REPORT ON THE CURRENT STATUS AND FUTURE OF UNDERWATER HEARING RESEARCH

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REPORT NMMF-001-14

May 2014

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National Marine Mammal Foundation
San Diego, CA 92106

Executive Summary

A workshop on the status and future of underwater hearing research was convened from September 10-12, 2013 in San Diego, California. The workshop was held to evaluate recent and current research, and identify future research avenues with the greatest potential for advancing the state of knowledge on underwater hearing in marine mammals. The workshop consisted of three days of presentations by members of the scientific community actively involved in the study of marine mammal hearing; in particular, research into the relationship between sound exposure and temporary threshold shift, masking, anatomically-based modeling of marine mammal auditory systems, and behavioral and evoked potential audiometry. The presentations were independently reviewed by experts that are active in both the marine mammal and terrestrial mammal/human hearing research communities. This report presents the results of the independent review of current and future research in underwater hearing that occurred at the workshop.

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Introduction

The evolution of marine mammals from terrestrial mammal ancestors required adaptations to the auditory system that enabled effective underwater hearing (e.g. signal detection, source localization). The evolution of underwater hearing was essential for dealing with an environmental medium that favored the transmission of sound; i.e. light rapidly attenuates in water, especially turbid aquatic environments, whereas sound efficiently travels through the medium. The evolutionary adaptations to the auditory system that permit effective underwater hearing vary considerably among the different families of marine mammals and major differences in auditory system structure exist between the fully aquatic and amphibious species.

Marine mammals are difficult species to study because they live in an environment where continual observation is difficult. Typically, in the ocean, marine mammals are visually observed only when at the surface. Acoustic observations and remote data loggers have improved observations while the animals are diving and have enabled data collection that is critical to understanding the ecology of a number of species. Nevertheless, most of the research on the hearing of marine mammals has been limited to a handful of species that have been maintained under human care or through anatomical investigations of post-mortem specimens. For decades, behavioral audiometry with trained animal subjects was the means by which most information on marine mammal hearing was obtained. This approach has permitted many aspects of marine mammal hearing for select species to be investigated. Consequently, species' hearing capabilities were represented by a handful of individuals specifically trained for psychophysical procedures. Technological advances in the area of evoked potential audiometry have enabled audiometric procedures to be performed on stranded and captive marine mammals. This has enabled the collection of basic audiometric information from a number of novel species as well as permitting the sample sizes for some species to be rapidly increased. Nevertheless, behavioral methods with trained subjects, which obtain results that more accurately represent the integration of auditory processes from the cochlea to cognitive function, remain the standard to which electrophysiological and anatomical modeling approaches are compared.

In recent decades, the realization that man-made sound was a potential source of negative impacts to marine mammals has spurred more research into marine mammal hearing and the behavioral and physiological consequences of exposure to man-made sounds. The relationship between the physical characteristics of received sound and marine mammal hearing abilities has been, and remains, the cornerstone for regulatory agencies charged with managing the impact of anthropogenic sound on marine mammals. Thus, the relevance of marine mammal hearing research has increasingly extended beyond understanding the acoustic ecology of marine mammals to applications of wildlife conservation.

The marine mammal hearing research community is small by most standards, and the funding of marine mammal hearing research is overwhelmingly supported by a few funding organizations. In conjunction with the fact that there are a limited number of subjects available for specialized psychophysical procedures, the limitations on the scope of marine mammal hearing research that can be conducted become apparent. The purpose of this report is to highlight recent advances in marine mammal hearing research, to have it evaluated in context of research capabilities and technological advances, and to

provide commentary on the areas of marine mammal research likely to be most fruitful and useful to advancing knowledge on marine mammal hearing in the near future. The evaluation and commentary are provided by an external review panel that predominantly represents expertise in mammalian hearing research outside of the marine mammal community. The report briefly describes presentations provided by workshop attendees and follows with the evaluation, questions, and recommendations of the external reviewers. The report is meant to be a useful tool for building collaboration within the marine mammal hearing research community and promoting those aspects of marine mammal hearing research with the greatest feasibility and potential for having significant positive impact.

Summary Recommendations

Below, summary recommendations are provided by the review committee. The summary recommendations are not all inclusive and do not repeat individual recommendations; rather, they provide a listing of the highest level recommendations given a synthesis of the topical research reviews.

1. Increase species representation and, where feasible, increase the sample size of subjects representing a species for temporary threshold shift (TTS), baseline audiometric studies, and other psychophysical studies. Variability between individuals and variability as a function of demography are poorly understood for nearly all marine mammal species and substantially increase the likelihood of erroneous conclusions when based on a handful of subjects. The testing of additional species will increase confidence in the categorization of functional hearing groups and facilitate cross-species comparisons.
2. Increase the number of comparisons between psychophysical and electrophysiological estimates of hearing function within the same subject. Electrophysiological approaches enable many subjects to be tested over a short period of time, but psychophysical approaches permit the integrated response of an animal to be obtained. To increase the utility of the emerging electrophysiological research methods, the information that can be obtained from such techniques needs to be assessed in conjunction with psychophysical experiments. This recommendation is relevant to evoked potential methods, TTS, masking, and hearing during echolocation.
3. Consistency among laboratories and between individual investigators is lacking. Both psychophysical and electrophysiological methods vary considerably among research groups, which complicate efforts to synthesize the collective research findings. Effort should be placed into standardizing approaches that allow the comparability between related, but different, studies (e.g. equal loudness vs. equal latency) and those that are assessing the same thing (e.g. auditory evoked potential thresholds) to be compared. Agreement on fundamental components of research methods (e.g. the baseline frequency for loudness comparisons) would improve consistency between research groups.
4. Until such time that hearing measurements are made on mysticete whales, anatomical models will be necessary for predicting mysticete hearing sensitivity. Validation of anatomical models is critical to gaining confidence in their predictive ability, but remains elusive. Effort should be placed into validating models against behavioral or electrophysiological information from available species prior to extrapolation to species for which no information exists. In this regard, validation of peripheral and middle-ear models is of high importance.

Temporary Threshold Shift

Temporary threshold shift (TTS) refers to a temporary change in hearing sensitivity. The change is commonly a reduction in hearing sensitivity and is most often induced through intense noise exposure. Similarly, a permanent threshold shift (PTS) is a permanent reduction in hearing sensitivity. Hearing threshold shifts were one of the first physiological effects to intense sound exposure observed in marine mammals (Kastak and Schusterman, 1996). Sound induced TTS has since been studied in a number of marine mammal species (e.g. Finneran et al., 2005; Finneran et al., 2003; Kastak et al., 2005; Nachtigall et al., 2003). Information from these studies have formed and informed the criteria and thresholds for federal agencies responsible for managing marine mammal stocks and regulating the impact of anthropogenic sound upon them. Studies have involved a breadth of sound types (e.g. impulsive, steady-state, narrowband, broadband), which has presented challenges to the synthesis of a common model explaining the relationships between sound exposure characteristics (e.g. stimulus amplitude, duration, duty cycle) and the onset, magnitude, and duration of TTS. Accumulating evidence suggests that the level of sound exposure required to induce TTS varies across species and across the frequency range of hearing within species, and relatively little information exists on the nature of the recovery from a TTS. Given the complexity in the relationship between TTS and the many factors contributing to it (species, hearing sensitivity, type of fatiguing sound source), there remain many avenues for research on the topic to be explored, each with varying degrees of difficulty and pay-off in understanding the factors of anthropogenic sound most likely to impact marine mammal hearing at a physiological level.

Summary of Presentations

Dr. James Finneran provided a summary of the TTS studies conducted in bottlenose dolphins (*Tursiops truncatus*) and belugas (*Delphinapterus leucas*) over a period of nearly twenty years at the Navy Marine Mammal Program (MMP). The studies focused on TTS as a result of exposure to tonal signals of varying frequency (0.4-80 kHz) and duration (1-64 s). Auditory threshold estimates, pre- and post-exposure, were obtained with both behavioral and electrophysiological methods. The collective findings of the work included: 1) demonstration of the upward spread of masking, with peak TTS occurring ~0.5 octave above the stimulus frequency; 2) the ability to predict the onset of TTS from the sound exposure level (SEL; measured in dB re 1 $\mu Pa^2 \cdot s$); 3) the breakdown of the equal energy assumption with increasing duration of stimulus exposure; 4) the impact of exposure frequency on the growth rate of TTS, with greatest amounts of TTS observed from exposure to frequencies where hearing is most sensitive, between 14.1-28.3 kHz; 5) and demonstration of the recovery of the ear when equal energy stimuli are interspersed with quiet intervals.

Dr. Paul Nachtigall reviewed work conducted at the Hawaii Institute of Marine Biology in which TTS in bottlenose dolphins was studied in response to exposure to ~30 minutes of broadband noise (5-11 kHz) presented at ~179 dB RMS sound pressure level (SPL; dB re 1 µPa). Auditory threshold estimates were obtained with behavioral methods and results demonstrated up to 11 dB of threshold shift with rapid recovery (i.e. no observed TTS 45 minutes post-exposure). Subsequent work utilizing electrophysiological methods to determine hearing thresholds demonstrated shifts at 8 and 16 kHz following a 30 minute exposure to broadband noise (4-11 kHz) presented at ~160 dB SPL. In combination

with TTS experiments performed with a recorded mid-frequency sonar signal played back for the exposure stimulus, results also demonstrated a dependency on duration of the exposure and failed to support the equal energy hypothesis. Animal exposure to recorded 53-C Sonar signals demonstrated reliable shifts (three consecutive sessions) at 214 dB re: 1 $\mu Pa^2 \cdot s$ (15 pings). Based on this finding, it was argued that a free-swimming dolphin would have to be ~ 50 meters from the sonar for five minutes to induce a TTS. Dr. Nachtigall concluded with a discussion of current efforts to investigate the occurrence of TTS following exposures to low frequencies, including the demonstration of low frequency comparisons of auditory evoked potential (AEP) and behavioral thresholds. Most AEP audiograms do not measure hearing below 4 kHz, but comparisons between behavior and AEP data down to 1.4 kHz utilizing tone pip stimuli showed good agreement.

Dr. Colleen Reichmuth summarized prior and continuing work on TTS in pinnipeds. The work relied only on psychoacoustic methods and capitalized on controlled and opportunistic noise exposures both underwater and in air (within a hemi-anechoic chamber). Exposure stimuli consisted of uncontrolled broadband noise (construction), mid-frequency octave band noise, impulsive sound, or mid-frequency tonal signals. Subjects represented three species – California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), and the northern elephant seal (*Mirounga angustirostris*). Measurements obtained underwater with octave-band noise demonstrated that small shifts could be induced with exposure levels < 75 dB above sensation level (SL) and exposure durations <22 minutes. TTS was most evident at the center frequency of the octave-band noise. Follow-on work demonstrated that threshold shifts were proportional to overall SEL, but that increasing exposure duration had a greater effect on TTS than increasing exposure level. Work conducted in a hemi-anechoic chamber demonstrated that equivalent TTS is induced in air and under water when exposures (referenced to SL) are similar. Robust information was also obtained and used to characterize the onset and growth of TTS from mid-frequency octave-band noise. Dr. Reichmuth concluded with a discussion of an unintentional permanent threshold shift (PTS) that was induced in a harbor seal repeatedly exposed to a brief (<1 min) 4.1 kHz tonal signal during training procedures. The shift was not predicted to occur, it occurred without any behavioral indicator of its occurrence, and the effect was most notable at 5.8 and 8.2 kHz (a half-octave and one-octave above the exposure frequency).

Dr. Ronald Kastelein presented on TTS investigations with harbor seals and a harbor porpoise (*Phocoena phocoena*). TTS was studied in relation to continuous noise (octave band centered at 4 kHz), playbacks of pile driving sounds, and playbacks of sonar sweeps from 1-2 kHz (LFAS) and 6-7 kHz (MFAS) at various duty cycles. The onset and recovery of TTS were demonstrated in both species exposed to broadband noise; the harbor porpoise was more sensitive than the harbor seal, but in both cases TTS occurred without any overt change in behavior. For exposure to pile strike playbacks, no TTS was observed to playbacks of strikes ranging from 46-173 strikes per minute and with a maximum cumulative SEL of 156 dB. More recently, TTS was elicited in a harbor porpoise by playbacks of pile driving sound and the affected hearing frequencies were determined. Presently, a TTS study is being conducted with long exposure times in order to elicit TTS in harbor seals. Dr. Kastelein also reported on a study of TTS in the harbor porpoise following exposures to 1.5 kHz continuous wave (CW) tones and 1-2 kHz down-sweeps. The study demonstrated the onset of TTS for a 100% duty cycle (onset <150 dB SEL) and highlighted the

importance of the duty cycle in the onset of TTS (i.e. intermittent signals require greater energy accumulation for the onset of TTS). Dr. Kastelein concluded with a description of recent and ongoing work, including that involving frequency sweeps from 6-7 kHz and 6.5 kHz CW tones.

Dr. Klaus Lucke reviewed a TTS study performed on a harbor porpoise exposed to single seismic airgun pulses. Threshold testing was performed using electrophysiological methods. A TTS was observed in the subject when the single pulse exposure reached 164 dB SEL and 200 dB SPL (p-p). Behavioral responses to the exposure occurred at single-pulse levels as low as 145 dB SEL. The implementation of these results by German regulatory agencies was discussed. Dr. Lucke concluded with a description of an ongoing study to increase the sample size for the TTS study by exposing by-caught porpoises to single and multiple seismic airgun pulses. In combination with complementary threshold audiometry work conducted with porpoises in rehabilitation, audiograms were presented for a number of harbor porpoises. To date, TTS has not been observed in any of the by-caught porpoises exposed to the seismic airgun pulses, but maximum levels have only equaled that used in the original study.

Dr. James Finneran concluded the session with a review of the TTS studies conducted at the MMP utilizing impulsive signals as the fatiguing stimulus. Historical studies included exposing belugas and bottlenose dolphins to signals produced from an explosion simulator and a seismic water gun, as well as those exposing California sea lions to an arc-gap transducer. Results from those studies demonstrated a TTS of 6-7 dB in belugas exposed to impulses of 186 dB SEL and 226 dB peak-to-peak SPL (or SPL (p-p)). No TTS was observed in dolphins exposed to impulses as high as 188 dB SEL and 228 dB SPL (p-p). Neither was TTS observed in the sea lions at the highest levels of exposure (198-203 dB SPL peak pressure, and 161-163 dB SEL). Dr. Finneran concluded with a report on more recent work in which three dolphins were exposed to up to ten pulses from a 150 cm^3 seismic airgun. As with prior studies, no TTS was observed in the dolphins at cumulative SEL from 189-195 dB SEL.

Reviewer Comments

The purpose behind the TTS studies is to determine the exposure parameters that lead to a modest, and reversible, threshold shift. There are multiple reasons to seek improved understanding of TTS. First, TTS deficits could compromise not only feeding, foraging, and localization, but also predator avoidance if sounds are not detected or cannot be localized. A second issue, not yet fully understood in either marine mammals or land mammals, is the longer-term relationship between TTS and PTS. Some evidence suggests repeated TTS can ultimately resolve as a PTS, but the mechanisms through which repeated TTS leads to PTS are not understood, and a causal relationship linking these two phenomena (TTS and PTS) has not been established. Finally, new data from terrestrial mammals suggest robust TTS can compromise neural integrity, perhaps resulting in supra-threshold perceptual deficits, even after complete threshold recovery. However, it should be noted that supra-threshold perceptual deficits after robust TTS have *not* been documented.

Over the course of multiple presentations on experimentally induced TTS in marine mammals, with data drawn from multiple species and multiple noise sources, a few factors became quite clear. First, despite differences in the transmission medium (air vs. water), the functional effect of noise on hearing is consistent across mammals. TTS increases with increasing sound pressure level and with increasing

signal duration. Therefore, just as in terrestrial mammals, both level and duration must be factored into noise risk criteria for marine mammals. A threshold shift one half-octave above the stimulus frequency, with an upward spreading of TTS to higher frequencies, has been documented in marine mammals, as in terrestrial mammals. Also, regions of maximum vulnerability have been identified for at least some species. There has indeed been robust progress in quantifying sound exposures that induce minimal TTS, as well as the growth of TTS with increasing exposure. The accomplishments are impressive given the time required to train and test subjects and the limited availability of subjects that can be used in these studies. Nonetheless, broad understanding of species vulnerability is uncertain.

It is clear from work with humans, mice, guinea pigs, and other terrestrial species that there are significant differences across individuals, and there is no reason to assume marine mammals will be any different. It is difficult to be certain if data from a small number of animals who participate in multiple studies are providing insight into the "average" condition, or reflect subjects that are relatively more (or less) vulnerable than the average animal subject would be. The small number of case reports in which a single animal has developed an unexpectedly large TTS (or even a PTS) is consistent with the suggestion that there may be significant individual variability. The only way to fully resolve this question is to increase sample sizes within studies, and to use experimentally naïve animals in new studies in order to provide additional rigor and understanding. Advances in the development of electrophysiological test protocols for marine mammals presumably increase feasibility of testing multiple subjects; the daily training over multiple months of time can be omitted in such studies.

In addition to the small number of individuals from any marine mammal species used to study TTS, there exists a reticence to cause PTS, which has led to a fairly conservative approach in terms of the magnitude of TTS that is allowed. Most of the marine mammal studies show minimal TTS, and thus it is difficult to identify true damage risk criteria for hearing loss without studies that expose animals to higher stimulus levels and/or longer exposure durations. In some studies, challenges in rapidly obtaining valid threshold estimations have led to an estimation of TTS at 4 minutes, rather than the more commonly used (in humans) TTS at 2 minutes (there is a maximum of TTS at 2 minutes, with TTS being smaller both before and after this time period). Recent studies in terrestrial mammals have suggested that there might be substantial anatomical damage to auditory nerve afferents before threshold shift is seen in noise exposed animals, and that the magnitude of response well above threshold may serve as an indicator of this 'subclinical' damage.

It is easy to assume that less TTS is better, but preventing all TTS, in even the most vulnerable animals, is probably no more achievable than prevention of all human noise-induced hearing loss, in even the most vulnerable humans. Understanding the specific changes in hearing that might compromise survival will provide important context for all previously collected data, and will provide a framework for new studies relevant to "safe TTS" and TTS hazard. With respect to long-term functional questions, there are two approaches that might be considered. TTS exposures that may result in PTS post-exposure (in the most vulnerable animals), or that may result in increased PTS in the future (during subsequent exposures), must be assessed if we are to fully understand "TTS risk". Some inferences can be drawn from terrestrial animals, given the extensive overlap across species, but critical levels at which risk begins for specific species will require empirical data. A database of hearing records from stranded animals might provide

some information if a notched configuration consistent with a history of noise exposure can be identified in stranded animals. However, such data are of limited value given unknown health status, unknown reason for stranding, and the potential that whatever health or environmental factors led to the stranding may have also influenced auditory function. Careful comparison of data collected from stranded animals and from animals maintained in captive environments will be important if data from stranded animals are to be incorporated into the database on marine mammal hearing. One novel approach is trapping of wild animals to allow health checks, hearing tests, etc., with release immediately following testing, although caution is needed to assure that pods and mother/offspring pairs are not separated or disrupted.

Questions regarding the types of noise exposure that result in TTS have compelling scientific value and are worth continued investment. Psychophysical test paradigms are an important component of this process, but evoked potential assessments may open up opportunities for improved understanding of species-typical function, rather than single animal function. Partnerships with scientists that study terrestrial mammals may also allow basic questions to be answered in larger numbers of animals at reduced cost, with translation to marine mammals to follow in smaller samples, given the protected status of marine mammals. Questions regarding noise-induced TTS/PTS will require careful discussion of the ethics of inducing hearing loss in a small number of marine mammals to better understand the point at which risk begins for larger numbers of animals. Discussion of the ethics of such studies is important, given the high scientific merit and existing technical information, to allow such studies to be initiated in the near future. In a similar regard, the objectives of how TTS results are to be used in context of improving scientific knowledge and improving species management and conservation need to be explicitly clarified.

Key questions that remain unanswered

1. How relevant are pure-tone insults to real-world noise hazards generated by military exercises and equipment, industrial exploration and development, and commercial transportation?
2. How much TTS is “needed” in order to compromise predation, foraging, localization, communication, etc.?
3. Is there any difference in noise conditions for animals in pools, in bays, and in the natural environment, which will influence the amount of TTS induced by a given signal?
4. Is there any effect of previous noise exposure on vulnerability to additional noise exposure (a “toughening” or “conditioning” like phenomena)?
5. What is the likelihood that an animal with TTS will develop PTS?
6. What are the fundamental sites of injury to the inner ear?
7. Does TTS result in physical injury (such as neural loss) that is not captured using threshold measurements? If so, what is the critical boundary for such injury? And, are there any functional deficits that emerge at supra-threshold levels?
8. What is the validity of testing single sources versus creating a matrix of single frequencies, durations and sound pressure levels? In terms of applying to actual real life scenarios, which one is most useful?

Recommendations

1. Look for opportunities to expose marine mammals to higher sound levels. The 'opportunities' might be stranded animals that will be sacrificed, or unhealthy animals that will be sacrificed. In these animals, explore physiologic changes (e.g. auditory brainstem response (ABR) or auditory steady-state response (ASSR)) comparing baseline to post-exposure responses, and harvest tissue (i.e. the inner ear) to identify early degenerative changes occurring post-exposure.
2. There is an emerging literature from Liberman and colleagues that the earliest anatomical changes in response to acoustic overexposure are not evoked potential threshold changes, but rather a reduction in response amplitude at high stimulus levels. In TTS studies that use AEP measures of threshold, it is critical that these studies add higher level stimuli to their protocol, to determine if response amplitude decreases at higher stimulus levels. Assessing variations in input/output (I/O) functions would also be beneficial.
3. Following a TTS, it is critical that ABRs be obtained for studies measuring AEPs. The amplitude of first ABR peak (reflecting the 8th nerve compound action potential) should be investigated, as well as the later ABR peak amplitudes, as brainstem plasticity might modify peripheral amplitude changes.
4. Increase the number of species tested to reduce uncertainty associated with interspecies extrapolations and better understand susceptibility of different species.
5. Increase sample sizes within studies and strive to include naïve subjects to address variation in individual vulnerability and "conditioning" phenomena.

Masking

Masking is the interference in the detection, recognition, or discrimination of one acoustic signal by the presence of another. In marine mammals, the issue of masking is relevant to intraspecific communication and social interactions, prey detection, predator avoidance, and navigation. The relevance of masking to real-world, anthropogenic signals is a subject of debate. Marine mammals have evolved in relatively noisy ocean environments and have likely evolved mechanisms for compensating for the interference of other noise sources. However, the addition of anthropogenic sound to the ocean noise budget, with substantial increases in ocean noise over the last 100 years, brings into question whether compensatory mechanisms are sufficient to mitigate potential masking effects. Traditional laboratory approaches to studying masking, though informative with respect to discovering underlying principles, often fail to capture the salient features of the masking signals most likely encountered by marine mammals in the wild, including the ambient noise of the environment within which they have evolved.

Understanding masking and the mechanisms by which marine mammals compensate for masking are important to predicting the manner by which anthropogenic signals affect the active space over which effective signal detection and discrimination occur. Relatively few studies of masking have been performed in marine mammals, and most of these have been performed in laboratory settings with fairly simple acoustic stimuli, i.e. only a handful have addressed real-world masking sounds likely to be experienced by marine mammals in the wild (e.g. Branstetter et al., 2013). As a result, errors in the prediction of masking resulting from exposure to real-world stimuli will exist, but will remain largely without quantification. Such errors will only become magnified as the prediction of masking impacts extends beyond simple detection to recognition and discrimination.

Summary of Presentations

Dr. Christopher Clark started the session with a presentation on how noises from anthropogenic sound sources influence the ocean acoustic environment. He discussed the potential for chronic noise from shipping to impose risks at large spatial and temporal scales for baleen whales, many of which communicate at frequencies <1 kHz. One form of risk is the loss of acoustic communication space due to masking. Dr. Clark provided several studies demonstrating the scales over which low-frequency noise persists in the ocean environment and presented an acoustic space overlap analysis in which shipping noise was compared to the frequency range of sound production for a number of marine mammal species. He concluded with a discussion of acute vs. chronic risk, e.g. ship strike vs. cumulative risks from direct and indirect stressors.

Dr. Christine Erbe summarized the dependency of masking on factors such as the signal-to-noise ratio, temporal variability of the signal, ambient noise and sound propagation conditions, and the hearing characteristics of the receiver (e.g. hearing sensitivity, frequency range of hearing, critical ratios). Distinctions were made between masking as it relates to signal detection and signal recognition and how the degree of masking varies depending upon which is of concern. Manners in which marine mammals potentially compensate for masking, e.g. the Lombard effect, frequency shifting, multiple looks, spatial

release from masking, were discussed. Dr. Erbe concluded with examples of how scientific information is combined for the purposes of noise risk management and reported on what is occurring with respect to noise risk management in some governments and industries.

Dr. Brian Branstetter presented on studies to determine the critical ratios of bottlenose dolphins and how the comodulation release of masking relates to dolphin signal detection. Critical ratios were experimentally determined utilizing seven different noise types with equal spectral densities. The results indicated that the spectral density does not capture all aspects of masking, but that variation in the time domain was also important to masking. Through a phase delay experiment, comodulation masking release, which is the decrease in masking when noise is amplitude modulated, was shown to be important to the degree that masking occurs. Follow-on investigations identified specific metrics to account for masked threshold data by employing different noise types and different noise levels. The power spectral density and the comodulation index, which measures across-channel coherence, were found to be the best predictors of masking for the given data.

Mr. Kane Cunningham concluded the session with a presentation on the application of a third-octave band/critical ratio model for signal detection, a model that is commonly used to predict the masking effects of noise on marine mammals. The model accurately predicts detection thresholds for simple sounds, but fails under certain complex conditions (e.g. the presence of multiple harmonics, comodulation). Model predictions were compared to empirical detection thresholds for pinnipeds under complex signal and noise conditions. The project is ongoing, but recently collected data were presented for a harbor seal. Based on differences between predicted and observed thresholds, additive correction factors that may improve model predictions were discussed. Mr. Cunningham concluded that third-octave band/critical ratio models could be significantly improved without overly increasing the complexity of the models.

Reviewer Comments

The ocean can be a noisy place and masking is an important issue to marine mammals. Masking may arise from biological sources (such as snapping shrimp), environmental conditions (such as wind, waves, or precipitation), or man-made sources (such as shipping, sonar, exploration activities, etc.). Noise from all of the above sources has the potential to result in a reduced ability to detect returning echolocation signals, mask communication calls, mask the sounds of prey that predators use to locate food, and also mask the sounds of predators. There are multiple ways in which noise might influence acoustic signals; it might reduce detectability, or, sounds might be detectable, but they may not be recognizable. Importantly, masking will vary not only as a function of the noise that serves as the masker and the signals that are subject to masking (i.e. do the frequencies fall within the same critical band, are there temporal distinctions, etc.), but also as a function of the listener. If the animal in that environment has existing hearing loss, from age or from TTS (see above), the effects of the masking noise may be greater than if the listener is a young, normal-hearing individual.

The workshop identified significant efforts to understand some of these factors, including effects of different maskers on specific acoustic signals, efforts to assess critical bands and signal-to-noise ratios required for detection within and outside critical bands, and the development of models for predicting

the disruption of communication space (i.e. the reduction in oceanographic space over which marine mammals can communicate in the presence of background noise). Auditory masking in natural environments such as the ocean remains difficult to predict. There remains a need for more comprehensive data on masking of species-relevant sound by noises that are biological and/or man-made. Disruption of detection is different from disruptions to the recognition or identification of sound, and knowledge gaps for both remain.

Much of the masking work performed in marine mammals has used behavioral testing methods. Hence, such work is typically only possible in a limited number of species and with only a few highly trained animals of a given species. As with the TTS studies previously mentioned, small sample size remains an issue that limits understanding of the variability across individuals and species. The tools are in place to answer a number of masking-related questions using lab protocols and recorded stimuli, and additional signals, species, and subjects could be added to the test paradigm.

A goal of the masking work is to better inform noise risk management. Noise risk management as it relates to marine mammals is in its early stages. There are clear examples throughout the literature that masking affects communication; however, there is a need for further exploration and data gathering to improve communication space models and to address other aspects of signal detection and discrimination as they relate to risk management. There is also a need to test the validity of the inputs to the models and improve the applicability of this type of analysis to other species and scenarios. Currently, this is a time consuming task and at several points assumptions are made that require further validation. Furthermore, it seems possible that information generated in masking studies could be used to inform weighting system guidelines, if it turns out that acoustic energy provides robust detrimental masking at frequencies that are not harmful to hearing and would otherwise be discounted in the scheme for rating noise risk.

Key questions that remain unanswered

1. Are man-made sounds more likely to result in acoustic masking than uncontrollable biological sources of noise?
2. What species are affected by different noise sources? What acoustic information will be most compromised by different man-made sources of aquatic noise?
3. Is there an interaction between hearing loss and masking noise? (Some maskers may not be detectable for an animal with hearing loss; masking noise may have less impact on performance and survival than the hearing loss itself. This will be difficult to assess, as it will vary as a function of the specific target signal, the specific masking signal, and the specific pattern of hearing loss.)

Recommendations

1. Perform studies that investigate masking of species-relevant signals by likely ocean noise sources.
2. Perform studies that differentiate between the impacts of masking on detection and discrimination.
3. In numerous far-field studies in terrestrial animals, it has been shown that masking noise reduces ABR peak amplitudes, increases peak latencies, and increases inter-wave intervals.

Evaluate the effects of a set of man-made sounds (e.g. ship noise, pile driving, sonar), used as background maskers, on the amplitude or latency of ABR peaks. (It is not unreasonable to assume that if a given masking noise affects the ABR amplitude (or latency), that it is having an influence on the audibility of a given sound.)

4. Study the critical band using the ABR or ASSR. A broadband noise can be raised in level until it masks (eliminates) the tone burst or SAM stimulus. Its bandwidth is gradually reduced (geometrically centers on the stimulus frequency) until the response emerges, and this can provide a reasonable approximation to the critical band.
5. Address applications to noise risk management. Specifically, apply results from recent masking studies to current models of masking.
6. Increase sample sizes and species representation.

Hearing and Echolocation

Echolocation is a biological system of sound navigation and ranging (biosonar) used by odontocete cetaceans. It is critical for odontocetes to forage and navigate, often in waters that are either very turbid or at depths where light is of little consequence. Echolocation consists of the emission of a sequence of sound pulses pneumatically generated at the phonic lips, which lie beneath the blowhole, and which are projected through a fatty body on the forehead known as the melon. Echoes from objects encountered by the projected signal are returned back to the odontocete and are received through fat bodies of the lower jaw, which then transmit the echo energy to the auditory bullae (see Au (1993), for review). Although the sound transmission and reception pathways of the odontocete biosonar system have been characterized, the neurological processing of received echoes remains largely unknown.

Echolocation has long been of scientific interest, not only because it is essential to odontocete biology, but also because it has demonstrated underwater target detection and identification that far exceed the capabilities of human-made sonar systems. Although most work on dolphin echolocation has been accomplished with bottlenose dolphins, these studies have shown the ability of the dolphin to detect small targets at ranges in excess of 100 m, discriminate material composition of targets, detect targets that are buried in the sediment, and differentiate target dimensions (e.g. wall thickness) on the order of millimeters. The last 20 years has seen a growth in the interest of echolocation of species other than the bottlenose dolphin, often in natural settings where laboratory constraints are removed but where control over the context of the measurement is lost. Additionally, efforts to study echolocation have extended beyond solely psychophysical efforts to measurements of central nervous system function during echolocation tasks. These latter efforts reflect the state of the art in odontocete echolocation studies and have provided insight into how odontocetes manage auditory processes, such as the regulation of hearing sensitivity, during echolocation.

Summary of Presentations

Dr. Paul Nachtigall started the session by presenting the results of an investigation of how echolocating animals hear low amplitude echoes following the production of their own high amplitude echolocation clicks, or more generally, how they hear while echolocating. By collecting auditory brainstem responses (ABRs) of a false killer whale (*Pseudorca crassidens*) to both its outgoing click and the echo returning from a target, the laboratory demonstrated that returning echoes are heard at the same level as higher amplitude echolocation signals and that echo-induced ABR amplitudes are relatively invariant to echo amplitudes that may differ by more than 35 dB. Follow-on work in which the envelope following response (EFR) was recorded to a 22.5 kHz tone during a target detection echolocation task demonstrated a change in the I/O function that was recorded during target present and target absent trials. The difference indicates a change in hearing sensitivity depending on whether targets were present or absent. Hearing sensitivity increased by more than 20 dB when targets were absent and the animal was required to search for the targets. The pseudorca was also exposed to a loud sound that was preceded by a neutral warning signal. By using similar electrophysiological methods, it was demonstrated that the pseudorca learned to change its hearing by as much as 13 dB when the warning

sound was provided. The results indicate learned control over hearing, but the process (e.g. stapedial reflex) underlying sensitivity change remains unknown.

Dr. Magnus Wahlberg presented on complimentary work conducted in the harbor porpoise. The ABRs to outgoing clicks and returning echoes were recorded during echolocation target detection trials. The porpoise was tested when it was stationary and also when it was allowed limited mobility. The work demonstrated that not only did the animal adjust the amplitude of its outgoing signal (~6 dB peak SPL) when target distances were increased, but also changed its threshold by 6 dB. Thus, the porpoise was able to actively compensate for the attenuation of the echo due to distance. This work also demonstrated that during the terminal approach of a free-swimming echolocation task, or the "buzz" phase, that the ABR peaks elicited by the outgoing clicks were not completely synchronous with the timing of echolocation click production. This was accompanied by an ~40 dB increase in ABR amplitude when compared to regular clicks. The meaning of the change in hearing sensitivity during the terminal approach is unknown.

Dr. James Finneran concluded the session by presenting on studies of the automatic gain control (AGC), previously discussed by other presenters, but at greater target detection distances (up to 100 m). Also included in the study was an investigation of changes in hearing sensitivity at a frequency of 113 kHz during the course of the echolocation task. The study utilized a phantom echo generator (PEG) as opposed to real targets, thus allowing the researcher control over echo attenuation and simulation of spreading loss. The task asked to be performed by bottlenose dolphins was a "change detection" task, in which they reported whether there was a change in the target echo. Using this paradigm, the AGC was found capable of compensating for spreading loss out to at least target distances of 80 m. Results from the hearing sensitivity investigation showed changes in neural potentials on time scales relevant to single click-echo pairs, similar to findings previously reported for the pseudorca.

Reviewer Comments

Echolocation is a unique adaptation that allows some marine mammals (e.g. dolphins) to find food and avoid predators while underwater where vision may be of limited use. Chiroptera also echolocate, and because ethical concerns regarding experimentation on bats is substantially less than that on marine mammals, there is a large body of invasive research (anatomical and electrophysiological) conducted on bats. As a result, the neural mechanisms underlying bat echolocation are fairly well understood. Perceptual work in bats (often neuroethologic research) has also demonstrated the acoustic cues useful for target location in the bat. It is not possible to use invasive approaches in marine mammals to study echolocation, but some very interesting work has been performed in recent years, some of which has used far-field auditory evoked responses. Auditory evoked responses can be recorded in select marine mammals to the emitted biosonar signal and the returning echo. Some interesting data suggest that there may be a sort of automatic gain function occurring in marine mammals during echolocation, which has interesting theoretical and practical implications. These data have provided intriguing evidence suggesting the potential for active central processing, with ABR amplitude being increased for returning clicks relative to the amplitude for detection of the initial outgoing pulse. Two possible mechanisms explaining this phenomenon are the active effects of attention (increased evoked potentials for returning signals) or the active suppression of the response to the outgoing signal. There is little

understanding of whether this may be mediated via a reflex response, such as might be mediated through an efferent reflex loop or a stapedial reflex induced during vocalization, or whether there is an active process mediated by the receiver, mediating its own sensitivity based on assumed target distance or other unknown factors that provide gain control. One of the unknowns that was not well addressed in the provided literature or in the presentations during the workshop was the extent to which this phenomena is evident in other echolocating species, such as bats. Although it has been demonstrated that bats invoke a form of automatic gain control during echolocation, a better understanding of the generality of the phenomena would be helpful in guiding next steps.

In humans (and a few other animals, such as gerbils), the relative contributions of various parts of the cochlea to an acoustic transient (such as a click) have been characterized by the use of high-pass subtractive masking. The relative contributions across the cochlea likely depend on the level of the stimulus. Similarly, as portions (especially lower frequency signal components) are often out of phase with other response components, a net increase in the response can be obtained when portions of the response that are out of phase with other cochlear regions contributing to the response are eliminated. It is possible that such a mechanism is contributing to the automatic gain function reported in echolocating sea mammals, and a high-pass subtractive masking study could identify (or eliminate) this possibility. Note that this study could be done with brief-duration impulses (such as clicks) as well as other simulated biosonar signals.

Key questions that remain unanswered

1. What is the mechanism by which automatic gain control is achieved in echolocating marine mammals?
2. How and in what manner does the automatic gain phenomenon generalize across bats and marine mammals?
3. How do variability in echolocation and echolocation strategies vary between controlled laboratory experiments and real-world scenarios (e.g. foraging)?

Recommendations

1. The biosonar data suggesting an automatic gain function are very interesting. However, the responses to the echoes are not simple time-shifted responses with morphology similar to that of the emitted biosonar signal. A number of experiments could clarify the nature of this automatic gain function:
    a. Eliminate the animal emitting a biosonar pulse and present a simulated pulse and simulated echo (with appropriate delays, amplitude changes, etc.) and investigate this phenomenon as a forward-masking experiment.
    b. Investigate the latency and amplitude of the ABR in response to the biosonar signal and returning echoes to see which portion of the response is enhanced and which is attenuated.
2. Develop and perform a high-pass subtractive masking study to characterize relative contributions of various parts of the cochlea to an acoustic transient.
3. Investigate possibilities for recording echolocation strategies and auditory processing while animals are free-swimming.

Weighting Functions and Related Research

Frequency weighting functions account for differences in the perceived loudness of an organism or species as a function of sound frequency. Within humans, it is often applied to instrumentation specific to the measurement of sound pressure level and has been incorporated in the prediction of damage risk criteria for humans exposed to industrial noise. The most common weighting function for humans is the A-weighting function, which is based on equal loudness studies conducted at low sound pressure levels. Other weighting functions have been developed based on changes in the perception of loudness that come with increasing signal amplitude. However, the A-weighting remains the most commonly used function for instrumentation and damage risk predictions for human use.

Weighting functions have recently been incorporated in the United States Navy approach to predicting impacts to marine mammals resulting from exposure to Navy sound sources. Weighting functions have progressed from simple to more complex, data-based functions with the latter having limited broad species applicability. Employing studies of equal loudness are difficult in non-verbal species, and data collections supporting the development of frequency weighting functions in marine mammals are challenged by additional logistical constraints (e.g. testing underwater). Debates over whether the collection of data near the threshold of auditory sensitivity are relevant to higher level sound sources are also germane to the implementation of the weighting functions, as they are within discussions of human damage risk criteria.

Summary of Presentations

Dr. James Finneran opened the session with a review of how the United States Navy utilizes auditory weighting functions in acoustic impact analyses involving marine mammals. Initial implementations of auditory weighting functions (ca. 2000) were simple in that they were “brick-wall” filters that discounted acoustic energy below a frequency limit; for mysticetes the frequency was 10 Hz, for odontocetes it was 100 Hz. Weighting functions more specific to the hearing ranges of low, mid, and high frequency hearing specialist cetaceans were later introduced by Southall et al. (2007). These “M-weighting” functions began to be used in Navy acoustic impact analyses (e.g. Mesa Verde Shock Trial), although the implementation was limited (e.g. used for impulsive sounds but not sonar) and inconsistent across analyses. More recently, data from TTS studies have been used to modify the mid-frequency specialist M-weighting functions to account for frequencies at which dolphins have been found to be most susceptible to TTS. In addition, weighting functions have been proposed for pinnipeds, mustelids, and ursids both in air and underwater. Numerous data gaps remain, particularly for the less common marine mammal species.

Dr. Colleen Reichmuth presented on work investigating the possibility of using equal latency functions to establish weighting functions for pinnipeds, i.e. the use of reaction time as a proxy for loudness. A California sea lion and harbor seal performed a signal detection task in an acoustic chamber. The response latency of each subject was measured to tones ranging from 250 Hz to 16 or 32 kHz and at levels that ranged from 0-40 dB above the hearing threshold of the subject. For the harbor seal, reaction times ranged from ~200-500 ms and were bounded by thresholds and asymptotic motor response times

within the dynamic range tested. The sea lion produced similar results but with reaction times ranging from only ~85-200 ms. Dr. Reichmuth concluded that reaction times were a suitable proxy for loudness, but only within a limited range (~40 dB above threshold). She also highlighted that this function, which is analogous to the 40 phon function used in humans, has limited utility for high level sound exposures, is not valid for non-tonal sounds, and has limitations in its application to high amplitude, low frequency signals. Dr. Reichmuth's laboratory is currently investigating similar reaction times for pinnipeds presented with tones while submerged. Dr. Reichmuth noted that the utility of reaction time extends beyond the equal loudness concept and provides a better understanding of perceptual salience, which is relevant to masking and its influence on sound detection, discrimination, and communication.

Dr. Ron Kastelein presented on work conducted in a harbor porpoise and in two harbor seals in which reaction times were used as a proxy for equal-loudness functions. For harbor seals, reaction times were determined from a retrospective analysis of prior hearing studies in which video recordings of the sessions were analyzed. Although there was a resolution limit of 40 ms based on the frame-rate of the video recording, the harbor seals demonstrated reaction times from 188-982 ms. Equal latency contours for sounds presented at near-threshold levels were found to closely follow the seal audiogram. For the harbor porpoise, reaction time was determined during a signal detection task by measuring the time it took the porpoise to leave the hearing station with an infrared light switch (8 ms resolution). Equal latency contours were developed for the porpoise for median latencies ranging from 92-522 ms (which corresponds to decreasing loudness). Equal-loudness functions were then created by fitting a smoothed function to the data. Dr. Kastelein concluded that reaction time data could be quickly collected and was a method that could also be used to derive equal-loudness contours in other marine mammal species. Although the derived weighting function was presumed to reflect relative loudness perception in the porpoise, he also cautioned that other studies (e.g. TTS) are needed to confirm this conclusion. The porpoise equal-latency study was part of the Ph.D. study of Paul Wensveen.

Dr. Jason Mulsow concluded the session by reviewing the only direct study of loudness perception performed in a non-human animal. The study involved having a bottlenose dolphin provide a differential response to sequential tone pairs, depending on which tone was louder. Reference tones were always at 10 kHz and ranged from 90-115 dB SPL, although the level was kept constant during a session. Comparison tones ranged from 2.5-113 kHz and were varied in amplitude. Baseline trials utilized comparison tones where the frequency was within ½ octave of the 10 kHz reference and the loudness relationship predictable. By introducing a small percentage of probe trials, where the loudness relationships were unknown, data were collected that were used in the first dolphin equal-loudness functions. The behavior was difficult to train, and the data collection time consuming. Dr. Mulsow then presented on current work being performed with a California sea lion and a dolphin to collect reaction times in a simple detection task and apply those to the development of equal-latency functions. For the sea lion, reaction times were collected for pure tones ranging from 0.125-32 kHz, and for the dolphin, they were collected for frequency-modulated tones ranging from 1.25-134.5 kHz. Reaction times were calculated as the time required to leave a test station or produce a burst pulse response, respectively. Preliminary equal-loudness functions derived from the equal-latency curves were presented. Dr.

Mulsow noted that more data at lower frequencies were needed, but that collection with other test subjects was underway.

Reviewer Comments

In human estimates of damage risk criteria to noise, we often use the A-weighting function, which attenuates low frequency sound (<1000 Hz sounds). This function, based on equal loudness contours for fairly low stimulus levels, represents the findings that low-frequency sounds are less damaging to hearing in humans. It would be inappropriate to assume that the risk of hearing damage in the various species of marine mammals (who, after all might have threshold audiograms that greatly differ from humans) would be closely related to humans.

There have been significant efforts to develop tests to assess equal loudness contours for marine mammals using equal latency contours. The rationale for these tests is that two sounds that are equally detectable will require equal time to respond. As sounds become more difficult to detect, the response times will slow, reflecting the more difficult detection and decision making process. A loudness matching test has also been conducted on a much more limited scale (i.e. a single dolphin), as there is more involved training and testing required in loudness matching tests. Data from the loudness matching study increases confidence in the studies that have used latency as “a measure” of perceptual loudness. At present there is little consensus regarding which frequency should serve as the baseline for comparison. In humans, a 1000-Hz tone served as the comparison, and different sound levels were used to generate different weighting curves. The A-weighting curve was based on 40-phon signals at 1000 Hz as the basis for comparison. The C-weighting curve is much flatter, and reflects the fact that at very high sound levels, there are fewer differences in perceived sound level. There is active discussion within the literature about whether to generate equal loudness contours based on quiet tones, at near-threshold levels, akin to A-weighting, or at higher supra-threshold levels, akin to C-weighing. The question initially appears to be academic, related more to increasing consistency of approaches between labs in order to improve consistency of protocols across species tested. The question is not simply academic, however, as the data are being used to argue for noise-hazard weighting functions for use in assessing risk to ocean-living animals.

Workshop attendees commonly referred to the M-weighting scheme identified by Southall et al. (2007) as the baseline against which changes should be compared. The Southall et al. (2007) M-weightings were generated in the absence of equal latency data and it is reasonable to suggest modifications based on new data. Some of the data presented at this workshop suggest the M-weighting will be overprotective (at least for porpoises) at low frequencies, and under-protective (at least for porpoises) at high frequencies. Overprotection is a problem for those that generate noise, as there is a real cost to equipment modifications needed to reduce noise output. In contrast to unnecessary financial costs incurred for noise abatement when there is inadequate discounting of energy at frequencies that “don’t matter,” there can be actual physical harm (in the form of hearing loss) when there is too much discounting of energy at frequencies that do matter in terms of auditory hazard. The most conservative approach from a hearing conservation perspective is not to apply any weighting, and the more weighting is applied, the greater the benefit to industry in that less abatement is required in order to meet the standards. This should be a high-priority area for continued research and investigation given

real-world impacts to both marine mammal hearing and the financial costs incurred due to mandated noise abatement procedures. Key questions are not only going to include the "best" weighting function, but also the total allowable noise exposure. At what point is a 100% noise dose reached? How is total noise dose going to be integrated? If every ship is regulated to provide no more than 100% percent noise dose, and 10 ships pass that area, the total accumulated exposure would be 1000%. Noise regulations for international ocean areas are potentially complex, and much more information is needed in order to assure that a frequency-weighting scheme is practical, useful, and worthwhile to incorporate and enforce. This should be a high priority topic as it directly influences abatement and risk.

Key questions that remain unanswered

1. What is the most appropriate weighting function?
2. What is the total allowable noise exposure for a given species/population? At what point is a 100% noise dose reached?
3. How will the total noise dose be integrated?
4. In the development of an auditory weighting function scheme applicable to a broad number of marine mammal species, what is the frequency that should be used for baseline comparisons?
5. What is the basis for clumping species under different weighting functions and what data exist to support this decision?

Recommendations

1. Investigate means by which the comparability between studies (e.g. equal loudness vs. equal latency) can be determined.
2. Strive for consistency among laboratories, at least with respect to fundamental factors such as the baseline frequency used for loudness comparisons.
3. It is possible that ABR latency/intensity functions or ABR/ASSR amplitude/intensity functions (using either absolute latencies/amplitudes, or the slopes of these functions) provide as good an estimate (or a better estimate) of loudness as do behavioral reaction time measures. It would be worthwhile to use several dolphins (and/or sea lions) with rigorous psychophysical training, and to compare psychophysical loudness measures with reaction time and with electrophysiological measures to determine if AEP measures can be used to predict loudness, and whether these electrophysiological measures are as good as, or better than, reaction time measures.

Auditory Evoked Potentials

Auditory evoked potentials (AEP) are small voltages produced by the brain in response to sound stimuli. The measurement of AEPs has been utilized for the measurement of hearing sensitivity in humans for decades, and has also been applied to numerous laboratory animals. The application of AEPs to the study of marine mammal hearing dates back over four decades (e.g. Bullock and Ridgway, 1972; Bullock et al., 1971), but until recently was largely limited to laboratory settings. Applications to determining auditory thresholds in marine mammals via AEP methods have advanced considerably over the last decade, largely due to hardware advancements and miniaturization that have allowed the techniques to be applied at non-laboratory marine mammal facilities and in the wild. The electrophysiological technique has greatly enhanced the ability to acquire audiometric information from larger numbers of certain marine mammal species as well as made feasible the testing of species that are rare or difficult to access except under stranding situations.

Summary of Presentations

Dr. Dorian Houser opened the session by summarizing AEP work conducted in cetaceans and in collaboration with Dr. James Finneran of the MMP. The collaboration was facilitated by Dr. Finneran's creation of the Evoked Response Study Tool (EVREST), which is a software package for the collection and analysis of AEP data. The software, which is incorporated into a ruggedized laptop system, provides a portable AEP system for use in field situations. Audiometry is performed with clicks and sinusoidal amplitude modulated signals, although arbitrary signal types can be generated. The system performs objective response detection and real-time analysis of evoked responses. The system has been used to record AEPs in 15 species of marine mammals, 13 species of new world monkeys, and several fish species. Dr. Houser then presented on the quantification of differences between behavioral audiograms and AEP audiograms collected in bottlenose dolphins. As with other odontocetes tested, signals were presented either in the direct field or through the use of a transducer coupled to the pan-region of the dolphin's lower jaw (the "jawphone"). The AEP audiograms predictably underestimated hearing sensitivity, particularly at the high and low ends of the hearing range, but reliably captured the audiogram shape. Through AEP methods, population variability in hearing has been quantified in bottlenose dolphins and has identified gender and age differences in the occurrence of presbycusis. Additional efforts demonstrated the similarity in audiograms across species and quantified relationships between the size of the test subject and the attenuation of the evoked response.

Dr. David Mann reported on the use of AEP methods to test the hearing of cetaceans, particularly those involved in stranding events. By monitoring the evoked response produced in response to clicks and SAM tones, Dr. Mann's group has tested the hearing of a number of species, including bottlenose dolphins, rough-toothed dolphins (*Steno bredoanensis*), Risso's dolphin (*Grampus griseus*), pygmy killer whales (*Feresa attenuate*), spinner dolphins (*Stenella frontalis*), short-finned pilot whales (*Globicephala macrorhynchus*), and a beaked whale (*Mesoplodon europaeus*). Notably, a number of the animals tested demonstrated severe hearing deficits, in some cases exhibiting no evoked response to the highest levels of sound that could be transmitted. Based on the acquisition of audiograms from a number of species, Dr. Mann proposed that the hearing ranges of small odontocetes could be differentiated between the

delphininae and the globicephalinae, with the latter having lower high frequency cut-offs to the range of hearing. Dr. Mann concluded with several case studies that highlighted the potential impact of hearing loss on free-ranging cetaceans (e.g. loss of foraging effectiveness) and the concern over the potential for ototoxic antibiotic use to damage hearing during the rehabilitation of stranded odontocetes.

Dr. Paul Nachtigall presented his laboratory's findings from evoked potential audiometry performed on wild-caught, stranded, and rehabilitating odontocetes. The audiometric approach utilized SAM tones and an estimate of threshold based on estimating the zero-crossing of a regression line fit to the linear region of the I/O function. The new species tested by the laboratory include a sperm whale (*Physeter macrocephalus*) infant, an infant Risso's dolphin, long-finned pilot whale (*Globicephala melas*), Blainsville beaked whale (*Mesoplodon densirostris*), pygmy killer whale, and striped dolphin (*Stenella coeruleoalba*). The audiogram for the infant Risso's dolphin demonstrated better sensitivity and a higher cut-off of the frequency range of hearing than was previously reported from an adult Risso's dolphin. The audiogram of the pilot whale showed a lower, high frequency cut-off than has been reported in smaller delphinids. The audiogram of the Blainsville beaked whale demonstrated a steep drop-off in sensitivity above 50 kHz. The region of best sensitivity (40-50 kHz) was consistent with the distribution of energy within the echolocation click produced by this species. When compared to other odontocete audiograms, the audiogram obtained from the striped dolphin suggested that the animal had hearing loss across a broad range of frequencies. Dr. Nachtigall concluded with a discussion of the need to continue collections on stranded marine mammals and to train people for rapidly responding to stranding situations in order to improve on data collection opportunities.

Dr. Klaus Lucke presented on efforts to perform evoked potential audiometry in harbor seals and grey seals (*Halichoerus grypus*). Studies were conducted at rehabilitation centers and in the wild. Seals were immobilized with ketamine and diazepam and AEPs were recorded through subcutaneous needle electrodes. Stimuli were presented in air either via headphones or through in-ear inserts, which were developed to try and minimize masking. Harbor seals were tested with tone pip stimuli from 1-22.4 kHz in ½ octave steps. Threshold estimation was performed via zero-crossing interpolation of a regression line fit to the linear region of the I/O function. Threshold determination was limited by background physiological noise and results were potentially masked. Nevertheless, the range of hearing was consistent with that previously reported for the species. Similar results were obtained in grey seals tested with tone pip stimuli, although the tone pips were more broadband than those used for the harbor seals. As with the harbor seals, the range of hearing was consistent with previous reports and there remained a concern for thresholds to be masked under the given test conditions. Dr. Lucke concluded with a discussion of future efforts, which included AEP and behavioral audiogram comparisons, underwater testing, TTS, cumulative exposure effects, and tests on other species, including arctic species.

Dr. Jason Mulsow presented on using the electrophysiological auditory steady-state response (ASSR) to test the hearing sensitivity of pinnipeds. Recent work conducted with the California sea lion and Steller sea lion (*Eumetopias jubatus*) compared behavioral and ASSR audiograms and showed good agreement between the two methods. As with other ASSR audiograms, the approach underestimates behavioral sensitivity and predictive power becomes progressively worse at the lowest and highest frequencies.

ASSR work with sea lions demonstrated the advantages of this method for making population-level sensitivity measurements and identified individuals with apparent hearing impairment. Steller and California sea lion audiograms were similar with respect to audiogram shape and variability in threshold estimates. Dr. Mulsow highlighted some of the limitations of ASSR work in pinnipeds, including challenges in estimating underwater hearing sensitivity, especially with regards to the extended frequency range of hearing exhibited by phocids when submerged versus when in air. Other issues included the challenge in trying to obtain evoked responses in large species, where size and differences in the auditory system make evoked potential audiometry difficult (e.g. elephant seals). Dr. Mulsow concluded with a brief discussion as to how audiometric information from ASSR testing can be used to address environmental issues related to underwater sound. It was noted that, although audiometric information has been obtained for a limited number of pinniped species, identification of easily accessible species as representatives of larger functional hearing groups may allow for conclusions to be made about the capabilities of more exotic species.

Dr. Dorian Houser concluded the session by providing an overview of how evoked potential methods are being delivered to stranding networks for the purpose of increasing the acquisition of hearing information from stranded cetaceans. The effort required pre-configuring the EVREST system for simplified use, building multiple ruggedized AEP systems, and providing training for individuals in the determination of AEP audiograms. Systems and training were given to the northeast, southeast and southwest regional stranding personnel. The pilot program, involving members of the International Fund for Animal Welfare, proved successful and generated audiograms for three Atlantic white-sided dolphins (*Lagenorhyncus acuta*), 17 common dolphins, and two harbor porpoises over the last three years. Collectively, the common dolphin audiograms demonstrated species variability and identified two animals with hearing deficits. Because of the success of the pilot, trained stranding personnel, in conjunction with members of the National Marine Mammal Foundation, were requested to assist in hearing tests of bottlenose dolphins captured as part of the Gulf of Mexico dolphin health assessments. More than 40 dolphins were assessed during the captures. Dr. Houser concluded with a description of a current effort to develop an AEP database to which data collected by stranding networks could be submitted. The database will eventually permit population-level audiometry to be assessed in species not under human care, and will provide a means for stranding network veterinarians to better determine the disposition of stranded animals which have had a hearing assessment.

Reviewer Comments

A large number of experimental auditory evoked potential (AEP) studies have been published in human subjects and other terrestrial mammals. Although a limited number of laboratories are currently investigating marine mammal AEPs, there is a substantial body of AEP data in marine mammals, but in a limited number of species. There have been rapid advances in the application of electrophysiological data collection protocols to marine mammals over the past 10 years; these techniques were first translated to dolphins some 30 years ago, but the literature was slow to accrue given a host of technical and methodological challenges.

Much of this work has focused on threshold estimation, and this work used both the auditory brainstem response (ABR) as well as the auditory steady state response (ASSR). There are challenges in recording

AEPs in sea mammals, e.g. electrodes can be shorted by conductive sea water and the mechanisms of hearing underwater are not well understood (leading to some spirited interchanges during the meeting about whether the jawphone represents bone-conduction stimulation). The development of a rugged, portable system with a user-friendly interface has greatly facilitated collection of new data, and protocols are now looking at more complex signals and responses and generating a wealth of new information. The system can be used in the field, can present stimuli via air conduction and via the jawphone, and not only collects but allows analysis of AEPs from marine mammals. In addition, the availability of systems that are capable of field deployment has created new opportunities to measure hearing in stranded animals and wild animals trapped for short periods of time. Opportunities are improved for captive animal testing as well, given that there is no training or extended behavioral testing required.

Some stimulation and recording parameters have not been standardized across marine mammal AEP laboratories, and the variations in these parameters at times makes the integration of information obtained across laboratories challenging. Also, AEPs are useful for investigations in numerous other paradigms than simply threshold estimation, and perhaps these AEP efforts in marine mammals can expand in new and interesting directions in future research studies. It might also be profitable to consider expanding the physiologic assessment of marine mammals to include areas not discussed in any detail during this meeting, such as otoacoustic emissions, acoustic reflectance and functional imaging.

The data from psychophysical studies remain critical, in that they are the only studies truly measuring hearing as a perceptual experience, and psychophysical techniques allow careful measurement of detection, recognition, and discrimination abilities. There is a tension between careful psychometric data collection which is slower and more expensive, and generates data for a small number of animals, and AEP testing, which is quicker and less expensive and can generate data from a large number of animals. Ultimately both models are needed. Psychophysical data can be readily used to validate the perceptual correlates of AEP data, particularly in the case of threshold measures, where there is a good correspondence between the lowest level signal that evokes a neural response and the lowest level signal for which a trained animal subject reports detection. Although more difficult to assess, supra-threshold functions might also be assessed both behaviorally and via AEPs using tools such as forward masking, oddball stimuli, or other tools adapted from the human or terrestrial animal AEP literature.

Key questions that remain unanswered

1. The observed variability in hearing thresholds within and across species is large. What actions can be taken to reduce measurement error so that the variability can be better interpreted?
2. How do neurophysiological correlates of perceptual phenomena correlate with behavioral studies using psychophysical procedures to address the same perceptual phenomena?

Recommendations

1. Continue the collection of data from larger numbers of captive animals, including captive-born animals at parks and aquaria that have a research/education mission. Age, drug history, and typical acoustic conditions should be relatively well documented for these captive animals.

2. Continue the collection of data from wild-caught animals to assess the extent to which hearing loss, including notched audiometric configurations that are consistent with a history of noise exposure, is a problem in ocean dwelling populations.
3. Continue the collection of data from stranded animals, building a database on hearing status in stranded animals, with the caveat that these data will not determine causal relationships; if hearing loss is present, it will not be possible to determine whether there was a pre-existing relationship, if pre-existing hearing loss contributed to the stranding, or if the hearing loss developed as a function of post-stranding stress and/or injury. As part of this latter mission, there will need to be careful monitoring of the test quality given that technicians will have variable skills and oversight.
4. Investigate the potential of standardizing procedures across laboratories, at least for commonly applied AEP methods.
5. Auditory evoked potentials can be used for much more than threshold estimation, and these non-threshold applications of AEPs should be expanded in marine mammals. Examples of such usages (not mentioned elsewhere in this report) include: 1) use of upward frequency-sweeping chirps as a means of characterizing traveling-wave delay in sea mammals; 2) evaluating peripheral tuning using tone-on-tone burst masking paradigms; 3) using high-pass masking techniques to evaluate whether traveling wave velocity is affected by peripheral hearing loss; 4) determining the optimal stimulus envelope (i.e. rise time) to elicit the ABR in marine mammals for a range of frequencies.
6. Most, if not all, marine mammal AEP studies have evaluated short latency AEPs (ABR, high-modulation frequency ASSR). The cortical responses, and especially the endogenous potentials, can be used to evaluate higher-level functions such as discriminating frequent from rare stimuli.
7. More within-animal (or at least within-species) comparisons of perceptual threshold to long-duration tones, ABRs to brief-duration tone bursts, and ASSRs to SAM tones are required. This is because differences in thresholds to long and brief duration tones are expected due to temporal integration, and in humans there are greater differences between perceptual and ABR/ASSR thresholds to low-frequency stimuli (as compared to high frequency stimuli). The relationship in threshold estimates across response measures (and stimuli) would enhance across-study threshold comparisons that used different threshold estimation approaches in marine mammals.
8. More within-species comparisons evaluating behavioral and electrophysiological responses to the three modes of marine mammal auditory stimulation are warranted: jawphone, air conduction, and underwater acoustic stimulation. Such comparisons might allow more across-lab comparisons of threshold estimation, and might shed light on whether jawphone stimulation can be considered a form of bone-conduction stimulation.
9. In pinnipeds, substantial information about the inner ear (including cochlear dynamics and outer hair cell function) could be gleaned by the use of otoacoustic emissions (OAEs), including: spontaneous OAEs, distortion product OAEs, transient OAEs, stimulus frequency OAEs, and contralateral suppression.
10. In recent years, in terrestrial animals (including humans), measures of middle-ear function have been obtained using acoustic reflectance/absorbance measures. These measures are able to

evaluate the transfer of acoustic power through the middle ear across a range of frequencies, and can be used as a sensitive measure of the acoustic reflex. Such measures might be profitably used in some marine mammals, such as pinnipeds.

11. Functional imaging studies (such as fMRI) are noninvasive measures useful to identify and evaluate those brain structures activated by acoustic stimuli. In marine mammals, such measures might, in some instances, be useful complementary studies (e.g. in cortical or endogenous evoked potential studies).
12. Mysticetes and other cetacean and pinniped groups are clearly missing or are under-represented in terms of data. A concerted effort should be made to get a good representative understanding of which functional hearing groups species fall into so that we can be confident in cross-species comparisons.

Anatomical Models

Modeling of the auditory system has a rich history in the human and laboratory animal world. Models range from the simple to the complex and can integrate the mechanical nature of the auditory system with psychophysical and/or electrophysiological measures of system function and performance. The difficulty in accessing many marine mammal species, particularly the mysticete whales, has been a major hurdle to determining the range of hearing and hearing sensitivity for most species. As a result, predictive modeling of auditory system function based on anatomical information has been relied upon as the primary means for predicting mysticete whale hearing. The auditory systems of marine mammals have anatomically evolved, sometimes extensively, to enable the effective detection, discrimination, recognition, and localization of underwater sound. The anatomical derivations of the auditory system present a challenge to understanding their function, particularly in species for which no psychophysical or electrophysiological assessments of the auditory system exist (e.g. no empirical hearing threshold measurements). Anatomical and functional information have been utilized from some available species (e.g. the bottlenose dolphin) to address model assumptions and predictions, but these have been largely restricted to animals accessible at marine mammal facilities. Nevertheless, until such time that hearing is directly measured on the mysticete whales, anatomical modeling will likely remain a focus for developing predictive hearing estimates.

Summary of Presentations

Dr. Darlene Ketten presented background on marine mammal auditory anatomy, compared it to land mammal data, and presented new functional models from her joint project with Dr. David Mountain. Hearing range models were shown for six Mysticetes (minke, blue, right, humpback, finback, gray whales); five beaked whales (Cuvier's, Blainville's, Sowerby's, Gervais's,True's), and live controls (porpoise, bottlenose dolphin, bats). Data were obtained from 29 specimens using multiple techniques: ultra-high resolution CT, MRI, microCT, Finite Element Models (FEM), Atomic Force Microscopy (AFM), dissection, and histology. The data show anatomically and biochemically distinctive fatty bundles connecting to the middle ear in both mysticetes and odontocetes. In odontocetes, these fats have sound speeds significantly lower than any other tissues (1420 to 1370 m/s test at 1-40 degrees C). In FEM multi-tissue models, they have the highest acoustic response pressures to incident plane wave sources. The inner ear hearing range models demonstrate beaked whales have a mid-range, high frequency auditory system, similar to bottlenose dolphins, with species peak sensitivities of 40 to 75 kHz and moderate to poor mid to low frequency sensitivity. Minke whale ear models indicate a low to mid frequency hearing range of 20 Hz to 33 kHz and peak sensitivities of 1-5 kHz. Most mysticete models demonstrated far lower ranges. Dr. Ketten concluded that this is consistent with their significantly greater radius of cochlear curvature (>8) and showed wave energy density distribution models that demonstrate low frequency energy propagation is far more effective in mysticete ears than in ultrasonic adapted odontocetes and bats.

Dr. David Mountain presented work from his laboratory modeling middle-ear function in cetaceans, which is a component of a longer term effort to predict hearing abilities in cetaceans for which

behavioral testing is not practical. The approach combines data obtained through measuring the mechanical properties of cetacean auditory structures with existing auditory models for terrestrial species. Verification of techniques is performed with control species (e.g. bottlenose dolphin and harbor porpoise) and then extended to other marine mammal species. The audiogram modeling approach treats the auditory system as a cascade of transfer functions (e.g. middle-ear transfer function and cochlear placement map). Transfer functions of the cochlea are based on basilar membrane stiffness measures, which have been measured in several cetacean species utilizing a customized system consisting of a needle coupled to a force transducer. The system is capable of measuring basilar membrane displacement and the restorative force applied to the needle following recovery from displacement. The middle-ear transfer function, which is believed to be the major factor affecting the low to mid-frequency hearing range of the audiogram, is determined via a combination of finite element modeling and bone elasticity measures of cetacean middle-ear structures with various assumptions regarding soft tissue properties.

Drs. Ted Crandford and Petr Krysl concluded the anatomical modeling session with a presentation of finite element modeling of acoustic pathways as determined from marine mammal CT data. Modeling efforts suggested the presence and importance of an internal acoustic pinna and gular pathway in Cuvier's beaked whale (*Ziphius cavirostris*). The work further suggested that the odontocete head operated like an acoustic antenna, delivering sound to the ears via multiple pathways. Modeling highlighted the anatomical relationship between terminal branches of the mandibular fat bodies and the tympano-periotic complex (TPC), as well as predicted the vibrational modes of the TPC based upon TPC structure. Head-related transfer functions (HRTF) were provided for the beaked whale and the bottlenose dolphin and the relevance of the HRTF to assessments of noise impacts was discussed. The authors concluded with a discussion of their "jawphone" simulations, which modeled a method of sound presentation to odontocetes used by a number of marine mammal bioacousticians. Results of the simulations led Drs. Cranford and Krysl to hypothesize that the jawphone creates abnormal or artificial jaw hearing, caused by localized "rattling" of the jaws by the hydrophone. They further hypothesized that the sound thus transmitted travels via sub-optimal pathways to the ear and that small variations in jawphone placement (on the order of an inch, or 30 mm) could result in amplitude differences in received level of 6-9 dB. The presenters suggested that this has implications for a large amount of data previously acquired with the jawphone methodology.

Reviewer Comments

One of the long-term goals of anatomical modeling is to make use of anatomical information to predict what hearing function might be expected in species that are difficult to access and/or assess. The models presented differ with respect to incorporation of different specific elements, such as skull structure, soft tissue, fatty layers, sinuses, and membrane stiffness. Several laboratories have used finite element models (or a similar technique) to model the middle ear and to try to estimate the threshold audiogram in marine mammals. There are a number of challenges in these modeling efforts. There are a large number of free variables, and there is no guarantee that a given solution is the one selected biologically by Mother Nature. Although an infinite number of models might explain a finite number of observations, convergence of evidence would be helpful in validating these modeling efforts.

It is critical that the anatomical models be validated. Some of the models have undergone limited validation, where models were used to predict hearing based on the anatomy/stiffness/etc., and those predictions were then compared against known hearing records obtained pre-mortem. More often, there are no functional data available from animals from which tissues were harvested, and the models are not explicitly validated. One very useful way of validating a model is to develop the model in one or more marine mammal species where good behavioral measures of threshold are available. A modeled audiogram that closely approximates behavioral or electrophysiological estimates of threshold would be compelling evidence that the model might reflect hearing reality. The value of these modeling efforts is, however, hampered by a very poor understanding of the role of the middle ear in odontocetes. Furthermore, there are a large number of free variables in the computational models of marine mammal hearing, with a limited number of known estimates of tissue factors such as stiffness. These modeling efforts are, then, at times little more than educated guesses

There is active debate about the "best" models and the "best" approach to modeling, and there are significant unknowns, such as the role of air spaces and pressurization of the air spaces at depth. Active management of air spaces while diving is an unknown possibility, with the potential that such active management would somehow protect the ear against pressure changes while diving, serve to preserve hearing at depth, or allow active manipulation of sensation level. These are important questions, with the potential for significant improvements in the understanding of basic biological function and endogenous protection strategies. Specific experimental models are not in place, and models may provide some suggestions as to potential impact of changes in air space pressure; ultimately, new empirical approaches will be needed to test model predictions. There is room for significant growth in this topic area, but the path forward and the optimal strategies remain relatively uncertain.

Key questions that remain unanswered

1. How faithfully do the predictions of anatomical models reproduce the known hearing characteristics of marine mammal species?
2. What will determine adequate validation?

Recommendations

1. Aggressive harvesting of appropriate tissues from animals who have died (e.g. from strandings), combined with investigation of their mechanical properties, should be performed (or continued, if currently underway). Over time, such information will help inform these models.
2. If the modeling efforts are aimed at predicting threshold, then these modeling efforts should begin with species of marine mammals that have behavioral or electrophysiological audiometric threshold data available across a wide range of frequencies. In these instances, the model can be validated against behavioral and/or electrophysiological estimates of threshold. The model, thus validated, can then be (cautiously) extended to marine mammal species that do not have such behavioral/electrophysiologcal audiometric threshold data.
3. It is critical that the roles of the peripheral auditory pathway and middle ears in cetaceans be better understood, including the role of anatomical specializations. Modeling efforts are fraught with difficulties in marine mammals without this understanding and both experimental models and means of empirically testing these models need to be developed.

Concluding Comments

The investment of resources into marine mammal hearing science has generated a wealth of knowledge about hearing in a variety of marine mammal species. Based on existing information from species that have been tested to date, anatomical information from cadavers, and models that infer function from structure, there are predictions about hearing function in a number of other species. Information about basic threshold sensitivity has been used to develop weighting functions that seek a compromise between protection of hearing function and noise abatement requirements. It is not a good investment of limited financial resources to abate noise that has no functional impact. Ongoing efforts to refine weighting functions are essential in developing noise abatement procedures that minimize cost to industry and government, while providing adequate protection to species that may be at risk due to noise exposure.

Some of the key questions that remain are the extent to which noise that is not harmful to hearing has other consequences, such as masking of biologically relevant information. Which noise, and at what levels, and for what species, are relatively unanswered questions, although there has been progress on these fronts. At a more fundamental level, there are critical unanswered questions about the point at which TTS becomes harmful. This is not a simple question. It incorporates not only how much TTS, but how long a duration of TTS is defined as harmful. Moreover, harm might be defined as overt hearing loss, or reduced function in a noisy environment, potentially compromising foraging or avoidance of predators. Questions regarding how weighting functions and their application are to balance protection with costs to noise producers remain: What percent of animals do we wish to protect? Every animal? Most animals? The average animal?

A number of additional factors hinder our understanding of marine mammal hearing. First, there is a robust national and international standardization of how air-borne sound is quantified and measured. This is not so true of water-borne sound. Improved underwater acoustics standardization, for both acoustics and bioacoustics usages, would be most helpful. Second, for both behavioral and electrophysiological measures, standardizing a hearing assessment protocol would make it easier to do across-lab comparisons, both within and across species. The goal is not to hinder innovation, but rather, when not a specific manipulation required to answer the experimental question, that certain standard specified stimuli (and, for electrophysiological studies, recording parameters) be used. Hearing threshold of one animal species with threshold estimation at 0.1 kHz, 1 kHz, 10 kHz, and 100 kHz behaviorally in 2 dB steps would be difficult to compare to threshold estimations (in the same, or different, species) obtained to 0.250 kHz, 4 kHz, 32 kHz, and 96 kHz obtained using four simultaneous ASSR frequencies in 10-dB steps. Finally, some observational studies during sound exposure have reported what appear to be aversive responses by the marine mammals to intense acoustic stimuli, which have been interpreted as the sounds being unpleasantly loud. It is equally possible that these responses are due to somatosensory or vestibular stimulation, and have nothing to do with an unpleasantly loud auditory sensation.

There is some existing interaction between scientists working with marine mammals and scientists working with terrestrial mammals, and continued interactions and new collaborations should be

encouraged and supported. Some questions may be 'easier' to answer in species other than marine mammals, with smaller numbers of marine mammals to be tested subsequent to the development of a significant knowledge base in other species. Protocols have been developed in terrestrial animals already for many questions, and there are "lessons learned" that can be shared through discussion and accessing the available literature. This is true not only for TTS, masking, equal latency, and AEPs, but also for echolocation, where there was little evidence of any existing interactions between those working with bats and those working with dolphins or other echolocating marine mammals. In-depth reviews, including comparisons/contrasts of echolocation in bats and dolphins, co-authored by experts on each, might be an excellent starting point, and could be an end-product of new workshops sponsored by groups such as ONR and the Joint Industry Program.

Recommendations

1. The marine mammal hearing community should work to develop national (ANSI) and perhaps international (IEC/ISO) standards related to underwater acoustics/bioacoustics. External financial support of this standardization effort would likely make this work move forward more quickly.
2. The marine mammal hearing community should sponsor a conference where a set of guidelines for marine mammal auditory evoked potentials are developed through a consensus process. Preferred frequencies, optimal level step size, preferred envelope characteristics and modulation rates, recording parameters, if selected sagely, could strongly promote across-experiment (across-laboratory) comparisons.
3. Fostering interactions between the terrestrial hearing community and the marine mammal hearing community is warranted. The current isolation of these two research communities could lead to less than fully informed experimental study design and execution. Such interactions (e.g. by the marine mammal community inviting those doing related terrestrial animal work to their meetings, and marine mammal researchers attending meetings mostly attended by terrestrial animal researchers) would be beneficial to both groups.
4. Those doing electrophysiological studies of marine mammal hearing should seek collaborations with investigators outside of the sea mammal community.
5. In studies where aversive responses to loud sound have been observed, care must be taken to assure that the stimuli are not in the acoustic near field, where water displacement and thus somatosensory stimulation is possible.
6. Studies of vestibular function in marine mammals are warranted. It is clear, even in terrestrial animals, that intense sounds are able to stimulate the vestibular end organ. It is thus likely that intense sounds can also stimulate the vestibular system in marine mammals. Vestibular stimulation can be disorienting, and might pose a threat to an individual animal. It is not possible to separate aversive responses to loud sounds from aversive responses to vestibular stimulation until experimental methods are developed to stimulate and record vestibular responses in marine mammals.

References

Au, W.W.L. 1993. The Sonar of Dolphins. Springer-Verlag, New York. 227 pp.

Branstetter, B.K., J.S. Trickey, K. Bahktiari, A. Black, H. Aihara, and J.J. Finneran. 2013. Auditory masking patterns in bottlenose dolphins (*Tursiops truncatus*) with natural, anthropogenic, and controlled noise. *J. Acoust. Soc. Am.* 133:1811-1818.

Bullock, T.H., and S.H. Ridgway. 1972. Evoked potentials in the central auditory system of alert porpoises to their own and artificial sounds. *Journal of Neurobiology*. 3:79-99.

Bullock, T.H., S.H. Ridgway, and S. Nobuo. 1971. Acoustically evoked potentials in midbrain auditory structures in sea lions (Pinnipedia). *Zeitshchrift für Vergleichende Physiologie*. 74:372-387.

Finneran, J.J., D.A. Carder, C.E. Schlundt, and S.H. Ridgway. 2005. Temporary threshold shift (TTS) in bottlenose dolphins (*Tursiops truncatus*) exposed to mid-frequency tones. *J. Acoust. Soc. Am.* 118:2696-2705.

Finneran, J.J., R. Dear, D.A. Carder, and S.H. Ridgway. 2003. Auditory and behavioral responses of California sea lions (*Zalophus californianus*) to single underwater impulses from an arc-gap transducer. *J. Acoust. Soc. Am.* 114:1667-1677.

Kastak, D., and R.J. Schusterman. 1996. Temporary threshold shift in a harbor seal (*Phoca vitulina*). *J. Acoust. Soc. Am.* 100:1905-1908.

Kastak, D., B.L. Southall, R.J. Schusterman, and C.R. Kastak. 2005. Underwater temporary threshold shift in pinnipeds: effects of noise level and duration. *J. Acoust. Soc. Am.* 118:3154-3163.

Nachtigall, P.E., J. Pawloski, and W.W.L. Au. 2003. Temporary threshold shifts and recovery following noise exposure in the Atlantic bottlenosed dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* 113:3425-3429.

Workshop Agenda

Tuesday Sept. 10 Temporary threshold shift (TTS)

0830-0850	Introduction and instructions
0850-0910	James Finneran – Review of TTS experiments at the Navy Marine Mammal Program: Tonal exposures
0910-0930	Paul Nachtigall – Measuring low frequency hearing shifts in the bottlenose dolphin
0930-0950	Colleen Reichmuth – Review of threshold shift studies in pinnipeds
0950-1010	Ronald Kastelein – Temporary hearing threshold shifts (TTS) in harbor porpoises and harbor seals
1010-1030	Break
1030-1050	Klaus Lucke – TTS thresholds in harbour porpoises
1050-1110	James Finneran - Review of TTS experiments at the Navy Marine Mammal Program: Impulsive exposures
1110-1200	Group Discussion
1200-1330	Lunch
1330-1410	Group Discussion (cont.)

Masking

1410-1430	Christopher Clark – Human impacts on the ocean acoustic environment
1430-1450	Christine Erbe – Acoustic masking
1450-1510	Break
1510-1530	Brian Branstetter – Critical ratios and comodulation masking release in bottlenose dolphins (*Tursiops truncatus*)
1530-1550	Kane Cunningham – Pinniped hearing in complex acoustic conditions
1550-1700	Discussion

Wednesday Sept. 11 Hearing and echolocation

0830-0850	Paul Nachtigall – Hearing sensation changes when a warning predicts a loud sound in the false killer whale
0850-0910	Magnus Wahlberg – Harbor porpoise hearing during echolocation
0910-0940	James Finneran – AEP measurements during echolocation at the Navy Marine Mammal Program

Weighting functions and related research

0940-1000	James Finneran – Use of auditory weighting functions in Navy acoustic impact analyses
1000-1020	Colleen Reichmuth – Evaluation of equal latency measures for application to noise exposure weighting functions in pinnipeds
1020-1040	Ronald Kastelein – Equal-latency contours in harbor seals and harbor porpoises
1040-1100	Jason Mulsow – Auditory weighting functions in sea lions and dolphins
1100-1200	Discussion

1200-1330 Lunch

Auditory evoked potentials (AEP)

1330-1350 Dorian Houser – Evoked potential audiometry in odontocete cetaceans
1350-1410 David Mann – AEP audiometry in wild dolphins
1410-1430 Paul Nachtigall – Measuring the Hearing of cetaceans using evoked auditory potentials
1430-1450 Klaus Lucke – In-air hearing thresholds in harbour and grey seals
1450-1510 Break
1510-1530 Jason Mulsow – Auditory evoked potential methods in pinnipeds
1530-1550 Dorian Houser – Stranding responder involvement and a national marine mammal AEP database
1550-1700 Discussion

Thursday Sept. 12 Anatomical models

0900-0920 Ketten – AFM to FEM: Comprehensive models of hearing in critical species for mitigating sound impacts
0920-0940 Mountain – Modeling middle-ear function
0940-1020 Krysl and Cranford – Modeling sound propagation in marine mammals
1020-1040 Break
1040-1130 Discussion
1130-1300 Lunch
1300-1400 Discussion of Future Research Directions
1400-1700 Reviewer discussion (*reviewers only*)

Submitted Participant Biographies

Brian Branstetter, Ph.D. - Brian Branstetter specializes in the sensory systems of humans and marine mammals. He currently holds a research scientist position with the National Marine Mammal Foundation where he investigates sensory and cognitive capabilities of marine mammals, with an emphasis on conservation and noise.

Christopher Clark, Ph.D. - Christopher Clark is the Imogene P. Johnson Senior Scientist in the Bioacoustics Research Program (BRP) at the Cornell Lab of Ornithology and in the Department of Neurobiology & Behavior at Cornell University. Christopher has a long history of successfully working at the interface between science, applied engineering, industry, regulations and NGOs in order to quantify and mitigate potential impacts of human activities on marine mammals. Christopher's current research areas include acoustic monitoring of large whale distributions, behaviors, and movements relative to environmental factors and man-made activities using a variety of passive acoustic detection, classification, localization and tracking technologies. He is also engaged in collaborative research efforts integrating physical oceanographic and biological productivity measures, aerial surveys, genetic and photo-ID data, and acoustic detections. He leads the development and application of distributed autonomous listening systems and near-real-time automatic acoustic detection systems to quantify the spatio-temporal occurrence of the endangered whales.

Ted Cranford, Ph.D. - Ted Cranford's research focuses on the functional morphology of biosonar in toothed whales and, more recently, hearing in baleen whales. The hallmark of his research is question-driven innovation, combining modern technology with traditional anatomic tools to develop new methods that allow investigation of the structure-function complex in marine organisms. These research innovations have led to significant discoveries. One seemingly insurmountable hurdle was to collect anatomic data from the broad size spectrum of marine mammals. The solution: Use an industrial CT scanner for large cetaceans heads and bodies, one such specimen weighed more than half a ton. This size-independent scanning capability is unique and has provided answers to questions that were previously intractable. The most important innovation implemented by Dr. Cranford and Dr. Petr Krysl (UCSD), is the application of engineering principles and analysis tools to simulate how ambient sounds interact with the anatomy of marine organisms. These "finite element modeling" tools have led to a new understanding for how whales hear. Dr. Cranford has published more than 30 peer reviewed papers, including 10 major papers. One of them, in the Journal of Morphology, is the most cited paper in that journal since 1996. Dr. Cranford excels at explaining complicated material to diverse audiences and received the Excellence in Science Communication Award from the Society for Marine Mammalogy in 2009.

Kane Cunningham - Kane Cunningham is a Ph.D. student working at the Pinniped Cognition and Sensory Systems Laboratory at the University of California, Santa Cruz. He first began studying marine mammals as a M.Sc. student in the Department of Electrical and Computer Engineering at Boston University, where he worked on modeling of communication masking in baleen whales. Kane's current research

focuses on the perception of complex stimuli and noise in pinnipeds, with the aim of furthering understanding of how anthropogenic noise effects these animals.

Christine Erbe, Ph.D. – Christine Erbe accidentally landed in marine bioacoustics in 1994 and has never looked back. Having grown up in Germany's coal belt, she relished Canada's sea breeze, yet discovered she got terribly seasick, hence chose to train captive beluga whales for masked hearing experiments. She worked for the Canadian Government (Fisheries & Oceans) from 1994-2001 on underwater noise, effects on marine mammals and noise regulation. She worked as a private consultant performing bioacoustic impact assessments until she joined JASCO Applied Sciences as Director of Australian Operations in 2006. In 2011, she couldn't resist the temptation to get back into academia, and became Director of the Centre for Marine Science & Technology at Curtin University in Perth, Western Australia. Christine's interests are underwater sound (ambient, anthropogenic and biological), sound propagation and noise effects on marine fauna.

James Finneran, Ph.D. - James Finneran is a research scientist with the US Navy Marine Mammal Program, at the Space and Naval Warfare Systems Center, Pacific, where he studies marine mammal hearing and echolocation, and the effects of noise on marine animals. He has a Ph.D. in Mechanical Engineering from The Ohio State University and has published over 75 peer-reviewed journal articles related to bioacoustics and hearing in marine animals. Dr. Finneran was awarded the Acoustical Society of America's R. Bruce Lindsay award in 2002, the Department of the Navy Top Scientists and Engineers Award in 2007, and the Chief of Naval Operations Environmental Award in 2010. At present, Dr. Finneran serves as an Associate Editor (Animal Bioacoustics) for the Journal of the Acoustical Society of America.

Dorian Houser, Ph.D. – Dorian Houser is the Director of Conservation and Biological Research at the National Marine Mammal Foundation. Dorian's research covers multiple aspects of marine mammal physiology, behavior and bioacoustics and he has published more than 90 peer-reviewed research articles and book chapters covering these topics. He was co-recipient of the Strategic Environmental Research and Development Program (SERDP) "Project of the Year" award in 2000 and received the R. Bruce Lindsay award from the Acoustical Society of America in 2007. He currently serves as the Vice-Chair of the Accredited Standards Committee (ASC) S3/SC 1, Animal Bioacoustics and is a member of ASC S3/WG2 Bioacoustics standards working group. Dorian has had significant involvement addressing marine mammal issues of concern to the Navy and has been involved in the development of numerous Navy environmental impact statements and environmental assessments involving marine mammals.

Ronald Kastelein, Ph.D. – Ronald Kastelein is the owner of SEAMARCO. Since 2005, SEAMARCO has conducted research with seals, harbor porpoises and various sea fish species. The studies resulted in more than 160 publications in scientific journals and books and covered a large variety of disciplines (anatomy, physiology, behavior, acoustics, biomechanics, sensory systems, animal medicine, animal welfare, psychophysics). For the last 20 years, SEAMARCO has been funded by private enterprise and the governments of the Netherlands (Ministry of Infrastructure and Environment, Ministry of Economic Affairs, and Ministry of Defense) and the UK (COWRIE) for applied research on prevention of bycatch of

harbor porpoises in fisheries and on the influence of underwater anthropogenic noise on marine mammals (windmill turbines at sea, acoustic underwater data communication systems, naval sonar systems, detonations). During the last 10 years, the government of the Netherlands has regularly used SEAMARCO's services to evaluate reports of technical institutes and ecological consultants companies. SEAMARCO regularly reviews manuscripts for scientific journals and also regularly evaluates research proposals of research institutes to governments and charities. In 2011, Ronald Kastelein became a Fellow of the Acoustical Society of America for his acoustic research with marine mammals.

Darlene Ketten, Ph.D. – Darlene Ketten currently holds joint appointments as a Senior Scientist in Biology at Woods Hole Oceanographic Institution and as Assistant Clinical Professor in Otology and Laryngology at Harvard Medical School. She is also the Director of the WHOI Computerized Scanning and Imaging Facility (http://csi.whoi.edu) and is an Adjunct Professor of Biology at MIT. Dr. Ketten has over twenty-five years' experience in high resolution radiology, auditory physiology, and head and neck pathology. She has published over 100 peer reviewed articles and case studies as well as specialist reviews and chapters on imaging, diagnostics of auditory system pathology, and hearing mechanisms. Her research comprises microscopic to gross imaging techniques for both humans and marine organisms, including whales, seals and sea lions, fishes, and sea turtles and focuses on modeling of hearing and mechanisms of hearing loss, with an emphasis on determining underwater hearing abilities of marine mammals and imaging of head and neck trauma and disease.

Petr Krysl, Ph.D. – No biography provided.

Klaus Lucke, Ph.D. – Klaus Lucke began his career as a private biological consultant and commenced as a researcher at the Science & Research Centre Westcoast (FTZ), University of Kiel, in 1998. His research focused on the impact of anthropogenic underwater sound on the hearing system of marine mammals, including development and testing of acoustic mitigation techniques, underwater acoustic measurements, marine mammal telemetry, and studies on the habitat use of marine mammals. Klaus was interim leader of the Department of Ecology of Birds and Marine Mammals at the FTZ and led the institute's Acoustics Research Group. Since 2011, he has been employed as a senior scientist at the Institute for Marine Resources and Ecosystem Studies (IMARES, Wageningen University), the Netherlands, where his primary focus is on biological and technical aspects of bioacoustics.

David Mann, Ph.D. - David Mann has extensive experience in the field of bioacoustics, starting with undergraduate training at Cornell University. He performed his doctoral work on sound production by damselfish at Johnston Atoll near Hawaii and for his post-doctoral research he studied hearing in fishes at the University of Maryland with Dr. Arthur Popper. Following his post-doc he spent several years working at Tucker-Davis Technologies (TDT), which manufactures signal processing workstations for hearing and neurophysiology research. During this time he became an adjunct scientist at Mote Marine Laboratory where he worked with Dr. Bill Tavolga on ultrasonic hearing in menhaden. In 2000, he joined the faculty at the University of South Florida College of Marine Science where he studied hearing and sound production in fishes and marine mammals. David formed Loggerhead Instruments based in

Sarasota, FL to develop and market acoustics research instrumentation. He is currently developing a line of open source animal tags to provide precise details of animal movement.

David Mountain, Ph.D. – David C. Mountain was a member of the Medical Engineering Department at Massachusetts General Hospital, Boston, from 1968 to 1970. He joined the Boston University faculty in 1979, where he is now Professor of Biomedical Engineering. His current research emphasis is on experimental and theoretical studies in auditory biomechanics, neuroinformatics, biomimetic acoustic signal processing, and the impact of anthropogenic sound on humans and cetaceans. Dr. Mountain is a fellow of the American Institute for Medical and Biological Engineering.

Jason Mulsow, Ph.D. - Jason Mulsow is currently a Research Scientist at the National Marine Mammal Foundation in San Diego, California. His research focuses on electrophysiological and behavioral measures of hearing in marine mammals. He is currently conducting research examining electrophysiological and behavioral correlates of loudness perception in bottlenose dolphins and California sea lions, as well as the auditory electrophysiology that underlies echolocation in dolphins. He is a member of the Acoustical Society of America and the Society for Marine Mammalogy. He publishes his research in and acts as a peer reviewer for journals including the Journal of the Acoustical Society of America, the Journal of Experimental Biology, and Marine Mammal Science.

Paul Nachtigall, Ph.D. - Paul Nachtigall is the Director of the Marine Mammal Research Program and is a Researcher Level 5 (full professor equivalent) within the School of Ocean Science and Technology, Hawaii Institute of Marine Biology. He has decades of research in the bioacoustics of marine mammals, particularly the use of echolocation by dolphins, assessing auditory evoked potential for hearing research, and the impact of anthropogenic sound on marine mammals. He has published numerous scientific papers and is the co-editor of a number of books on marine mammal bioacoustics. He is an Honorary Member of the European Association of Aquatic Mammals and is a Fellow of the Acoustical Society of America. Paul also served as the editor of the journal *Aquatic Mammals* and was a Charter Member and Past President of the Society for Marine Mammalogy.

Colleen Reichmuth, Ph.D. – Colleen Reichmuth is a Research Scientist at the University of California Santa Cruz. Trained primarily as an animal behaviorist, she has spent the past 20+ years conducting research in the areas of comparative cognition, bioacoustics, and behavioral ecology. Colleen currently heads the Cognition and Sensory Systems Laboratory, based at UC Santa Cruz's Long Marine Lab, where resident seals, sea lions, and sea otters are trained for participation in studies examining how these amphibious marine mammals acquire and process information. She has extensive experience with laboratory and field methods addressing how marine mammals produce, perceive, and are affected by sound, and expertise in operant studies of discrimination learning and emergent behavior. While her research program emphasizes psychophysical methods, Colleen also has worked in the areas of electrophysiology, brain imaging, and controlled exposure studies to gain a better understanding of auditory function in marine mammals.

Magnus Wahlberg, Ph.D. - Magnus Wahlberg is an Associate Professor at the University of Southern Denmark, specializing in measuring sound production and hearing abilities of marine animals. He lives in Kerteminde and works at the Marine Biological Research Center there, which together with the public institution Fjord&Bælt, houses harbour porpoises in a harbour facility for scientific research and public outreach.

Submitted Reviewer Biographies

Robert Burkard, Ph.D. – Robert Burkard is the Professor and Chair, Department of Rehabilitation Science, University at Buffalo. His research interests include calibration, auditory electrophysiology (in particular, auditory evoked potentials), vestibular/balance function/dysfunction, functional imaging and aging. His professional interests include calibration standards and health care economics. Robert has served as Vice-Chair and Chair of American National Standards Institute (ANSI) S3 Bioacoustics, which is responsible for U.S. audiometric standards development. He is currently the Chair of the working group that is responsible for developing an ANSI auditory evoked potential standard. He has served as the Editor for the American Journal of Audiology and currently serves as a member of the American Speech-Language-Hearing Association's (ASHA) Health Care Economics Committee. He was named ASHA Fellow in 2005 and received the Honors of the Association in 2011.

Colleen Le Prell, Ph.D. - Colleen Le Prell is an Associate Professor in the Department of Speech, Language, and Hearing Sciences at the University of Florida, where she also directs the Center for Hearing Research. She has received research funding from the National Institutes of Health, several foundations, and she has led industry-sponsored contracts. Current research programs in her laboratory at the University of Florida include an effort to identify and prevent the progression of biochemical processes that lead to cell death in the inner ear, as well as collaborative translational research programs directed at prevention of noise-induced hearing loss. Colleen served as Director of Education for the National Hearing Conservation Association from 2012-2014.

Sofie Van Parijs, Ph.D. - Sofie Van Parijs has worked on passive acoustic research from the poles to the Tropics for over 19 years. She worked as a postdoctoral scientist at the Norwegian Polar Institute, James Cook University in Australia and Cornell University before moving to the Northeast Fisheries Science Center (NMFS/NOAA) in 2004. At NMFS, she is the program leader for the passive acoustic research program within the Protected Species Branch (http://www.nefsc.noaa.gov/psb/acoustics/), which consists of postdoctoral scientists, Ph.D. students, research analysts and summer interns. She has published over 60 papers in international journals and represents NMFS in a wide range of fora within the US and internationally. Her expertise in marine bio-acoustics has addressed questions on behavioral ecology, distribution, abundance, long term monitoring, mitigation and effects of ocean noise on marine mammals. This has given her extensive experience collecting data with archival, real time acoustic recorders and autonomous vehicles.

Acknowledgments

The workshop and report were jointly sponsored by Navy Living Marine Resources, the Office of Naval Research, and the National Oceanic and Atmospheric Administration - National Marine Fisheries Service. Funding and logistical support were facilitated by the Naval Postgraduate School and the Naval Facilities Engineering Command.