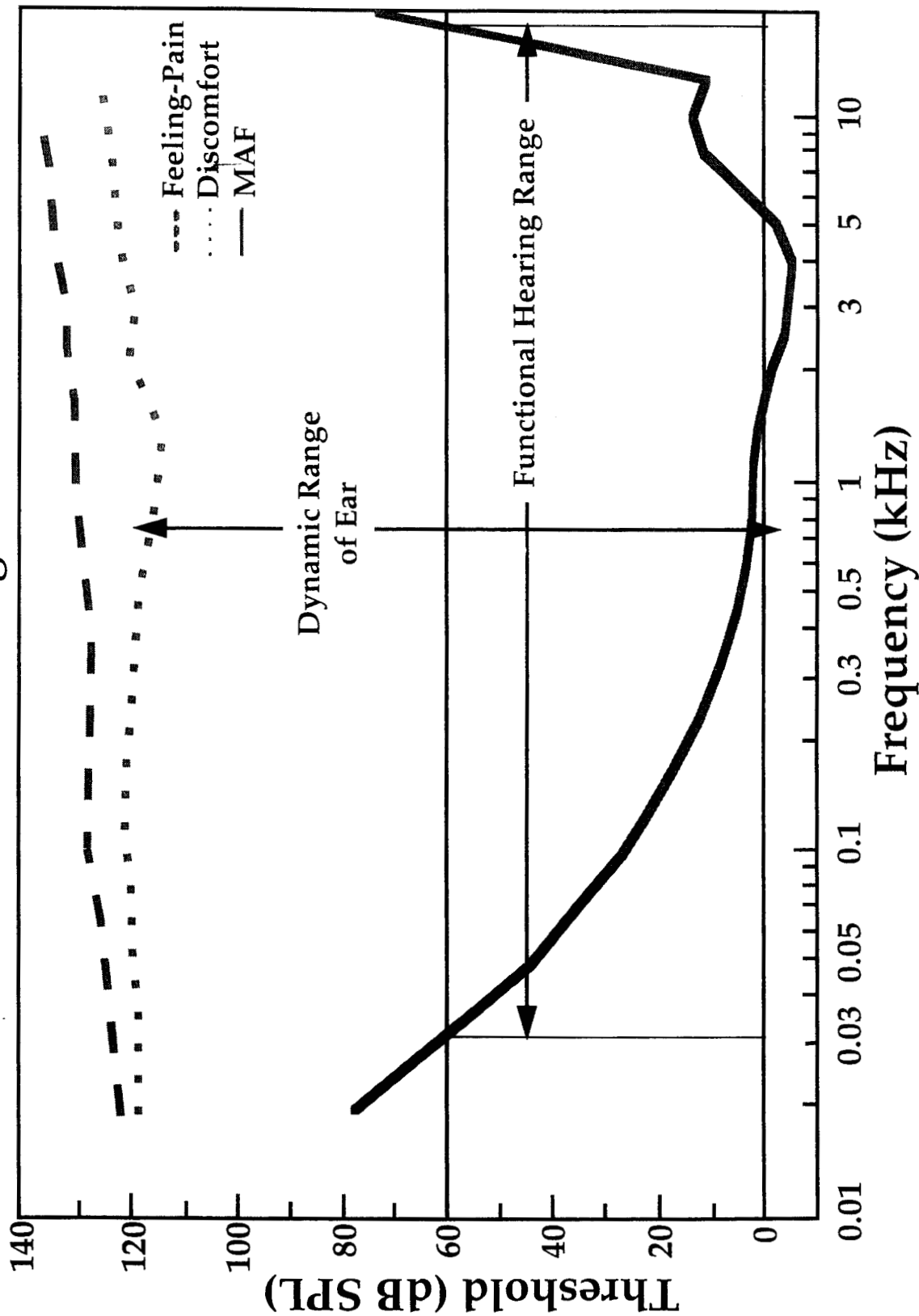


Figure 2. The human audiogram shown represents a minimum audible field (MAF) response for an average adult tested in quiet. This curve can be compared with the audiograms for land mammals in air with the underwater audiograms for cetaceans and pinnipeds in Figure 3, taking into consideration the effect that differing reference pressures have on reported threshold values. A transposition of this curve with some of the marine mammal curves is shown also in Figure 7, but to accomplish this, a conversion of all curves to watts/m^2 was required before they were subsequently replotted for with a common reference pressure of $\text{dB re } 1 \mu\text{Pa}$.

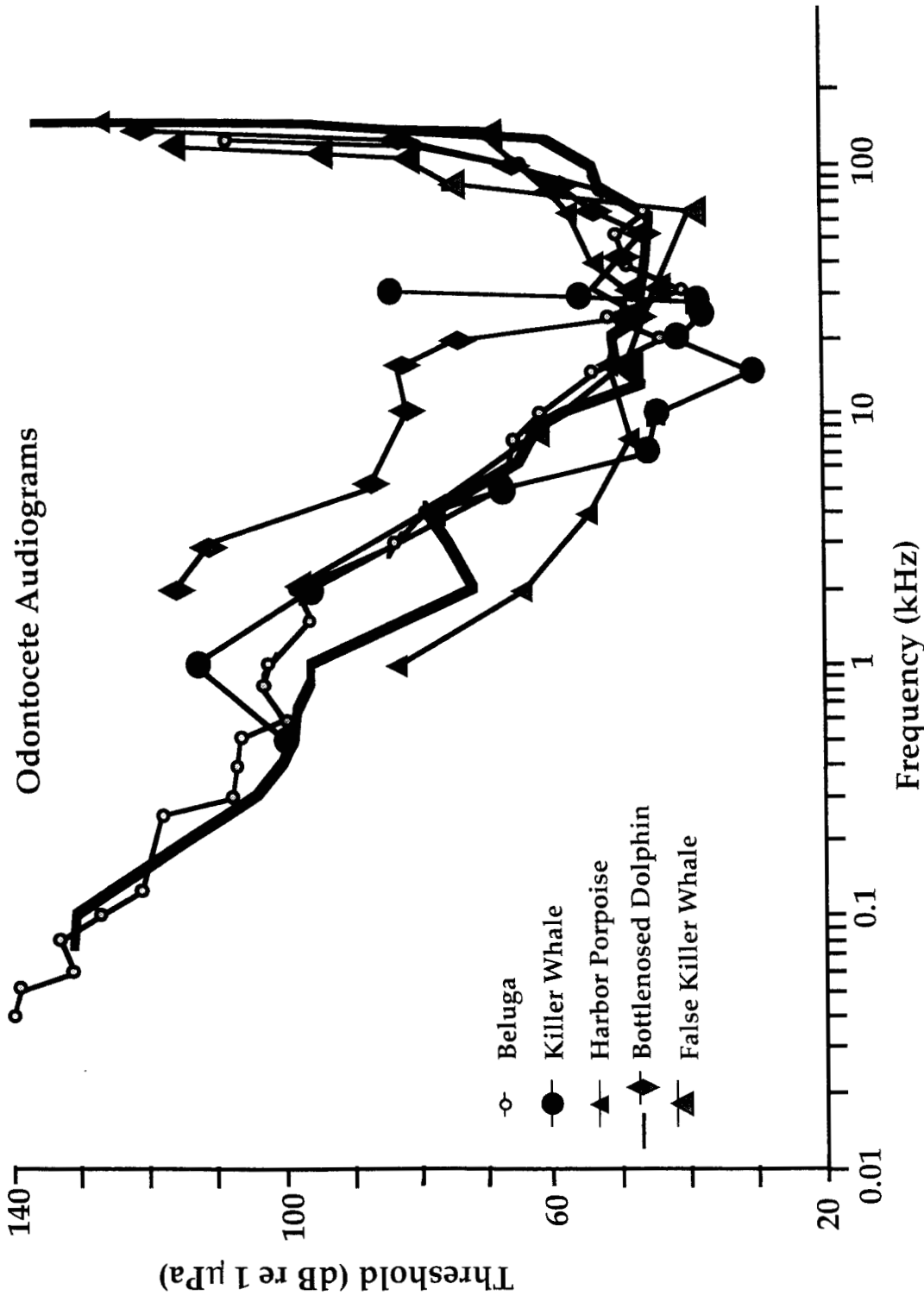


Figure 3. Underwater audiograms for (A) odontocetes and (B) pinnipeds. For some species, more than one curve is shown because data reported in different studies were not consistent. Note that for both the bottlenose dolphin and the sea lion, thresholds are distinctly higher for one of the two animals tested. These differences may reflect different test conditions or a hearing deficit in one of the animals. (Summary data compiled from Popper 1980; Fay 1988; Au 1993; Richardson *et al.* 1995. **Beluga:** White *et al.* 1978; Awbrey *et al.* 1988 and Johnson *et al.* 1989. **Killer Whale:** Hall & Johnson 1971 and Hall & Johnson 1972. **Harbor Porpoise:** Anderson 1970 and Anderson 1970a. **Bottlenose Dolphin:** Johnson 1967 and Ljungblad *et al.* 1982b. **False Killer Whale:** Thomas *et al.* 1988a. **California Sea Lion:** Schusterman *et al.* 1972; Kastak & Schusterman 1995 and Schusterman, Balliet & Nixon 1972. **Northern Fur Seal:** Moore & Schusterman 1987; Babushina *et al.* 1991 and Schusterman & Moore 1978a. **Harbor Seal:** Mohl 1968; Kastak & Schusterman 1995 and Terhune & Turnbull 1995. **Ringed Seal:** Terhune & Ronald 1975a. **Harp Seal:** Terhune & Ronald 1972. **Monk Seal:** Thomas *et al.* 1990b.).

Pinniped Audiograms

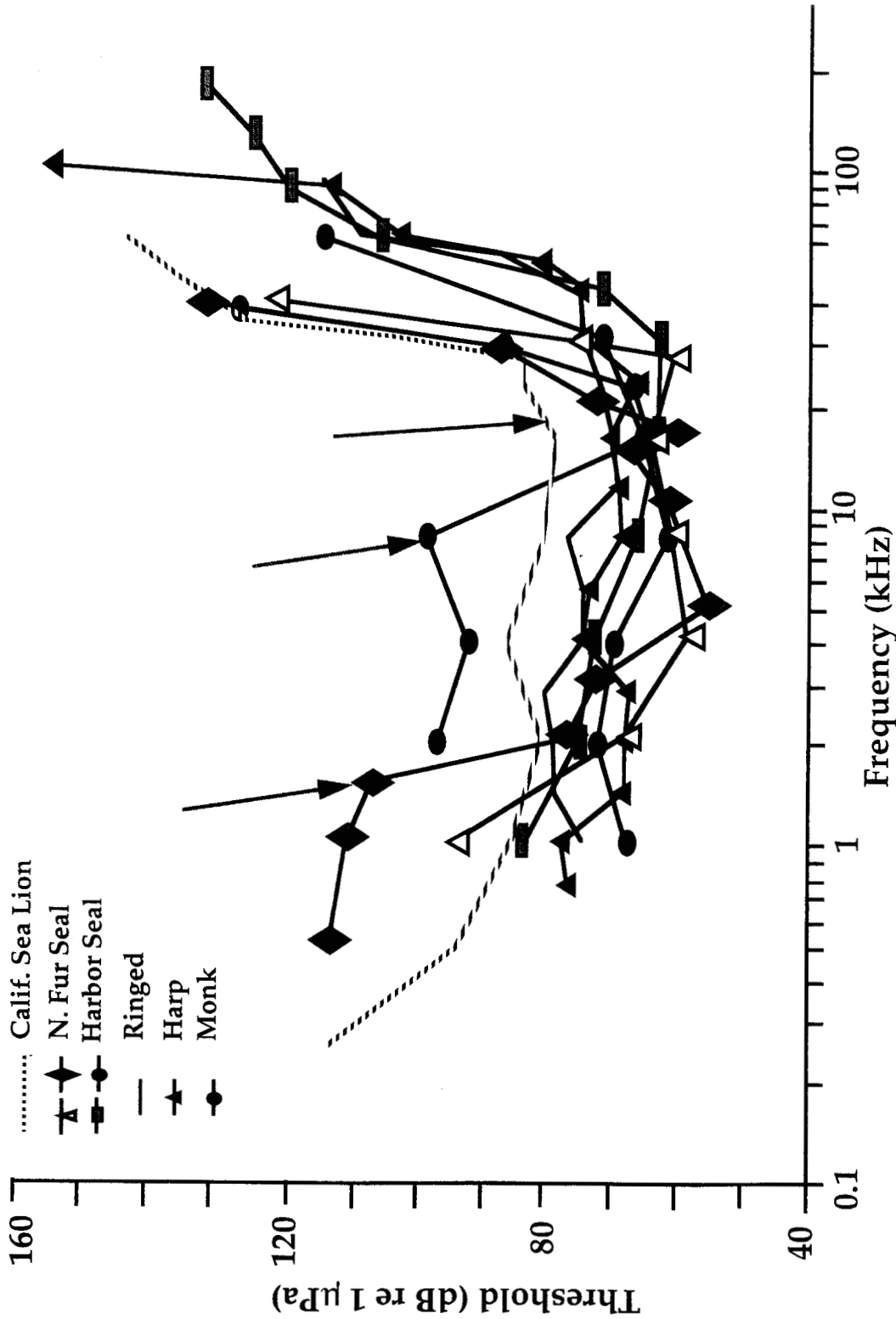


Figure 3. Underwater audiograms for (A) odontocetes and (B) pinnipeds. For some species, more than one curve is shown because data reported in different studies were not consistent. Note that for both the bottlenose dolphin and the sea lion, thresholds are distinctly higher for one of the two animals tested. These differences may reflect different test conditions or a hearing deficit in one of the animals. (Summary data compiled from Popper 1980; Fay 1988; Au 1993; Richardson *et al.* 1995. **Beluga**: White *et al.* 1978; Awbrey *et al.* 1988 and Johnson *et al.* 1989. **Killer Whale**: Hall & Johnson 1971 and Hall & Johnson 1972. **Harbor Porpoise**: Anderson 1970 and Anderson 1970a. **Bottlenose Dolphin**: Johnson 1967 and Ljungblad *et al.* 1982b. **False Killer Whale**: Thomas *et al.* 1988a. **California Sea Lion**: Schusterman *et al.* 1972; Kastak & Schusterman 1995 and Schusterman, Balliet & Nixon 1972. **Northern Fur Seal**: Moore & Schusterman 1987; Babushina *et al.* 1991 and Schusterman & Moore 1978a. **Harbor Seal**: Mohl 1968; Kastak & Schusterman 1995 and Terhune & Turnbull 1995. **Ringed Seal**: Terhune & Ronald 1975a. **Harp Seal**: Terhune & Ronald 1972. **Monk Seal**: Thomas *et al.* 1990b.)

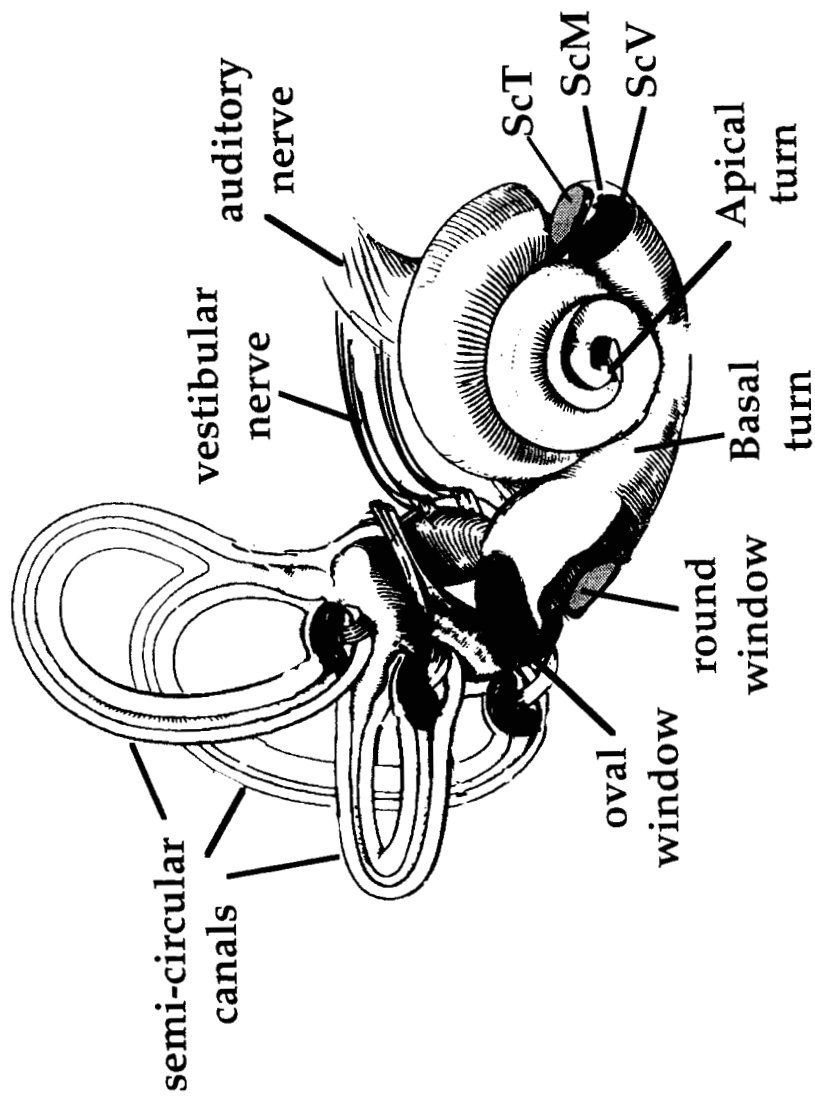


Figure 4A. The two drawings (A and B) illustrate the fundamental structure of a mammalian inner ear. 4a shows an average mammalian 2.5 turn cochlea and 3 semicircular canals. A wedge has been removed from the basal turn to show the three chambers or scalae in the cochlea. ScV scala vestibuli; ScM scala media; ScT scala tympani. A hypothetical mammalian cochlea is "unrolled" in 4b to illustrate changes in basilar membrane width with cochlear length. The broader apical end which responds to low frequencies is in the foreground. A membrane place vs. frequency distribution is shown for this ear's theoretical hearing range with the approximate envelope of membrane displacements for three pure tone sounds. The approximate widths for this membrane would be 100 μ at the base and 400 μ at the apex (Redrawn redrawn from an archive illustration of the Dept. of Otolaryngology, Mass. Eye and Ear Infirmary).

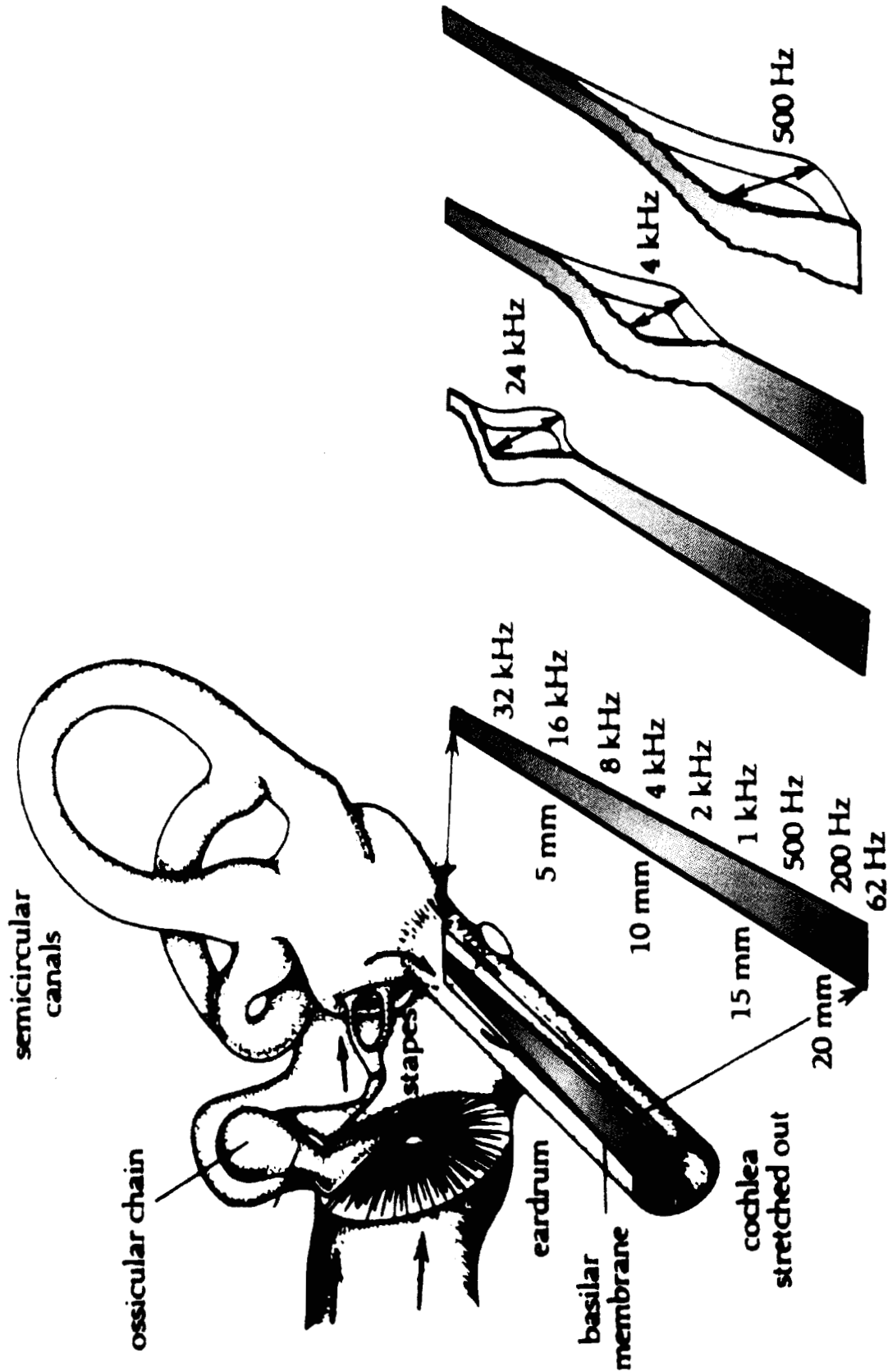


Figure 4B. The two drawings (A and B) illustrate the fundamental structure of a mammalian inner ear. 4a shows an average mammalian 2.5 turn cochlea and 3 semicircular canals. A wedge has been removed from the basal turn to show the three chambers or scalae in the cochlea. ScV scala vestibuli; ScM scala media; ScT scala tympani. A hypothetical mammalian cochlea is "unrolled" in 4b to illustrate changes in basilar membrane width with cochlear length. The broader apical end which responds to low frequencies is in the foreground. A membrane displacement vs. frequency distribution is shown for this ear's theoretical hearing range with the approximate envelope of membrane displacements for three pure tone sounds. The approximate widths for this membrane would be $100\ \mu$ at the base and $400\ \mu$ at the apex (Redrawn from an archive illustration of the Dept. of Otolaryngology, Mass. Eye and Ear Infirmary).

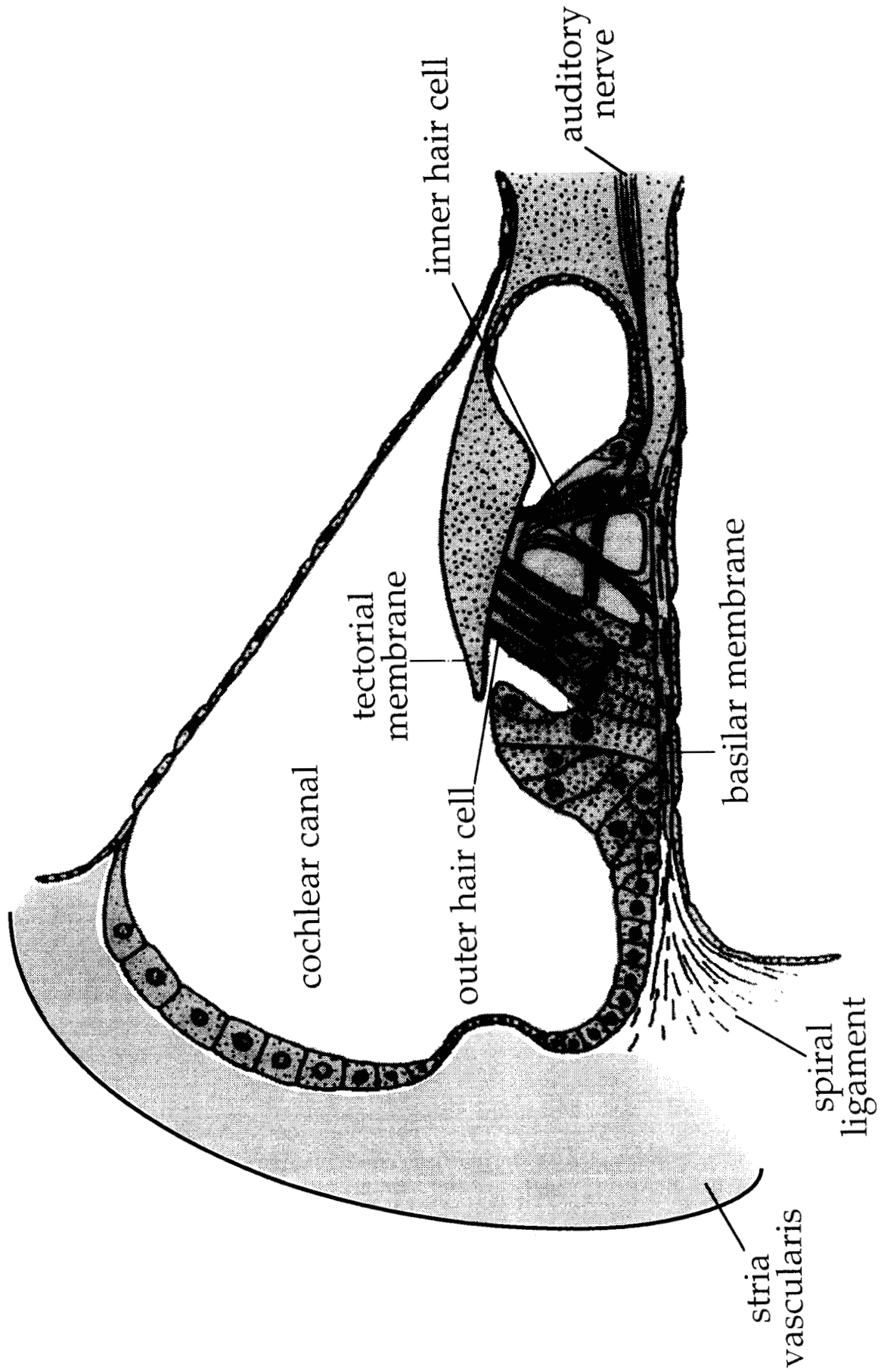
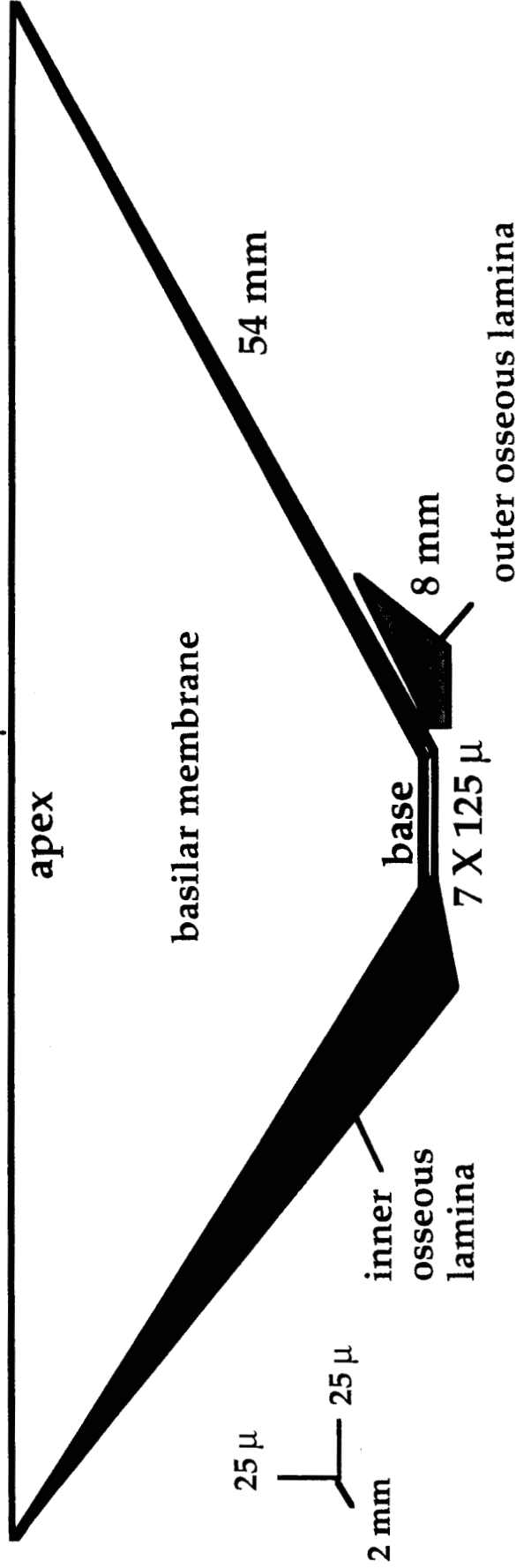


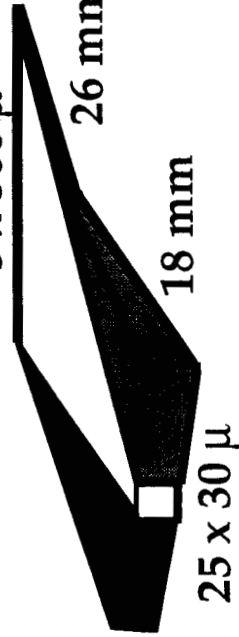
Figure 5. A schematic of the cochlear duct and the Organ of Corti are shown for a generic mammal ear.

RIGHT WHALE *Eubalaena glacialis* - Type M

2.5 x 1400 μ

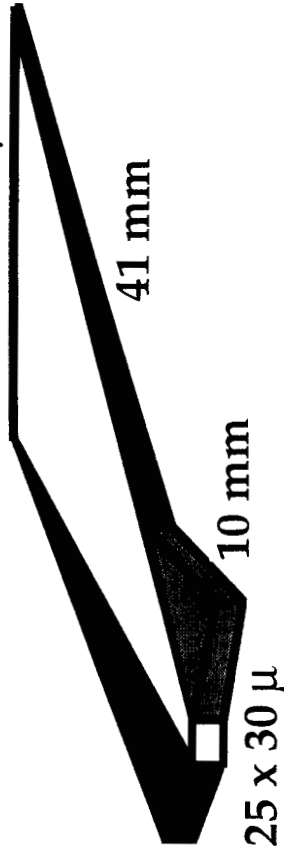


5 x 300 μ



**HARBOR PORPOISE
Phocoena phocoena - Type I**

5 x 380 μ



**BOTTLENOSED DOLPHIN
Tursiops truncatus - Type II**

Figure 6. Differences in basilar membrane dimensions and outer lamina distributions that are primary dictates of hearing ranges in odontocetes and mysticetes are represented schematically and to scale.

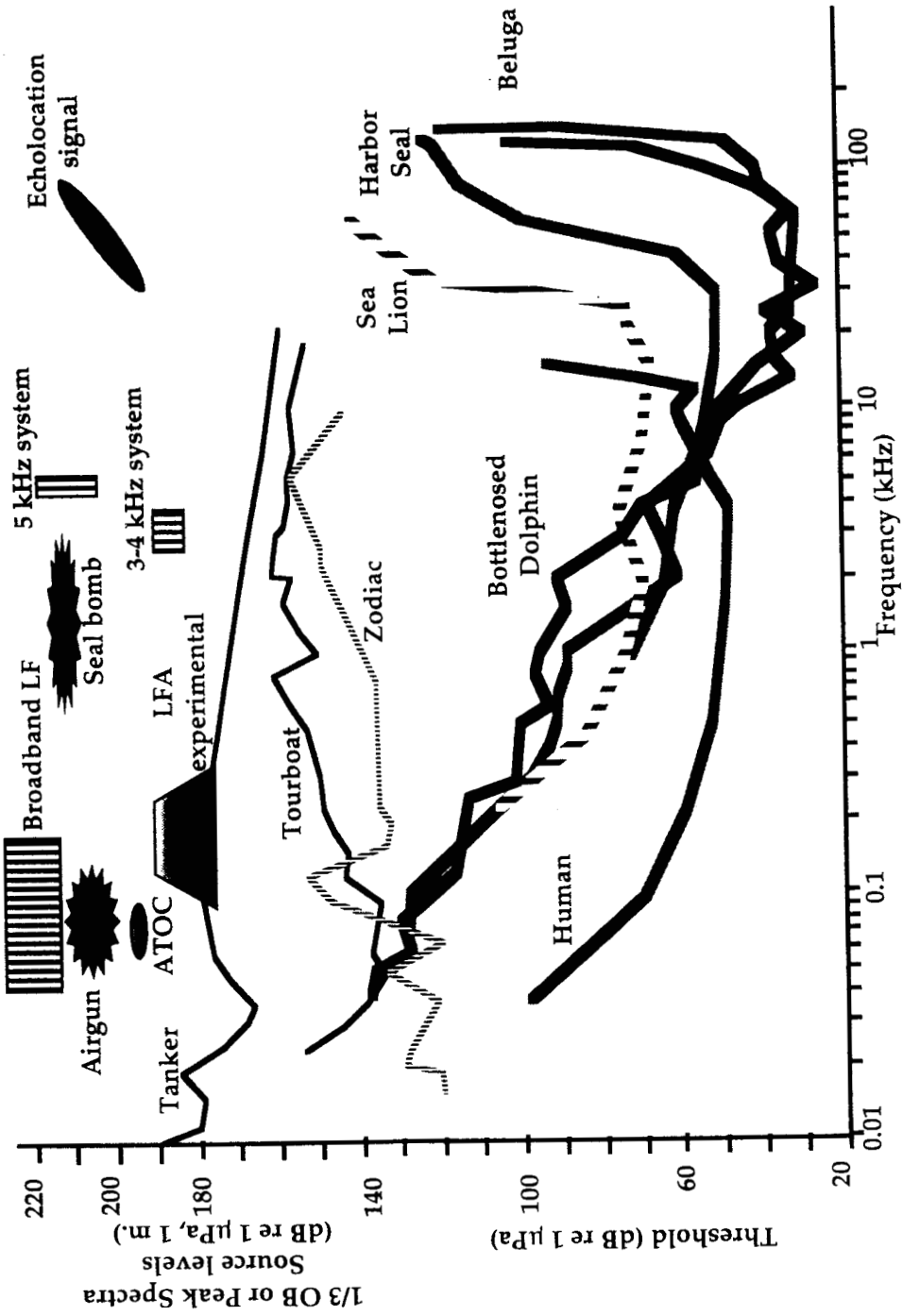


Figure 7. Audiograms for representative odontocetes and pinnipeds are compared with source level data for shipping noise (1/3 octave band) and source levels for airguns, the ATOC source, and two theoretical sonic censusing devices (Au 1995; Richardson et al 1995; Ketten, 1998). The human in-air audiogram and marine mammal underwater audiograms were recalculated as watts/m² to allow direct comparison with marine mammals before replotting on common SPL axes. If marine mammals had an equivalent relationship between sensitivity and onset of TTS as that reported for human and land mammals, any source providing a received level greater than 80 dB over the audiograms has significant potential to produce TTS. Note that the data shown are source levels at 1 m. . Bear in mind that this figure offers only gross comparisons. Because of the variable nature of the measures reported here, exact comparisons are not intended. Equally important, received levels, which are the key to estimating the probability of threshold shifts, will vary considerably depending upon the animal's proximity and the acoustic propagation characteristics of the area. (Adapted from Ketten, (1998).

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