PROCEEDINGS

WORKSHOP ON THE

EFFECTS OF

ANTHROPOGENIC NOISE

IN THE MARINE ENVIRONMENT,

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FOREWORD

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BACKGROUND

This volume is intended to provide a current summary of the state of knowledge about the effects of human-generated noise on marine organisms, along with suggestions about where additional scientific research is most needed, most ready for further development, or both. Marine mammals were emphasized, but fish, sea turtles and other marine animals were considered to some extent.

WORKSHOP FORMAT AND REPORT PREPARATION

Thirty-seven experts from five relevant subject areas were convened for a three-day workshop in February 1998. The subject areas were ocean (physical) acoustics, non-hearing physiological effects of sound, hearing, behavior, and monitoring and mitigation of noise effects. The subject areas were not mutually exclusive and the workshop format was also designed to allow all members to participate in the half-day discussions of subjects other than their own. All
participants were provided with read-ahead materials so that they could participate in the one to two hour review of each team leader's proposed format for discussions and reports that were to follow. After the workshop, team leaders for each of the five discussion groups prepared an initial draft report of the proceedings for their topic area, and then distributed it for review by the entire membership. Some team members were asked to prepare additional special material after the workshop. These special reports are labeled to indicate that they were not part of the workshop discussion, but were prepared later at the request of the membership. The five topic area chapters in this volume therefore represent a considerable amount of interdisciplinary scrutiny by top professionals across the range of subject matter.

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ORGANIZATION AND SUPPORT
This workshop arose from a mutually recognized need among several federal agencies that the issue of anthropogenic noise is of considerable public interest and that their agencies have a potential role to play in addressing the issue and its impacts. Representatives of the Department of Defense, National Marine Fisheries Service, Geological Survey, Minerals Management Service, and Coast Guard met under the leadership of the Marine Mammal Commission to devise a process for providing their respective agencies with the information they would need to make informed decisions about acoustic effects on the underwater environment. This workshop was planned as a first step in a process intended to lead to a national policy and plan of action on this topic. This policy and plan should be integrated across agencies, should include a solid foundation of accurate scientific information, and should address public concerns about national security, economics, and environmental quality.

GOALS The reader may view this report as a "blueprint". It should not be treated as an exhaustive in-depth look at the scientific data, but rather as a framework to provide context to subsequent more exhaustive efforts focused on critical technical areas. Likewise, it should not be treated as a fully-realized template for policy, guidelines or regulations, but again as a framework upon which project proponents, resource managers, biologists and acousticians, legal experts, economic experts, advocacy groups and the public can structure their discussions during the formulation of policies and plans of action with regard to anthropogenic underwater noise.

Since many people view the environmental impact from anthropogenic noise as potentially serious and extensive, there is a sense of urgency to many discussions of the subject. We urge the users of this document not to allow their sense of urgency to shortcut the above process by treating this document either as an encyclopedic reference on all relevant information (which it is not) or as a set of recommendations as to what are "safe" levels of acoustic exposure for marine life (in fact, this question was deliberately avoided).

TEAM REPORT SUMMARIES

OCEAN ACOUSTICS
During the past fifty years, significant progress has been made in our understanding of sound generation, propagation, and signal processing in the ocean. This report summarizes those aspects of underwater acoustics which are relevant to the subject of anthropogenic noise in the marine environment. These topics are addressed in the context of the passive sonar equation and include source level, transmission loss, ambient noise, and processing gain. In addition, a discussion of sound measures and boundary conditions is presented. Finally, recommendations
are made for future collaborative research efforts between the ocean and animal bioacoustic communities.

HEARING

The following summarizes the major issues targeted in this section of the report: 1) Sounds of high intensity and/or long duration are known to cause physiological effects on the auditory system of terrestrial mammals and birds and there is evidence that such sounds can effect the ears of fishes. Effects may be temporary or permanent. Multiple exposures causing temporary hearing loss may ultimately result in permanent hearing loss, 2) Loss of hearing, whether it be temporary or permanent, can affect animals in a number of ways. As a minimal effect, a temporary loss could prevent an animal from detecting predator or prey, or result in the animal entering an area that would be dangerous for its survival. In addition to these effects, permanent loss of hearing could result in loss of an animal's ability to communicate with conspecifics, find mates, care for young, or find food. Over the long term, loss of hearing capabilities by large numbers of a species could lessen reproductive potential and survival of the species, 3) Permanent effects that are most readily seen clinically involve damage to the sensory hair cells (the mechanotransducers) in the inner ear. In mammals these cells are not replaced once they are damaged, and damage to these cells results in permanent loss of hearing. Replacement does occur in birds and fishes, but it is not clear that their hearing returns to normal even with the new hair cells, 4) the aquatic environment has numerous natural sound sources, including wind on the surface, rain, shoaling waves, and seismic events. There are also substantial biological sources such as from snapping shrimp, fishes, and marine mammals that are significant sound sources within their own right. Sounds are widely used by aquatic animals in their everyday survival including foraging, detecting predators, finding mates, and caring for young, etc. Any sounds present in the environment that interfere with natural communication or perception of relevant sounds potentially compromise the survival of an animal, 5) There is a wide range of human-generated (anthropogenic) sounds in the aquatic environment. These include sounds produced by ships, for exploration, hydroelectric plants, etc. There is substantial evidence that the overall level of sound in the aquatic environment has increased significantly in the past 50 years and this is cause for concern vis a vis effects on aquatic organisms. At the same time, because the major increase is attributable to shipping, most added noise is likely to be below 500 Hz, and so the major effects of anthropogenic sounds may only be on those species that readily detect sounds at lower frequencies, 6) The effects of intense sound on the hearing of aquatic animals is not well known and has only been minimally investigated to date. However, there is evidence that temporary and permanent hearing loss occurs in dolphins and some pinnipeds, as well as in at least one species of fish. There are no data on the effects of sound on hearing capabilities of mysticete whales, or semi-aquatic mammals such as otters, 7) There are also almost no data on the effects of intense sounds on hearing by aquatic birds, reptiles, or invertebrates. The concern for hearing loss in these animals needs to be as great as it is for marine mammals since many of these species are of economic importance to humans and/or keystones in the marine food chain. Damage to hearing, and thus to the ability of these animals to survive, may affect the survival of other animals that interact or depend upon these species; 8) The levels of sounds needed to cause permanent hearing loss in aquatic mammals are not known.
These levels are very hard to assess using behavioral techniques since it would be necessary to damage hearing capabilities in order to assess these effects. Other techniques are under development, including ABR and morphological methods, which may enable us to predict the levels of sound that will damage hearing based upon extrapolation of the effects from lower levels of sound stimulation.

NON-HEARING PHYSIOLOGICAL EFFECTS OF SOUND

The major focus of this group was on physiological effects of sound in the marine environment apart from effects on hearing. The paucity of current information in this area was underscored in the read-ahead materials by Richardson, Popper, and Cudahy and Sims. In view of the lack of information, it was decided to use some of the work done with human divers to investigate physiological effects of low-frequency sound as a starting point and relate diver target areas to marine research areas. The primary research areas reviewed included blast, extreme vibration, impulse noise, and stress along with low-frequency sound. Factors identified during the session that limited conclusions about the effects of underwater sound included the diversity of sound stimuli, the diversity of target animals (marine mammals, fish, reptiles, seabirds, and invertebrates), and the diversity of marine environments. The information presented therefore was scattered rather than focused and there was considerable discussion regarding measurement technology, such as the least intrusive way to track and get real-time information on animals in the ocean, and what constitutes the most cost-effective research strategies, such as focusing on acute versus long-term effects.

BEHAVIOR

The team recognized the significance of assessing both the immediate and long-term direct effects of alteration of behavior by anthropogenic noise. The team also recognized the role of behavior assessment as a means of predicting and thus preventing more immediately serious physically injurious effects. Background discussions focused on issues of data collection methods and data interpretation that must be considered in the generation of useful behavioral data in this topic area. Biological significance was a recurring theme in discussions of acoustic behavior and alteration of acoustic behavior by introduced noise. Biological significance has very specific meaning in population biology and is the baseline scientific metric used to measure the impact of both natural and manmade environmental changes on the living world. The group recognized that many measurable behavioral responses to anthropogenic noise, such as brief temporary alterations in heart rate or breathing, may have little or no biological significance, and that possibly significant behaviors may currently go unassessed, particularly those behaviors that are associated with cumulative long-term effects. New developments in monitoring technology were discussed in light of their ability to better reveal and quantify biologically significant behavioral change. The team made recommendations on the use of behavior to assess noise impacts. In addition to emphasizing the selection of behaviors that have clear biological significance the team discussed the implications of cessation or alteration of vocal behavior in response to an introduced noise source, since these easily measured behaviors can indicate impacts ranging from profound immediate adverse effects to trivial and easily accommodated effects. Additional recommendations included the measurement of sound fields to more accurately determine the cumulative "dosage" of sound an individual animal might receive as it travels through an acoustically heterogeneous three-dimensional world. The importance of
control procedures in behavior assessment was also emphasized, since few areas of scientific
endeavor are more sensitive to observer biases, or more influenced by uncontrolled variables.

**MONITORING AND MITIGATION**

The session focused on marine mammals. It began with a discussion of the reasons
(regulatory and research) for monitoring, and some of the limitations. The participants reviewed
the capabilities and limitations of several monitoring methods, including currently-used and
potential methods. Topics included visual surveys from ship, shore or aircraft; photographic,
electro-optic and remote methods; passive and active acoustics; dataloggers and telemetry; and
determination of sound exposure. There was consensus that, in most situations, no single

**CONCLUSION**

This volume is, therefore, a broad, inclusive (but not exhaustive) summary of the current
scientific knowledge relevant to assessing the effect of anthropogenic noise on marine life. It is
intended to be a guide to the topics that should be included in policy, legal, regulatory and
management plans for dealing with this issue. It includes a review of current scientific
knowledge along with expert opinions about the science areas in which information is most
needed and/or in which there is a high probability of near-term success in obtaining more
information. However, no attempt was made to recommend a particular course of action with
regard to using the information in policy and legal matters. In fact, such a course was
deliberately avoided because it would necessarily involve issues other than science, and should
therefore be addressed by a broader spectrum of participants. In spite of that caveat, we are
gratified that scientific evidence is given such great importance by all sides of the debate on this
issue, and are acutely aware of our societal responsibility to provide high quality information as
quickly as practicable.
best to interpret and implement relevant legislation such as the Marine Mammal Protection Act. The workshops are products of consultations initiated early last year (1997) among representatives of the Navy, the National Marine Fisheries Service, the Marine Mammal Commission, the Minerals Management Service, the U.S. Geological Survey, the U.S. Coast Guard, and other federal government agencies with interests and responsibilities related to human sources of ocean noise.

This workshop was organized by Dr. Gisiner and was funded by the Office of Naval Research. Participants include invited experts in the relevant fields of science and engineering (see Appendix A).

The fact that this workshop is being held reflects growing interest in the possible effects of sound from human sources on the marine environment. That interest has scientific, political, and legal components, all of which need to be kept in mind. The scientific interests are well known, and need no introduction here. The political interests and related statutory matters may be less well known. They are the products of concerns raised by scientists, environmental groups, and others regarding the possible effects of anthropogenic sound on marine mammals, fish, and other components of the marine environment, and conflicting concerns regarding regulation of sound-producing activities raised by affected scientists, industries, and other producers and users of anthropogenic sounds.

Nationally, much of this concern has been precipitated by three things:
1. the Acoustic Thermometry of Ocean Climate (ATOC) Program funded in 1993 by the Defense Department's Advanced Research Projects Agency;
2. the National Defense Authorization Act's requirement that new designs for the hulls and other critical components of Navy ships and submarines undergo shock tests before service in the fleet; and
3. the Navy's planned operational deployment of a surveillance towed array sonar system (SURTASS) low-frequency active (LFA) sonar.

In Alaska and California, there has been much concern expressed regarding the possible effects of noise associated with offshore oil and gas exploration and development. Much of what we know about the effects of sound on marine mammals and other marine organisms is the result of research that either has been conducted or supported by the Navy and by the Minerals Management Service in response to these types of concerns.

When the Marine Mammal Protection Act was enacted in 1972, there was no apparent recognition that noise could or would be a marine mammal conservation problem. For example, there is no mention of noise or noise-producing activities in any of the Congressional Committee reports that explain the rationale for the various provisions in the Act.

The Act was unique in several respects. One was that it placed the burden on those wanting to take marine mammals for commercial or other purposes to show that the taking would not have adverse impacts, rather than on the regulatory agencies or the conservation community to show that it would, which had been the traditional approach to regulation until that time. That is, prior to passage of the Marine Mammal Protection Act, marine mammals, like fish and other wildlife, were generally viewed as common property resources that could be used without restriction until someone could show that the use was adversely affecting the resource.
As originally written and subsequently interpreted, the Act made it illegal, with certain specified exceptions, to hunt, capture, kill, or harass marine mammals in any area under U.S. jurisdiction without first obtaining a waiver of the Act's moratorium on such taking. The conditions for obtaining a waiver were procedurally burdensome and, as a consequence, few waivers were sought or granted. The Act was amended in 1981 and again in 1986 to make it easier to obtain taking authorization when only small numbers of animals are expected to be taken and certain other conditions are met -- i.e., the taking is unintentional; the effects on population size and productivity will be negligible; and the responsible regulatory agency (either the National Marine Fisheries Service or the Fish and Wildlife Service) have prescribed regulations specifying the permissible methods of taking and setting forth requirements for monitoring and reporting to ensure that no more than the authorized number of animals are taken and that the effects are in fact negligible. In 1994, the Act was amended again to make it easier to get authorization for taking that is by unintentional harassment only.

Several points regarding these amendments merit special mention. One is that the House of Representative's Report that accompanied the 1981 amendments stated that the term "negligible" impact was intended to mean an impact that was so insignificant that it could be disregarded. In this regard, the report noted that Webster's Dictionary defines the term "negligible" to mean "so small or unimportant or of so little consequence as to warrant little or no attention." Although it has not been subject to interpretation in any court suits, it appears that this negligible impact standard is more restrictive than the "no significant impact" standard in the National Environmental Policy Act.

A second point meriting special mention is the provision in the 1994 MMPA amendments in which Congress differentiated two types of harassments. The first, titled "Level Effects of Anthropogenic Noise in the Marine Environment"

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A harassment" is defined as "any act of pursuit, torment, or annoyance which has the potential to injure a marine mammal or marine mammal stock in the wild." The second, titled "Level B harassment" is defined as "any act of pursuit, torment, or annoyance which has the potential to disturb a marine mammal or marine mammal stock in the wild by causing disruption of behavioral patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering."

The National Marine Fisheries Service and the Fish and Wildlife Service are responsible for interpreting and promulgating regulations to implement these and the other provisions of the Act, and for insuring compliance with the Act and its implementing regulations. It is important in this regard to keep in mind that any individual or organization can challenge the actions of the regulatory agencies in court suits if they believe that those actions do not reflect Congressional intent. Thus, the courts often are the final interpreter of Congressional intent.

Recognizing this, the National Marine Fisheries Service plans to hold a workshop later this year (1998) to seek expert advice as to how -- given the available information -- guidelines or regulations can be best formulated to reflect Congressional intent regarding authorization of the taking marine mammals incidental to sound-producing activities. It is hoped that this workshop will provide the foundation for the follow-up workshop. In particular, it is hoped that this workshop will --
provide a thorough and objective summary of what is known about
the sources, characteristics, transmissions, and effects of
anthropogenic sound on marine mammals and other marine
organisms;

* identify uncertainties that should be taken into account in
developing appropriately precautionary management guidelines or
regulations; and

* describe the research that will be required to resolve the
uncertainties and, pending their resolution, the kinds of monitoring
programs that would be required to verify that sounds from
anthropogenic sources are not having unacceptable effects on
marine mammals or other marine organisms.

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**Team Reports**

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**Ocean Acoustics**

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INTRODUCTION

The ocean acoustics component of the effects of manmade sound on the marine environment can be analyzed in terms of the passive sonar equation, which describes the signal excess \( SE \) in decibels (dB) measured at a receiver in the ocean (Urick, 1975),

\[
SE = SL - TL - AN + AG,
\]

(1)

where \( SL \) is the source level, \( TL \) is the transmission loss, \( AN \) is the ambient noise, and \( AG \) is the processing gain associated with the receiving system. Since the decibel is inherently a relative quantity,

\[
SE(dB) = 20 \log_{10} \left( \frac{\text{Measured Pressure}}{\text{Reference Pressure}} \right),
\]

(2)

it is essential to define a reference pressure level when we attempt to describe absolute signal levels in terms of dB. In ocean acoustics, the convention for quite some time has been to choose the reference pressure level as 1 microPascal. The source level is then defined as the pressure at a unit distance, typically 1 meter, from the source, while the transmission loss describes all of the attenuating effects of the medium associated with propagation, scattering, and absorption as the signal travels from a position 1 meter from the source to the location of the receiver. The ambient noise is a descriptor of the acoustic level that would be measured under conditions where the source of interest is absent and may arise from sources that are natural and manmade, near and far, and discrete and continuous. Finally, the processing gain indicates the enhancement of the received signal that can occur through the application of clever signal processing techniques and, perhaps, through the use of multiple sensors in the receiving system. Thus, Eq. (1) states that the excess signal level detectable at a sensor in the ocean due to a source with output level \( SL \) depends upon the degradation which the transmitted signal suffers as a result of the propagation process (\( TL \)) and the ambient noise context (\( AN \)) within which the signal is observed. Once the signal is received at the sensor(s), some of these losses may be recovered through signal processing techniques (\( AG \)).

During the past fifty years, primarily because of Naval interest and support, significant progress has been made in our understanding of all of the components of the sonar equation. However, there is a unique set of problems which offer challenging research opportunities to both the ocean and animal bioacoustic communities working in collaboration. These include both basic and applied issues ranging from instrumentation development and database transfer to theoretical wave propagation and signal processing. In what follows, we will provide a brief summary of state-of-the-art knowledge in each one of the four areas associated with the sonar equation and offer recommendations for future research.

SOURCE LEVEL

In this section, we will consider sources of sound whose origins are well defined and for which the output levels can be measured in controlled experiments. Furthermore, we will focus on sources whose occurrence is sufficiently episodic that they are not typically considered a part of the long-term ambient noise environment. Thus, in this context, a continuous wave (CW) projector used in a shallow water acoustics experiment would be considered a source, while the
sound produced by breaking waves would be treated as ambient noise. We point out that, in the context of Eqs. (1) and (2), a correct and unambiguous description of the output level of such a single-frequency source would be, for example, 150 dB re 1 microPascal @ 1 m. In the case of signals which are not pure tones, the source level may be described in terms of a peak pressure in the time domain or as a power spectral density (dB re 1 microPascal squared per Hz @ 1 m) in the frequency domain. The issue of appropriate and consistent units among the various sub-disciplines continues to be an active area of debate in the acoustics community (Carey, 1995; Medwin and Clay, 1998; Appendix).

SHIPPING
The sound radiated by the enormous number of ships plying the world's seas is the single largest contributor to the total acoustic budget of the ocean. The effects of these vessels are both local, where they act as discrete sources of sound, and global, where they comprise the dominant component of the overall ambient noise level at frequencies below 500 Hz. As examples, the source levels associated with low-frequency pure tones radiated by supertankers and container ships lie in the range 180-190 dB re 1 microPascal @ 1 m, while drillship and dredging operations generate broadband source levels of 185 dB re 1 microPascal per Hz @ 1 m (Richardson et al., 1995). There is a considerable amount of information available in the literature on both ship traffic and source levels (Gray and Greeley, 1980; Institute of Shipping Economics and Logistics, 1989; Jennete, 1993; Lloyd's Register of Ships, 1989; Molinelli et al., 1990; Revello and Klingbeil, 1990; Ross, 1987; Scrimger et al., 1990; Scrimger and Heitmeyer, 1991).

OFFSHORE OIL EXPLORATION
The activities associated with the oil exploration industry have historically constituted a major source of acoustic activity in shallow water (<200 meters) and, in recent years, in deeper water (several hundred meters) as well. These activities range from oil and gas drilling and production operations to marine geophysical surveys and, in some geographic areas (e.g., the Gulf of Mexico), are of sufficient extent that they might be considered to be part of the background ambient noise level. Richardson et al. (1995) provides an extensive and comprehensive summary of the available data in this area and clearly shows that the strongest sources of sound are associated with seismic surveys. The extent to which our knowledge base is limited by the proprietary nature of oil exploration activities is unclear. Airguns and arrays of airguns are the most commonly used geophysical survey tools and are typically fired repeatedly every several seconds, providing broadband signals at tens of Hz with peak levels ranging from 216 to 259 dB re 1 microPascal @ 1 m. Other less commonly used sources in the exploration industry include sparker, boomer, and water guns, all of which produce levels comparable to those generated by airguns. By far, the most powerful sources of underwater sound are explosive charges of TNT, with charge weights in the range 0.5-20 kg producing broadband, peak levels in the range 267-279 dB re 1 microPascal @ 1 m (Richardson et al., 1995). For a variety of reasons, the use of explosives as acoustic sources has diminished dramatically in both the oil industry and the ocean acoustics community since the 1960s.

SONARS AND OCEANOGRAPHIC RESEARCH
Sonar signals permeate the ocean environment from the most practical to the most esoteric levels in the sense that every ship on earth has at least an echo sounder to determine
bottom depth and almost every oceanographic experiment has at least a pinger to determine instrument depth. In some cases, the transmission, reception, and positioning systems are far more elaborate and complex. Typically, pulsed high-frequency (kHz) signals are used over relatively short ranges (km) for echo sounding, bottom imaging (side scan and multibeam sonars), bottom and surface scattering studies, fish finding, navigation, communication, and Acoustic Harassment Devices (AHD's). Their output levels range from 180 to 230 dB re 1 microPascal @ 1 m (Richardson et al., 1995). It should be noted that high frequencies are rapidly attenuated in range, and therefore the sound emitted by even high source level devices diminishes quickly. For example, the absorption at 100 KHz is 0.01 dB/m, so that owing to absorption alone, a 200 dB emission @ 1 m is reduced to a 100 dB level at a range of 10 km. Geometrical (spherical) spreading loss reduces this an additional 80 dB at that range. In underwater acoustic and acoustical oceanographic research, low-frequency (tens to hundreds of Hz) CW (Constant Wavelegth) and coded signals are normally used to study the transmission characteristics of the ocean waveguide and to infer oceanographic properties of the surface, the water column, and the seabed. These experiments are typically conducted over short to moderate ranges (ones to hundreds of km), are of relatively short duration (2-4 weeks), and utilize sources such as the NRL J15-3, with an output level of 170 dB re 1 microPascal @ 1 m. In isolated instances (e.g., the ATOC Project), low-frequency sources with output levels of 195 dB re 1 microPascal @ 1 m have been used to study long-range (thousands of km) transmissions and their oceanographic implications.

**Effects of Anthropogenic Noise in the Marine Environment**

**RECOMMENDATIONS**

One of the exciting possible areas of future research involves the use of animals as sources of sound for the study of ocean acoustics in conjunction with investigations of animal behavior. A significant challenge here lies in localizing and tracking the sources in an uncertain environment. But both the inverse source and inverse environment problems have been studied extensively in ocean acoustics using matched field processing and inversion, as well as other, techniques (Brekhovskikh and Lysanov, 1991; Frisk, 1994; Jensen et al., 1994). The use of marine mammals as sources therefore offers a unique opportunity for collaborative research between the ocean and animal bioacoustic communities.

Another interesting area is the electroacoustic/physiological mechanism by which animals generate sound. Although some research work exists in this area, a unified effort among physicists, engineers, and biologists would be very useful and productive.

**TRANSMISSION LOSS**

During the past twenty-five years, enormous progress has been made in our understanding of the physics of acoustic wave propagation through the ocean and our ability to model, both analytically and numerically, the interaction of sound with complex ocean environments (Brekhovskikh and Lysanov, 1991; Frisk, 1994; Jensen et al., 1994). These include oceanographic features, such as fronts, eddies, currents, internal waves, bubbles, and surface gravity waves, as well as multilayered, rough, heterogeneous, elastic seabeds. The classical approaches of ray theory, normal modes, and wavenumber integration have all been extended to include both range and depth-dependent properties of the ocean. The parabolic equation method, originally intended for paraxial (small angle), range-dependent propagation in the water column, has been extended to accommodate steep angles and elastic bottoms. In
addressing the realities of the ocean environment, these computer codes are typically most effective and efficient in dealing with 2D (depth and range-dependent) problems, and must invoke some approximation (e.g., Nx2D slices) in order to deal efficiently with the full 3D problem. Thus, with these approaches, as well as the less commonly used finite-difference and finite-element methods, the computational complexity increases at least as rapidly as kR, where k is the characteristic wavenumber in the problem, and R is the distance (in each of the three spatial dimensions) over which we desire to compute the acoustic field. In practice, therefore, efficient and accurate high-frequency 3D calculations are limited to short ranges, while effective low-frequency calculations can be made for longer ranges. The computational challenge is further escalated in broadband calculations, where the typical, though time consuming, approach is Fourier synthesis of the time-dependent signal from its frequency components.

RECOMMENDATIONS

Despite the above-mentioned limitations, our modeling capabilities far exceed our ability to measure the ocean environment with the level of accuracy required for input data to the models (e.g., 3D sound velocity profiles in the water column and seabed on spatial scales of an acoustic wavelength or less). That is to say, inaccuracies in the transmission loss calculations are more likely due to inadequate input data than they are to deficiencies in the models. This is particularly true in shallow water environments, where our knowledge of lateral variability lags far behind that in deep water. Since surface, bottom, and water column effects can easily introduce spatial and temporal fluctuations in the received acoustic signal that are 5-10 dB or more, acoustic characterization of the ocean environment continues to be an important area of research.

Another important area lies in the creation of a virtual ocean/animal bioacoustic model that integrates ocean acoustic environmental information as well as animal behavior data. Such a model would be very useful in experiment planning as well as monitoring and assessment studies and could be continually updated as new measurements are acquired. Such an effort would also involve the transfer of the appropriate oceanographic, bottom geoacoustic and ambient noise databases to the animal bioacoustic community.

Still another exciting area for collaborative research is the investigation of animal exploitation of the marine acoustic environment. For example, do animals in some sense anticipate acoustic shadow and convergence zones and use noise sources as navigational benchmarks? This is one of many areas in which human sonar system designers may benefit from investigations of animal sonar systems.

Finally, the variable nature of the ocean environment implies that the components of the sonar equation are, in general, statistical variables. The ramifications of the stochastic nature of the problem must be incorporated into the bioacoustic context.

AMBIENT NOISE

Considerable effort has been expended over the years in attempts to measure and model both natural and manmade ambient noise in the sea. The early work is summarized in the Wenz curves (Richardson et al., 1995; Wenz, 1962), which are still very useful, but more recent efforts have added significantly to our knowledge base in this area (e.g., Hamson and Wagstaff, 1983; Jensen et al., 1994; Kerman, 1988; Kuperman and Ingenito, 1980; Medwin and Clay, 1998; Renner, 1993; Richardson et al., 1995; Ross, 1987; Wagstaff, 1973; Zakarauskas, 1986).
Generally, the ambient noise spectral level is about 140 dB re 1 microPascal squared per Hz at 1 Hz and decreases at the rate of 5 to 10 dB per octave to a level of approximately 20 dB re 1 microPascal squared per Hz at 100 kHz. The dominant sources of ambient noise and their frequency ranges are (Richardson et al., 1995): seismic activity, turbulent-pressure fluctuations, and second order pressure effects due to surface gravity waves (1-100 Hz); ship traffic and industrial activity (10 Hz-10 kHz); biologics (10 Hz to 100 kHz); sea ice activity (10 Hz-10 kHz); breaking waves, bubbles, and spray (100 Hz-20 kHz); precipitation (100 Hz-30 kHz); thermal (molecular agitation) effects (30-100 kHz). There are also airborne sources of noise from aircraft, helicopters, and industrial activity, and these are discussed extensively in Richardson et al. (1995). The relative prevalence and frequency of occurrence of these various noise sources are not well understood, particularly in shallow water. Furthermore, it is important to attempt to relate ambient noise levels to actual source levels by taking into account the propagation conditions associated with a particular ambient noise measurement. Thus, although the ambient noise level due to ship traffic may be nominally 75 dB re 1 microPascal squared per Hz at 100 Hz, the source level associated with a large tanker is actually 186 dB re 1 microPascal per Hz @ 1 m.

**RECOMMENDATIONS**

The time is ripe for the translation of existing ambient noise databases and models into a useful and accessible set of curves for the animal bioacoustic community. These will need to be location and time specific. Ambient noise varies on small to large time scales, and can depend on time of day and season. Rather than plotting broad means as in the Wenz curves, spectrum percentiles as employed in LGL and Greeneridge (1995) might be more useful. In addition, the determination of the total sound budget of the ocean and its principal constituent parts is a pressing need. Another interesting question which ocean acoustics can help to answer is whether and how animals could use ambient noise, e.g., for navigation using (fixed) noise sources. Also, do they have means of ambient noise imaging? Could they use acoustic daylight (Buckingham, Potter, and Epifanio, 1996)?

**PROCESSING GAIN**

It is important to recognize that the signal level measured at a sensor can be enhanced by subsequent signal processing by the total receiving system, whether it is designed by humans or marine mammals. These processing gains can be achieved through a variety of techniques including matched filtering, correlation processing, and array processing (Burdic, 1984; Johnson and Dudgeon, 1993; Medwin and Clay, 1998; Urick, 1975; Van Trees, 1968). The method used to process the signal received at a sensor depends critically upon whether it is perceived to be a real signal of interest or largely undesirable background noise.

**RECOMMENDATIONS**

The determination of the signal versus noise context in which marine mammals place the large variety of sounds in the ocean described above is an important area of research. In addition, the investigation of the signal processing systems employed by animals in both the transmission and reception modes is of considerable interest both to ocean and animal bioacousticians. In the area of technology and instrumentation, a high-frequency active sonar system for tracking animals should be investigated. We should also be pursuing more advanced, compact, and robust sensors and tags for these animals.
APPENDIX: SOUND MEASURES AND BOUNDARY CONDITIONS

SOUND MEASURES

Sound is manifested by two physical influences: sound pressure and particle velocity. Sound pressure is force per unit area and has amplitude. Particle velocity is length traveled per unit time and has a direction associated with it as well as an amplitude. The "particles" moving in sound are not the molecules of the medium, but millions of molecules whose motion can be viewed as that of a unit of the medium. Sound sensors detect either sound pressure or particle velocity, or some quantity related to particle velocity like displacement or acceleration. In the MKS system of units in physics, sound pressure is measured in micropascals and particle velocity is measured in meters per second.

Sound intensity is the product of sound pressure and particle velocity. Sound intensity has the same direction as the particle velocity. One usually computes sound intensity as some average of the product of pressure and particle velocity over some period of time. The MKS unit of intensity is watts per square meter, which represents the power flow through an area in a direction normal to the area.

There can still be sound in a medium even if the intensity is zero. That is, the intensity is zero if either the pressure or the particle velocity is zero, but it is not necessary for both to be zero. This is important in considering sound in standing waves (in which the average power flow is zero, so the time-averaged intensity is zero) and sound at boundaries between media. Acousticians accustomed to working in only one medium (usually air or water) use the fact that for plane waves the pressure and particle velocity are related by the characteristic impedance of the medium, given by the product of the density and the sound velocity. That is, sound pressure equals the particle velocity times the characteristic impedance. Then, they can relate intensity to either the pressure or to the velocity by substituting appropriately. In fact, the intensity is then proportional to the pressure squared or to the particle velocity squared, where the constant of proportionality is the characteristic impedance or its inverse. All this is true for plane waves, or for spherical waves, but not for waves in general.

Sound pressure is much easier to measure than particle velocity, and it serves us well. A consequence is that acousticians speak of sound intensity in terms of sound pressure, even to the point of referring a sound intensity level in decibels to a unit of pressure (the micropascal). This is naturally confusing to non-acousticians who wonder how intensity, which they have been told is power per unit area, can simply be a pressure, or force per unit area. The answer lies in the assumptions of one medium and plane waves/spherical waves, and therefore a simple characteristic impedance relating intensity to pressure squared.

In general, source level can be a function of angle; it is the power level per unit area at unit distance (or per steradian) at the angle of emission. Total power is the surface integral over the unit sphere of the angle-dependent source intensities. For an omnidirectional source, the source power level is about 11 dB greater than the source level.

BOUNDARY CONDITIONS

Boundaries between media are special places to sound waves. The ocean has two major boundaries: the surface, above which is very "soft" air, so different in characteristics from water as to be little different from a vacuum, in which there can be no sound; and the bottom, below which is sand or muck or rock. The greatest contrast between the water and bottom media is
when the bottom is very hard rock.

The surface is important to marine mammals, they all have to breathe, and therefore they
use the surface regularly. What happens to sound from underwater sources when it encounters
the surface? The pressure and the horizontal components of particle velocity effectively go to

zero (the air is too "soft" to support pressure or horizontal particle motion at the boundary).

However, the vertical particle velocity is actually enhanced by a factor of two compared to what
it would have been had the boundary not been there and the sound wave had continued
unimpeded. Here is an important case of there being sound but no intensity.

The reverse happens at a hard boundary, such as a rock bottom. The sound pressure and
horizontal particle velocity are doubled compared to what they would have been without the
boundary being present. However, the vertical particle velocity goes to zero, the boundary below
being too "hard" to move. This boundary condition is important in airborne acoustics when
sound waves hit the hard ground and the sound pressure is doubled compared to what it would
have been in "free space".

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Effects of Anthropogenic Noise in the Marine Environment

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Effects of Anthropogenic Noise in the Marine Environment

EFFECTS OF ANTHROPOGENIC SOUNDS ON THE HEARING OF MARINE ANIMALS

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INTRODUCTION and BACKGROUND

Noise and other loud sounds can have a detrimental effect on animals by causing stress, increasing risk of mortality by changing the delicate balance in predator/prey detection and avoidance, and by interfering with their use of sounds in communication especially in relation to reproduction and in navigation. Very significantly, acoustic overexposure can lead to temporary or permanent loss of hearing (e.g., Kryter, 1994; Richardson et al., 1995; see chapter 14 in Yost, 1994). While temporary hearing loss (often called temporary threshold shift - TTS) is reversible over time, more prolonged and/or intense exposure (as from cumulative TTS) can result in non-reversible permanent hearing loss (or permanent threshold shift - PTS) in mammals. The situation can be more complicated in fish and birds, where regeneration of damaged hair cells is also possible. Over the long term, large-scale loss of hearing can potentially affect the viability of a population or species if there is a significant reproductive consequence of hearing loss in a sufficiently large segment of the population. More specifically, loss of hearing can affect behavior since it alters the ability of an animal to process acoustic signals providing information about reproductive behavior, parental care, feeding, predator avoidance, navigation, and migration (e.g., Green et al., 1994).

The anatomical and physiological effects of acoustic overexposure on the auditory systems of some experimental animals such as guinea pigs, chinchilla, and several avian species, have been well documented (e.g., Miller, 1974; Bohne et al., 1985; Nielsen et al., 1986; Salvi et al., 1986; Awbrey, 1993). While less is known about the effects of acoustic overexposure on the hearing of wild mammals or on fish (including elasmobranchs), amphibians and reptiles (reviewed in Myrberg, 1990a,b; Richardson et al., 1995), we can hypothesize that similar parametric effects are likely to exist for these animals since there are significant inter-specific similarities in the ear and receptor cells in most vertebrates. Thus, since acoustic overexposure has deleterious effects on hearing and on the ear in humans and various experimental mammals, it is likely that it also has similar effects on many other species including marine mammals.
anthropogenic (human-generated) sounds on animals in the wild, and particularly on marine mammals (e.g., Richardson et al., 1995). Interest by the public has been heightened with the Heard Island study and the ATOC program, as well as by ship-shock tests. However, the sounds associated with this work represents only a very small portion of all of the anthropogenic sound in marine and freshwater environments today (e.g., Myrberg, 1990a, b; Green et al., 1994; Richardson et al., 1995). As described elsewhere in this document, there is very substantial anthropogenic underwater sound produced by sonars, shipping, oceanographic oil and mineral exploration methods, offshore construction, ocean drilling, etc. In the frequency range of hearing for marine mammals, the prevailing background noise in the vast majority of ocean areas is composed of ship-generated and sea-surface noise. As for the shipping noise component, it has been observed (Ross, 1987) that the increase in ship traffic led to an increase in ambient noise (in the low-frequency bands) of as much as 10 dB over the period from 1950 to 1975. Ross predicted a continuing increase, by as much as an additional 5 dB by the year 2000. Thus, Ross estimates a 15 dB increase in noise levels in the past 50 years, with ship noise as a major factor in the environment. Of course, it is also the case that ambient noise levels vary in different parts of the ocean, depending upon human and non-human activity in different areas.

Freshwater environments also contain anthropogenic sounds. In addition to boating and shipping sounds, there are also significant levels of noise associated with hydroelectric dams and power plants. These sources not only put a great deal of acoustic energy into the water by the nature of how they operate, a number of power plants also use underwater sound in attempts to keep fish from water intakes and turbines (reviewed in Popper and Carlson, 1998).

Responses by animals to anthropogenic sounds and noise overexposure can take several forms. At lower sound levels, animals might detect the sound before damage could occur and simply leave the area of maximum ensonification. This decreases the duration of sound exposure and may protect the animal from noise damage if the sound is very loud. Alternatively, the animal might be involved in feeding, breeding, or caring for its young, and therefore remain in the area of ensonification for a longer period. In these instances, the animal may suffer TTS or PTS or some other physiology and/or behavioral effects such as increases in stress level, cardiovascular effects, etc. The same would be true for animals not mobile enough to move from the site of ensonification. Intense acoustic overexposure, on the other hand, might damage an animal's hearing even before it has a chance to move.

**IMPORTANCE OF SOUND TO AQUATIC ORGANISMS**

*Effects of Anthropogenic Noise in the Marine Environment*

Sound is an important communication channel for a large number of terrestrial and aquatic vertebrates and invertebrates (e.g., Atema et al., 1988; Hauser, 1996; Fay and Popper, 1998; Zelick et al., 1998). The advantages to sound over other channels (e.g., light, chemical) are that it is relatively fast (typically at least 4.5 times greater in salt water than in air), highly directional, independent of light levels or water clarity, and not subject to disruption by currents as are chemical signals (although density differences in current speeds can alter sound propagation).

We are just beginning to become aware of how important environmental sound has been for the evolution of hearing. Indeed, it has been suggested that one of the major factors affecting the evolution of vertebrate (and perhaps all) hearing was to provide animals with an acoustic image of their environment (e.g., Popper and Fay, 1997; and see Bregman, 1990). The marine
environment is naturally noisy, with sounds being produced by animals (fish, invertebrates, marine mammals) (e.g., Tavolga, 1960, 1964; Tavolga et al., 1981; Myrberg, 1990a, b), as well as by wind and rain, water hitting the shoreline, seismic events, etc. (Richardson et al., 1995). This information can potentially provide an acoustic image that encompasses a broad expanse of the ocean, enabling an organism to know about portions of its environment far beyond visual range. It is not hard to imagine that such information might enhance the ability of an animal to survive. One of the consequences of increased anthropogenic sound is the considerable increase in ambient aquatic noise. Thus, we need to be concerned not only that anthropogenic sounds alter the ability of aquatic organisms to communicate and use sound in normal behavioral situations, but also that such sounds alter the ability of these organisms to glean an overall acoustic image of their environment that might be very necessary for survival. Such sounds might mask the ability of aquatic organisms to hear their environment, with potential serious consequences for the organism.

**AQUATIC NOISE LEVELS**

One of the major issues with underwater sound is determining what noise levels can impact animals. Another issue is identifying the sources of sounds that are most likely to affect animals. A number of sound sources are likely to be the major cause of damage or annoyance. Shipping noises are generally considered to be the single biggest factor, contributing energy in the region of 20 Hz to 500 Hz. At higher frequencies (1 - 100 kHz), noise is dominated by sea surface and wind action. The primary significance of ship-generated sounds would be for those animals that detect and use sounds in the lower frequency ranges. This clearly would at least include baleen whales, some pinnipeds, and fishes (Fay, 1988; Kastak and Schusterman, 1998). The significance of such sounds to odontocetes is less clear since there are few data on low frequency hearing in these species (see Green et al., 1994; Richardson et al., 1995; Au et al., 1997). Of the approximately nine species of small odontocetes that have had hearing thresholds measured, all appear to have relatively poor hearing at frequencies below about 500 Hz, where shipping noise dominates. In fact, thresholds for these species over 120 dB (re 1 µPa) for tones are not unusual and would preclude detection of ship noise in most areas.

The number of ships in various sea lanes has increased substantially over the past decade. Among commercial ships, radiated noise increases with ship speed and with ship displacement (usually correlated with length). The supertanker, large tanker, fast container ship, and other large merchants are all important contributors, with radiated noise levels being nearly 10 dB of the average level. The broadband radiation is dominated by noise from propeller cavitation and resembles a dipole source because of surface-image interference. For a typical deep ocean case, a large tanker might have a source spectrum level of 180 dB (re 1 µPa/Hz 1/2 at 1 m) at 50 Hz.

The contribution to the ambient noise at 10 miles might be about 85 dB and at 100 miles 75 dB and 1000 miles 65 dB. For a typical, North Atlantic noise spectrum level of 85 dB at 50 Hz, the level may be dominated by noise from one nearby ship or ten ships at 100 miles or 100 ships at 1000 miles. It is usually a dynamic combination of many ships at many ranges. Nonetheless, in medium to high noise areas, the long-term average levels tend to be stable and predictable.
Ship radiated noise tends to fall off at a rate 6 dB per octave (Ross, 1987) above 50 Hz, and the shipping-generated ambient noise at about 8 dB per octave. In even the heaviest shipping areas and calm seas, the ship-generated component becomes secondary to the sea-surface noise above 1000 Hz. It is rare to detect the effects of shipping noise above 500 Hz. Spectrum levels must be compared to the auditory filter bandwidths of the animal in question. In beluga whales, for example, hearing sensitivity increases by -10 dB/octave up to 20 kHz. All other things being equal, this will result in increasingly higher perceived sound levels. Because noise levels are integrated within the animal's so-called critical band filters, that widen with increasing frequency, this effect counteracts any density spectrum drop-off (Erbe, 1997).

There are any number of potentially harmful anthropogenic underwater noise sources in operation today, and these are discussed at length in other parts of this workshop report. While shipping may be the most significant source of sounds, oil drilling, removal of oil rigs by blasting and other construction-related explosions, etc. may all be significant sources of impulse and short-duration noise-related impacts.

SPECIES OF CONCERN

Sound is used for communication by a wide range of aquatic and semi-aquatic animals including invertebrates, fishes, aquatic birds, aquatic reptiles (e.g., turtles), and various mammals that are obligate or semi-obligate water dwellers. Thus, the presence of anthropogenic sounds in the environment of these animals potentially affects their behavior and their physiology (Green et al., 1994). When considering anthropogenic sounds, we must not only consider the most `visible' aquatic animals, the marine mammals, but also be concerned about other taxa. In particular, it must be remembered that not only are all of these species important members of the aquatic ecosystem, but many non-mammalian species make up important components of the marine mammal food chain, or are of economic importance to humans. Thus any physiological damage to aquatic animals lower on the food chain could have profound effects on organisms higher on the chain. It must also be remembered that if anthropogenic sounds effect the physiology or behavior of rare and endangered species, this could profoundly alter the survival of those species.

An important issue to raise is whether data from one species or group of species dealing with the physiological effects of anthropogenic sounds can be accurately extrapolated to other species. One of the major issues here, as discussed below, is whether it is possible to extrapolate from levels of sounds that effect the ear and hearing of terrestrial vertebrates to the levels of sounds that would have similar effects on aquatic vertebrates. One difficulty in such an extrapolation is interpreting absolute levels of sounds in two very different environments. Another difficulty arises because of significant differences in the structure of the peripheral auditory system of aquatic and terrestrial animals and the possibly different pathways for sound to get to the ear. But, until new data are available, the general pattern of damage to the ear in terrestrial mammals from acoustic overexposure provides the best estimate as to the effect on marine animals (e.g., damage to hair cells of the inner ear). Extrapolation from terrestrial mammals to fishes and invertebrates may be even more difficult since the structure of the auditory system is so different between these groups.

It is also important to note, as pointed out by Schusterman (1981), that it may be difficult to extrapolate data on physiological effects of sound among mammalian species that are different
anatomically, physiologically, and phylogenetically (also see Moore and Schusterman, 1987; Renouf, 1991). Moreover, there are also likely to be differences between species that only need to hear in water and other species, such as pinnipeds, otters, walruses, etc. that have to be able to hear in air as well as in water (e.g., Schusterman, 1981; Fobes and Smock, 1981). Thus, interspecific differences in aspects of hearing such as the role of the middle ear in sound conduction, and whether detection is via bone or soft tissue conduction, the hearing bandwidth of a species and whether it can detect sounds in the range of the human-made sounds in its environment, could all influence whether a particular sound can damage hearing (see discussion by Ketten below). As a consequence, what we ultimately can say about the general effects of anthropogenic sounds on marine mammal hearing may be most germane to only some species, or perhaps related species, rather than to larger phyletic groupings.

AIR VS. WATER ISSUES FOR HEARING

This section considers the essential differences in the medium; i.e., how do the physics of air vs. water relate to parameters of hearing. While this discussion primarily considers issues related to marine mammals, it must be remembered that the physical principles involved in air vs. underwater sound may also be important for understanding differences in hearing mechanisms between fishes and terrestrial vertebrates.

All marine mammals, including whales, evolved from land-based animals with air-adapted ears (Barnes et al., 1985). Over the next 50 million years, their ears evolved in tandem to effectively process underwater sound. Water, with a density nearly 800-times that of air (\(=1.03 \text{ g/cc} \text{ vs.} 0.0013 \text{ g/cc}\)), has a sonic velocity that is over 4 times faster than the speed of sound in air (\(c=1530\text{m/sec vs.} c=340\text{m/sec}\)). To examine the sensory implications of these values, consider a hypothetical mammal, that hears equally well in water and in air. An animal with an intensity based ear would require the same acoustic power/unit area in water as in air to have an equal sound percept, or (\(I_{\text{air}} = I_{\text{water}}\)):

\[
I_{\text{air}} = \frac{p_{\text{air}}^2}{0.442 \text{ g-m/sec-cc}} = \frac{p_{\text{water}}^2}{1575. \text{g-m/sec-cc}} = I_{\text{water}}
\]

(1)

which implies the sound pressure in water must be 59.7 times that required in air to produce the same intensity and therefore the same sensation. The units of intensity are watts/m2, but to put this into the context of conventional hearing measures, recall that intensity is related to the mean square pressure of the sound wave over time. Consequently, most studies report hearing thresholds as effective sound pressure level (SPL), expressed in decibels (dB), which in turn are complicated by arbitrary reference pressures. For air-borne sound measures, the reference is generally dB SPL or dB re 20 µPa rms; for underwater sound measures, the reference pressure is dB re 1 µPa. Thus, accounting both for the function of 59.7 dB and the difference in reference levels, underwater sound pressure levels numerically are about 61.5 dB greater than sound pressure levels in air for an equal intensity. Whether viewed in terms of pressure or intensity responses, there are substantial differences implied in the measures and physics for an equal percept at the mammalian ear in water. (Note, the pressure level of a sound under water is 35.5 dB greater than that of an airborne sound of equivalent intensity. Because the standard reference level under water (1 µPa) is lower than that used in air (20 µPa), 26 dB must be added to this difference, but only if comparisons are made with respect to the two different reference levels...
[i.e., a sound level of 90 dB re 20 µPa in air has the same intensity as a sound level of 151.5 dB re 1 µPa under water - thus, 90 + 35.5 + 26]). Therefore, one of the most interesting aspects of hearing in marine mammals is the fact that anatomically they follow much of the basic land mammal pattern, but they have also solved the fundamental problems of how to hear in water including the attendant complications for acoustic cues; e.g., increased pressures and shortened interaural arrival times. This successful coupling of a mammal ear to water-borne sound also has some intriguing implications for the potential for marine mammal ears to sustain acoustic impacts. On one hand, having inner ears that are similar to those of land mammals implies they may be susceptible to conventional mechanical loss mechanisms. If this is so, what is worrisome is that even moderate increases in the naturally noisy oceanic environments could accelerate loss from simple acoustic impacts. On the other hand, perhaps these ears have adaptations that could prevent ear damage from barotrauma, pressure changes, and concussive forces. That is why careful research is required to answer these questions.

**EFFECTS OF SOUND ON THE AUDITORY SYSTEM**

This section considers the effects of sound on the auditory system. At the same time, sound or vibration can have other effects than on organs of hearing, and these effects are discussed in the section on "Non-hearing Effects of Anthropogenic Noise."

Noise trauma is a well-investigated phenomenon for air-adapted ears (see Lehnhardt, 1986; Lipscomb, 1978; and Richardson et al., 1995 for reviews). Noise trauma has been divided into lethal and sub-lethal impacts, although only sub-lethal impacts are likely to be relevant except in extraordinary or blast-related events.

**LETHAL 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; e.g., profound injuries related to shock wave or blast effects which are not, technically, simple acoustic trauma. Sub-lethal impacts are those in which a hearing loss is caused by exposures to sounds that exceed the ear's tolerance to some acoustic parameter. In general, the ear component which is the most fragile or liable to acoustic impact is the inner ear, and specifically, the hair cell and its support structure in the organ of Corti, although intense sounds can also damage the middle ear and outer ear.

**SUB-LETHAL IMPACTS: TEMPORARY AND PERMANENT THRESHOLD SHIFT**

To determine whether any one animal or species is subject to a sub-lethal 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. Hearing losses of this type may be temporary (TTS - temporary threshold shift) or permanent (PTS). Whether a sound causes TTS or PTS is highly correlated with the extent of inner ear damage. Moreover, all frequencies do not produce equivalent damage at the same exposure level, nor will the same frequency-exposure combination cause equivalent damage in all species. The extent and duration of a threshold shift depends upon several acoustic features, including the sensitivity of the subject, and the level, frequency, and duration of 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: that is, what sounds, at what levels, for how long, or how often will commonly produce temporary (TTS) vs.
permanently (PTS) hearing loss. Three fundamental effects are well documented at this time.
1. There can be considerable variation within and between species.
2. For tones and narrow-band noises, the loss centers around the exposure frequency or slightly above.
3. For all types of exposures, there is some combination of noise level and exposure time for which the loss is irreversible.

Temporary threshold shifts might extend over a wide range of frequencies or be restricted to a narrow frequency range, according to source characteristics. The majority of studies have been conducted with cats and rodents (especially chinchilla) using relatively long duration stimuli (> 1 hr.) and mid to low frequencies (1-4 kHz) (see Lehnhardt, 1986, for summary). Virtually all studies show that losses are centered around the peak spectra of the source and are highly dependent upon the sensitivity of the subject. There is always some spread to other frequency regions of the ear, but this is generally greater in the high frequency direction. For narrow band high frequency signals, maximum losses typically occur in or near the signal band or slightly above, 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 (e.g., Saunders et al., 1991). 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. Generally, for sounds that are less than 80-90 dB SPL, with exposures of a few hours or less, and are relatively narrow band, the loss is limited and temporary, with recovery periods taking from hours to days. The amount of TTS is correlated with both the length of time and the intensity of exposure. The actual effect is related to sound pressure level, signal spectrum, and signal duration. To give a general idea of the kinds of signals that result in hearing damage, note that the current allowable limits for human workplace exposures for broad spectrum signals over an 8 hour period is 80-90 dB re 20 µPa (Lehnhardt, 1986; NIOSH, IO 1999).

PERMANENT THRESHOLD SHIFT (PTS)
The majority of PTS effects are also complex. In the case of impulse signals, rise-time and duration of peak pressure are significant factors. If the exposure is short, hearing thresholds are often recoverable (depending on signal level); if long, or the sound has a sudden, intense onset and is broadband, hearing, particularly in the higher frequencies, is more often permanently lost. Experimentally, PTS can be induced by high intensity multi-hour exposures to narrow- or broad-band noise or by tones. It can also be induced by impulse signals. In humans, PTS occurs most commonly from protracted, repeat intense exposures (e.g., occupational auditory hazards from background noise) or sudden onset of intense sounds (e.g., rapid, repeat gunfire). In humans, hearing loss with aging (presbycusis) is essentially the accumulation over time of PTS and TTS insults to the ear at multiple frequency regions. In presbycusis, sensitivity to high frequencies is lost first with the permanent loss gradually spreading to lower frequencies with age.

Although the inner ear changes related to TTS are fairly well documented, to date, only the PTS level effects of impulse noise have been reliably mathematically modeled (Price and Kalb, 1996). While the correlation between sound level and damage to the inner ear is high and well established, far less is known about the fate of neural centers in the brain stem and cortex to
intense acoustic stimulation. Recent data show evidence for "toughening" or "sound conditioning" of neurons in the auditory brain stem to sound exposure once these neurons have been previously stimulated with moderate to loud sound levels (Canlon et al., 1988). That is, following previous sound exposure some brain stem neurons appear less affected by high sound levels. The functional consequences of such neural toughening have not been elucidated.

UNDERWATER HEARING LOSS IN HUMANS

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 µPa (Smith and Wojtowicz, 1985; Smith et al., 1988). Taking into account differences in measurements of sound pressure in air vs. water (see above), these underwater levels are consistent with the 80-90 dB re 20 µPa exposure levels that induce TTS in humans at similar frequencies in air, assuming an appropriate media-dependent shift in the human minimum sensitivity. It should be noted, however, that, sharp rise-time, impulsive signals produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water, as has often been demonstrated both experimentally in animals and accidentally in humans through occupational or recreational noise exposures (Lipscomb, 1978; Lehnhardt, 1986; Price et al., 1989).

NOISE EFFECTS ON MARINE MAMMALS AND ACOUSTIC TRAUMA

There are simply too many structural and functional differences between marine mammal and land mammal ears to assume that acoustic trauma effects are isomorphic between the two groups.

Vocalization data 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 µPa at 1 m (Au, 1993; Richardson et al., 1995). 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 precisely coincident and recorded intensity may have little to do with sensitivity. Animals, including humans, commonly produce sounds which would produce discomfort if they were received at the ear at levels equal to the emitted level. Mammal ears are protected generally from self-generated sounds by both intervening tissues (head shadow and impedance mismatches) as well as active mechanisms (eardrum and ossicular tensors).

Arguments that marine mammals can tolerate higher intensities simply because of their size and tissue densities are also not persuasive. The large head size of a whale is not acoustically exceptional when the differences in pressure and sound speed in water vs. air are taken into account. 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 provide some useful insights into both facets of the paradox that also need further investigation. In one study, inner ears from a long-term captive male dolphin with a documented hearing loss were compared with the ears of two young adult dolphins (Ketten et al., 1995). 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 five times as many cell layers in the...
The stria vascularis is considered to be the principal dictator of mammalian cochlear metabolism and the health and resiliency of the spiral ligament is a key factor in basilar membrane response. If these results are confirmed in other odontocete ears, these structural differences could mean dolphins in general have faster hair cell recovery times than air-adapted ears and/or some resistance to degenerative processes within the cochlea and may therefore be less subject to temporary threshold shifts. It is also quite possible that these are simply adaptations in response to increased acoustic pressures, etc. inherent in an aquatic environment and do not infer any special protection, but in any case they do suggest that dolphins may be more resilient than the typical land animals or pinnipeds, which are subject to similar ambients and have cochleae without any apparent hypertrophy.

CT, MRI, and histologic studies of the older dolphin ears showed cell loss and laminar demineralization like that found in humans with presbycusis. The location and degree of neural degeneration in these ears implied a substantial, progressive, hearing loss beginning in the high frequency regions. This too is consistent with the pattern commonly observed in humans. Recently, a behavioral audiogram from a second older dolphin showed a parallel loss (Brill et al., 1997; Ketten et al., 1997). Similar significant differences in the hearing thresholds of two

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Zalophus have also been reported by Kastak and Schusterman (1995) that are consistent with age-related hearing differences between animals. The reasonable conclusion from these data is that despite any resistance to acoustic trauma that any marine mammal may be shown to have to threshold shifts in the short term, they are not immune to long term degenerative effects of noise exposure.

Unfortunately, the present data are far from definitive, and in some ways, only beg the basic question of what are the most sensitive species and what noises cause significant impacts. The problem of hearing loss has not been systematically explored until very recently (Ridgway and Carder, 1993, 1997). The most studied group to date, the odontocetes, are also the least likely to sustain a substantial impact from common anthropogenic sources because odontocetes have relatively poor low frequency sensitivity. Still, there are some high-frequency sources within the most sensitive range of many odontocetes. Further, the sensitivity of the odontocete ear to intense low-frequency sounds has not been investigated. In some cases, a captive animal's age or history has not been considered in analyzing its auditory responses, and, in the absence of overt data (e.g., antibiotic therapy), we assume any 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 above suggest age and/or exposure to noise can significantly alter hearing in marine mammals. In some cases, it is clear that some individual differences observed in "normal" captives may be the result of permanent hearing loss. The fact that some studies show losses in marine mammals consistent with age-related hearing changes considerably complicates the diagnosis and assessment of hearing loss from anthropogenic sources based on small samplings of exposed populations. Cetaceans ears are purely aquatic and are structurally more derived than land mammal ears and are probably incapable of hearing in air in any normal functional sense. Whale and dolphin middle and outer ears are adapted exclusively to hearing underwater with specialized
fatty tissue elements that have acoustic impedances comparable to water that are unique soft
tissue analogues to the external canals of other mammals (Brill et al., 1988, 1998; Ketten, 1994,
1997). Given the acuity of odontocetes, this group should be among the most liable to acoustic
impacts from sources within their hearing ranges, but it is possible that inner ear hypertrophy in
odontocetes provides protective mechanisms from high intensity noise. If the middle ear is
dysfunctional in cetaceans, that could also substantially affect the potential for acoustic impacts
by eliminating the filter and reflex attenuation functions common in land mammal ears.
Pinnipeds, however, present more complex pictures and may be the most fragile marine mammal
ears because of their similarity to land-based ears (Kastak and Schusterman, 1998; Wartzok and
Ketten, 1998). (See section by Schusterman, below.)

NOISE-DAMAGE IN NON-MAMMALIAN SPECIES
There is evidence that high intensity sounds can temporarily alter hearing sensitivity in
goldfish (Popper and Clarke, 1976) and cause permanent loss of sensory cells of the ear in
several species (Enger, 1981; Hastings et al., 1996). While TTS in fish was followed by
complete recovery of hearing over several hours, noise damage resulted in hair cell death.

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Although these data support the idea that fish could be affected by anthropogenic sounds,
only a few studies give any insight into this problem. Moreover, there is very substantial
interspecific variation in the structure of the ears of fishes, and how sound gets to the ear. For
example, the ear of the goldfish and the oscar are very different from one another (e.g., Popper
and Platt, 1993), and there are also differences between these species in how sound gets to the
ear (e.g., Fay and Popper, 1974, 1975). Thus, it may be almost impossible to extrapolate results
between fish species that have very different ear structures. Moreover, whereas many fish
species could be expected to move rapidly from areas of high ensonification, there are other
species that move very little in times of stress, and their potential exposure to damaging
anthropogenic sounds could be much higher than in species that move rapidly and readily.
The effects of anthropogenic sounds on other aquatic species, such as reptiles, aquatic
birds, invertebrates, etc. is totally unknown. We might be able to extrapolate to aquatic birds
from TTS and PTS data on terrestrial birds (see below); however, the exposure to anthropogenic
underwater sounds by aquatic birds, other than diving species such as penguins, is likely to be
limited due to their short time under water. Of course, if the sound levels are sufficiently intense,
even a short exposure could be problematic.

For land birds, there are considerable data available on the effect of acoustic
overexposure (see, for example, Saunders et al., 1996; Ryals and Dooling, 1996; Saunders and
Dooling, 1974; Saunders et al., 1991). As with terrestrial mammals, the amount of TTS, and
whether it leads in PTS, depends on factors such as the spectral characteristics of the acoustic
stimulus as well as its duration and level and the amount of exposure (Saunders and Tilney,
1982; Roberto et al., 1996). In general, birds are less susceptible to both TTS and PTS than are
mammals (Saunders and Dooling, 1974). Moreover, relatively severe acoustic overexposures
that would lead to irreparable damage and large permanent threshold shifts in mammals are
moderated somewhat in birds by subsequent hair cell regeneration. Interestingly, recent work
has also shown that birds may have other mechanisms for reducing the damaging effects of
continuous acoustic overexposure altering the transmission characteristics of the tympanum
(Larsen et al., 1997).
RECOVERY OF SENSORY HAIR CELLS
While there is no evidence to suggest that damaged hair cells are replaced or recover after
cell death in mammals, there is ample evidence showing that such recovery occurs in both fish
and birds. Lombarte and colleagues (1993) showed hair cell recovery in the cichlid fish, the
oscar, after treatment with ototoxic drugs (gentamicin). In addition, a large and growing body of
literature shows that a number of avian species can regenerate sensory hair cells after noise or
drug damage (e.g., Corwin and Cotanche, 1988; Ryals and Rubel, 1988; Ryals and Westbrook,
1990). Still, such recovery does not mean that the replacement hair cells are sending the same
kinds of information to the brain as were sent by the original hair cells, or that there is full
recovery of function in either birds or fishes. However, if such recovery occurs, this could mean
that effects of noise damage are only temporary. At the same time, there would likely be some
significant TTS during the recovery, and this could significantly compromise the survival of
these species.

Effects of Anthropogenic Noise in the Marine Environment
If acoustic overexposure is so great that other structures in the cochlea are damaged, in
addition to hair cells, then the prospects for long term recovery of hearing are reduced. If only
hair cells are lost or damaged, studies in several species of birds have now shown that hair cell
regeneration results in the return to near normal auditory sensitivity with a lingering PTS of only
about 10-15 dB (Ryals and Dooling, 1996; Niemiec et al., 1994).

RESEARCH REPORTS
In the following sections, several investigators report on the results of studies that are
germane to the issues of the effects of noise on hearing. These include investigations that
directly assess TTS in both odontocetes (Ridgway and Carder, 1997a) and pinnipeds
(Schusterman). The impact of sounds on the ear itself are considered by Ketten, while Erbe
discusses the potential effects of ship noise on cetaceans. Dooling provides an overview of the
effects of sounds on birds that could readily be applicable to aquatic birds, and also demonstrates
that results from avian studies are applicable to a general understanding of the effects of sound
on marine organisms. Finally, Price provides theoretical methods to evaluate the effects of
sound on marine animals.

DETERMINATION OF HEARING CAPABILITIES IN MARINE MAMMALS (prepared by
Randy Brill and Sam Ridgway after the workshop at the request of the team leader)
The Navy's marine mammal program and its associated activities have provided most of
the available data on the auditory capabilities of small cetaceans. There is an awareness that
certain antibiotic regimes, especially high-dose aminoglycosides, can cause hearing damage.
The application of behavioral and clinical techniques with animals of known health histories and
hearing capabilities throughout its history has provided an important database that continues to
grow.
Audiograms have been measured for several species of small odontocetes including the
Atlantic bottlenose dolphin,
Tursiops truncatus
(Johnson, 1967; Brill et al., 1997) and its Pacific
relative,
Tursiops truncatus gilli
spp. (Ljungblad et al., 1982), the harbor porpoise,
Phocoena phocoena (Andersen, 1970), the beluga whale, Delphinapterus leucas (White et al., 1978), the killer whale, Orcinus orca (Hall and Johnson, 1972), and the false killer whale, Pseudorca crassidens (Thomas et al., 1988). These audiograms reveal typically mammalian, U-shaped, broadband curves that are all, by comparison to humans and other terrestrial mammals, shifted to higher frequencies with greater sensitivity. Johnson (1968) and Au and Moore (1990) reported measurements of critical ratios and bandwidths that likewise suggest adaptation for high frequencies. There are few, if any, data regarding low-frequency hearing for cetaceans.

The biosonar capabilities of the Atlantic bottlenose dolphin have received a good deal of attention (cf. Au, 1993). Ancillary investigations have provided useful measurements of several characteristics of hearing in these marine mammals; not the least being their ability to localize on a sound source. Renaud and Popper (1975) reported a minimal audible angle (MAA) of less than 1° of arc. Au and Moore (1984) described receiving beam patterns. Moore et al. (1995) reported interaural thresholds for time, 7 µsec, and intensity differences of less than 1 dB.

As discussed above, TTS is an important indicator of sound beginning to exceed the ear's ability to respond. With the intent to determine whether TTS occurs in marine mammals, efforts are currently underway to investigate the effects of loud sounds on the hearing thresholds of five bottlenosed dolphins (Tursiops truncatus), and two white whales (Delphinapterus leucas).

Following measurement of baseline hearing thresholds, animals were exposed to 1-second tones at 3, 10, 20, and 75 kHz at gradually increasing levels up to 202 dB re: 1µPa. Masking noise was used to create a floor effect, thereby eliminating between-session threshold variability due to an ever-changing ambient noise floor in San Diego Bay. Both dolphins and whales began to exhibit alterations in their behavior at levels around 180 dB. TTS was determined to have occurred when there was at least a 6 dB increase in hearing thresholds from baseline testing. TTS was considered to have occurred when tone levels increased to 194-201 dB at 3 kHz, 192-196 dB at 10 kHz, 193-196 dB at 20 kHz, and 192-194 dB at 75 kHz. In all cases, hearing thresholds were back to pre-exposure levels by day's end. Future plans for this study include extending the range of test frequencies and the inclusion of California sea lions, Zalophus californianus, to examine taxonomic differences. Evidence of behavioral alteration and TTS in
marine mammals will be used to establish criteria for safe noise levels around marine mammals both in open ocean, and in zoos and aquaria.

There are no audiometric data regarding the hearing sensitivity of baleen whales, although there are models based upon anatomical data. Two different groups have developed portable equipment (Carder and Ridgway, 1990, 1994; Dolphin, 1997) to do an audiogram as a function of the auditory brainstem responses. ABR may be used to gather data from stranded, beached, or entrapped whales, and if the animals die, an examination of the health of the ear and other organs that might be impacted by intense sound would assist our understanding of natural incidence of hearing loss.

Biomedical and husbandry studies conducted by the Navy's marine mammal program have provided reason to consider that medical ultrasound techniques can be used to study bubble formation in tissue or blood and CNS effects. The issue of bubble formation is especially important because it appears to be a mechanism that could produce acute death under certain circumstances. Bubble formation and possible embolism are mechanisms that could explain sudden deaths of whales in the presence of intense acoustic events such as have recently been described (Frantzis, 1998). Human divers are susceptible to bends or decompression sickness, a disabling and sometimes fatal condition in which gas bubbles form in blood, joints and other tissues. In human divers whose tissue is saturated due to breathing pressurized gas at depth, low frequency sound might induce bends episodes that would not otherwise occur. Crum and Mao, (1996) suggested that intense low-frequency sound (160 to 220 dB) may induce bubble growth in tissues (also see Lettvin et al., 1982) and therefore divers radiated with low-frequency pulsed sound when they are near decompression limits could be severely injured (Crum and Mao, 1996).

Although cetaceans do not carry a tank of pressurized breathing gas as divers do, they do make repetitive dives to great depth which may produce overpressure of nitrogen in muscle after repetitive dives (Ridgway and Howard 1979, 1982). Dolphins do not bend even at nitrogen overpressures that would produce the disease in humans; however, in light of the suggestions of (Lettvin et al., 1982) and (Crum and Mao, 1996), we must consider whether intense sound might be a bends threat to diving cetaceans.

TEMPORARY THRESHOLD SHIFT IN PINNIPEDS (prepared by Ronald Schusterman after the workshop at the request of the team leader)

During aerial threshold testing at 100 Hz, a male harbor seal (Phoca vitulina) was fortuitously exposed to loud, broadband construction noise, which occurred intermittently for about a week. Kastak and Schusterman (1996) took advantage of this situation, and measured several reliable shifts in the animal's threshold at 100 Hz immediately following cessation of the noise, on each of several occasions. Unfortunately, not only did this experiment not control the intensity of the noise or the period that the seal was exposed to the noise, but the measurements were all made in air, and it was important to determine whether similar results would be obtained under more controlled conditions and also under water. Because of the uncontrolled aspects of the initial aerial TTS experiment, and following completion of basic underwater audiometric
work with this 8-year-old harbor seal, (Kastak and Schusterman, 1996) then tested for TTS in a much more controlled fashion in water. The purpose of this work was not to get into issues involving PTS, but merely to demonstrate small but statistically reliable noise induced TTS in pinnipeds.

Octave band noise (OBN) levels of about 60 dB above the subject's threshold at center frequency and exposure durations of 20 minutes were used. Thresholds were obtained using an up-down psychophysical procedure prior to noise exposure, immediately following noise exposure (1-2 minutes between cessation of noise and first trial of threshold testing), and following a variable recovery period. Frequencies of 1 kHz and below were tested with the harbor seal, and 2 kHz and below for the two California sea lions. The subjects were trained to submerge and station in a chin cup near the bottom of a 2.5-meter deep pool. While stationed, filtered white noise was projected from two underwater speakers built into the stationing platform. Noise levels were calibrated before and after daily sessions were completed.

Threshold testing was conducted at a separate apparatus.

Results for the harbor seal showed a reliable TTS of approximately 5 dB, followed by recovery within at least 24 hours. In this animal, there was also an effect separate from threshold shift, but clearly related to the signal detection task. The effect manifested itself as a change in response criterion on the majority of post-exposure sessions. The change in criterion was reflected in an average 15% increase in false alarm responses from baseline sessions. When a signal detection analysis was applied, the average adjustment to threshold shift (to account for response bias) was 3.7 dB (producing a corrected average TTS of about 8 dB). False alarm rates during recovery fell back to approximately baseline levels. These results are suggestive of noise-induced tinnitus, changes in motivational state subsequent to exposure, or simply the lack of ability to discriminate previously supra-threshold tones from background noise. Regardless of the physiological mechanism, such dramatic changes in response criterion are likely to have effects as severe as temporary threshold shift in free-ranging circumstances (i.e., inappropriate responding to irrelevant or non-biological acoustic signals).

Results with the two California sea lions showed that a 22-year-old animal showed statistically reliable TTS (in the range of about 5 dB) at the time of the experiments. However, a 12-year-old animal showed only a marginal and statistically insignificant TTS of only about 1 dB, even when she was exposed to OBN levels up to 69 dB above her threshold at center frequency. Unlike the harbor seal, in the sea lion that did show reliable TTS, there appeared to be no change in the animal's response criterion.

It is important to emphasize that these studies were designed to induce small, temporary threshold shifts with exposure noises of moderate intensity. It was not desirable to produce permanent hearing loss in these subjects due to repeated TTS's. Two reasons for avoiding levels sufficient to induce PTS are 1) ethical concerns about inducing deafness in the subjects; and 2) future experiments involving the same subjects will require that there be no loss of hearing sensitivity or acuity (in terms of frequency discrimination and temporal resolution). It is very clear from these early experiments that TTS can be readily induced both in air and under water in pinnipeds, and that future experiments should take advantage of both harbor seals and sea lions being at least as sensitive to airborne noise as they are to underwater noise. The advantage here refers to the fact that duration and intensity of noise exposure is much more readily controlled in...
aerial testing than in underwater testing. TTS data will assist in predicting the potential for auditory damage resulting from short exposures to more intense sounds and prolonged exposure to less intense sounds (i.e., aid in the development of noise exposure risk criteria).

MARINE MAMMAL EARS AND MODELS (prepared by Darlene Ketten after the workshop at the request of the team leader)

A fundamental assumption in hearing models is that hearing capacities are the output of the integrated components of the whole ear. All mammalian ears, including those of marine mammals, have three basic divisions: 1) an outer ear, 2) an air-filled middle ear with bony levers and membranes, and 3) a fluid-filled inner ear with mechanical resonators and sensory cells. In terms of the common models used to analyze mammalian hearing, the outer ear acts as a sound collector; the middle ear transforms acoustic components into mechanical ones detectable by the inner ear, and the inner ear acts as a band-pass filter and mechano-chemical transducer of sound into neural impulses.

Hearing models are generally anatomically derived but use electrophysiologic and behavioral data as controls. Modeling of land mammal ears has a long and well-established pedigree (Fay, 1992). One strength of models is that they emphasize species-specific structural differences and, given that there are sufficient anatomical data, models can provide an extraordinarily accurate estimate of the hearing characteristics for virtually any species (Fay, 1992). Clearly an important issue is model accuracy, and this is where the interface of behavioral or electrophysiologic data plays an important role, particularly for marine mammals. As marine mammal ear anatomy data becomes more comprehensive, and as we gain more information on the comparative aspects of marine vs. land species, anatomically derived models become more sophisticated and more reliable. While some aspects of land based inner ear models are valid for marine mammals, it has been shown that there is a different frequency to ear morphometric relationship in marine mammals compared to land mammals which must be taken into consideration (Ketten, 1992). That is, while conventional land mammals models provide a starting point, they must be modified to incorporate the underwater bauplan. Because there are sufficient control data (e.g., Brill et al., 1997), primarily in the form of behavioral audiograms correlated with ear lesion data (discussed below), a basic Tursiops frequency model has been properly tested. The high level of correlation between the model and the Tursiops audiogram means that we can now be reasonably confident that current frequency-membrane mapping models for delphinids and phocoenids are good predictors of hearing ranges for species in those groups (Ketten, 1994; Ketten et al., 1997). Hearing range models have also been generated for some mysticetes (e.g., right whales, humpbacks, and bowheads) using these techniques, but as indicated earlier, while these models have good agreement with vocalization data, no audiometric data are available to definitively test baleen models. No model data are yet available for pinniped inner ears.

Major issues in marine mammal hearing that are unresolved, but for which anatomy is providing some useful indicators are: (1) what are the paths to the ear; (2) what is the function of the middle ear; (3) how is localization accomplished underwater; and (4) what structural
mechanisms account for the exceptional frequency ranges of cetacean ears? Mammalian outer ears are subdivided into a pinna or ear flap that assists in localization, a funnel-shaped concha, and the ear canal or auditory tube. In most mammals, the pinnal flaps are distinct flanges that may be mobile and aid in localization (Heffner and Heffner, 1992). Of course, these structures are reduced or absent in most marine mammals. Whales have no external ear and the canal is blocked by debris and wax. Currently, the lower jaw is considered the primary reception path for ultrasonic signals in odontocetes. Norris (1968, 1969) speculated that fat filling the lower jaw as a preferential low impedance path to the middle ear and the pan bone as an acoustic window to the middle ear region. Brill et al. (1988) confirmed this role, but some studies also found best thresholds for low to sonic frequencies near the external meatus (Popov and Supin, 1990). Recent CT and MRI data, suggest there are two discrete, orthogonal fat channels, one inside the jaw and a larger one underlying the meatus that may conduct sound to the inner ear (Ketten, 1994, 1997). The presence of two channels may first explain reported discrepancies among sensitivity measures, but equally important it suggests relatively complex dual channel processing that may be unique among mammals.

Pinniped ears are less derived. External pinnae are reduced or absent and ear canal shapes vary. The exact role of the canal underwater has not clearly been determined. Otariids have terrestrial-like, broad bore external canals; phocids, particularly M. angustirostris, have narrow ear canals that are nearly occluded (Ketten and Schusterman, unpublished). Whether the external canal remains patent and air-filled, collapses, or becomes flooded during dives continues to be debated. There are strong theoretical arguments for each position. Flooding the canal would provide a low impedance channel to the tympanic membrane, if the middle ear is fluid-filled, the oval and round windows can receive simultaneous stimulation that would compromise normal basilar membrane response. If the canal remains air-filled, the canal should be less efficient for sound conduction to the middle and inner ear than surrounding soft tissues when the animal is submerged. Mohl and Ronald (1975) found that underwater, the most sensitive region was not the canal but a region parallel to it. CT and MRI data from live harbor seals suggest there are distinctive fats near the meatus (Ketten et al., 1998). Therefore, fatty tissues may also play a role in underwater hearing for some seals, but no discrete soft channels have yet been clearly identified and tested in any pinniped.

Land mammal middle ears are commonly described as impedance-matching devices or amplification transformers that counteract the expected 36 dB loss between air and a fluid-filled inner ear. The gain is achieved by the mechanical advantages provided by area differences of the middle ear membranes (large tympanic vs. small oval window) and by the lever ratio of the bony chain of ear ossicles which create a pressure gain and a reduction in particle velocity at the inner ear.

Improving the efficiency of power transfer to the inner ear may not, however, be the only middle ear function. Recent studies suggest a "tuning" (see Yost, 1994 for overview). Each species has a characteristic middle ear resonance based on the combined chain of impedances. The sum of impedances is lowest; i.e.
middle ear admittance is greatest and energy transmission most efficient, at a species-specific middle ear resonant frequency, which depends upon middle ear mechanical characteristics. This frequency is generally at or near the frequency of best sensitivity for that species (Fay, 1992). Ultrasonic species like microchiropteran bats and dolphins have high frequency middle ears with ossicular chains stiffened with bony struts and fused articulations; low frequency species, like heteromyid desert rodents, mole rats, elephants, and mysticetes, have large, flaccid tympanic membranes and massive middle ears components (Fleischer, 1978; Ketten, 1992).

Middle ear function in cetaceans and pinnipeds is still debated. Mass and stiffness of the ossicles and the size and shape of the eardrum vary widely among marine mammals. None are overtly degenerate or vestigial. Both cetaceans and pinnipeds have specialized middle ear mucosa that lines and may fill the middle ear when submerged but has not been definitively shown to do so. Logically, whales would seem to have little need for the classic amplification role of the middle ear, given that they have fluid (ambient) to fluid (inner ear) coupling. CT shows the middle ear of dolphins is air-filled in vivo, but some authors hypothesize it does not remain so when submerged. It has been suggested that seal middle ears are capable of operating entirely liquid-filled and that this may enhance high-frequency sensitivity in water (Renouf, 1992). Neither suggestion has been proven. At this point, neither a tuning role nor a particle velocity related role can be ruled for any marine mammal middle ear.

The inner ear consists of the cochlea (hearing) and the vestibular system (orientation and balance). Marine mammal inner ears have the same general format as land mammal ears, but again, there are unusual extremes, particularly in basilar membrane construction. Key components of mammalian cochleae are the basilar membrane, which is a tonotopically ordered resonator, and the organ of Corti that rests atop the membrane. When the basilar membrane moves, cilia on the hair cells of the organ of Corti are deflected eliciting chemical changes that release neurotransmitters. Damage to the hair cells is the primary mechanism underlying most hearing loss.

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Differences in hearing ranges are dictated largely by differences in basilar membrane thickness and width along the cochlear spiral. From the base of the spiral to its apex, the basilar membrane becomes progressively thinner and broader. Consequently, the highest frequency an animal hears depends upon the membrane's resonant frequency at the base where the membrane is generally stiffest (narrow and thick). Moving towards the apex, the lowest frequency region of the spiral, the membrane becomes broader and more pliant.

Like land mammals, pinniped and cetacean basilar membranes scale with animal size, and most marine mammals have basilar membranes longer than the human average. If marine mammals had the same stiffness characteristics vs. length as land mammals, most would have relatively poor high frequency hearing. For example, the conventional land mammal length-based hearing model (Greenwood, 1961) predicts an upper limit of hearing of ~16 kHz for bottlenosed dolphins rather than the actual functional high frequency hearing limit of 160 kHz for this species (Au, 1993). This is because marine mammals, and particularly odontocetes, do not have the same thickness gradients, or basilar membrane ratio of width to thickness over
length as land mammals. In addition, some odontocetes also have extensive stiffening support elements in the basal regions of the inner ear. By incorporating all these factors, the marine specific model that has been developed not only accurately predicts odontocete hearing ranges but also led to the development of generic multi-feature hearing models that are better predictors of hearing characteristics for all mammals than traditional, single-dimension models (Ketten, 1994; Roitblat et al., 1996).

Anatomically and acoustically, cetacean inner ears divide into three formats. Type I ears, found in the highest frequency animals (functional upper bound >160 kHz), have basal membrane ratios (t/w) >0.8. Type II ears (functional upper bound <160 kHz), have less acute basal membranes (ratio ~0.6) and slightly wider apices, which is consistent with their broader hearing range. Type M ears, common to baleen whales, have unremarkable basal ratios but exceptionally broad apical membranes (up to 2200 µ) and apical ratios near 0.002, consistent with infrasonic resonances and suggestive of a functional hearing limit as low as 10 Hz. Odontocetes have extensive hypertrophy of virtually all cellular elements of the cochlear duct. Mysticetes have no obvious cochlear duct specializations, but both odontocetes and mysticetes have auditory nerve to hair cell innervation ratios three-times those of land mammals, which suggests that both infrasonic mysticetes and ultrasonic odontocetes are capable of equivalent complexity in acoustic processing (Ketten, 1997).

Seal inner ears have not been extensively studied. The consensus of available data suggest that pinnipeds include both high and low frequency adapted species as well as aerial vs. aquatic specialists (Renouf, 1992), but there is no evidence for extreme functional hearing ranges as was found in cetaceans. Most pinnipeds have inner ears that resemble terrestrial high frequency ears, and there are no exceptional developments in either the cochlear duct or auditory nerve. Preliminary data on larger species suggest they may have some low frequency adaptations consistent with their size. Pinnipeds share one feature with cetaceans, a large cochlear aqueduct. Mohl (1968) suggested that this would facilitate bone conduction, but this theoretical function is not consistent with equally large aqueducts in odontocetes.
Ketten, 1997). These data for odontocetes are consistent with the jaw fat hypothesis of (Norris, 1969) and the results of (Brill et al., 1988). Similar efforts to measure IATD in a variety of pinnipeds would be extremely helpful for solving the question of air vs. water sound conduction mechanism for seals and sea lions.

EFFECTS OF NOISE ON ACOUSTIC COMMUNICATION IN BIRDS - A HEURISTIC EXAMPLE (prepared by Robert J. Dooling after the workshop at the request of the team leader)
The potential for noise to adversely affect acoustic communication by masking is probably the most ubiquitous but least well understood effect of noise on animals. Moreover, the complexities of studying acoustic communication in the sea greatly exacerbate this situation. For this reason, examples of similar problems in land vertebrates, such as birds, can serve to highlight the important issues, identify the critical variables for consideration, and suggest approaches to solving the problem of noise interference on acoustic communication. Clearly, when noise masks the biologically important signals of animals in the wild, and interferes with their ability to communicate effectively, it almost surely has a detrimental effect on their normal behavior and breeding biology. However, the situation is really quite complex and different species of birds (as well as other vertebrates) each have their own unique ecology and have evolved various strategies for communicating in noise. The proper approach to the problem of whether anthropogenic noise interferes with acoustic communication, then, is a combined approach involving rigorous hearing and masking studies on the animals in question combined with ethological and ecological data. For example, two of the well known strategies used by humans and other animals include binaural release from masking (e.g., the ability to improve signal-to-noise ratio by turning the head when the signal and noise come from different locations) and either voluntary or involuntary control over the level of vocal output (e.g., the ability to increase the level of vocal output to enhance communication in noise).

It is rare that such considerations enter into discussions on the effect of anthropogenic noise acoustic communication. As a result, attempts to assess the effects of noise on acoustic communication are often simple-minded, unrealistic, and incorrect. As one recent example illustrates, recent concerns that traffic noise might interfere with acoustic communication in several endangered species of birds in California (the California Gnat-catcher and the Least-Bell's Vireo) have led to the impractical adoption of single noise level (60 dB(A) SPL) as the environmentally acceptable limit of noise produced by freeways.

Taking this problem as an example, a better approach for birds might include the following elements. Most of what we know about hearing sensitivity of birds comes from laboratory tests with simple stimuli such as pure tones. Also, there is a wealth of data from laboratory studies measuring the masking of pure tones by noise (Dooling, 1982, 1991). Pure tone thresholds in the quiet and in noise can be combined with the scattered information available on other more ethological and ecological factors that we know influence the distance over which biologically meaningful signals can be used under natural conditions (Dooling, 1982). These other factors include such things as the location and source intensity of a singing bird, the sound-attenuating and masking characteristics of the environment, and the location and hearing sensitivity of the bird receiving the signal. By combining such laboratory and field data, we can at least roughly estimate possible communication distance between birds for detecting...
simple sounds such as pure tones in noise. This is a first step. One should not assume that the ability to detect a sound in noise is the only relevant variable. To understand how environmental noise might affect acoustic communication, laboratory tests must be conducted on how noises of different types effect not only the detection, but also the discrimination, and identification of species-specific vocalizations. Such laboratory data are critical for understanding the full effect of noise on acoustic communication and for developing reasonable guidelines for noise abatement. At present, predictions made for detection of vocalizations in the environment only address the simplest case, the ability of a bird to tell whether a sound occurred (i.e. detection). It is clear that such a measure does not reflect a bird's ability to communicate effectively in a particular acoustic environment, and may, in fact, have little bearing on it. One need only consider the case of human speech communication. It is one thing to hear a voice, and it is quite another to understand what is said. That is the problem that must be addressed, so that from the perspective of the receiver, acoustic communication abilities can be divided into three broad categories. The ability to detect a signal involves only being able to tell whether a sound occurred or not (Wiley and Richards, 1978, 1982; Klump, 1996). The ability to discriminate or distinguish whether a sound is different from another sound requires yet a higher signal-to-noise ratio than simple detection (Miller, 1974). And identification, or the ability to recognize a specific, biologically relevant signal, may require even higher signal-to-noise ratios. We are now acquiring equivalent data for birds and we need such data on marine animals in order to fully understand communication in noise. It is the ability to discriminate or identify relevant sounds - not just detect the presence of a sound - that are the critical pieces of information.

It is known from recent laboratory tests that, in cases where the signal (a tone) and a masker (a noise) come from different locations, small birds (as well as humans and other animals) can gain a tremendous advantage (up to 10-15 dB) by simply turning their heads (Dent and Dooling, 1997). Moreover, at least some birds can voluntarily control the level of their vocal output and can learn to increase or decrease the level of their vocal output by as much as 15 dB (Manabe et al., 1998). In humans, the increase in vocal level in the presence of noise is called the Lombard effect. If vertebrates as different as humans and birds show the combined effect, it would not be too surprising to find a similar capability in marine animals. Another robust phenomena in human speech communication is that of binaural unmasking or, as it is sometimes called, "the cocktail party effect." Under free-field conditions, both speech detection and speech intelligibility in humans are considerably improved as the signal is spatially separated from a masker such as noise (Santon, 1986, 1987; Saberi et al., 1991). Using pure tones, it has been shown that this is true for birds as well using broadband
noise as the masker (Dent et al., 1997). Such spatial "release" from masking is a relatively well-known characteristic of the binaural auditory system. A separation in space of signal and noise sources will certainly improve a bird's ability to hear biologically-relevant signals. The degree to which separation in space between noise and signal sources improves the ability of birds to detect the presence or absence of a communication signal must be a part of any effort to understand the effect of noise on communication since this strategy may enable a bird to communicate effectively even in noisy environments.

Finally, there is the type of ecological environment in which an animal lives that can be a critical parameter in estimating interference by noise. Calculating the maximum distance for song detection has to be considered in relation to the animals ecology. Song sparrows have relatively small territories (a diameter of 20 - 30 m) and reside in relatively open habitats (Wingfield, 1994). Thus, in contrast to many other songbird species, signal attenuation and masking is therefore expected to be minimal for this species. Songbirds occupy a wide array of habitat types and have a broad range of territory sizes, with some songbirds having territory diameters in excess of 200 - 300 m (Catchpole and Slater, 1995). Therefore, predictions for distances over which a tone may be detected in the environment will vary widely depending on the species in question.

With appropriate laboratory studies on hearing and knowledge of the sound attenuating characteristics of the environment, excellent estimates can be obtained for the maximum distance over which a song produced by one bird can be heard and understood by another. But this information is only valuable in the context of the animal's ecology as the song sparrow example shows. Because this species has a relatively small territory, a given level of noise will be much less disruptive on intraspecies acoustic communication in this species than on another species which may have a much larger territory size.

**ZONES OF MASKING IN THE WILD** (prepared by Christine Erbe after the workshop at the request of the team leader)

As part of an environmental assessment of icebreaker noise in the Canadian Arctic, the masking of beluga whale vocalizations was studied. The work presented included acoustic experiments with a beluga whale at the Vancouver Aquarium, various software methods to model such experiments, and the application of ocean sound propagation models to calculations of zones of masking in the wild (Erbe, 1997).

Similar to a shortage of data for birds pointed out by Dooling, masking in marine mammals has so far only been studied in experiments where the signal was a pure tone and the masker either a pure tone or a random, white noise. As hearing is highly nonlinear and depends on both frequency and temporal structure of signal and noise, results from pure tone experiments cannot be superposed to predict the masking of complex communication signals by structured noise. A different approach is necessary.

At the Vancouver Aquarium, masked hearing thresholds were measured behaviorally with a trained beluga whale (Erbe and Farmer, 1998). The signal was a typical beluga vocalization; the maskers were two types of icebreaker noise (bubbler system noise and propeller cavitation noise) and naturally occurring, thermal ice cracking noise for comparison. Results showed that bubbler system noise was strongly masked with a detection threshold at a signal-to-noise ratio of -15 dB, followed by propeller cavitation noise (-18 dB), then natural ice...
cracking noise (-29 dB). The reason for the different thresholds lies in a complex interplay between the individual time and frequency characteristics of call and noise. In general, pulsed noise as compared to temporally continuous noise exhibited a smaller potential of masking, because the animal could identify the call from very short pieces that emerged through quieter gaps in the noise field.

For the same reason, temporally continuous calls such as whistles are more robust to masking than are pulsed calls. Furthermore, masking depends on the amount of energy call and noise share in so-called critical bands which are characteristic of the animal's auditory frequency filter.

As pointed out by Dooling, there is a need to develop a set of algorithms for predicting noise interference. Animal experiments are very time and cost consuming and often impractical, but necessary. Reliable software models could produce data very efficiently. The detectors tested for their ability to simulate the masking of beluga vocalizations included human listeners, matched filtering, adaptive noise cancellation, spectrogram cross-correlation, critical band cross-correlation, visual spectrogram discrimination and artificial neural networks. The only software algorithm which produced masked hearing thresholds similar to those of the whale was a back propagation neural network (Erbe et al., 1999). The neural net was then used to predict the masking of artificially created, Gaussian white noise. Afterwards, data were collected from the whale. The net's prediction was accurate to within 5%. This raises confidence in the network's ability to replace animal experiments. At this stage, further ground-truthing with different calls and noises as well as comparison to data from other beluga whales of different age and sex would be advisable. Ultimately, the applicability of the neural net technique to other marine mammal species should be tested.

Masked hearing thresholds (measured or predicted) are of little use unless they can be related to noise types and levels in the wild. An ocean sound propagation model was applied to a conversion of critical signal-to-noise ratios to distances between a noise source, a calling whale and a listening whale. Results were that propeller cavitation noise masked furthest with a maximum radius of masking of 22 km. Bubbler system noise masked over 15 km. A naturally occurring ice cracking event only masked if the listening whale was within 8 m of the event. This study produced the first data on the masking of animal vocalizations by real underwater noise. Assumptions made previously in hypothetical analyses of masking turned out to be inadequate. For example, results showed that the zone of masking around a noise source will in general be smaller than the zone of audibility. In addition, ambient noise will often not add to the masking effect of man-made noise.

This project identified the following primary research needs: (1) The utilization of tools from computer science to develop robust models for masking and other effects of noise on marine life is invaluable. (2) Because masking cannot be isolated from other effects described in this report; an integration of data from behavioral, physiological and other studies is needed. For example, arctic beluga populations show disturbance reactions to large vessels long before masking occurs; whereas for the St. Lawrence population, the disturbance distance is shorter than the masking distance. Are habituation or hearing impairment due to PCB contamination an explanation? (3) Do animals have means of avoiding masking? Evidence exists that animals can increase the source level of transmitted signals in the presence of noise. Also, active
frequency-shifting has been reported in the case of echolocation (Au, 1993), but in the case of communication, can a call with different spectral characteristics convey the same information? It seems "reasonable" that if vocal communication involves variable signals such as mating or warning signals, then masking will be "biologically significant." However, we basically don't have any data on the importance of communication for survival and on long-term effects on an individual and an entire population.

MODELS OF AUDITORY PROCESSING (prepared by J. Richard Price after the workshop at the request of the team leader)
The list of incomplete knowledge in the area of noise effects on marine mammals is staggering; however there are a few welcome instances where lines of inference can be drawn and previous work in related areas can shed some light on avenues of likely approach. There is an interesting similarity between the natural environment and the military environment. In both, hunter and prey seek to survive, one at the expense of the other. The US Army has dealt with problems of auditory detectability through measuring the source, then modeling the propagation path, the noise background, and the properties of the detector (ear). This program (Garinther et al., 1985) has served as the basis for the Army's non-detectability standard (DOD, 1996) and its structure fits the structure of the marine mammal problem, if not the medium. With the assistance of these algorithms it was possible to calculate the effects of noise on detectability and identifiability of complex sounds or to predict the effects of any particular change in hearing on a soldier's ability to perform various tasks (Price et al., 1989).

If one simply trusts in the great similarity of the basic structure of mammalian ears (as we are usually asked to do when animal models are used to predict human responses), or in the similarity of detection of speech signals (complex transient sounds) and those complex transient sounds used by other animals to communicate, then the applicability of this work to the problem of predicting the effects of man-made sounds on marine mammals is obvious. As always there is the caveat that unique qualities may exist in the model or the system modeled and that these differences may be not only interesting but crucially significant; but development of this parallel has promise. In fact, work is underway under a collaborative effort by Ketten and Price to determine minimal anatomical measures to make these transitions.

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A similar parallel also exists where intense sound exposure is concerned. Both the battlefield and the underwater environments have exceedingly intense sound sources and the mammals in both have similar cochleas (the primary site for structural changes which fundamental to hearing loss). It is apparent that an important dividing line exists in the mammalian ear's response to intense sound as pressures rise higher and higher. At lower pressures, the ear can be thought of as "tiring out." Thresholds are elevated for a short while, but they recover to normal and the cycle can be repeated almost indefinitely. However, at higher pressures the damage mechanism may shift into effectively irreversible mechanical stress (the ear is "torn up") (Price, 1981; Liberman, 1987). In this case, the loss is immediate and shows only limited recovery. The damaged cells are replaced by scar tissue and the hearing loss is permanent. The important parameter here is the intensity of the sound rather than what source produced it. In this case also, the Army has developed a mathematical model of the mammalian
ear to predict hearing loss from such intense sounds (Price and Kalb, 1991; Price, 1998). The model is an electroacoustic analog of the ear and predicts hearing loss based on displacements within the cochlea. The path to applicability of this technology in the case of marine mammals is to develop methods to predict stapes displacements (which drive the inner ear) from pressures in water. Given the great parallelism of mammalian cochleas, it seems likely that the loss algorithms that work within the cochlea should also be useful for predicting the responses of the marine mammals. If so, then it should be possible to make some useful statements with respect to the hazard from really intense sounds in the marine world as well.

MAJOR QUESTIONS

In general, the effects of anthropogenic sounds on aquatic organisms are likely to be essentially the same as the effects of air-borne sounds on terrestrial organisms. While we have much less knowledge of the effects on aquatic organisms and on the sources of the sounds underwater, the same kinds of questions asked regarding problems in air are applicable underwater.

During discussions, we identified several areas that are particularly important if we are to understand the effects of anthropogenic sound on marine organisms. These areas are briefly discussed in this section.

What are the effects of anthropogenic sounds on the ability to communicate, navigate, find food, avoid predators, etc.?

It was agreed that this issue is somewhat different than masking per se since the amount of noise needed to interfere with detection may be quite different from the amount of noise that would interfere with the understanding of a biologically relevant communication signal. In the speech perception literature, it is well known that intelligibility of speech in a noise background continues to improve from no intelligibility when speech is completely masked by noise to complete intelligibility as the speech-to-noise ratio improves over a 20-30 dB range (Hirsh, 1952). At the same time, if it is not possible to measure the effects of sounds on understanding of communication sounds, a second best approach would be to understand masking effects.

Specifically with regard to marine mammals, (Erbe, 1997) found that when measuring the hearing threshold for a complex vocalization consisting of a fundamental frequency and four harmonics, the animal stopped reacting to the call as soon as the lowest frequency either dropped below the audiogram in the absence of noise or was masked in the presence of noise. The higher frequency components, however, were still audible at much lower signal levels. The difference between the call detection and call recognition (identification) level was about 15 dB.

What level stimulus is needed to produce temporary vs. permanent damage to the underwater auditory system?

A critical question is whether anthropogenic sounds have the potential to damage the function of the auditory receptors in different animals. Our knowledge on this subject is minimal. With the exception of a few studies on fishes (Enger, 1981; Hastings et al., 1996), no investigators have ever demonstrated that acoustic overexposure can damage the auditory receptors of aquatic organisms. In the most quantitative of these studies, Hastings et al. (1996)
found damage only after the most intense sound stimulation, and then only after the animals were
allowed to survive for four days following one hour of stimulation. Whether such results are
meaningful for organisms that may avoid or flee from the region of intense sounds is highly
questionable (e.g., Popper and Carlson, 1998). Indeed, this question is germane not only to fish,
but also to marine mammals. The effects of intense sounds may be much greater on slow
moving or sessile organisms, particularly if they are located near stationary sound sources.
Two aspects of the question of direct damage to auditory receptors were discussed. The
first was whether sounds can result in a temporary loss of hearing ability that has short-term
consequences for an animal. The second was whether sounds can permanently damage the
auditory system and lead to long-term consequences. Within the consideration of permanent
damage, it is important to keep in mind that damage could be to the hair cells or to any other
component or set of structures in the outer, middle, or inner ear. Unlike the inner ear, which is at
least fundamentally the same in marine and land mammals, the outer and middle ear anatomies
of many marine mammals are rather different and very diverse (see above). For instance, it is
still a matter of debate how or if the eardrum and middle ear ossicles function in cetaceans. Even
among pinnipeds which have ears that are more similar to land animal ears than to whales, the
external ear canals vary considerably from those of land mammals. It is likely that many of the
differences found in marine mammals are in part related to their diving requirements, but these
adaptations surely imply an acoustic price as well. By example, in land mammals, damage due
to high intensity impulse sounds can, presumably, cause a tear in the tympanic or round window
membranes, and thus alter the contributions of the eardrum and middle ear to hearing. At the
same time, the tympanic membrane, unlike the hair cells of the mammalian inner ear, generally
will repair spontaneously and rapidly (within 24 to 48 hours) if less than one-third of the eardrum
is compromised. In marine mammals, the tympanic membrane is extraordinarily varied in size,
shape, and thickness. In some animals, it is like that of a dog or cat; in others, it is both far larger
and tougher, which may well mean it is resistant to high acoustic pressure based tears.
The only information we have on permanent hearing loss in marine mammals comes
from several recent studies showing that different individuals of a single species can have
different hearing sensitivities
(see sections above by Brill and Ridgway, and by Schusterman),

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and that some have inner ear damage consistent with their hearing loss (Ketten et al., 1997).
For example, age related hearing loss has been found in a female California sea lion, especially at
high frequencies (Kastak et al., 1995). This sea lion's aerial hearing had originally been
measured when she was two years-old. Sixteen years later, audiometric reassessment using
extrapolated comparisons ranging in frequency from 800 to 6,400 Hz showed that the animal had
an aerial hearing loss averaging about 22 dB. Comparing the underwater hearing of this older
female California sea lion (18 years-old) and that of a younger counter