MARINE MAMMAL AUDITORY SYSTEMS:

A SUMMARY OF AUDIOMETRIC AND ANATOMICAL DATA AND ITS IMPLICATIONS FOR UNDERWATER ACOUSTIC IMPACTS

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Terminology

Audiogram: A graph of hearing ability charting frequency (abcissa) vs. sensitivity measured as sound pressure or intensity (ordinate).
Cetaceans: Whales and dolphins
decibel (dB): a scale based on the log ratio of two quantities. It is commonly used to represent sound pressure level or sound intensity. The value of the decibel depends upon the denominator used, or reference pressure. Therefore the decibel level of sound is properly stated in the form of n dB re n microPa . The microPascal is a unit of pressure; e.g., 100 dB re 20 microPa in air equals 160 dB re 1 microPa in water.
infrasonic: below 20 Hz, the lower limit of human hearing
kHz: kilo Hertz. A Hertz (Hz) is a measure of sound frequency equal to 1 cycle/sec, therefore a kHz is one thousand cycles per second.
Mysticetes: Baleen or moustached whales, which include rorquals. The largest whales, all of which are opportunistic gulp or seine feeders. They are not known to echolocate.
Octave: An octave is broadly defined as a doubling of frequency. Thus, a one octave shift from 500 Hz is 1,000 Hz, and from 3,000 Hz, it is 6,000 Hz. Adult humans have on average an 8-9~~,~~ octave functional hearing range from 32 to 16 kHz..
Odontocetes: toothed whales. All are believed to echolocate; i.e., to use a biosonar for imaging the environment via sound and sound analyses.
Pinnipeds: Seals, sea lions, walruses.
ultrasonic: above 20 kHz, the upper limit of human hearing.

Introduction

Concomitant with man's increasing use of the oceans is an increase in the ocean's acoustic budget. In the mid 1970's, it was estimated that noise from human related activity was increasing in coastal areas and shipping lanes at 10 dB per decade. Given our ever increasing activity in all seas and at all depths, this figure is not surprising. It may even be too conservative., Anthropogenic noise is an important component of virtually every human endeavor in the oceans, whether it be shipping, transport, exploration, research, military activities, construction, or recreation. For some activities, such as military and construction, impulsive and explosive devices are fundamental tools that are intermittent but intense; for others, such as shipping, the instantaneous noise may be less, but sound is inherent in daily operations and is therefore a constant, pervasive by-product.. Because these activities span the globe and produce sounds over the entire audible range of most animals, it is reasonable to assume that man-made noise in the oceans can have a significant adverse impact on marine species. Because marine mammals are especially dependent upon hearing and in many cases are endangered, the concern over noise impacts on these animals is particularly acute. Our concern is both logical and appropriate, but it is also, at this time, unproved and the range of concerns is unbounded. For responsible stewardship of our oceans it is imperative that we begin to measure and understand our impacts, and, more important, that we proceed with a balanced and informed view. To that end, this hearing is a significant, positive step.

Hearing for any animal is an important sense. Many sensory cues are limited in their distribution and utility. Sound however is literally universal While many animals inhabit lightless environments and are blind, there are no known vertebrates that are naturally, profoundly deaf. . There is no habitat, except space, that is soundless, and sound is such a significant cue, carrying such a wealth of information that hearing is well developed in virtually every animal group. We employ sound and hearing both passively and actively, listening not only in the dark but even while asleep. The cues are constant and diverse, providing information on the direction and nature of the sources and how they change through time. Sound is a key element for survival and hearing is a key component of communication, mate selection, feeding, and predator avoidance.

For marine mammals, hearing is arguably their premier sensory system. It is obvious from their level of ear and neural auditory center development alone. Dolphins and whales devote three fold more neurons to hearing than any other animal. The temporal lobes, which control higher auditory processing, dominate their brain, and they appear to have faster auditory and signal processing capabilities than any other mammal. Since the late 1950's we have been aware that dolphins, at least, use very high ultrasonic signals as a form of biosonar. Using sound they can distinguish amongst different metals and detect differences as small as a few mm in two objects. To date, despite 50 years of research on dolphin biosonar, we are still incapable of duplicating some of their feats. However, despite the multifaceted evidence we have for exceptional and diverse hearing in marine mammals, we still know very little about how and what they hear.

This statement summarizes and critiques existing auditory data for marine mammals. It was compiled primarily as a background document for assessing potential impacts of anthropogenic sounds, including long-range detection or sonar devices. To that end, it has the following emphases: a description of currently available data on marine mammal hearing and ear anatomy, a discussion and critique of the methods used to obtain these data, a summary and critique of data based on hearing models for untested marine species, and a discussion of data available on acoustic parameters that induce auditory trauma in both marine and land mammals. In order to place these data in an appropriate context, summaries are incorporated also of basic concepts involved in underwater vs. air-borne sound propagation, fundamental hearing mechanisms, and mechanisms of auditory trauma in land mammals. Lastly, to maximize the utility of this document, a brief discussion has been included on the potential for impact on hearing from several recently proposed devices and an outline of research areas that need to be addressed if we are to fill the relatively large gaps in the existing data base.

Mammalian Hearing Fundamentals

The term "auditory system" refers generally to the suite of components an animal uses to detect and analyze sound. There are two fundamental issues to bear in mind for the auditory as well as any sensory system. One is that sensory systems and therefore perception are species-specific. The ear and what it can hear is different for each species. The second is that they are habitat dependent. In terms of hearing, both of these are important issues.

Concerning the first issue, species sensitivities, all sensory systems are designed to allow animals to receive and process information from their surroundings which means they act as highly selective filters. If every environmental cue available received equal attention, the brain would be barraged by sensory inputs. Instead, sensory organs are essentially multi-level filters, selecting and attending to signals that, evolutionarily, proved to be important.

Most animals have vocalizations that are tightly linked to their peak hearing sensitivities in order to maximize intra-specific communication, but they also have hearing beyond that peak range that is related to the detection of acoustic cues from predators, prey, or other significant environmental cues. Consider, in general, how predator and prey are driven to be both similar and different sensorially. Because their activities intersect in place and time, they need, for example, to have similar visual and auditory sensitivities, but, ideally, different fields of view and hearing ranges. Similarly, two species living within similar habitats or having common predators and prey have some hearing bands in common but will differ in total range because of anatomical and functional differences that are species dependent and reflect other "species-specific" needs. Thus, each animal's perceived world is a different subset of the real physical world; *i.e.*, it is a species-specific model, constructed from the blocks of data its particular sensory system can capture and process. Two species may have overlapping hearing ranges, but no two have identical sensitivities. This is of course the case with piscivorous marine mammals, their fish targets, and with their prey competitors. It is also the case with whales and ships. They both have navigational and predator detection needs.

In animal behavior, this concept is called the Umwelt (von Uexküll 1934). As a technical term, Umwelt means an animal's perceptually limited construct of the world. In common usage, it means simply the environment. This dual meaning reflects the complex interaction of sensory adaptations and habitat, which leads us to the second issue; i.e., the relation or influence of habitat on sensory abilities. While senses are tuned to relevant stimuli by evolution they are nevertheless limited by the physical parameters of the habitat.

Mechanistically, hearing is a relatively simple chain of events: sound energy is converted by bio-mechanical transducers (middle and inner ear) into electrical signals (neural impulses) that provide a central processor (brain) with acoustic data. Mammalian ears are elegant structures, packing over 75,000 mechanical and electrochemical components into an average volume of 1 cm^3. Variations in the structure and number of ear components account for most of the hearing capacity differences among mammals.

Hearing ranges and the sensitivity at each audible frequency (threshold, or minimum intensity required to hear a given frequency) vary widely by species). "Functional" hearing refers to the range of frequencies a species hears without entraining non-acoustic mechanisms. In land mammals, the functional range is generally considered to be those frequencies that can be heard at thresholds of 60 dB SPL, a decibel measure of sound pressure level. The basis for this measure and how it differs in air and water is explained in the next section.

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 (Fig. 1). In humans, best sensitivity (lowest thresholds) occurs 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 (beyond 120 dB SPL) will generally produce discomfort and eventually pain. To hear frequencies at the extreme ends of any animal's total range generally requires intensities that are uncomfortable, and frequencies outside or beyond our hearing range are simply undetectable because of limitations in the ear's middle and inner ear transduction and resonance characteristics. Through bone conduction or direct motion of the inner ear, exceptionally loud sounds that are outside the functional range of the normal ear can sometimes be perceived, but this is not truly an auditory sensation.

"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. We know that many animals hear sounds inaudible to humans;consider the training whistles in common use that are silent to humans but clearly audible by dogs . 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 and communicate with infrasonic signals (<20 Hz).

That brings us to three major auditory questions: 1) what are the differences marine and land mammal ears, 2) how do these differences relate to underwater hearing, and 3) how do these differences affect the acoustic impacts?

To address these questions requires assimilating a wide variety of data. Behavioral and electrophysiological measures are available for some odontocetes and pinnipeds, but there are no published hearing curves for any mysticete. We have anatomical data on the auditory system for approximately one-third of all marine mammal species, including nearly half of the larger, non-captive species. These data allow us to estimate hearing based on physical models of the middle and inner ear. To some extent it also allows us to address potentials for impact. For marine mammals it is necessary to bring both forms of data, direct from behavioural tests and indirect from models, to bear. Before beginning those discussions, however, it is necessary to explain a few of the "rules" for sound in water vs. air.

Sound in air vs. water

Hearing is simply the detection of sound. "Sound" is the propagation of a mechanical disturbance through a medium. In elastic media like air and water, that disturbance takes the form of acoustic waves. Basic measures of sound are frequency, speed, wavelength, and intensity. Frequency, measured in cycles/sec or Hertz (Hz), is defined as:

f = c/lambda (1)

where c = the speed of sound (m/sec) and lambda is the wavelength (m/cycle).

The speed of sound is not invariable; it depends upon the density of the medium. Because water is denser than air, sound in water travels faster and with less attenuation than sound in air. Sound speed in air is approximately 340 m/sec. Sound speed in sea water averages 1530 m/sec but will vary with any factor affecting density and any ocean region can have a highly variable sound profile that may change both seasonally and regionally. For practical purposes, in water sound speed is 4.5 times faster and, at each frequency, the wavelength is 4.5 times greater, than in air.

How do these physical differences affect hearing? Mammalian ears are primarily sound intensity detectors. Intensity, like frequency, depends on sound speed and, in turn, on density. Sound intensity (I) is the acoustic power (P) impinging on a surface perpendicular to the direction of sound propagation, or power/unit area (I=P/a). Intensity for an instantaneous sound pressure for an outward traveling plane wave in terms of pressure, sound speed, and density is defined mathematically as:

I = pv = p (p/rho c) = p2/rho c

The combined factor (rho c) is the characteristic impedance of the medium. If we take into account the differences in sound speed in air c=340 m/sec vs. sea water c=1530 m/sec; and in density which in air=0.0013 g/cc vs. sea water=1.03 g/cc:

Iair = p2/(340m/sec)(0.0013 g/cc) = p2/(0.442 g-m/sec-cc)

Iwater = p2/(1530m/sec)(1.03 g/cc) =p2/(1575 g-m/sec-cc)

To examine the sensory implications of these numbers, consider a hypothetical mammal, that hears equally well in water and in air. For this to be true, an animal would require the same acoustic power/unit area in water as in air to have an equal sound percept, or (Iair = Iwater):

Iair = pair2/(0.442 g-m/sec-cc) = pwater2/(1575.g-m/sec-cc) = Iwater

pair2(3565.4) = pwater2 (5)

pair(59.7) = pwater

This means the aquatic ear needs and must tolerate sound pressures in water that are ~60 times greater than are required in air to produce the same intensity and therefore the same sensation in the ear.

For technological reasons, we commonly use effective sound pressure level (SPL) rather than intensity to describe hearing thresholds (see Au 1993 for discussion). Sound pressure levels are conventionally expressed in decibels (dB), defined as:

dB SPL = 10 log (pm2/pr2) (6)

= 20 log (pm/pr)

where pm is the pressure measured and pr is an arbitrary reference pressure. Currently, two standardized reference pressures are used. For air-borne sound measures, the reference is dB re 20 Pa rms, derived from human hearing. For underwater sound measures, the reference pressure is dB re 1 Pa.

Decibels are a logarithmic scale that depends on reference pressure. In the earlier hypothetical example, with identical reference pressures, the animal needed a sound level ~35.5 dB greater in water than in air. However, if conventional references for measuring levels in air vs. water are used, the differences in reference pressure must be considered as well. This means he underwater sound pressure level in water if measured with conventional reference pressures would need to be 61.5 dB re 1 Pa greater in water to be equivalent to the decibel in air or dB re 20 Pa in air. Thus, the rule of thumb is that to compare air vs underwater sound intensities, the numerical value of the water sound pressure level must be thought of as being reduced by ~61.5 dB to be comparable numerically to an intensity level reported in air.

It is important to remember that these equations describe idealized comparison of air and water borne sound. In comparing data from different species, particularly in comparing air based land mammal and marine mammal hearing, experimental condition differences are extremely important. We have no underwater equivalent of anechoic chambers, often results are obtained from one individual that may not have normal hearing, and test conditions are highly variable.

Mechanisms of Acoustic Trauma

Temporary vs, Permanent Threshold Shifts

Because of our considerable interest in human hearing and how hearing is lost or may be ameliorated, noise trauma is a well-investigated phenomenon. For the sake of completeness in the following discussion, noise trauma has been divided into lethal and sublethal impacts, although only sublethal impacts are likely to be relevant in the case of long-range sonar devices. 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 exhaustion or over-extension of one or more ear components. Of course, sublethal impacts may ultimately be as devastating as lethal impacts, causing death through impaired foraging, predator detection, communication, stress, or mating disruption, but the potential for this type of extended or delayed impact from any sound source is not well understood for any mammal.

Essentially whether there is any hearing loss and, if so, what portion of hearing is lost, comes down to three interactive factorst:

Intensity, frequency, and sensitivity.

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 permanent (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 and *received* sound level causes. 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 *only* in or near the signal band, but intensity and duration can act synergistically to broaden the loss.

The point cannot be made too strongly that this is a synergistic and species-specific phenomenon. Put simply, for a sound to impact an ear, that ear must be able to hear the sound, and, equally important, the overall effect will depend on just how sensitive that ear is to the particualr sound. For this reason there is no single, simple number; i.e., no one sound byte, for all species that accurately represents the amount of damage that can occur.

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. In most cases a signal intensity of 80 dB over the individual threshold at each frequency is required for significant threshold shifts (see Fig. 1). This finding led to the current OSHA allowable limit of 90 dB re 20 Pa for human workplace exposures for broad spectrum signals (Lehnhardt, 1986).

Unlike TTS which is highly species dependent, PTS onsets are more general. One important aspect of PTS is that signal rise-time and duration of peak pressure are significant factors. Commonly, 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). In humans, PTS results most often from protracted, repeat intense exposures (*e.g.*, occupational auditory hazards from background industrial 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 with land mammals, multi-hour exposures to narrow band noise are used to induce both TTS and PTS and initial shifts are often in the 10's of decibels. Work to date on marine mammals has been much more conservative with relatively short exposures that induce less than 10 dB of shift which is considered invariably temporary. Consequently there are serious concerns that the numbers from current experiments cannot be used to extrapolate PTS from TTS data as the current curves are not yet at the conventional or comparative TTS fronteir as defined for land mammals and humans. As noted above, most mammals with air-adapted ears commonly incur temporary losses when the signal is 80 dB over threshold. The only other available data for underwater shifts are from experiments that produced TTS 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 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.

Blast Injury

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:

MILD - Recovery	MODERATE - Partial loss	SEVERE - Permanent loss - death
Pain		
Vertigo	Otitis media	Ossicular Fracture/Dislocation
Tinnitus	Tympanic membrane rupture	Round/Oval window rupture
Hearing Loss	Tympanic membrane hematoma	CSF leakage into middle ear
Tympanic tear	Serum-blood in middle ear	Cochlear and saccular damage
	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) becauseit is the result of saturation or in simpler terms extension past the breaking point of body and certainly auditory tissues.

There is no well defined single criterion for sublethal ATS from blasts, 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 can repair spontaneously if less than 25% of the membrane is involved or can be repaired surgically with no hearing loss if greater areas are compromised), 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. Trauma to other areas of the auditory system such as the outer canal and middle ear bones are not nearly as well investigated. In light of concerns from the Bahamian beaked whale incident, this is an area warranting more research.

Concerning survivable blast trauma, 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 Hearing

Hearing research has traditionally focused on mechanisms of hearing loss in humans. Animal research has therefore emphasized experimental work on ears in other species as human analogues. Consequently we generally have investigated either very basic mechanisms of hearing or induced and explored human auditory system diseases and hearing failures through these test species. Ironically, because of this emphasis, remarkably little is known about natural, habitat-and-species-specific aspects of hearing in most mammals. With marine mammals we are at an extreme edge of not only habitat adaptations but also of ear structure and hearing capabilities.

The same reasons that make marine mammals acoustically and auditorally interesting; i.e., that they are a functionally exceptional *and* an aquatic ear - also make them difficult research subjects. Marine mammal hearing has for many decades been the poor stepchild of our country's auditory research program. Consequently, we now find ourselves for multiple reasons in need of precisely the basic research information that we lack. Nevertheless, we can address some issues about marine mammal hearing, both directly and inferentially from the data in hand. While there are large gaps remaining in our knowledge, progress has been made on some fronts related to sound and potential impacts from noise.

Marine mammals, and whales in particular, present an interesting hearing paradox. On one hand, marine mammal ears physically resemble land mammal ears. Therefore, since many forms of hearing loss are based in physical structure, it is likely hearing damage occurs by similar mechanisms in both land and marine mammal ears. On the other hand, the sea is not, nor was it ever, even primordially, silent. The ocean is a naturally relatively high noise environment. Principal natural sound sources include seismic, volcanic, wind, and even biotic sources. Whales and dolphins in particular evolved ears that function well within this context of high natural ambient noise. This may mean they developed "tougher" inner ears that are less subject to hearing loss. Recent anatomical and behavioral studies do indeed suggest that whales and dolphins may be more resistant than many land mammals to temporary threshold shifts, but the data show also that they are subject to disease and aging processes. This means they are not immune to hearing loss, and certainly, increasing ambient noise via human activities is a reasonable candidate for exacerbating or accelerating such losses

Unfortunately, existing data are insufficient to accurately predict any but the grossest acoustic impacts on marine mammals. At present, we have relatively little controlled data on how the noise spectrum is changing in oceanic habitats as a result of human activities. We also have little information on how marine mammals respond physically and behaviorally to intense sounds and to long-term increases in ambient noise levels. Our current inability to predict the impact of man-made sounds in the oceans has spawned serious and occasionally vituperous debates in the scientific community as well as costly legal battles for environmental and governmental organizations. Ironically, our data gaps may also be hampering the development and deployment of even simple devices such as effective acoustic deterrents that could decrease marine mammal by-catch. This testimony will not fill the gaps in our knowledge but rather will discuss our current data base on both acoustic trauma and on the sound profiles of ocean habitats in the context of what we know about species variations in marine mammal hearing. It will focus on how species vary in their potential for impact and on how we may go about determining whether auditorially fragile species coincide with "acoustic hotspots" where man's sonic activities, particularly sonars as an issue for this committee, may damage hearing and disrupt key behaviours.

The data available show that all marine mammals have a fundamentally mammalian ear which through adaptation to the marine environment has developed broader hearing ranges than are common to land mammals. Audiograms are available for only 10 species of odontocetes and 11 species of pinnipeds. All are smaller species which were tested as captive animals. However, there are 119 marine mammal species, and the majority are large wide-ranging animals that are not approachable or testable by normal audiometric methods. Therefore we do not have direct behavioral or physiologic hearing data for nearly 80% of the genera and species of concern for coastal and open ocean sound impacts. For those species for which no direct measure or audiograms are available, hearing ranges are estimated with mathematical models based on ear anatomy obtained from stranded animals or inferred from emitted sounds and play back experiments in the wild.

The combined data from audiograms and models show there is considerable variation among marine mammals in both absolute hearing range and sensitivity. Their composite range is from ultra to infrasonic. Odontocetes, like bats, are excellent echolocators, capable of producing, perceiving, and analyzing ultrasonics frequencies well above any human hearing. Odontocetes commonly have good functional hearing between 200 Hz and 100,000 Hz (100 kHz), although some species may have functional ultrasonic hearing to nearly 200 kHz. The majority of odontocetes have peak sensitivities (best hearing) in the ultrasonic ranges although most have moderate sensitivity to sounds from 1 to 20 kHz. No odontocete has been shown audiometrically to have acute; i.e., best sensitivity or exceptionally responsive hearing (<80 dB re 1 Pa) below 500 Hz.

Good lower frequency hearing appears to be confined to larger species in both the cetaceans and pinnipeds. No mysticete has been directly tested for any hearing ability, but functional models indicate their functional hearing commonly extends to 20 Hz, with several species, including blue, fin, and bowhead whales, that are predicted to hear at infrasonic frequencies as low as 10-15 Hz. The upper functional range for most mysticetes has been predicted to extend to 20-30 kHz.

Most pinniped species have peak sensitivities between 1-20 kHz. Some species, like the harbour seal, have best sensitivities over 10 kHz. Only the elephant seal has been shown to have good to moderate hearing below 1 kHz. Some pinniped species are considered to be effectively double-eared in that they hear moderately well in two domains, air and water, but are not particularly acute in either. Others however are clearly best adapted for underwater hearing alone.

To summarize, marine mammals as a group have functional hearing ranges of 10 Hz to 200 kHz with best thresholds near 40-50 dB re 1 Pa. They can be divided into infrasonic balaenids (probable functional ranges of 15 Hz to 20 kHz; good sensitivity from 20 Hz to 2 kHz; threshold minima unknown, speculated to be 60-80 dB re 1 Pa); sonic to high frequency species (100 Hz to 100 kHz; widely variable peak spectra; minimal threshold commonly 50 dB re 1 Pa), and ultrasonic dominant species (200 Hz to 200 kHz general sensitivity; peak spectra 16 kHz to 120 kHz; minimal threshold commonly 40 dB re 1 Pa).

Impacts and Sonar

Since the development and use of SONAR in World War II, acoustic imaging devices have been increasingly employed by the military, research, and commercial sectors to obtain reliable, detailed information about the oceans. On one hand, these devices have enormous potential for imaging and monitoring the marine environment. On the other hand, because echo-ranging techniques involve the use of intense sound and because hearing is an important sensory channel for virtually all marine vertebrates, existing devices also represent a potential source of injury to marine stocks, both predator (marine mammals) and their prey. Therefore, a reasonable concern for any effort involving active sound use in the oceans is whether the projection and repetition of the signals employed will adversely impact species within the "acoustic reach" of the source. Realistically, because of the diversity of hearing characteristics among marine animals, it is virtually impossible to eliminate all acoustic impacts from any endeavor, therefore the key issues that must be assessed are: 1) what combination of frequencies and sound pressure levels fit the task, 2) what species are present in an area the device will ensonify at levels exceeding ambient, and 3) what are the potential impacts to those species from acoustic exposures to the anticipated frequency-intensity combinations.

In order to assess potential impacts, it is necessary to obtain the best possible estimate of the coincidence of acoustic device parameters and auditory sensitivities for animals that may be exposed. Because marine mammals are both an important group in terms of conservation and are generally considered to be acoustically sensitive, the primary goal of this document is to provide a detailed summary of currently available data on marine mammal hearing and auditory systems, and where possible to put that data into a functional or comparative context. The key issues addressed are: 1) how do marine mammal ears differ from terrestrial ears, 2) how do these differences correlate with underwater sound perception, 3) what is known from direct measures about marine mammal hearing sensitivities, 4) what can be reliably extrapolated about the frequency sensitivity of untested species from currently available auditory models, and 5) how sensitive to acoustic impacts are these ears.

Conclusions

The consensus of the data is that virtually all marine mammal species are potentially impacted by sound sources with a frequency of 300 HZ or higher. Any species can be impacted by exceptionally intense sound, and particularly by intense impulsive sounds. However, at increasing distance from a source, which is the realistic scenario as opposed to at source, the effects are a composite of three aspects: Intensity, Frequency, and Individual Sensitivity. Briefly, if you cannot hear the sound or hear it poorly, it is unlikely to have a significant effect. If however, you have acute hearing in the range of a signal, be it prop noise or a sonar, there is a potential for impact at a greater range than for a source you hear poorly. Because each species has a unique hearing curve that differs from others in range, sensitivity, and peak hearing, it is not possible to provide a single number or decibel level that is safe for all species for all signals.

Relatively few species are likely to receive significant impact for lower frequency sources. Those species that currently are believed to be likely candidates for LF acoustic impact are most mysticetes and the elephant seal as the only documented lower frequency sensitive pinniped. Most pinnipeds have relatively good sensitivity in the 1-15 kHz range while odontocetes have peak sensitivities above 20 kHz. It must be remembered that received levels that induce acoustic trauma, at any one frequency, are highly species dependent and are a complex interaction of exposure time, signal onset and spectral characteristics, as well as received vs. threshold intensity for that species at that frequency.

Pilot studies show that marine mammals are susceptible to hearing damage but are not necessarily as fragile as land mammals. The available data suggest that a received level of approximately 140 dB re 1 microPascal which is in the 80-90 dB range over species-specific threshold for a narrow band source will induce temporary for hearing in and near that band in pinnipeds and delphinids (Ridgway, pers. comm.; Schusterman, pers. comm.). Estimates of levels that induce permanent threshold shifts in marine mammals can be made, at this time, only by extrapolation from PTS and trauma studies in land mammals.

Blasts are cardinal sources, capable of inducing broad hearing losses in virtually all species but some resistance or tolerance may occur based on body mass of marine mammals compared to most land mammals tested.

For all devices, the question of impact devolves largely to the coincidence of device signal characteristics with the species audiogram. Because the majority of devices proposed use frequencies below ultra or high sonic ranges, odontocetes, with relatively poor sensitivity below 1 kHz as a group, may be the least likely animals to be impacted. Mysticetes and pinnipeds have substantially greater potential than odontocetes for direct acoustic impact because of better low to mid-sonic range hearing.

Behavioral perturbations are not assessed here but a concern is noted that they are an equal or potentially more serious element of acoustic impacts. While auditory trauma, particularly from short or single exposures may impair an individual, that is unlikely to impact most populations. Long term constant noise that disrupts a habitat or key behaviour is more likely to involve population level effects. In that sense, the question of individual hearing loss or animal loss form a single intense exposure is far less relevant to conservation than more subtle, literally quieter but pervasive source that induces broad species loss or behavioural disruption.

Mitigation of any source or estimation of impact requires a case by case assessment, and therefore suffers from the same chronic lack of specific hearing data. To provide adequate assesments, substantially better audiometric data are required from more species. To obtain these data requires an initial three-pronged effort of behavioural audiograms, evoked potentials recordings, and post-mortem examination of ears across a broad spectrum of species. Cross-comparisons of the results of these efforts will provide a substantially enhanced audiometric data base and should provide sufficient data to predict all levels of impact for most marine mammals. To achieve this goal without bias involves advocacy and funding from a broader spectrum of federal and private sources. That in turn is likely to require a significant effort in public education about the real underlying issues that will supplant current misdirections or precipitous reactions on the part of many groups concerned with marine conservation.

Summary

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 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.

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. 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 and even reception of incoming sounds 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). 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 implied a substantial, progressive, hearing loss beginning in the high frequency regions, precisely the pattern commonly observed in humans. 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 consistent with age-related loss in two *sea lions*have also been reported by Kastak and Schusterman (1995).

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 abovr clearly suggest age and/or exposure to noise can significantly alter hearing in marine mammals, and in some cases (compare the two curves shown in figure 2A for bottlenosed dolphins), it is clear that some individual differences have been observed in "normal" captives that may be the result of permanent hearing loss. The fact that some studies show losses in marine mammals consistent with age-related hearing changes. Disease also complicates the assumptions that any animal has normal hearing or that the only source of a loss found is 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.

Of course, acoustic trauma is a very real and appropriate physiologic concern. It is also one for which we can ultimately, given proper research, obtain a data that will allow us to provide a usable metric. 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. 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.

However, it is equally important to consider that sub-trauma levels of sound can have profound effects on individual fitness. 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 usefully 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 higher than typical tolerances for noise 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 sonars or in effect any human acoustic device, the principal concerns are to determine a balance of frequencies vs. level vs. duty cycle that will effectively detect targets at long ranges but will not repel 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 operation.

2. What are the hearing curves for species within the sound field?

The fundamental concern is to avoid impact or harassment in the short term, as well as preventing long-term, multiple exposure effects that can compound the probability of hearing loss.

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 that which if any of these measures is important to the marine mammal ear has not been determined. Further, it is also important to consider the trade-offs each implies in operational effectiveness of the sonars in question. If decreasing one aspect increases the parameters of another, the composite effects must always be kept in mind.

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, 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 3 for marine mammals audiograms compared with a human audiogram.

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. What the figure suggests is that theMysticetes (which are speculated to have a hearing curves similar to but at lower frequencies than odontocetes)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 by LF sonars or other devices, 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 and depths ensonified 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.

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 be 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.

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.

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