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Pinniped hearing in a changing acoustic environment

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PINNIPED HEARING IN A RAPIDLY CHANGING ACOUSTIC ENVIRONMENT

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PINNIPED HEARING IN A RAPIDLY CHANGING ACOUSTIC ENVIRONMENT

Kane Cunningham

ABSTRACT

Increasing levels of anthropogenic noise in the world's oceans are a matter of concern for the conservation of pinnipeds (seals, sea lions, and walruses). Sound from noise-generating human activities—such as marine construction, oil exploration, and shipping traffic—may alter the lives of pinnipeds in a variety of ways. For example, anthropogenic noise can interfere with an individual's ability to detect calls from conspecifics or the sound of an approaching predator; and loud, aversive sounds can cause animals to abandon preferred habitats. Laboratory studies of hearing in pinnipeds over the past 50 years have expanded knowledge of the basic auditory capabilities of certain species, and data from these studies are currently being used to predict how specific noise-generating activities may affect wild animals. However, predicting the effects of anthropogenic noise is a complex process, and certain knowledge gaps must be addressed before accurate predictions can be made. First, it is unclear how well standard hearing data—which are generated using simple, synthetic sounds—can predict pinniped auditory sensitivity to spectrally and temporally complex anthropogenic sounds. Second, hearing sensitivity data above 80 kHz are scarce for most species, which is problematic given the recent proliferation of high-frequency, high-energy acoustic marine technologies such as commercial sonar and recreational fish finders. The research described in this dissertation addresses these two knowledge gaps using behavioral hearing experiments with trained pinniped subjects combined with mathematical models of hearing and sound propagation.

The data presented here improve the ability of regulators to predict the effects of anthropogenic noise on pinnipeds and indicate future research directions. The reported sensitivity data for complex sounds show that certain spectral and temporal features can significantly alter detectability. Comparison of detection thresholds for complex stimuli to predictions from hearing models based on standard hearing metrics showed differences of up to 8 dB in both quiet and noisy conditions. Such discrepancies indicate the need for future research into how complex features influence the detectability of underwater sound. High-frequency sensitivity data for two seals and one sea lion show that these animals can detect underwater sound at frequencies well above their traditional high-frequency hearing limits, with all three subjects able to detect tonal signals centered at 180 kHz. The shapes of the sensitivity profiles for all subjects indicate that the idea of a traditional high-frequency hearing limit is problematic for underwater pinniped listeners, a fact that regulators must take into account.

DEDICATION

For my father, Kelly Cunningham, who taught me the value of books, learning, skepticism, and independent thought.

Thank you for giving me the intellectual self-confidence I needed to complete this work.

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America: “Auditory detection of ultrasonic coded transmitters by seals and sea lions” (Cunningham, KA, Hayes, SA, Wargo Rub, AM, and Reichmuth, C, 2014, vol. 135), and “Auditory sensitivity of seals and sea lions in complex listening scenarios” (Cunningham, KA, Southall, BL, and Reichmuth, C, 2014, vol. 136). Co-author Dr. Colleen Reichmuth directly supervised the research that forms the basis for this dissertation. As co-authors on the former publication, Drs. Sean Hayes and Michelle Wargo Rub provided expert knowledge and advice regarding the use of acoustic tags on spawning salmon. As co-author on the later publication, Dr. Brandon Southall provided expert advice on experimental design as well as editorial comments on an earlier draft of the article. As the primary author on these publications and the author of this dissertation, I (Kane Cunningham) designed all experiments, collected all experimental data, and was in charge of writing and revising all drafts.

Last but certainly not least, I would like to thank the animals that participated in these studies: Sprouts, Ronan, and Tunu, this dissertation would not have been possible without your enthusiastic participation.

GENERAL INTRODUCTION

The superfamily Pinnipedia is contained within the order Carnivora. All extant pinniped species come from one of three families within this superfamily: the Phocidae (true seals), Otariidae (sea lions and fur seals), and Odobenidae (walruses). Modern pinnipeds are thought to have evolved from a common amphibious ancestor that lived in the early Oligocene (Rybczynski *et al*., 2009). As such, their sensory biology is the result of approximately 30 million years of the selective pressures of a semi-aquatic lifestyle.

Aquatic environments present significant obstacles to the sensory systems of terrestrial mammals due to the different physical properties of air and water. The ear is a particularly interesting case. In air, the three bones of the mammalian middle ear act as an impedance matching device allowing acoustic energy to be efficiently transferred from the air surrounding the head, to the fluid contained within the cochlea. However, because the middle-ear bones are suspended within an air-filled cavity, the middle ear amplifier loses its effectiveness under water due to the inverse impedance matching problem of transferring energy from the water surrounding the head, to the air within the cavity. This is why terrestrial mammals, including humans, have poor underwater hearing abilities (Wainwright, 1957; Brandt & Hollien, 1967). Marine mammals, in contrast, tend to have superior underwater hearing relative to marine fish and invertebrates (Fay, 1988), indicating that their mammalian ears have adapted to the challenges of underwater energy transmission. This is not entirely surprising given that acoustic energy in the marine environment is efficiently transferred over large distances relative to electromagnetic energy within the visible spectrum. Animals that can access the information contained within acoustic energy channels will have an advantage over those that cannot.

Pinnipeds are known to utilize sound for social interactions, and most species likely rely on sound to avoid predators, detect prey, and navigate in three-dimensions. The importance of sound to pinniped species means that any changes to their acoustic environment could affect individual fitness and survival. The acoustics of the world's oceans have indeed been changing rapidly over the past century due to increases in noise-generating human activities such as shipping, marine construction, and seismic exploration (Richardson *et al*., 1995; NRC, 2003). Comparisons of historic ocean ambient noise levels with current data indicate that such activities are making the ocean a noisier place (Andrew *et al*., 2002; McDonald *et al*., 2006). The extent to which these changes will impact pinniped life histories remains uncertain; however, cases of observed effects can be cited in a variety of marine mammal species (Southall *et al.*, 2007), demonstrating a need for improved understanding.

In order to predict the effects of anthropogenic noise, we must understand how pinnipeds receive and process sound in their environment; that is, we must understand how these animals hear. Pinniped underwater hearing has been of interest to researchers since at least the 1950's, and multiple behavioral hearing studies have examined the basic auditory capabilities of pinnipeds. These studies have largely focused on measuring standard comparative hearing metrics using simple sounds that are easily replicated in the laboratory. The most common of these metrics are auditory detection thresholds in quiet conditions as a function of frequency (audiograms), and auditory detection thresholds in the presence of white masking noise as a function of frequency (critical ratios and critical bandwidths). Such studies indicate that pinnipeds can detect underwater sound at low sound pressure levels across a broad range of frequencies (e.g., Møhl, 1968; Kastelein *et al*., 2009; Reichmuth *et al*., 2013; Sills *et al*., 2014), and that the sharpness of frequency tuning within their auditory systems is on par with or exceeds that of representative terrestrial mammals (e.g., Southall *et al*., 2003; Sills *et al*., 2014). While hearing data are available for only a subset of extant pinniped species, consistent trends can be identified across families. Most notably, phocids seem to have a broader frequency range of underwater hearing than otariids, and it has been hypothesized that the phocid ear is more adapted to a aquatic environment than the otariid ear (Hemilä, S., 2006; Reichmuth *et al*., 2013). Comparison of hearing data across pinniped species with data for other marine organisms suggests that the ears of all pinnipeds have adapted to the acoustic challenges of underwater sound reception over time.

While laboratory hearing experiments have greatly increased understanding of the basic capabilities of hearing in pinnipeds, knowledge gaps still exist. First, there is uncertainty as to how hearing data generated in a laboratory setting, using carefully controlled and relatively simple stimuli, can be generalized to the wide range of complex sounds that pinnipeds encounter in their marine habitats. Further, underwater sensitivity measurements have mostly been restricted to frequencies 80 kHz and below, but the increased presence of high-frequency acoustic marine technologies such as commercial sonars and recreational fish finders (Hildebrand, 2004) has made understanding pinniped hearing at higher frequencies of critical importance. The aim of the research described here was to address these two knowledge gaps, and in the process, create a better understanding of pinniped hearing and how it may be affected by the presence of anthropogenic noise.

This dissertation is divided into three chapters, presented in the chronological order in which the research was conducted. Each chapter describes a separate study, composed of one or two experiments. All of the studies in this dissertation were based on behavioral hearing experiments conducted under water with trained animals, which has proven to be the most accurate method for measuring auditory sensitivity in pinnipeds (Mulsow *et al*., 2011). Each chapter also contains a modeling component, used either to predict hearing capabilities from existing audiometric data, or to help resolve the physiological mechanisms shaping observed patterns of auditory sensitivity. All of the experiments described in this dissertation were designed to improve understanding of how anthropogenic noise may affect wild pinnipeds in complex natural environments.

Chapter 1 introduces the difficulties inherent to predicting which types of anthropogenic sounds will affect pinnipeds while addressing a practical hearing question relative to a specific acoustic technology. In 2011, our research laboratory was approached by biologists from the National Marine Fisheries Service who were using acoustic fish tags to track survivorship rates of salmon in the San Francisco Bay Delta and the Pacific Northwest. These biologists were concerned that resident pinnipeds, which naturally prey upon spawning salmon, could detect the acoustic tag outputs and were selectively predating tagged fish, thereby skewing their survivorship data. This was unexpected because the tag outputs were at high frequencies and were of short duration; baseline hearing data seemed to indicate that pinnipeds would not be able to detect such tags at meaningful distances. The experiments described in Chapter 1 were designed to investigate this issue and demonstrated that both a California sea lion and a harbor seal could likely detect tag outputs at large distances on the order of hundreds of meters. These results underline the issues inherent in extrapolating from laboratory hearing data to actual marine sounds, as well as the lack of understanding of underwater hearing at high frequencies.

The two knowledge gaps introduced in Chapter 1 are addressed individually and systematically in Chapters 2 & 3. The experiments in Chapter 2 were designed to test how well baseline hearing data can predict detection thresholds for spectrally and temporally complex sounds. Baseline hearing data are measured in the laboratory using simple sounds, such as pure tones and white noise. Such sounds can be replicated in a variety of testing environments making it possible to compare hearing data across studies and species. Natural sounds, in contrast, tend to be much more complex and baseline data therefore may not reliably predict sensitivity in natural listening scenarios. The wide variability in natural sounds makes it impossible to measure sensitivity for even a small portion of existing sound types. This study approaches this problem by isolating three complex features commonly found in animal vocalizations and ambient noise: frequency modulation (FM), amplitude modulation (AM), and the presence of multiple harmonics. Results from Chapter 2 indicate that baseline hearing data predict auditory capabilities relatively well in certain complex listening scenarios, but rather poorly in many others. The findings demonstrate that, in order to generate accurate and meaningful predictions of noise effects on wild pinnipeds, understanding of how auditory capabilities differ for complex sounds must be improved.

The experiments described in Chapter 3 were designed to test underwater hearing at ultrahigh frequencies, that is, frequencies presumed to be above the species specific high-frequency hearing limit. The results for three subjects from three different species show that pinniped underwater audiograms are characterized by two distinct slope-regions on the high-frequency end, an initial steep slope followed by a much shallower slope. The presence of the shallower slope-region at ultrahigh frequencies represents a significant deviation from typical hearing patterns for terrestrial mammals and complicates the idea of a traditional high-frequency hearing limit for these animals. This fact must be taken into account when estimating the potential effects of rapidly-proliferating high-energy, high-frequency anthropogenic noise sources. This chapter also presents evidence that the physiological mechanisms that limit high-frequency hearing may be different from previously thought.

Taken as a whole, the three chapters of this dissertation describe and address some of the challenges inherent in understanding how acoustic changes to the world’s oceans may affect pinnipeds. The results of these studies expand the current state of knowledge of pinniped hearing in a focused manner so that anthropogenic noise in the marine environment can be properly managed. While the findings of this research program are intended to improve the present state of noise management, they also indicate future directions for research in pinniped hearing by revealing in which cases extrapolation from current knowledge leads to inaccurate predictions of sensitivity to human-generated marine sound. Continued research effort along these lines is needed to ensure the conservation of wild pinnipeds in a rapidly changing acoustic environment.

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CHAPTER 1

Auditory detection of ultrasonic coded transmitters by seals and sea lions

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ABSTRACT

Ultrasonic coded transmitters (UCTs) are high-frequency acoustic tags that are often used to conduct survivorship studies of vulnerable fish species. Recent observations of differential mortality in tag control studies suggest that fish instrumented with UCTs may be selectively targeted by marine mammal predators, thereby skewing valuable survivorship data. In order to better understand the ability of pinnipeds to detect UCT outputs, behavioral high-frequency hearing thresholds were obtained from a trained harbor seal (*Phoca vitulina*) and a trained California sea lion (*Zalophus californianus*). Thresholds were measured for extended (500 ms) and brief (10 ms) 69 kHz narrowband stimuli, as well as for a stimulus recorded directly from a Vemco V16-3H UCT, which consisted of eight 10 ms, 69 kHz pure-tone pulses. Detection thresholds for the harbor seal were as expected based on existing audiometric data for this species, while the California sea lion was much more sensitive than predicted. Given measured detection thresholds of 113 dB re 1μPa and 124 dB re 1μPa respectively, both species are likely able to detect acoustic outputs of the Vemco V16-3H under water from distances exceeding 200 m in typical natural conditions, suggesting that these species are capable of using UCTs to detect free-ranging fish.

I. INTRODUCTION

Ultrasonic coded transmitters (UCTs) are acoustic tags commonly used in fisheries research. These tags emit a series of short duration, high-frequency pulses containing a signature by which spatially distributed receivers can identify individual tags. In order for receivers to be effective, they must be able to detect signals from tags at relatively long distances. The fact that underwater high-frequency sounds attenuate quickly with distance from the sound source, combined with constraints on receiver placement, necessitates a high sound pressure level (SPL) for tag outputs. Tag acoustic source levels (SPL at 1 m) typically range from 140-165 dB re 1μPa. Tag outputs consist of a series of 8-9 discrete, 10 ms pulses with a total duration of approximately 3 seconds; tags are programmed to emit a single output at a variable delay, usually between 30-90 seconds. The discrete pulses that compose a UCT output consist of a sinusoidal signal in the frequency range of 50-400 kHz, depending on the tag type and model. Because UCTs are relatively small and inexpensive, they have been widely used for studying fish life history parameters such as behavior, migration patterns, and survivorship.

On the West Coast of the United States, researchers commonly employ UCTs to conduct large-scale survivorship studies on vulnerable, economically important salmonid species. In California alone, thousands of migratory fish are instrumented with 69 kHz tags annually (Moustahfid *et al.*, 2011). A fundamental assumption of these life history studies is that survivorship rates for instrumented fish are similar to those of untagged fish. However, this assumption is inconsistent with recent observations of higher mortality in juvenile salmon implanted with active acoustic tags relative to those implanted with passive integrated transponder (PIT) tags, as well as to those implanted with sham acoustic tags having physical characteristics similar to active tags, but producing no output (Wargo-Rub, 2012a; Wargo-Rub, 2012b). One possible explanation for this discrepancy has been termed the "dinner bell" hypothesis: marine mammals that can hear acoustic tag outputs use this information to selectively predate tagged fish, thereby skewing survivorship data (Bowles *et al.,* 2010).

While UCT outputs are designed to be above the frequency range thought detectable by most fish, these tags might still be detectable by some marine mammals, including seals, sea lions, and odontocetes. A recent report by Bowles (2010) showed that harbor seals reacted with apparent aversion to 69 kHz acoustic tags, suggesting that the outputs of at least some UCTs are salient to this species. This finding is consistent with pre-existing hearing data for pinnipeds. Using behavioral techniques with captive pinnipeds, Møhl (1968a) determined that a harbor seal could reliably detect an 180 kHz pure-tone with a sound pressure level of 133 dB re 1μPa, and Schusterman *et al.* (1972) reported that a California sea lion could detect a 64 kHz pure-tone with a sound pressure level of 145 dB re 1μPa. Considering these hearing thresholds relative to typical UCT frequencies (50-400 kHz) and source levels (140-165 dB re 1μPa), it becomes apparent that harbor seals should detect all but the highest frequency, lowest SPL UCTs at considerable distances, while

California sea lions should detect only the lowest frequency, highest SPL UCTs at close range, if at all.

Bowles *et al.* (2010) estimated detection ranges for pinnipeds and small cetaceans to certain UCTs. In order to accomplish this, transmission loss for a tag output was directly measured as a function of distance in a nearshore marine environment. This transmission loss function was then used to determine the distance that a UCT output could travel before its SPL fell below the auditory threshold of a hypothetical listener. Auditory thresholds for UCT outputs were derived from the available literature on detection of high-frequency signals by marine mammals, as well as from related studies on auditory summation and pulsatile (brief) stimuli. This source-path-receiver analysis indicated that harbor seals should detect a 69 kHz tag output with a source level around 140 dB re 1µPa at a minimum distance of 25 m and a maximum distance of 200 m. A similar analysis indicated that the 69 kHz tag output would likely be inaudible to a California sea lion at distances greater than 1 m. Note that these calculations assume that the ambient noise in the frequency range of the UCT output is at least one critical ratio lower than the detection threshold. This is a safe assumption given that ambient noise in the habitats of interest (i.e. large rivers where resident pinnipeds prey on spawning salmonids) tends to decrease with increasing frequency, to the point where the spectrum level of the noise is much lower than pinniped detection thresholds (Vračar and Mijić, 2011).

The aim of the present study was to directly measure pinniped hearing capabilities at 69 kHz, a common operational frequency for UCTs, creating a basis for detection range estimates. Auditory threshold measurements were made for two common predators of salmonids on the West Coast of the United States: the Pacific harbor seal and the California sea lion. To ensure adequate understanding of the influence of signal frequency and duration on signal detectability, hearing thresholds were measured for a trained individual from each species to an extended (500 ms) narrowband 69 kHz stimulus, a brief (10 ms) narrowband 69 kHz stimulus, and a series of eight 10 ms, 69 kHz pure-tone pulses recorded directly from a Vemco V16-3H UCT. These auditory data were used to empirically refine the earlier predictions by Bowles *et al.* (2010), and to test the viability of the “dinner bell” hypothesis with direct hearing measurements.

II. METHODS

A. Experimental design

This study was designed to test the ability of a trained harbor seal and a trained California sea lion to detect the acoustic output of a Vemco V16-3H UCT. The Vemco V16-3H projects a series of eight 10 ms pulses over an interval of approximately 3.5 seconds. Each pulse comprises a 69 kHz pure tone within a 10 ms envelope including a brief linear ramp up and down, and has an SPL of 165 dB re 1 μPa at 1 m.

Auditory measurements were conducted in three matched phases with each phase employing a unique stimulus. The three stimuli, in the order tested, were:

Treatment 1) a 500 ms, 10% linear frequency-modulated (FM) sweep centered around 69 kHz, Treatment 2) a 10 ms, 2% FM sweep centered around 69 kHz, and Treatment 3) the recorded output of the tag itself. Narrowband FM sweeps were used for synthesized signals because these types of stimuli result in detection thresholds similar to pure-tone signals, but tend to exhibit less spatial variation in SPL when presented in a reverberant testing environment (Finneran and Schlundt, 2007; Kastelein *et al.,* 2002). A duration of 500 ms was used for Treatment 1 so as to be greater than the estimated temporal integration time at 69 kHz (Kastelein *et al.*, 2010; Holt *et al.*, 2012), resulting in detection thresholds that represent maximum sensitivity at this frequency.

The stimuli used in Treatments 1, 2 and 3 had rise times of 25 ms, 5 ms, and approximately 0.1 ms, respectively. Because rise times and signal duration can affect signal bandwidth and lead to spectral energy at frequencies distant from the center frequency, received signals for all three treatments were analyzed across the functional range of hearing for these species. No low-frequency energy was detected above the noise floor of the test environment for the range of signal SPLs used during behavioral testing. Received spectrum levels, relative to ambient noise levels in the testing environment, are depicted for each treatment in Fig. 1.

The experimental progression from Treatment 1, to Treatment 2, to Treatment 3 was chosen for two reasons. First, both animal subjects had prior experience working with 500 ms, 10% FM stimuli as used in Treatment 1. Therefore, this experimental design allowed the subjects to transition from the most familiar type of stimulus to the least familiar. Second, because different features of the stimulus changed between treatments, this design allowed for a better understanding of which aspects of the signal influenced changes in threshold. That is, the difference between Treatments 1 and 2 is mainly duration, while the difference between Treatments 2 and 3 is mainly the number of pulses presented. Hence, any observed threshold change between the first two stimuli is likely due to decreased duration, and similarly, any threshold change between the second two stimuli is likely due to the number of available pulses.

B. Test subjects

Two subjects participated in this study: a 24 year-old male harbor seal identified as *Sprouts* (NOA0001707), and a 3 year-old female California sea lion identified as *Ronan* (NOA0006602). Both subjects had multiple years of experience participating in psychophysical hearing studies and both have measured audiograms that demonstrate species-typical hearing (Reichmuth *et al.*, 2013). Testing was conducted at Long Marine Laboratory in Santa Cruz, California.

C. Testing procedure

Animal testing took place at a depth of 1 m in an outdoor circular, concrete test pool (7.6 m diameter, 1.8 m depth) filled with natural seawater at temperatures between 10°C to 15°C. Signals were projected from an ITC 1042 hydrophone mounted on PVC pipe and suspended into the test pool. Outgoing signals were bandpass filtered with a Krohn-Hite 3364 analog filter, attenuated by 10 dB using a TDT PA5 programmable attenuator, and amplified using a Hafler P1000 amplifier when necessary. Analog to digital conversion was performed through a National Instruments USB-6259 data acquisition system at a sampling rate of 500 kHz. Signals were calibrated and the received sound fields mapped using a Reson 4032 hydrophone and custom software (HTP; Finneran, 2003). HTP software was also used to generate the FM sweep stimuli used in Treatments 1 and 2. The tag stimulus used in Treatment 3 was recorded without environmental influence by coupling the Vemco V16-3H to an ITC 1042 hydrophone *via* ultrasound gel in air. This method effectively eliminated multipath reflections and produced a recording representative of the projected tag signal with a high signal-to-noise ratio.

Daily signal calibration was performed at the position of the center of the subject's head during testing. The calibration routine tested linear attenuation of the signal and mean error across the desired range of SPLs. For all stimuli, SPL was calculated relative to the root-mean-square pressure over the duration of the stimuli, except in the case of Treatment 3, where the SPL was calculated over the duration of the first pulse within the eight-pulse sequence. During daily calibration, received signals were visually inspected in both the time and frequency domains for temporal distortions as well as for any energy at frequencies other than 69 kHz. For each treatment, SPLs were measured at 24 positions within a 3 x 3 x 3 cubic grid encompassing the position of the subject's head during testing. Points on the grid were separated by 7 cm, making the outer dimensions of the grid 14 cm x 14 cm x 14 cm. The criterion for acceptable spatial variability in received sound fields was +/- 3 dB at all measured positions; if this criterion was not met, the transducer was moved until a suitable configuration was obtained.

The psychoacoustic procedures were the same for all treatments. A standard go/no-go procedure was used. First, the subject swam down to a listening station, which provided a fixed location for the animal to rest its head, and waited for an underwater light to come on indicating the beginning of the trial. The light would remain on for a four-second trial duration, during which a signal might be presented at any time. The subject had been previously trained to move from the listening station to touch its nose to a target positioned at the left of the station when a signal was presented. Correct responses occurred when the subject touched the target after a signal had been presented, but before the trial interval ended (termed a "hit"), or when the subject remained positioned at the station for the full trial interval when no signal (i.e. an output of 0 volts) was presented. Correct responses were marked by a brief buzzer sound followed by a fish reward delivered by a trainer who was blind to the trial condition. No reward was given and the subject was recalled to the surface when it either touched the target when no signal had been presented ("false alarm"), or when it failed to touch the target when a signal had been presented ("miss").

Signal-present and signal-absent trials were presented in a pseudorandom sequence with a maximum run length of four for either trial type. On signal-present trials, HTP was used to adjust the outgoing signal voltage (and, consequently the received signal SPL) in between trials using an adaptive staircase procedure

(Cornsweet, 1962). Testing began at an SPL approximately 20 dB above threshold, estimated from either pre-existing audiometric data or preliminary performance on the task. The stimulus amplitude was decreased in 4 dB steps following each correct detection, until the subject failed to detect a signal. The amplitude was then increased in 4 dB steps until the subject successfully detected the signal, at which point the amplitude was decreased by 2 dB steps until the subject again failed to detect the signal. This 4 up/2 down procedure was continued until the subject demonstrated consistent performance through five consecutive hit-to-miss transitions, after which the subject was given several supra-threshold level trials that were approximately 20 dB above threshold. A stable response bias was maintained by adjusting the ratio of signal-present to signal-absent trials in between sessions as necessary. As a result, the proportion of signal-absent trials within a session varied between 35% and 50%.

D. Threshold analysis

From each session, thresholds were estimated in terms of SPL by taking the mean of the last five hit-to-miss transitions. The criterion to finish testing for a given treatment was three sessions with estimated thresholds within 3 dB of one another, all with false alarm rates greater than 0% but less than 30% for the trials encompassing the last five hit-to-miss transitions. Probit analysis (Finney, 1947) was used to fit a Gaussian distribution to the proportional response data. The cumulative distribution function of this Gaussian distribution is equivalent to the psychometric function.

Thresholds were defined as the SPL corresponding to the 50% detection probability as determined by taking an inverse prediction from this psychometric function.

III. RESULTS

For synthesized stimuli (Treatments 1 and 2), as well as for the stimulus recorded directly from the VEMCO V16-3H (Treatment 3), received signals contained no significant energy outside of the 69 kHz frequency region within the range of SPLs used in this study. Further, for brief stimuli (Treatments 2 and 3), energy occurring at times beyond the duration of the projected signal due to reflections was minimal. A small amount of energy due to acoustic reflection appeared between 15-25 ms after the initial projection of the signal; however, the energy contained in this interval was 10 dB less than the energy contained within the 0-10 ms period. Therefore, the signals received by the subject were similar to those that would be received from an acoustic tag in a free-field.

For Treatment 1, the calculated detection threshold for the harbor seal was 106 dB re 1 μPa, and for the California sea lion it was 112 dB re 1 μPa. Because Treatment 1 employed a narrowband stimulus with duration much greater than the expected temporal integration time (Kastelein *et al.*, 2010; Holt *et al.*, 2012), these results can be construed as data points in an audiogram. Fig. 2 depicts these data points along with pre-existing audiogram data for these subjects, as well as for other individuals from these species. The threshold for the harbor seal agrees well with the available species data in this frequency range and appears to fall within the region of the audiogram where sensitivity is decreasing rapidly with increasing frequency, i.e. the high-frequency roll-off. There is limited pre-existing data in this frequency range for the California sea lion; however, the threshold determined in this study is 33 dB lower than the lone existing data point in this range (64 kHz, Schusterman *et al.,* 1972) and appears to fall beyond the high-frequency roll-off region of the audiogram.

For Treatment 2, the calculated threshold for the harbor seal was 115 dB re 1 μPa, and for the California sea lion it was 127 dB re 1 μPa. For the stimuli used in Treatments 1 and 2, both narrowband FM sweeps with center frequencies of 69 kHz, but with durations of 500 ms and 10 ms respectively, the difference in threshold was calculated to be +9 dB for the harbor seal and +15 dB for the sea lion.

For Treatment 3, the calculated threshold for the harbor seal was 113 dB re 1 μPa, and for the California sea lion it was 124 dB re 1 μPa. The primary difference between Treatments 2 and 3 was the number of pulses within the employed stimuli (1 and 8 respectively), and the difference in thresholds between these treatments was calculated to be -2 dB for the harbor seal and -3 dB for the California sea lion.

Measured thresholds for both subjects and all three treatments are summarized in Table I, along with threshold estimations based on Bowles *et al.* (2010) for comparison. False alarm rates for each of the three Treatments were between 10% and 15% for both subjects.

By combining the calculated detection thresholds for the Vemco V16-3H (Treatment 3) with a propagation model, detection ranges can be estimated for both species relative to the output of this tag. This is accomplished using the equation:

$$\mathrm{DT} = \mathrm{SL} - 15\log(r) - \alpha r \quad (1)$$

where DT is the detection threshold, SL is the tag source level, r is the distance from the source in meters, and α is the attenuation coefficient in dB/m. The $15\log(r)$ term serves as an estimate of the spreading loss and is halfway between spherical and cylindrical spreading. The αr term accounts for loss of energy due to absorption. The value of α is based on the Francois-Garrison model of acoustic absorption and is a function of frequency, temperature, depth, salinity and pH (Francois and Garrision, 1982a & 1982b). For any given distance, the transmission loss estimated by this model will be higher than that estimated by the model of Bowles *et al.* (2010), which was developed based on direct transmission loss measurements of a 69 kHz Vemco tag. Consequently, the detection ranges generated by Equation 1 are conservative relative to empirical measurements of transmission loss.

Two sets of input values were used to calculate to values for α. The first set was selected to represent a large riverine habitat such as the Columbia River and is particularly relevant for this study as this is the type of environment where pinnipeds may selectively predate tagged fish. The second set of values was chosen to represent a mid-latitude, coastal marine environment, where acoustic tags are used on a variety of fish species (*e.g.* Zimmerman *et al.*, 2013). Chosen environmental input parameters and the corresponding values for α are summarized in Table II.

Using the propagation model from Equation 1 with the empirical auditory detection threshold of 113 dB re 1 μPa for the harbor seal, and a source level of 165 dB re 1 μPa for the VEMCO V16-3H, yields detection ranges of 933 m and 501 m in the hypothetical riverine and coastal marine environments respectively. Similarly, the auditory threshold of 124 dB re 1 μPa for the California sea lion yields detection ranges of 352 m and 236 m for the riverine and marine environments. For comparison purposes, detection ranges for the VEMCO V16-3H were also calculated using seal and sea lion auditory thresholds estimated from Bowles *et al.* (2010) combined with Equation 1. Both sets of detection ranges—those based on the estimated detection thresholds and those based on the directly measured detection thresholds—are summarized in Table III.

IV. DISCUSSION

When compared with relevant existing data, the auditory detection thresholds determined in this study for extended (500 ms) and brief (10 ms) 69 kHz stimuli were as expected for the harbor seal, but much lower than expected for the California sea lion. Treatment 1, which produced standard audiometric data for the relatively long duration 69 kHz signal, confirmed the sensitivity of a harbor seal at this high frequency. The measured threshold was 106 dB re 1 μPa, similar to the available threshold measurements of 106 dB re 1 μPa at 64 kHz (Møhl, 1968a) and 106-109 dB re 1 μPa at 63 kHz (Kastelein *et al.,* 2009). Data in this high-frequency range are much scarcer for the California sea lion because the upper functional hearing limit for this species has generally been considered to be around 32 kHz (Mulsow *et al.*, 2012) and testing has rarely occurred at frequencies higher than this. The calculated threshold for the current study was 112 dB re 1 μPa, 33 dB lower than the one previously existing data point in the frequency range of interest (64 kHz, Schusterman *et al.*, 1972). This 33 dB difference in absolute sensitivity is the major factor driving the large discrepancy in the predicted Vemco V16-3H detection threshold for the California sea lion estimated from Bowles *et al.* (2010) versus the empirical threshold from this study.

One known contributor to the higher threshold reported by Schusterman *et al.* (1972) versus the threshold determined for the sea lion in this study is a methodological difference in the manner in which thresholds were calculated. In the present study, thresholds were determined at the 50% correct response rate, where in Schusterman *et al.* (1972), thresholds were determined at the 75% correct response rate. However, based on the psychometric function provided by Schusterman *et al.* (1972), this contribution accounts for a difference of approximately 5 dB, a small portion of the total discrepancy (see Reichmuth & Southall 2012 for a complete discussion of differences in psychophysical methods). How to account for the remaining discrepancy is unclear, but given the limited number of subjects tested thus far, individual variation in absolute sensitivity at high frequencies should be considered a potentially important factor.

In addition to potential differences in high-frequency hearing between individuals within a species, there are documented differences in the auditory capabilities of otariid (sea lion and fur seal) versus phocid (true seal) species. Particularly, the functional hearing ranges of phocids tend to include a broader range of frequencies relative to otariids, the largest differences occurring at the upper frequency range of hearing (Reichmuth *et al.*, 2013). However, the shape of the underwater audiograms of both phocids and otariids share certain characteristics at higher frequencies. For both, when frequencies increase beyond a critical point, sensitivity decreases dramatically with increasing frequency (known as the high-frequency roll-off). This critical point occurs around 32 kHz for the California sea lion, and around 40 kHz for the harbor seal (*e.g.* Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013).

A critical point followed by a dramatic high-frequency roll-off is characteristic not only of pinniped underwater audiograms, but also of the aerial audiograms of many terrestrial mammals, including humans (Masterson *et al.*, 1969). However, pinniped underwater audiograms deviate from the standard mammalian aerial template at frequencies more than one octave above this critical point. At these ultra-high frequencies, the rate of decrease in sensitivity relative to the increase in frequency is much less, i.e. the slope of the audiogram is shallower (Møhl, 1968a;

Schusterman *et al.*, 1972). This phenomenon can be seen in the audiometric data summarized for harbor seals and California sea lions in Fig. 2. For harbor seals, sensitivity decreases dramatically with increasing frequency in the 40-80 kHz range, but after 80 kHz, sensitivity decreases less rapidly with increasing frequency. For California sea lions, the initial sharp decrease in sensitivity occurs in the 32-50 kHz range, but in the two studies that tested at higher frequencies (Schusterman *et al.*, 1972 and this study), this decrease appears much less dramatic above 50 kHz. It is this pattern of decreased slope at ultra-high frequencies that allows for the audibility of sufficiently high level sounds well above the nominal high-frequency hearing limit under water. Interestingly, a similar pattern holds for the audiograms of human subjects listening *via* a bone vibrator directly coupled to the skull leading to the ability of these subjects to detect tones at frequencies well above the expected upper frequency limit of 20 kHz (Corso, 1963). Further, this ability to detect high-intensity tones at frequencies above 20 kHz is also found in humans immersed in an under water sound field (Deatherage *et al.*, 1954), suggesting similar mechanisms for humans listening *via* a bone vibrator, humans listening under water, and pinnipeds listening under water.

While ultra-high frequency tones can be heard under water at high intensities, pitch discrimination is either severely impaired or non-existent within the frequency range where the slope of the audiogram levels off in both pinniped and human listeners (Schusterman & Moore, 1978; Møhl, 1968b; Deatherage *et al.*, 1954). This suggests that although the end of the tonotopic map on the basilar membrane has been reached, energy is somehow still reaching hair cells near the basal end of the membrane. Because energy at these frequencies does not seem to stimulate the basilar membrane during conventional aerial hearing, it has been hypothesized that a pathway other than the traditional in-air route (through the meatus and middle ear) is involved in the transmission of energy to the cochlea for underwater hearing at these ultra-high frequencies. This phenomenon is known as bone conduction and a variety of mechanisms have been proposed (see Hood, 1962 for review of bone conduction in humans; Repenning, 1972 for discussion of possible mechanisms in pinnipeds). Further research is needed to determine the precise mechanism of hearing at these ultra-high frequencies. However, it is apparent that when underwater hearing is involved, the fact that the frequency of a signal is above the nominal high-frequency hearing limit for a species is insufficient to rule out the possibility that the signal is detectable, as demonstrated by the much lower than expected detection thresholds for the California sea lion in all three treatments of the current experiment.

It is important to note that the lower than predicted threshold for the sea lion listening for a 500 ms narrowband signal with a rise time of 25 ms (Treatment 1) minimizes the potential relevance of any low-frequency energy resulting from the brief rise time and duration of the amplitude envelope of acoustic tag outputs. Bowles *et al.* (2010) speculated that a low-frequency click associated with the envelope of VEMCO tag pulses may be audible to sea lions when the 69 kHz signal is not. However, the experimental design used here shows that not only is the detection threshold for the California sea lion listening for the recorded tag stimulus (Treatment

3) around 30-35 dB lower than expected, so is the sea lion threshold for the long duration stimuli with a 25 ms rise time (Treatment 1). This indicates that increased sensitivity at 69 kHz is the major factor in the discrepancies between the observed and predicted thresholds for all three treatments, not a low-frequency click. This observation is entirely consistent with the observed absence of low-frequency energy for all three stimuli at the SPLs used in this experiment, indicating that any low-frequency energy associated with the envelope was below the noise floor of the testing environment.

In order for seals and sea lions to effectively use high-frequency acoustic cues from UCTs as an aid in foraging, these cues must be detectable at ecologically relevant distances. The calculated Vemco V16-3H detection ranges for the harbor seal based on this study are similar to the detection ranges calculated based on pre-existing data. In both cases, data indicate that the harbor seal would be able to detect this tag at distances on the order of hundreds of meters in both marine and riverine environments. This suggests that, for this species, signals from the tag are cues that could increase foraging success. For the California sea lion, the estimated detection ranges are much greater when based on data from this study versus previously existing data. Based on previously existing data, the maximum detection range would be only 10 m for this tag. It is unclear whether this close-range information would be useful in foraging. In contrast, the results of the present study indicate that detection ranges for the sea lion would exceed 200 m in both environments, indicating that these signals may indeed be useful as foraging cues.

In the absence of direct measurements of signal propagation in the environment of interest, it should be noted that the detection ranges calculated here are rough estimates. However, when compared with empirical measurements of transmission loss of a similar Vemco 69 kHz UCT by Bowles *et al.* (2010), the propagation model used in this study is conservative. It should also be noted that, given the large discrepancy in sea lion detection thresholds for stimuli in the 64-69 kHz range between this study and Schusterman *et al.* (1972), a considerable degree of individual variation in sensitivity at ultra-high frequencies above the nominal high-frequency hearing limit may exist. It is possible that the data reported here for a young, female subject are not typical of all California sea lions.

In summary, this study confirms the viability of the "dinner bell" hypothesis relative to the hearing capabilities of both harbor seals and California sea lions. Prior to this study, existing data showing low auditory sensitivity around 69 kHz in California sea lions implied that these animals could likely not detect UCT outputs at distances that would be useful in foraging. In contrast, this study indicates that high-frequency sensitivity, and consequently detection ranges for 69 kHz UCTs, may be much greater than previously thought, presumably due to bone conduction of high-frequency sounds under water. The sensory capabilities of harbor seals and California sea lions, combined with the fact that both harbor seals and California sea lions are creative and opportunistic foragers, make it likely that these animals exploit signals from UCTs when foraging. This would logically lead to the selective predation of acoustically tagged fish, and might explain the anomalies in survivorship data for many vulnerable and economically important fish species.

These findings are also relevant to recent studies deploying high-frequency transceivers (tags that act as both transmitters and receivers of ultrasonic coded signals) on free-ranging pinnipeds to track encounters with conspecifics or other tagged species (Lidgard *et al.*, 2012; Hayes *et al.*, 2013). Our results indicate that the output of a UCT transmitter physically attached to a seal or sea lion would be perceptually quite loud and, as such, could alter the normal behavior of the tagged animal as well as other animals within the vicinity. Future research should focus on seal and sea lion hearing capabilities in the 100-400 kHz frequency range so as to better understand the capacity of these animals to detect a wide variety of UCTs, as well as on the ability of these animals to localize tag outputs in three-dimensional aquatic environments.

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	Detection threshold at 69 kHz (dB re 1 μPa)	Threshold increase for 10 ms signal (dB)	Threshold decrease for multiple pulses (dB)	Threshold for VEMCO V16-3H (dB re 1 μPa)
Harbor seal	106[1]	+9[1]	- 2[1]	113[1]
	109-112[2,3]	+ 6-10[4,5]	-1[6]	114-121[7]
California sea lion	112[1]	+15[1]	-3[1]	124[1]
	145[8]			150-154[7]

TABLE I. Directly measured and estimated auditory detection thresholds for an extended (500 ms) 69 kHz tone, the increase in threshold for a brief (10 ms) 69 kHz tone, the decrease in threshold when multiple (8) pulses are available, as well as detection thresholds for a Vemco V16-3H UCT. Estimated values (those not from this study) and the corresponding references are from Bowles *et al.* (2010).

[1] This study

[2] Møhl, 1968a

[3] Kastelein *et al.*, 2009

[4] Terhune, 1988; 64 kHz

[5] Kastelein *et al.*, 2010; 40 kHz

[6] Turnbull and Terhune, 1993

[7] Calculated by combining estimates of 69 kHz sensitivity, duration effect, and multiple pulse effect from existing literature (columns 1, 2, and 3). For this calculation, estimates of duration effect and multiple pulse effect were based on harbor seal studies for both the harbor seal and sea lion.

[8] Schusterman *et al.*, 1972; 64 kHz

	Frequency (kHz)	Temperature (°C)	Depth (m)	Salinity (psu)	pH	α (dB/m)
Riverine[1]	69	12	30	10	8	0.008
Marine[2]	69	14	100	35	8	0.023

TABLE II. Input values used to estimate the attenuation coefficient (α) for a representative riverine environment and a marine environment. Riverine values were approximated for the Columbia River and marine values for a typical nearshore, mid-latitude environment.

[1] Temperature and pH values estimated from Fuhrer *et al.* (1996). Salinity values are heavily dependent on location as well as tides. Conservative values resulting in a larger value for α were chosen for salinity and depth.

[2] Temperature, salinity and pH estimated from Kennish (2001)

	Environment	Detection Range based on Bowles *et al.* (2010)	Detection Range based on this study
Harbor seal	Riverine	478-867 m	933 m
	Marine	299-473 m	501 m
California sea lion	Riverine	0-10 m	352 m
	Marine	0-10 m	236 m

TABLE III. Estimated detection ranges for the VEMCO V-16 3H UCT for harbor seals and California sea lions based on the auditory detection thresholds estimated from Bowles *et al.* (2010), or on the detection thresholds directly measured in this study. Detection range estimates are given for representative riverine and nearshore marine environments using Equation 1, with the absorption coefficients provided in Table 2, and a tag source level of 165 dB re 1 μPa.

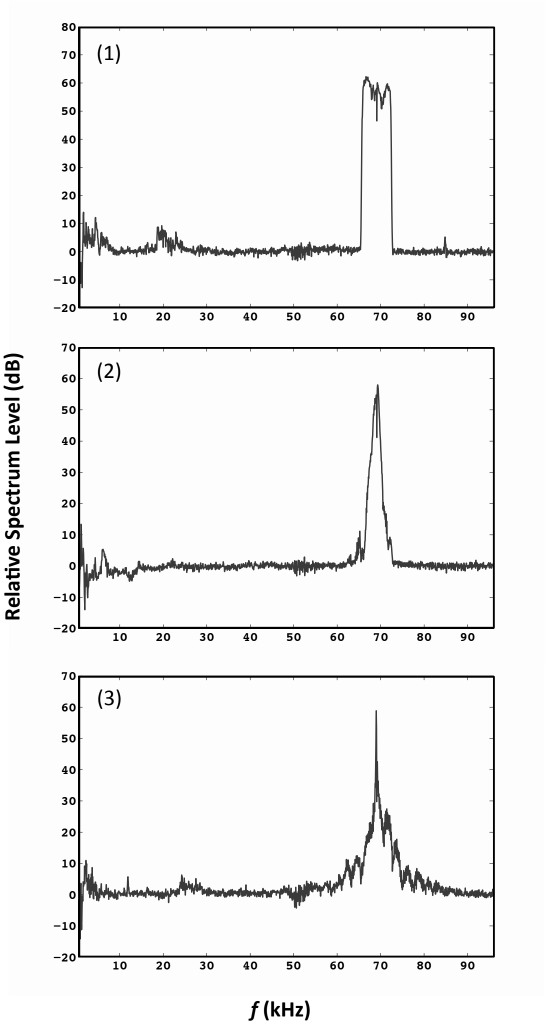

FIG 1. Received spectra for (1) a 500 ms, 10% linear frequency-modulated (FM) sweep centered around 69 kHz, (2) a 10 ms, 2% FM sweep centered around 69 kHz, and (3) the recorded output of a Vemco V16-3H UCT. Signals were recorded at the position of the test subject's head and spectrum levels are normalized to the ambient noise in the test environment recorded immediately prior to signal projection (figures show the difference in decibels between the received spectrum level for the signal-plus-ambient and the spectrum level for the ambient noise alone). Note the absence of any low-frequency components above the noise floor in all three stimuli. In the 100-72000 Hz range, average ambient noise spectrum levels in the test environment tend to decrease with increasing frequency, ranging from 74 dB re (1 μPa)^2/Hz at 100 Hz to 28 dB re (1 μPa)^2/Hz at 72000 Hz.

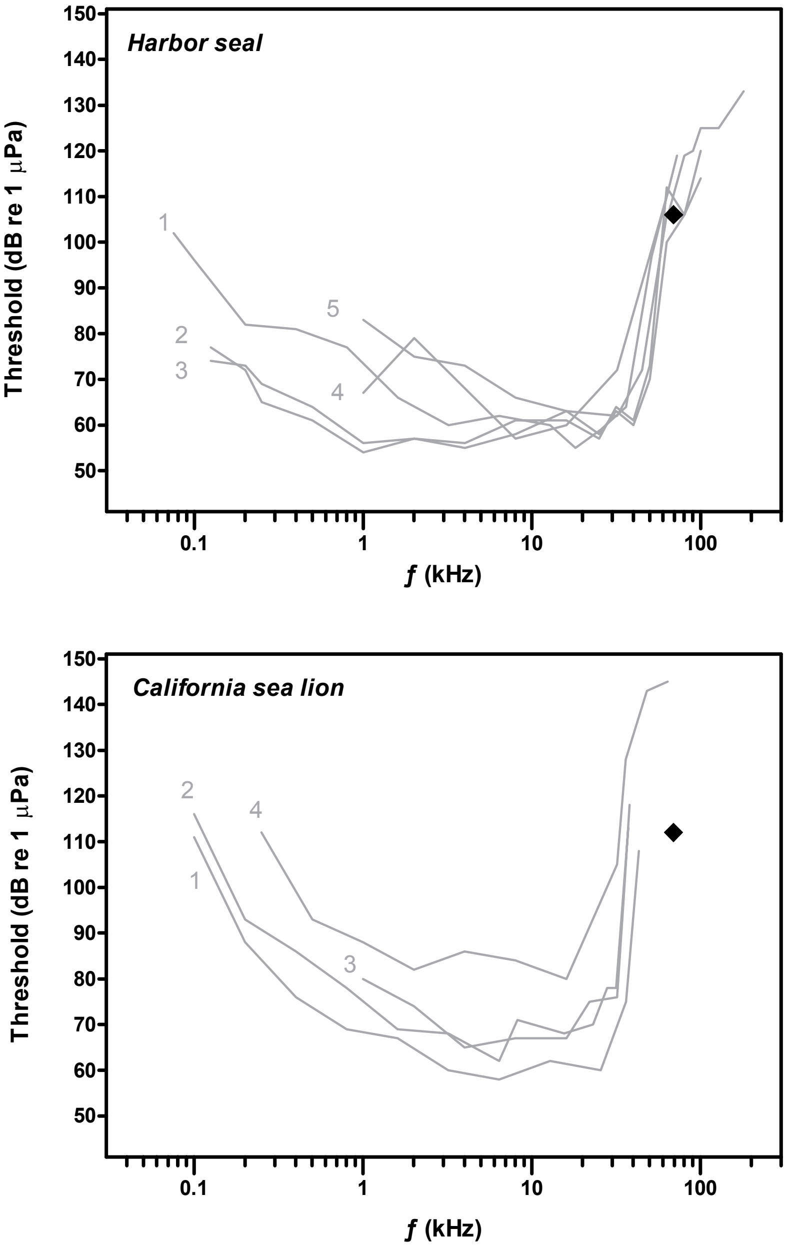

FIG 2. Auditory detection thresholds for a 69 kHz (500 ms) narrowband signal from this study (◆) for a harbor seal and a California sea lion as compared to published audiograms for these species. Note that lower detection thresholds indicate better auditory sensitivity. Harbor seal references: 1 (Reichmuth *et al.*, 2013); 2, 3 (Kastelein *et al.*, 2009); 4 (Terhune, 1988); 5 (Møhl, 1968a). California sea lion references: 1 (Reichmuth *et al.*, 2013); 2 (Reichmuth and Southall, 2012); 3 (Mulsow *et al.*, 2012); 4 (Schusterman *et al.*, 1972).

CHAPTER 2

Auditory sensitivity of seals and sea lions in complex listening scenarios

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ABSTRACT

Standard audiometric data, such as audiograms and critical ratios, are often used to inform marine mammal noise-exposure criteria. However, these measurements are obtained using simple, artificial stimuli—i.e. pure tones and flat-spectrum noise—while natural sounds typically have more complex structure. In this study, detection thresholds for complex signals were measured in (I) quiet and (II) masked conditions for one California sea lion (*Zalophus californianus*) and one harbor seal (*Phoca vitulina*). In Experiment I, detection thresholds in quiet conditions were obtained for complex signals designed to isolate three common features of natural sounds: frequency modulation, amplitude modulation, and harmonic structure. In Experiment II, detection thresholds were obtained for the same complex signals embedded in two types of masking noise: synthetic flat-spectrum noise and recorded shipping noise. To evaluate how accurately standard hearing data predict detection of complex sounds, the results of experiments I and II were compared to predictions based on subject audiograms and critical ratios combined with a basic hearing model. Both subjects exhibited greater-than-predicted sensitivity to harmonic signals in quiet and masked conditions, as well as to frequency-modulated signals in masked conditions. These differences indicate that the complex features of naturally occurring sounds enhance detectability relative to simple stimuli.

I. INTRODUCTION

Increases in marine ambient noise levels coincident with increases in certain human activities—such as commercial shipping and seismic exploration—indicate that anthropogenic noise has altered the acoustic environment of the world's oceans over the past century (NRC, 2003; McDonald *et al.*, 2006). This has raised concern over the negative effects that altered soundscapes may have on marine mammals, including behavioral disturbance, temporary or permanent hearing loss, and auditory masking of ecologically relevant sounds (e.g. Richardson *et al.*, 1995; Southall *et al.*, 2007; Clark *et al.*, 2009). The ability to predict such effects for specific noise-generating activities is important for noise management that adequately protects marine mammal populations.

In order to accurately predict anthropogenic noise effects, an understanding of the basic auditory capabilities of marine mammals is needed. Scientists examining auditory abilities within and across species often begin by measuring audiograms and critical ratios. Audiograms are absolute sensitivity profiles constructed from detection thresholds measured in quiet conditions for narrowband signals across a range of frequencies. Audiograms are often used in comparative hearing assessments because they indicate to which frequencies an auditory system is most sensitive (e.g. Masterton *et al.*, 1969). Critical ratios are measures of sensitivity to narrowband signals in the presence of flat-spectrum masking noise. Specifically, the critical ratio is the minimum ratio of the sound pressure level (SPL) of a narrowband signal to the spectral density level of a flat-spectrum masking noise required for auditory detection (Fletcher, 1940). Like audiograms, critical ratios are commonly used as comparative hearing metrics as they provide an indirect measure of preciseness of frequency tuning in the auditory system, which partially determines ability to detect sounds in noise as well as ability to discriminate sounds from one another (e.g. Saunders *et al.*, 1979).

Recently, these traditionally comparative metrics have been applied as foundational components in quantitatively predicting how anthropogenic noise may affect different marine mammal species. For example, audiograms have been used to create auditory weighting functions, which are utilized in predicting the effects of noise at different frequencies for a particular species (e.g., Nedwell, 2007; Southall *et al.*, 2007), and species-specific critical ratios have been used as the basis for predictive models of auditory masking (Jensen *et al.*, 2009; Dooling *et al.*, 2013). While the use of audiograms and critical ratios as comparative metrics within and across species is well established, using these measures to predict noise effects is a relatively new phenomenon, and as such, must be empirically evaluated.

Of particular concern is the uncertainty regarding how well these two metrics predict auditory sensitivity in natural listening conditions. This uncertainty stems from the fact that both audiograms and critical ratios are measured using simple audiometric stimuli—i.e., narrowband signals and flat-spectrum masking noise—while natural sounds tend to have more complex spectral and temporal features. Using simple stimuli in the laboratory is practical as they are controllable and replicable, unlike most natural sounds. However, several studies indicate that mammalian auditory systems have evolved to process certain spectro-temporal features of natural sounds—such as frequency modulation (FM), amplitude modulation (AM), and the presence of multiple harmonics (Mendelson and Cynader, 1985; Rees and Møller, 1987; Frisina *et al.*, 1990; Suga, 1992; Nelken *et al.*, 1999) — suggesting that sensitivity to complex sounds may be fundamentally different from sensitivity to simple sounds. If audiograms and critical ratios are to play central roles in the management of noise-exposure levels for marine mammals, the question of how accurately these metrics predict sensitivity to complex sounds must be addressed experimentally. In this study, behavioral detection thresholds were measured in quiet and masked conditions and compared to predictions based on subject audiograms and critical ratios for one California sea lion (*Zalophus californianus*) and one harbor seal (*Phoca vitulina*).

II. EXPERIMENT I

A. Methods

1. Overview

In Experiment I, behavioral detection thresholds were measured for complex signals in quiet conditions. Experiments were conducted from January to October 2013 in an acoustically mapped underwater testing environment. Thresholds were measured for three types of complex signals: FM signals, AM signals, and multi-component harmonic signals. Four center frequencies for FM and AM signals were chosen to span the known functional range of hearing for each subject (Reichmuth *et al.*, 2013), and two fundamental frequencies were chosen to build harmonic signals with all components within the functional range of hearing. The detection thresholds measured for these ten complex signals were compared to threshold predictions based on audiogram data for the same two subjects.

2. Subjects and test environment

Two trained pinnipeds participated in this study: a 3-year-old female California sea lion identified as *Ronan* (NOA0006602) and a 24-year-old male harbor seal identified as *Sprouts* (NOA0001707). Both subjects had multiple years of experience participating in psychophysical hearing studies.

Experimental sessions were conducted at Long Marine Laboratory in Santa Cruz, CA in an outdoor, semi-in-ground, circular, concrete test pool (7.6 m diameter, 1.8 m depth) filled with natural seawater ranging in temperature from 10-16°C. An experimental apparatus made of perforated polyvinyl chloride (PVC) pipe was suspended into the pool such that the pipes filled with water. A PVC chin station was located on the apparatus such that the subject's head was at 1 m depth during testing. An underwater light was placed 40 cm in front of the chin station and a flat, square, PVC response target was positioned 20 cm to the left of the station. A closed-circuit underwater camera was located slightly above the underwater light so that the chin station, light, and response target were all within the field of view.

Sessions were conducted by a trainer, who was in direct contact with the animal subject, and a remote experimenter, who was not. The trainer was blind to the specific trial condition and was responsible for directing the animal to the station at the appropriate time, as well as providing fish rewards. The experimenter was located in a control room that was hidden from the subject's view, but had visual access to the subject during trials via the underwater camera. The experimenter controlled the onset of test trials as well as the presentation of acoustic stimuli.

3. Psychophysics

A go/no-go procedure was established as the signal detection task. On each trial, the trainer cued the subject to dive to the chin station. Once the subject was motionless in the station, the experimenter turned on an underwater light, indicating the beginning of a 4-s trial interval during which an acoustic signal might be presented. The subject had been previously trained to leave the station and press its nose to the response target upon hearing a signal. Correct responses occurred either when the subject touched the target after a signal presentation (termed a "hit"), or when the subject remained on the station for the full trial interval when no signal had been presented. Incorrect responses occurred either when the subject failed to touch the target after a signal presentation (a "miss"), or when the subject went to the target when no signal had been presented (a "false alarm"). All correct responses were reinforced with a single piece of fish; incorrect responses were never reinforced.

Experimental sessions consisted of 40-60 trials. Signal-present and signal-absent trials were presented in a mixed order, with a maximum run length of four for either trial type. During each session, the signal level was varied using an adaptive staircase procedure with a 4 dB ascending step size and a 2 dB descending step size (as in Reichmuth *et al.*, 2013; Sills *et al.* 2014). The subject's response bias was maintained at a stable level by adjusting the ratio of signal-present to signal-absent trials between sessions (Schusterman and Johnson, 1975). The proportion of signal-present trials varied from 50% to 70%.

Complex signals were tested in a mixed order that differed for each subject. Subjects completed testing with each signal-type/frequency combination before progressing to the next treatment. In order for a subject to complete testing for a given treatment, three experimental sessions that met the following criteria had to be completed: Within each session, the last five consecutive hit-to-miss transitions were within 6 dB of one another; within-session averages of hit-to-miss transitions were within 3 dB of one another; and the false alarm rate—defined as the proportion of signal-absent trials that resulted in false alarms calculated over the trials encompassed by the last five hit-to-miss transitions—was greater than 0 and less than 0.3.

For each signal treatment, the most recent three experimental sessions that met these criteria were used in the final threshold calculation. From each of these sessions, the trials bracketed by the last five hit-to-miss transitions were extracted and probit analysis (Finney, 1947) was used to calculate the 50% detection threshold, 95% confidence intervals, and standard errors. Criteria for final threshold determination were confidence intervals no wider than 5 dB and $p \geq 0.1$ for a Chi-squared goodness of fit test applied to the probit model.

4. Audiogram data

In order to generate threshold predictions for complex sounds, recent and reliable underwater audiogram data were needed for both subjects. An underwater audiogram for the California sea lion had been recently measured (2011-2012) at the same facility, under similar test conditions, using similar psychophysical procedures (Reichmuth *et al.*, 2013). Because of this, additional audiogram measurements were deemed unnecessary for this subject. For the harbor seal, only a composite audiogram, measured under similar test conditions, consisting of recently measured mid- to high-frequency data (2008-2010) combined with older low-frequency data (1998) was available (Kastak and Schusterman, 1998; Reichmuth *et al.*, 2013), and it was deemed necessary to re-measure low- to mid-frequency hearing thresholds for this subject.

Two major factors made retesting necessary: The harbor seal subject's thresholds at low-frequencies were elevated relative to other harbor seal data (Kastelein *et al.*, 2009), suggesting that the previous measurements for this subject may have been constrained by background noise; and in 2007 this subject suffered a permanent threshold shift of 7-10 dB at 5.8 kHz (Kastak *et al.*, 2008). The frequency regions tested in this experiment were intentionally distant from the frequency region of PTS.

The narrowband signals used to collect audiogram data in this study were similar to those used in several recent pinniped hearing studies (e.g., Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013; Sills *et al.*, 2014), and consisted of 10% bandwidth, linear FM sweeps. Narrowband FM sweeps were chosen over pure-tones because it has been shown that, while both signal types result in similar detection thresholds, narrowband FM sweeps exhibit less spatial variability in reverberant testing environments (Kastelein *et al.*, 2002; Finneran & Schlundt, 2007). Center frequencies of 0.5, 2, and 3.2 kHz were chosen to target uncertainties in the harbor seal subject's audiogram as needed for threshold predictions. Narrowband signals were generated using HTP software (Finneran, 2003).

5. Signal types

Three types of complex signals were synthesized for this experiment using MATLAB (MathWorks, Natick, MA). While each signal type had different features, all were of 500 ms duration with 25 ms linear on and off ramps.

Each FM signal comprised an octave-band linear upsweep at a given center frequency. Mathematically, the amplitude of these signals as a function of time is given by

$$A(t) = \sin\left(2\pi \int_0^T \left\{ f_{start} + \frac{f_{stop} - f_{start}}{T} t \right\} dt\right), \qquad (1)$$

where T is the duration of the signal, f_{start} is the start frequency of the upsweep, and f_{stop} is the end frequency of the upsweep. FM signals were synthesized at center frequencies 0.5, 2, 16 and 38 kHz, chosen to span the subjects' functional hearing ranges and to encompass the frequencies of many biologically relevant sounds.

AM signals were created through sinusoidal modulation of a pure-tone carrier with a modulation rate of 50 Hz and a modulation depth of 0.5. A 50 Hz modulation rate was selected based on an *ad hoc* analysis of a variety of pinniped vocalizations, which revealed common modulation rates between 1 and 80 Hz. A modulation depth of 0.5 was chosen to ensure that the modulation was detectable. Mathematically, the amplitude of these signals as a function of time is given by:

$$A(t) = \sin(2\pi f_c t)(1 + A_m \sin(2\pi f_m t)), \quad (2)$$

where f_c is the frequency of the carrier signal, f_m is the modulation frequency, and A_m is the modulation depth. AM signals were synthesized at carrier frequencies 0.5, 2, 16, and 38 kHz, mirroring the center frequencies of the FM signals.

Harmonic signals contained components at the fundamental frequency and its first three linear multiples. All components had the same bandwidth, which was set to 1/4-octave of the fundamental frequency. Harmonic signals were synthesized with fundamental frequencies of 0.5 and 2 kHz. Higher fundamental frequencies (16 and 38 kHz) were not used because the higher-frequency components would have been beyond the subjects' high-frequency hearing limits. When the harmonic signals were designed and calibrated, each component was filtered such that the difference in SPL at the location of the subject's head between the first harmonic and the fundamental was -3 dB, between the second harmonic and the fundamental was -6 dB, and between the third harmonic and the fundamental was -9 dB. To account for day-to-day variability in the relative SPL between harmonic components due to environmental factors (e.g., changes in water temperature) levels for each component were recorded immediately prior to the start of each session and the appropriate adjustments were made in the threshold analysis.

6. Signal generation and calibration

Outgoing signals were sent from a PC to a NI USB-6259 data acquisition system for digital-to-analog conversion, band-pass filtered using a Krohn-Hite 3364 analog filter, attenuated using a TDT PA5 programmable attenuator, and amplified using a Hafler P1000 amplifier when necessary. Depending on frequency, signals were projected from either an ITC 1042 hydrophone mounted on PVC pipe and suspended into the test pool, or from an NUWC J11 projector suspended from a metal cable. The projected signal was received by a Reson TC4032 hydrophone located at the position of the center of the subject's head during testing. Analog-to-digital conversion of the received signal was performed using the same NI USB-6259 at a sampling rate of 500 kHz.

Before testing began with a specific signal type, the signal SPL was measured at 24 positions within a 14 cm x 14 cm x 14 cm cubic grid—centered around the daily calibration position—to ensure that received SPLs were within +/- 3 dB of one another (as in Sills *et al.*, 2014). Prior to each experimental session, projected signals were calibrated using HTP software and the ambient noise in the test environment was measured using a B&K 2250 sound-level meter connected to the Reson TC4032.

In the calibration process, received signal SPLs were calculated within specific frequency bands, the limits of which changed depending on the signal. For narrowband, FM, and AM signals, received levels were measured within the full signal band limits, i.e. across a band encompassing all spectral energy of the particular signal. For harmonic signals, received levels were measured relative to the band limits of the fundamental component. The frequency range of calibration was taken into account when calculating threshold predictions (as described below).

8. Predictions based on audiograms

Threshold predictions for FM, AM, and harmonic signals were made based on linear interpolation of subject-specific audiogram data: The two closest available audiogram data points that bracketed a given complex signal center frequency were selected, and a straight line was fit between these two points. This line was then used to make an inverse prediction of detection threshold at the desired center frequency.

The hearing model used for this experiment assumed that the auditory periphery acts as a series of non-overlapping 1/3-octave, band-pass filters, and that signal detectability is determined entirely by the filter with the highest probability of detection (i.e., information from multiple filters cannot be combined to enhance detection). The choice of a 1/3-octave bandwidth is consistent with human hearing models and is appropriate for pinnipeds based on direct critical bandwidth measurements (Southall *et al.*, 2003). Within this model, signals with bandwidths exceeding 1/3-octave relative to the center frequency (FM and harmonic signals) are processed piecewise by different auditory filters. To simulate this, wideband signals were decomposed into multiple narrowband components for which predictions were generated. Octave-band FM sweeps were decomposed into three, 1/3-octave-band FM sweeps with center frequencies:

$$f_{1/3} = f_c * 2^{\frac{k}{3}}, for\ k = -1, 0, 1 \quad (3)$$

where f_c is the center frequency of the octave-band signal. The durations of the 1/3-octave-band FM sweeps were determined by the length of time for which the instantaneous frequency of the signal fell within the given 1/3-octave band limits (131, 163, and 206 ms for the lower, middle, and upper 1/3-octave bands). Three predictions were calculated for FM signals based on interpolation of audiogram data, one at the center frequency of each 1/3-octave band component. Harmonic signals were decomposed into their four individual harmonic components. Four predictions were then calculated based on interpolation of audiogram data, one at the center frequency of each component.

Because the durations of the 1/3-octave band components of the decomposed octave-band FM sweep were likely less than the auditory integration time at three of the four center frequencies tested, threshold predictions at these frequencies were adjusted based on studies of temporal integration of narrow band signals in harbor seals (Kastelein, *et al.*, 2010) and a California sea lion (Holt *et al.*, 2012). Predictions for FM signals at 0.5, 2, and 16 kHz were increased by 4, 2, and 1 dB respectively. The 0.2 kHz integration data from Kastelein *et al.* (2010) that were inconsistent with data from Reichmuth *et al.* (2012) were not applied.

Further adjustments to predicted thresholds were made depending on how the received levels of FM and harmonic signals were calibrated. For example, because harmonic signals were calibrated relative to the SPL at the fundamental frequency, threshold predictions were adjusted according to the SPL of each harmonic component relative to the fundamental component. That is, if the received SPL of the second harmonic component was 3 dB less than the fundamental, 3 dB would be added to the threshold prediction for that component. Similar adjustments were made for the three 1/3-octave band signals that composed the octave-band FM sweep. In this case, predictions were adjusted relative to the SPL of the full octave band (the level used for calibration).

Once thresholds were estimated for all components of a given signal, the minimum of these thresholds was taken as the final prediction. The selection of the minimum predicted threshold is consistent with a hearing model in which the listener attends to auditory filters independently, and the individual filter with the greatest sensation level at threshold determines detection. As a practical metric of comparison, the difference between this final prediction and the measured detection threshold was calculated, where a positive difference indicated that sensitivity was greater than predicted, and a negative difference indicated that sensitivity was less than predicted. This metric is subsequently referred to as the *sensitivity difference from predicted*.

B. Results

1. Narrowband Signals and Audiograms

The harbor seal's detection thresholds measured for narrowband signals were 69, 62, and 66 dB re 1 μPa at 0.5, 2, and 3.2 kHz respectively. The thresholds at 0.5 and 3.2 kHz exceeded the spectrum level of the background noise by at least one critical ratio (as measured in Experiment II), indicating that these measurements were not limited by ambient noise in the enclosure. However, higher than expected critical ratio measurements made it impossible to rule out noise limitation of the harbor seal subject's threshold at 2 kHz. The threshold measured at 0.5 kHz in this study was more than 10 dB lower than the thresholds at 0.4 and 0.8 kHz measured by Kastak and Schusterman (1998), suggesting that the older threshold data may have been noise limited; therefore, only the new measurements were used to generate audiogram predictions for this study. The harbor seal's present and prior audiogram data, along with prior audiogram data for the sea lion, are provided in Fig. 1.

2. Frequency modulated, amplitude modulated, and harmonic signals

Detection thresholds measured for the octave-band FM signals were well predicted by the audiogram for both the sea lion and the harbor seal (Table I). For the sea lion, the mean sensitivity difference from predicted across all center frequencies was -2 dB. At center frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the sea lion were 3, -1, -5, and -4 dB, respectively. For the harbor seal, the mean sensitivity difference from predicted was -1 dB. At center frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the harbor seal were 1, 0, -2, and -3 dB, respectively.

Detection thresholds measured for the 50 Hz AM signals were well predicted by the audiogram for both the sea lion and harbor seal (Table I). For the sea lion, the mean sensitivity difference from predicted across all carrier frequencies was 0 dB. At carrier frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the sea lion were 4, 1, -1, and -4 dB, respectively. For the harbor seal, the mean sensitivity difference from predicted was -1 dB. At carrier frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the harbor seal were 4, -1, -8, and 1 dB, respectively.

The measured detection thresholds for harmonic signals were lower than predicted for both subjects (Table I). For the sea lion, the mean sensitivity difference from predicted across both fundamental frequencies was 4 dB. At fundamental frequencies 0.5 and 2 kHz, sensitivity differences from predicted for the sea lion were 2 and 7 dB respectively. For the harbor seal, the mean sensitivity difference from predicted was 7 dB. At fundamental frequencies 0.5 and 2 kHz, sensitivity differences from predicted for the harbor seal were 8 and 6 dB respectively. Sensitivity differences from predicted for FM, AM, and harmonic signals are summarized in Fig. 2.

C. Discussion

Absolute detection thresholds were well predicted by the audiogram for octave-band FM and 50 Hz AM signals, but harmonic signal thresholds were consistently lower than predicted, indicating greater than predicted sensitivity to harmonic signals in quiet conditions. These trends were consistent across both subjects, despite the fact that they represent two distinct pinniped lineages. The enhanced sensitivity measured for harmonic signals is consistent with data for human subjects. Buus *et al.* (1998) demonstrated that human detection thresholds for multi-tone harmonic complexes were lower than detection thresholds for any isolated tone within the complex by as much as 9 dB. These combined results suggest that information from multiple auditory filters is integrated in order to enhance detection of harmonic signals in both pinniped and human listeners.

Thresholds for octave-band FM signals were well predicted by the audiogram despite the fact that the bandwidth of these signals was greater than the bandwidth of an auditory filter at the signal center frequency (i.e., greater than one critical band; Southall *et al.*, 2003). This indicates that there was no gain in sensitivity as the result of integration of energy across multiple auditory filters for these signals. However, the nature of these FM signals is such that while the spectrum taken over the 500 ms signal duration is broadband, the signal is narrowband at any moment in time. The absence of simultaneous energy in multiple auditory filters may prevent across-channel comparisons.

For the harbor seal subject, the mean sensitivity difference from predicted for AM signals was low, but detection thresholds varied less than predicted as a function of carrier frequency. Predicted thresholds ranged from 57-69 dB, but observed values ranged only from 63-67 dB, indicating that sensitivity was near constant across frequencies. Because the modulation rate is constant for the AM signals, the amplitude envelope of the signal is the same at all carrier frequencies. The observed constant sensitivity combined with the constant modulation rate suggests that the amplitude envelope of the signal—not just the carrier frequency—may have played an important role in determining detection thresholds for this subject. Further experimentation is necessary to test this hypothesis.

III. EXPERIMENT II

A. Methods

1. Overview

In Experiment II, detection thresholds for complex signals were measured for the same pinniped subjects in noisy (masked) conditions. Octave-band FM, 50 Hz AM, and multi-component harmonic signals were masked by either a white noise with no regular amplitude fluctuations, or by recorded shipping noise that exhibited regular amplitude fluctuations. The objective of Experiment II was to compare masked thresholds for complex stimuli to predictions based on traditional critical ratios. To generate these predictions, critical ratios were measured for both subjects using simple stimuli and combined with a basic hearing model.

Psychophysical procedures were similar to those used in Experiment I, with the addition of masking noise on each trial. Masking noise was projected from the same underwater transducer as the signal to prevent spatial release from masking (Turnbull, 1994). The onset of the masking noise coincided with the onset of the light indicating the start of a trial; the noise offset occurred after the end of the 4-s trial interval. The masking noise level was identical for all trials within a session, while the signal level was varied between trials. Threshold analysis (probit analysis: Finney, 1947) and completion criteria were the same as in Experiment I. Testing for

Experiment II was conducted from July 2013 through January 2014.

2. Signals

Narrowband, FM, AM and harmonic signals were used as in Experiment I. Experiment II tested low signal frequencies (2.4 kHz and lower), where much anthropogenic noise energy is concentrated.

Narrowband signals were the same 10% bandwidth FM sweeps that were used in Experiment I, but with center frequencies 0.3, 6, 1.2, and 2.4 kHz. Octave-band FM and 50 Hz AM signals were also the same as in Experiment I, but with a center or carrier frequency of 0.6 kHz. A single harmonic signal with a fundamental frequency of 0.3 kHz was created for Experiment II. In order to create a harmonic signal that was most comparable to the signals used in Experiment I in terms of both bandwidth and number of components, a five-component signal was used with components at 0.3, 0.6, 0.9, 1.2, and 1.5 kHz, each with bandwidths 1/4-octave of the fundamental frequency. The harmonic signal was selectively filtered such that the individual SPLs of all five harmonic components of the received signal were equal.

3. Masking Noise

Two types of masking noise were used in this experiment: Flat-spectrum, white noise bands and recorded shipping noise. The creation of flat-spectrum masking noise took place in three steps. First, 6 seconds of white noise with 50 ms linear on and off ramps was generated, band-pass filtered, and saved as a WAV file using MATLAB. This noise was then projected into the test pool and the received spectrum was measured at the location of the subject's head during testing. The received spectrum was examined visually and the noise selectively filtered using custom MATLAB functions to obtain a flat spectrum for the received sound. This process of projection and filtering was repeated until fluctuations in the spectrum level were minimal, and the 1/3-octave band levels were within +/- 3 dB of the center 1/3-octave band level.

Two flat-spectrum masking noises were created for testing with complex signals. The first had a noise band ranging from 0.3-1.2 kHz (one octave below and one octave above 0.6 kHz). This masking noise was combined with the FM and AM signals. The second masking noise was combined with the harmonic signal and had a noise band ranging from 0.15-3 kHz (note that a wider noise band was needed to encompass all components of the harmonic signal). Three additional flat-spectrum masking noises were used in measuring predictive critical ratios. These were created using the same procedure as above and had noise bands of 0.15-0.6, 0.6-2.4, and 1.2-4.8 kHz.

In addition to flat-spectrum noise, a 6-s sample of recorded shipping noise was used to mask signals (Fig. 3). This sample was taken from a longer recording of the Bulk Carrier *Hanjin Istanbul* made at a distance of 3 km. Linear on and off ramps of 50 ms duration were applied to the 6-s sample. This noise had energy concentrated below 1 kHz and exhibited regular temporal fluctuations in amplitude. In addition, this noise exhibited comodulation across multiple 1/3-octave frequency bands below 1 kHz. The shipping noise was combined with narrowband, FM, and AM signals, but not with the harmonic signal due to incompatible bandwidths.

4. Signal and noise calibration

The procedure used to generate and calibrate signals in Experiment II was the same as that used in Experiment I. Masking noise was sent from Windows Media Player software on a PC, through a Hafler P1000 amplifier, to the same NUWC J11 that was used to project signals. During calibration, masking noise was received using a Reson TC4032 hydrophone connected to a battery-powered laptop PC through a Roland QUAD-CAPTURE external sound card set to a sampling rate 192 kHz. SpectraPlus software was used to measure the 1/3-octave band SPLs. Prior to each session, the amplifier level was adjusted until the masking noise SPL within the 1/3-octave band (ANSI standard, 1985) encompassing the center frequency of the signal being tested—or the fundamental frequency for harmonic signals—was within 1 dB of 110 dB re 1 μPa (Note that by maintaining a constant 1/3-octave band SPL, masking noises at lower center frequencies had lower spectrum levels than noise at high center frequencies). This SPL was chosen to ensure that masking noise levels were at least 20 dB above the noise floor of the test environment, and 10-20 dB above the absolute hearing threshold at the frequency of the signal. In order to generate critical ratio based threshold predictions for all auditory filters that contained signal energy, the SPL of the noise was also measured for all 1/3-octave bands that overlapped with the spectrum of the signal prior to each session.

Prior to testing with any specific signal/noise combination, SPL measurements of both signal and noise were taken within the same 24-point cubic grid used in Experiment I to ensure that: (1) all signal SPLs were within +/- 3 dB of one another, and (2) noise SPLs within all 1/3-octave bands that overlapped with the signal spectra were within +/- 3 dB of one another.

5. Predictions based on critical ratios

In order to generate masked-threshold predictions for complex stimuli, critical ratios were measured at frequencies 0.3, 0.6, 1.2, and 2.4 kHz. To determine a critical ratio, the subject's 50% detection threshold for a narrowband signal masked by constant-volume white noise was measured, and the spectrum level of the masking noise at the signal center frequency was estimated. To estimate the spectrum level, the average SPL of the flat-spectrum masking noise within the 1/3-octave band encompassing the signal was calculated for the three experimental sessions used in threshold analysis; 10log(B) was subtracted from this value, where B is the 1/3-octave bandwidth of the noise band. The critical ratio was then calculated as the difference between the detection threshold and the estimated noise spectrum level.

In order to predict detection thresholds for complex signal and noise combinations, a 1/3-octave band plus critical ratio model of masking was applied. This type of model has been used to predict masked thresholds for a variety of species (e.g. Jensen *et al.*, 2009; Dooling *et al.*, 2013), and is derived from the power spectrum model of masking. The power spectrum model is based on a number of assumptions, including that (1) the auditory periphery can be modeled as a series of linear band-pass filters, (2) the listener attends to the output of a single filter, and (3) the long-term energy spectra of the signal and noise determine detectability, rather than variations in temporal fine structure or phase (Moore, 1993). The model used in this study is similarly built on these assumptions with the added assumption that auditory filter bandwidths are well approximated by 1/3-octave bandwidths, which is consistent with direct critical bandwidth measurements in pinnipeds (Southall *et al.*, 2003).

These model assumptions were combined with masking noise levels and critical ratio measurements in order to predict detection thresholds. Critical ratios were estimated for each animal at the center frequency of the signal being tested using a linear interpolation of the measured critical ratios at 0.3, 0.6, 1.2, and 2.4 kHz. These estimates were then added to noise spectrum levels—calculated from 1/3-octave bands—giving an estimate of the minimum received signal SPL necessary for 50% correct detection.

In this hearing model, signals with bandwidths greater than 1/3-octave of their center frequency are processed by multiple filters, and because of this, critical ratios and noise spectrum levels were calculated at multiple center frequencies when wideband signals—harmonic or FM—were being tested. For harmonic signals, these calculations were made at the center frequencies of all five harmonic components. For FM signals, the octave-band signal was processed as three discrete, 1/3-octave band signals with center frequencies of 0.476, 0.600, and 0.756 kHz and durations of 131, 163, and 206 ms respectively. Because the durations of the individual 1/3-octave components of the octave-band FM signal are likely less than the integration time for both species at 0.6 kHz, 4 dB was added to the predicted thresholds for these signals. This value was estimated based on studies of the effect of duration on detection thresholds for harbor seals (Kastelein *et al.*, 2010) and a California sea lion (Holt *et al.*, 2012).

Because threshold predictions were based on 1/3-octave bands, but the calibrated level of the signal was not, predictions were adjusted relative to the calibrated level. For signals with bandwidths less than 1/3-octave of the center frequency—narrowband and AM signals—no adjustment was necessary because the 1/3-octave band signal level was the same as the calibrated level. For signals with bandwidths wider than 1/3-octave—harmonic and FM signals—the signal SPL within each 1/3-octave band containing signal energy was measured relative to the calibration level in HTP. For the harmonic signal, received SPLs were calibrated relative to the fundamental component. So, for example, if the average SPL measured prior to experimental sessions for the first harmonic component was 1 dB less than the SPL of the fundamental, 1 dB would have been added to the predicted threshold for the first harmonic component, giving a prediction relative to the calibration level for that component. For the FM signal, SPL was calculated for each of the 1/3-octave bands encompassed by the octave-band signal. These levels were compared to the calibration level taken over the entire octave-band sweep and the appropriate adjustments were made to threshold predictions for each 1/3-octave component of the broadband signal.

In the power spectrum model of masking, detectability is determined entirely by the output of the single auditory filter that gives the highest probability of detection. In line with this model, once predicted levels were determined for the individual 1/3-octave bands of interest (relative to the calibration level), the minimum of these values was used as the final masked-threshold prediction. As in Experiment I, the sensitivity difference from predicted was calculated as the difference between this final prediction and the measured detection threshold, where a positive difference indicates greater sensitivity than predicted, and a negative difference indicates poorer sensitivity than predicted.

B. Results

1. Critical ratio measurements

Critical ratios for the sea lion were measured as 16, 21, 23, and 24 dB at frequencies 0.3, 0.6, 1.2, and 2.4 kHz, respectively (Table II). These values are similar to existing data in this frequency range for California sea lions (Southall *et al.*, 2000), and show a slope of 2.8 dB/octave (Fig. 4), similar to the expected mammalian pattern of 3 dB/octave (Fay, 1988).

Critical ratios for the harbor seal were 17, 19, 27, and 24 dB at frequencies 0.3, 0.6, 1.2, and 2.4 kHz, respectively (Table II). These data also showed a slope of 2.8 dB/octave. Measured critical ratios were greater than existing values for this species, with the only other available data in this frequency range coming from the same harbor seal subject, but 16 years younger (Southall *et al.*, 2000; measurements taken in 1997). Comparison of the two datasets suggest that the subject's critical ratios increased by 4-7 dB across the entire 0.3-2.4 kHz range, but that the pattern as a function of frequency remained the same (Fig. 4).

2. Complex signals in flat-spectrum and shipping masking noise

Sensitivity was greater than predicted for complex signals embedded in flat-spectrum masking noise for both subjects across all three signal types, indicating an enhanced ability to detect complex signals relative to simple signals in noisy conditions (Table III). Observed thresholds for AM signals were the most accurately predicted, with a sensitivity difference from predicted of 1 dB for both the sea lion and the harbor seal. For the FM signals, sensitivity differences from predicted were 4 and 2 dB for the sea lion and the harbor seal, respectively. Observed thresholds for the harmonic signals were the least accurately predicted, with sensitivity differences from predicted of 7 and 4 dB for the sea lion and the harbor seal, respectively.

Observed detection thresholds for the narrowband signal masked by recorded shipping noise were lower than predicted for both the sea lion and harbor seal; sensitivity differences from predicted were 6 and 3 dB respectively (Table III). Observed detection thresholds for both subjects were also lower than predicted for the octave-band FM signal embedded in the shipping masking noise, with sensitivity differences from predicted of 8 dB and 7 dB for the sea lion and harbor seal respectively. For the AM signal, the sensitivity difference from predicted was 4 dB for the sea lion subject, and -3 dB for the harbor seal subject. A summary of sensitivity differences from predicted for complex signals in masked conditions is given in Fig. 5.

C. Discussion

Auditory detection thresholds were measured for a total of six masking scenarios involving complex signals and noise for two pinniped subjects. Greater-than-predicted sensitivity was observed in 11 of the 12 treatments. This indicates an enhanced ability to differentiate signal and noise when complex spectral and temporal features were present. Masking release was most prominent for FM and harmonic signals, and the thresholds were lower for signals embedded in shipping noise versus white noise. The results likely reflect the capacity of the subjects' auditory systems to exploit the complex acoustic features found in natural sounds to enhance detection.

The phenomenon of greater-than-expected sensitivity to harmonic signals in noise is consistent with observations in human listeners of enhanced sensitivity to noise-masked multi-tone complexes relative to their individual components (Green, 1958; Buus *et al.*, 1986). Further, this phenomenon is consistent with the results of Experiment I, and with the proposed explanation: detection is enhanced by the ability of the auditory system to integrate information across multiple auditory filters.

The observation of enhanced detectability of FM signals in noise is consistent with observations that natural noise can often be expressed as the product of a function of frequency alone and a function of time alone (i.e., a carrier and an envelope), while many natural signals—such as animal vocalizations containing FM—can not, and the corresponding hypothesis that signals that are not separable in such a way may be more easily extracted from separable noise by the auditory system (Nelken *et al.*, 1999).

It was possible to test the narrowband, FM, and AM signals using both the shipping noise and the flat-spectrum noise, resulting in six conditions (3 signals x 2 subjects) that were tested with both masking noises. Detection thresholds were lower when signals were masked by shipping noise versus white noise in 5 out of 6 of these conditions, indicating that a release from masking occurred in the shipping noise condition. This masking release was likely due to comodulation within the shipping noise, that is, it exhibited consistent temporal amplitude fluctuations across multiple frequency bands. Comodulation masking release has been observed in multiple mammalian species (e.g. Hall *et al.*, 1984; Branstetter and Finneran, 2008; Klink *et al.*, 2010), and is hypothesized to result from the comparison of amplitude envelope patterns across multiple auditory filters.

The AM signal in shipping noise for the harbor seal was the only instance in Experiment II where the observed threshold exceeded the predicted threshold. The reasons for this are unclear, but as both the signal and noise exhibit regular amplitude fluctuations in time, it is possible that detection of the AM signal was limited by perceptual similarities between signal and noise, rather than merely by overlapping spectral energy. A similar effect has been observed in a bottlenose dolphin (*Tursiops truncatus*) subject listening for a tonal signal embedded in perceptually similar ice-squeak noise (Branstetter *et al.*, 2013). However, why perceptual similarities between signal and noise would affect the harbor seal, but not the sea lion, is uncertain.

It is worth noting that, because only a single 6-s sample of shipping noise was used here, these results are not necessarily generalizable to all types of shipping noise, which tends to vary with vessel type, speed, and distance. Further, it is possible that the unpredictability of actual shipping noise could make signal detection more difficult compared to a laboratory task involving a familiar masking noise. It is also important to mention that the elevated critical ratios measured for the harbor seal indicate that this subject may not have species-typical hearing. These elevated critical ratios are likely the result of deterioration of frequency selectivity with age. Patterson *et al.* (1982) demonstrated a similar pattern of reduced frequency selectivity for human listeners aged 60 years relative to listeners aged 20 years, but such patterns have yet to be demonstrated in pinnipeds. Whether or not decreased frequency selectivity would impact the relative effects of complex acoustic features on the subject's signal detection abilities is unknown.

IV. CONCLUSIONS

The results of this study indicate an enhanced ability to process sounds with certain complex features—similar to those found in natural sounds—for two pinniped subjects. Both subjects consistently detected signals at lower than predicted SPLs in certain complex listening scenarios, with maximum differences between observed and predicted thresholds of 8 dB in both quiet and masked conditions. This suggests that the audiogram and critical ratio based hearing models used in this study will not accurately predict the effects of anthropogenic noise in certain natural listening scenarios. Consequently, regulators charged with determining safe levels of anthropogenic noise should exercise caution when employing such models.

The data from this study suggest two underlying auditory abilities that allow for enhanced detectability of complex sounds: The ability to integrate information across multiple auditory filters, and the ability to separate a sound into a carrier signal and its amplitude envelope to enhance detection in noise. The ability to integrate information across multiple channels likely leads to the enhanced detectability of harmonic signals in both quiet and masked conditions (Buus *et al.*, 1986). The ability to separate a sound into a carrier and an envelope may account for the enhanced detectability of FM signals in masked conditions by the fact that only the noise is separable, and not the signal (Nelken *et al.*, 1999). Both of these abilities are combined in the case of the comodulation release from masking seen for the shipping noise: the auditory system is able to extract and compare amplitude envelopes from multiple auditory filters in order to enhance detectability (Hall, 1984). Given the similar trends for two pinniped subjects from distinct families, as well as similar patterns found in humans and other mammals (e.g. Green, 1958; Hall *et al.*, 1984; Buus *et al.*, 1986; Buus *et al.*, 1998; Branstetter and Finneran, 2008; Klink *et al.*, 2010), it is likely that such abilities are shared across many species. Because of this, it is advisable that hearing models used to predict the effects of anthropogenic noise on marine mammals and other animals take these two factors into account.

As this study included only two subjects and a small set of complex signals, further investigation is needed to understand how the auditory systems of pinnipeds and other mammals exploit the complex features of natural sounds. Particularly, future studies should examine how subjects detect inseparable signals in separable noise relative to scenarios where both signal and noise are separable, neither signal nor noise are separable, and the signal is separable, but the noise is not. Such studies will further test the hypothesis of Nelken et. al. (1999) that is supported by the findings reported here, and provide insight into the extent to which baseline audiometric data can be used to predict noise effects.

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Signal Type	**Subject**	**Frequency [kHz]**	**Predicted Threshold [dB re 1 μPa]**	**Observed Threshold (Std. Err.) [dB re 1 μPa]**	**Sensitivity Difference from Predicted [dB]**	**FA Rate**
Octave FM	Sea lion	0.5	76	73 (0.4)	2.9	0.10
Octave FM	Sea lion	2	65	67 (0.5)	-1.2	0.15
Octave FM	Sea lion	16	61	66 (0.5)	-5.2	0.21
Octave FM	Sea lion	38	73	77 (0.5)	-4.0	0.15
Octave FM	Harbor seal	0.5	71	70 (0.5)	1.0	0.15
Octave FM	Harbor seal	2	62	62 (0.5)	0.0	0.15
Octave FM	Harbor seal	16	56	58 (0.5)	-2.5	0.22
Octave FM	Harbor seal	38	67	70 (0.5)	-3.1	0.21
50 Hz AM	Sea lion	0.5	74	70 (1.0)	4.5	0.16
50 Hz AM	Sea lion	2	65	65 (1.0)	0.7	0.09
50 Hz AM	Sea lion	16	61	62 (0.5)	-0.7	0.03
50 Hz AM	Sea lion	38	84	87 (0.7)	-3.6	0.10
50 Hz AM	Harbor seal	0.5	69	65 (1.2)	3.8	0.16
50 Hz AM	Harbor seal	2	62	63 (0.5)	-1.4	0.04
50 Hz AM	Harbor seal	16	57	65 (0.4)	-8.0	0.17
50 Hz AM	Harbor seal	38	68	67 (0.3)	1.0	0.12
Harmonic	Sea lion	0.5	69	67 (0.5)	2.1	0.15
Harmonic	Sea lion	2	60	53 (0.4)	6.9	0.20
Harmonic	Harbor seal	0.5	67	59 (0.5)	7.7	0.10
Harmonic	Harbor seal	2	62	56 (0.3)	6.2	0.14

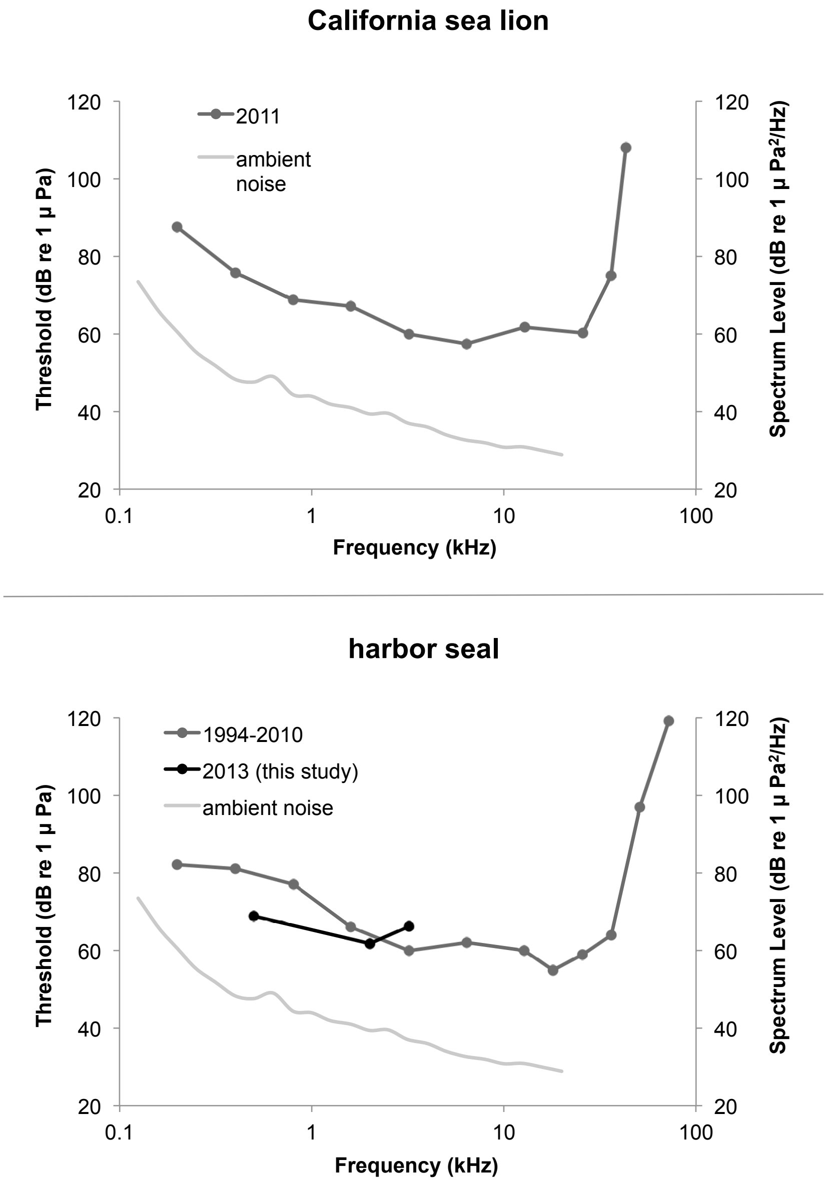
TABLE I. Predicted and observed unmasked detection thresholds from Experiment I for one harbor seal and one California sea lion and three types of complex signals: Octave-band FM, 50 Hz AM, and multi-component harmonic signals. Frequency values represent center frequency for FM signals, carrier frequency for AM signals, and fundamental frequency for harmonic signals. Thresholds for FM and AM signals are given in terms of the overall signal SPL, and for the harmonic signal are given in terms of the SPL of the fundamental component. A positive sensitivity difference indicates that the animal was more sensitive to the signal than predicted, i.e., the observed threshold was lower than predicted. False alarm rates and standard errors are also included.

Subject	Center Frequency [kHz]	Noise Spectrum Level [dB re 1 μPa^2/Hz]	Observed Threshold (Std. Err.) [dB re 1 μPa]	Critical Ratio [dB]	FA Rate
Sea lion	0.3	91	107 (0.5)	16	0.11
Sea lion	0.6	88	109 (0.4)	21	0.25
Sea lion	1.2	85	109 (0.6)	23	0.20
Sea lion	2.4	82	106 (0.3)	24	0.08
Harbor seal	0.3	91	109 (0.4)	17	0.24
Harbor seal	0.6	88	107 (0.6)	19	0.13
Harbor seal	1.2	85	113 (0.4)	27	0.17
Harbor seal	2.4	82	106 (0.5)	24	0.05

TABLE II. Critical ratio data for one harbor seal and one California sea lion in the low- to mid-frequency range, including false alarm rates. The critical ratio is calculated as the difference between the observed narrowband signal threshold in terms of sound pressure level and the spectrum level of a white masking noise.

Noise Type	Signal Type	Subject	Predicted Threshold [dB re 1 µPa]	Observed Threshold (Std. Err.) [dB re 1 µPa]	Sensitivity Difference from Predicted [dB]	FA Rate
Flat	Narrowband	Sea lion	-	109 (0.4)	-	0.25
Flat	Narrowband	Harbor seal	-	107 (0.6)	-	0.13
Flat	Octave FM	Sea lion	111	107 (0.6)	4	0.19
Flat	Octave FM	Harbor seal	109	107 (0.5)	2	0.26
Flat	50 Hz AM	Sea lion	109	109 (0.5)	1	0.17
Flat	50 Hz AM	Harbor seal	107	106 (0.8)	1	0.13
Flat	Harmonic	Sea lion	107	100 (0.9)	7	0.12
Flat	Harmonic	Harbor seal	108	104 (0.5)	4	0.17
Shipping	Narrowband	Sea lion	109	103 (0.6)	6	0.13
Shipping	Narrowband	Harbor seal	107	104 (0.6)	3	0.13
Shipping	Octave FM	Sea lion	111	103 (0.4)	8	0.10
Shipping	Octave FM	Harbor seal	110	103 (0.4)	7	0.13
Shipping	50 Hz AM	Sea lion	109	105 (0.6)	4	0.19
Shipping	50 Hz AM	Harbor seal	107	111 (0.3)	-3	0.17

TABLE III. Predicted and observed masked detection thresholds from Experiment II for narrowband and complex signals masked by either flat-spectrum noise or shipping noise. The narrowband and FM center frequencies, as well as the AM carrier frequency, were all 0.6 kHz. The harmonic signal fundamental frequency was 0.3 kHz. A positive sensitivity difference indicates that the animal was more sensitive than predicted, i.e., the observed threshold was lower than predicted. Narrowband signals in white noise (critical ratios) are treated as controls because they served as the basis for predictions. False alarm rates and standard errors are also included.



California sea lion

harbor seal

FIG 1. Audiograms for the California sea lion and harbor seal subjects. Audiogram data are plotted as 50% correct detection thresholds (left axis) and ambient noise data for the test enclosure are plotted as spectrum levels estimated from 1/3-octave band levels (right axis). All data were collected at the same facility using similar methods. Dates indicate the years over which data were collected. Note that threshold predictions for the harbor seal at frequencies below 6.4 kHz were based on the more recent (2013) data. Data not from this study are summarized in Reichmuth *et al.* (2013). Ambient noise measurements were made in 2011-2012 and validated during testing.

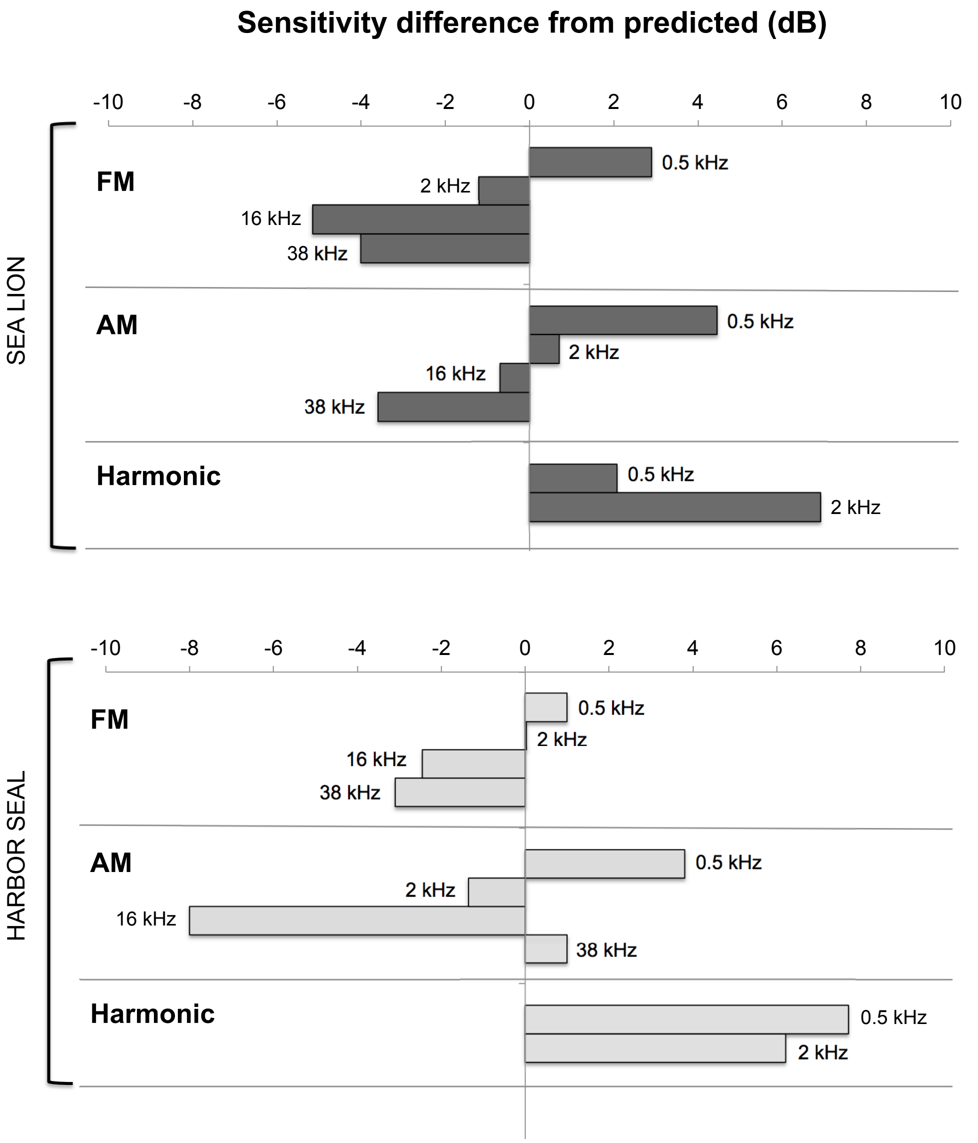


FIG 2. Sensitivity differences relative to predicted values for two pinniped subjects performing a detection task with complex signals in quiet conditions (Experiment I). Positive values indicate greater than predicted sensitivity. Three types of signals were tested: Octave-band FM, 50 Hz AM, and multi-component harmonic complexes. Frequencies indicate center frequency (FM), carrier frequency (AM), or fundamental frequency (harmonic). Predictions were based on subject audiograms combined with a basic hearing model.

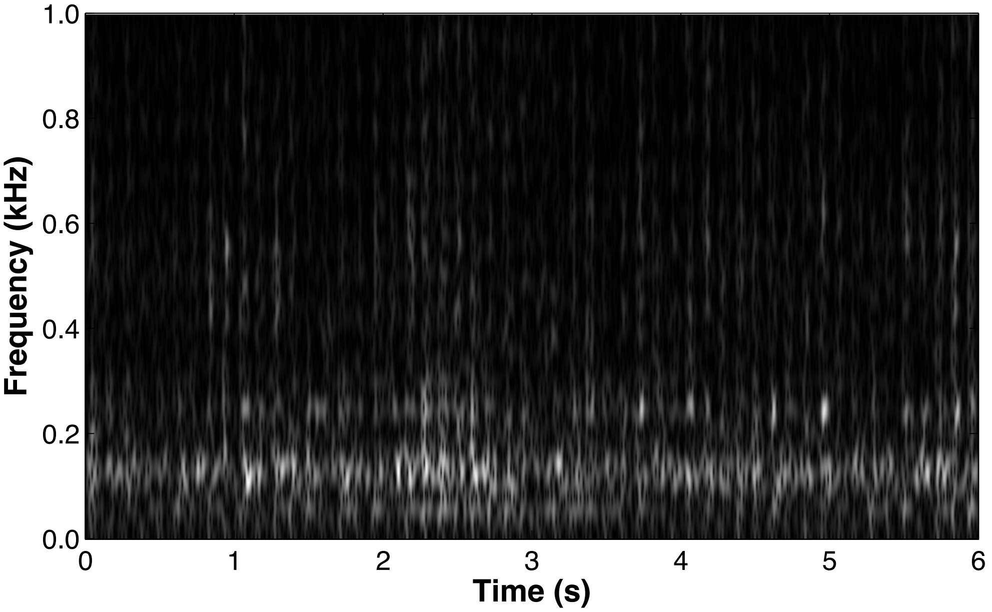


FIG 3. Spectrogram of the shipping noise used to mask simple and complex signals in Experiment II. Lighter shades represent high-energy regions. The presence of repeated vertical bands of energy indicate that this noise is comodulated.

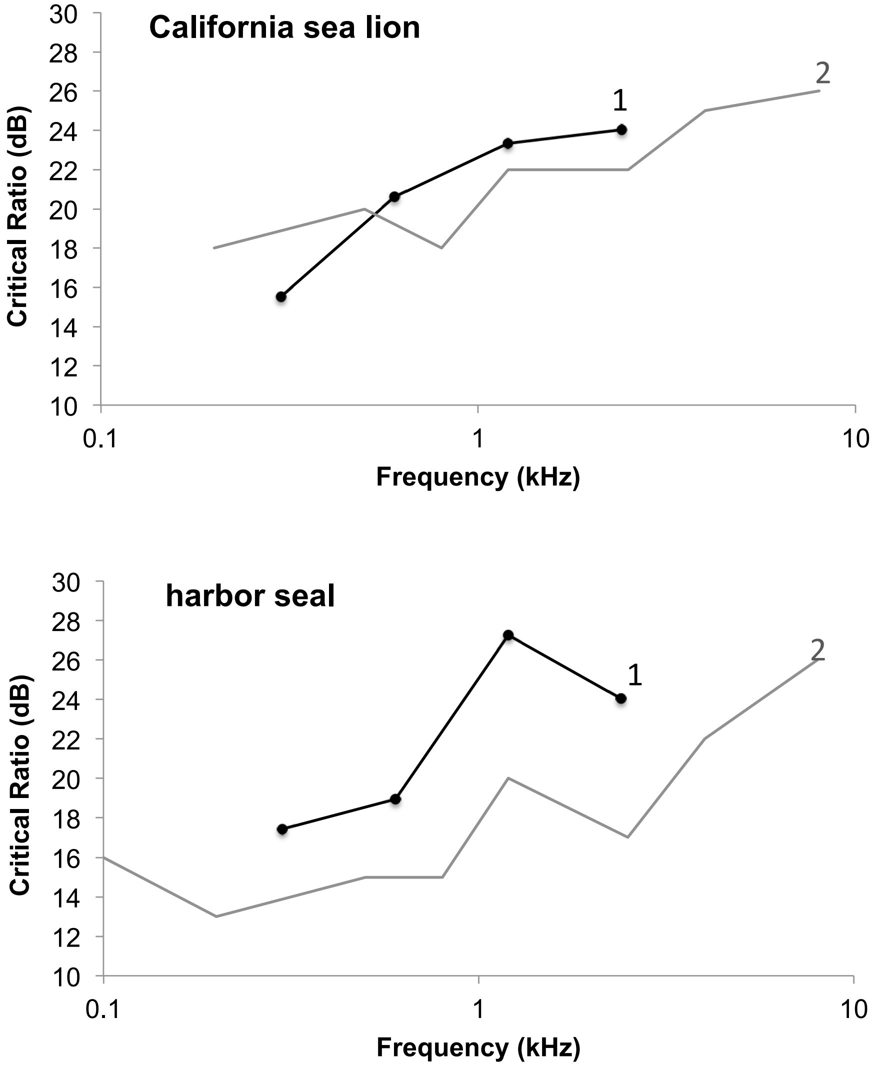


FIG 4. Critical ratios for one California sea lion and one harbor seal plotted with existing data for these species. Data are from either (1): this study, or (2): Southall *et al.*, 2000. Sea lion data represent two different female subjects; harbor seal data were collected from the same male subject at 9 and 25 years old. While the harbor seal sensitivity patterns are similar at both ages, the more recent data from this study are elevated relative to the older data, likely as a result of age-related loss of frequency selectivity

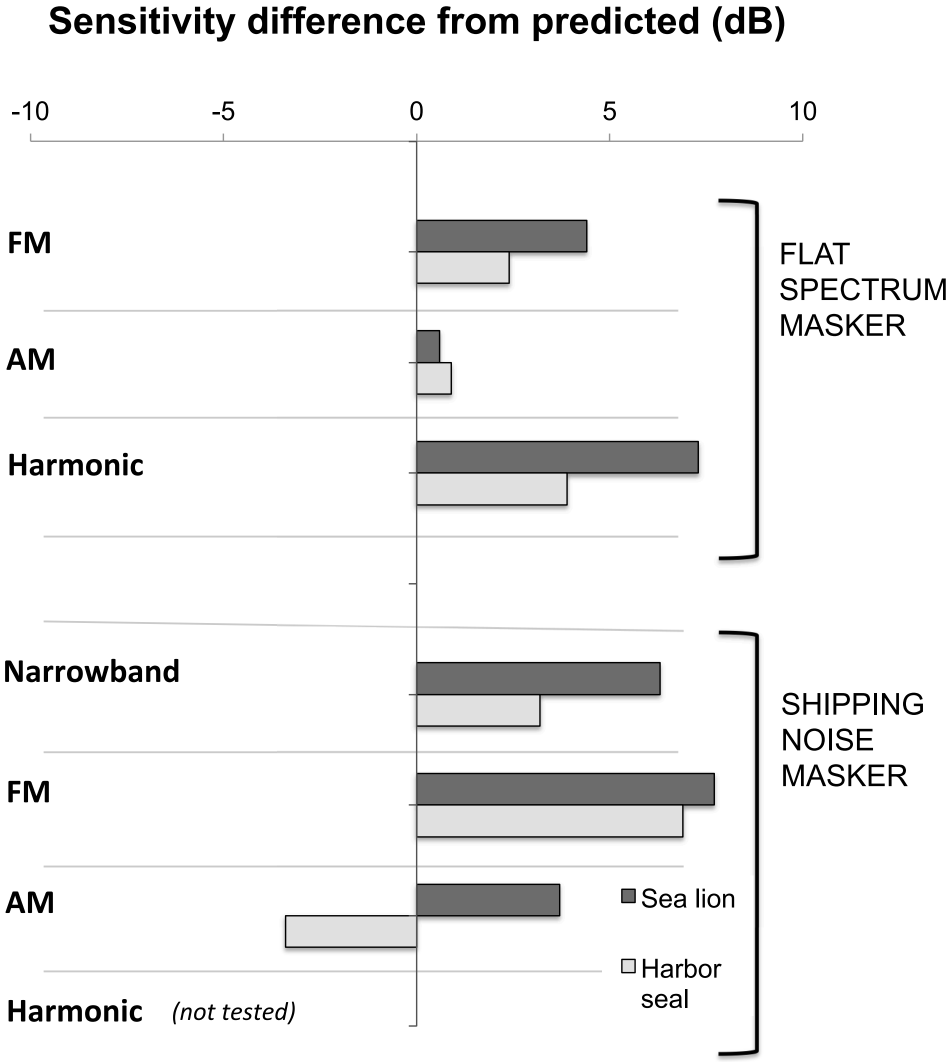


FIG 5. Sensitivity differences relative to predicted values for two pinniped subjects performing a detection task with complex signals masked by either flat-spectrum noise or recorded shipping noise (Experiment II). Positive values indicate greater than predicted sensitivity. Four types of signals were tested: Narrowband, 50 Hz AM, octave-band FM, and a multi-component harmonic complex. Predictions were based on subject critical ratios combined with a power spectrum model of auditory masking.

CHAPTER 3

High-frequency hearing in seals and sea lions

ABSTRACT

Limited evidence suggests that the underwater audiograms of seals and sea lions may exhibit two distinct regions on the high-frequency end, the first characterized by a rapid decrease in sensitivity with increasing frequency—i.e. a steep slope—followed by a much less rapid sensitivity decrease—i.e. a shallower slope. If confirmed, the presence of two slope-regions would complicate the traditional under water high-frequency hearing limits for these animals. This is problematic given the rapid increase in high-frequency, high-energy marine acoustic technologies—such as commercial sonars and recreational fish-finders—the outputs of which may disturb wild pinnipeds. Further, the presence of two distinct slope-regions does not agree with the prominent hypothesis that underwater high-frequency hearing in pinnipeds is primarily limited by cochlear constraints. In this study, sensitivity patterns in the 50-180 kHz range were measured for a California sea lion (*Zalophus californianus*), a harbor seal (*Phoca vitulina*), and a spotted seal (*Phoca largha*). In addition, a masking experiment was conducted to determine how ultrahigh frequency energy is encoded on the basilar membrane. Results confirm the presence of two distinct slope-regions at the high-frequency end of the audiogram and suggest that the initial, rapid decrease in sensitivity is not due to cochlear constraints, but rather to constraints on the conductive mechanism.

I. INTRODUCTION

The ears of pinnipeds are amphibious, meaning that they operate effectively both in air and under water (Reichmuth *et al*. 2013). This is remarkable given the different obstacles presented by the two media. In air, the major difficulty is the large impedance mismatch between the gaseous media surrounding the head and the cochlear fluids, which makes the efficient transfer of acoustic energy from one to the other challenging. In mammals, this problem is solved by the middle-ear ossicles, which act as an amplifier and impedance matcher. Under water, however, the air-filled middle-ear cavity that contains the ossicles creates the inverse impedance-matching problem, effectively blocking the traditional air-conduction energy-transmission pathway to the cochlea. Because of this, it has long been assumed that sound must travel along an alternate pathway (or pathways) to the inner ear in order for pinnipeds to hear effectively under water, and that different auditory mechanisms must therefore be responsible for energy transmission in air versus under water (Møhl, 1968a). In other words, pinniped underwater hearing is thought to be bone conducted, meaning that sound energy travels to the cochlea via direct coupling of the surrounding fluid to the animal's flesh and bone, allowing the air-filled middle-ear cavity to be bypassed (Møhl, 1968a; Repenning, 1972).

Psychophysical studies show that pinniped hearing capabilities are markedly different in air versus under water, supporting the hypothesis that different auditory mechanisms operate in the two media. Phocid seals, in particular, have an expanded frequency range of hearing in water relative to in air—a difference of over an octave (Reichmuth *et al*., 2013; Sills *et al*., 2014). Hemilä *et al.* (2006) hypothesized that this difference is primarily due to the massive middle-ear ossicles characteristic of phocids. These authors argued that ossicular inertia would impede the transmission of high-frequency energy in air, but could aid the transmission of bone-conducted underwater sound via amplification of the relative motion that occurs between the ossicles and the cochlea when the head vibrates. They further hypothesized that, while middle-ear inertia acts to constrain aerial high-frequency hearing in phocids, cochlear constraints—such as the end of the tonotopic map of the basilar membrane (BM) or an upper frequency limit of the cochlear amplifier—are the primary limit on underwater high-frequency hearing in both phocid and otariid pinnipeds.

The hypothesis that high-frequency underwater hearing is limited by cochlear constraints has recently been used to interpret auditory data for several pinniped species (e.g., Reichmuth *et al*., 2013; Mulsow *et al*., 2012). The apparent shape of pinniped audiograms at ultrahigh frequencies, however, challenges this influential idea. Studies of both California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*) suggest that the portion of the audiogram near the high frequency hearing limit—around 40 kHz for California sea lions and 80 kHz for harbor seals—may be characterized by two distinct regions with different slopes (Møhl, 1968b; Schusterman *et al*., 1972; Kastelein, 2009; Cunningham, 2014). In both species, the rate at which sensitivity decreases with increasing frequency is initially very rapid, but appears to decrease once a certain frequency is reached. In other words, the slope of the audiogram near the high-frequency hearing limit starts off very steep, but then becomes shallower at even higher frequencies (Fig. 1). However, data at these ultrahigh frequencies (frequencies in the second, shallow slope region) are relatively scarce and the two-slope phenomenon has yet to be shown conclusively. The confirmed existence of a second, shallower slope-region would indicate that the cochlea is capable of processing sounds at ultrahigh frequencies, suggesting that the steep-slope portion of the audiogram is the result of constraints on the bone-conducted energy transmission mechanism, rather than constraints on the inner ear.

Overall, underwater high-frequency hearing in pinnipeds is poorly understood—both in terms of the underlying mechanism, and in terms of the shape of the audiogram. This is partially due to the fact that auditory sensitivity at high and ultrahigh frequencies is relatively low. Low sensitivity means that few naturally occurring ultrahigh-frequency sounds will be audible to pinnipeds, which can lead to the assumption that hearing at these frequencies is not biologically relevant. However, there are an increasing number of human-made marine technologies that generate sounds in the 80-180 kHz range at source levels as high as 230 dB re 1 μPa @ 1m[a]—such as commercial sonar and recreational fish finders (Hildebrand, 2004; Hildebrand, 2009). Such noises may indeed be audible to pinnipeds, and depending on the shape of individual audiograms, could be perceptually quite loud. The relative lack of hearing data at ultrahigh frequencies has therefore become problematic and

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[a] Note that other factors in addition to source level, such as beam width and transmission loss must be taken into account when predicting the effects of noise on wild animals.

has led to confusion as to which underwater sounds pinnipeds may be able to detect (Cunningham *et al*., 2014).

The primary goal of this study was to extend the existing underwater audiograms of one California sea lion, one harbor seal, and one spotted seal (*Phoca largha*) to 180 kHz by measuring behavioral auditory detection thresholds in quiet conditions. The secondary goal was to conduct an auditory masking experiment with a single pinniped subject (the harbor seal) to determine how ultrahigh frequency sounds are encoded on an individual's BM, thereby providing insight into the physiological factors contributing to the shape of the audiogram at ultrahigh frequencies.

II. MATERIALS AND METHODS

Two experiments were conducted as a part of this study. Both involved the measurement of underwater auditory detection thresholds for experienced animal subjects using behavioral methods. Experimental testing was conducted in an outdoor, semi-in-ground, circular, concrete test pool (7.6 m diameter, 1.8 m depth) filled with natural seawater, with the subject at a depth of 1 m and the projector approximately 60 cm in front of the subject. Two psychophysical methods were used in succession for all threshold measurements. A staircase (up/down) procedure was used for the first three to five sessions to obtain an initial threshold estimate. This was followed by two to three sessions of testing using a method of constant stimuli from which final thresholds were calculated. To ensure that threshold measurements were comparable to earlier measurements made for the same individuals, the test environment, psychophysical procedure, and threshold analysis methods were kept the same as in Reichmuth *et al*. (2013) and Sills *et al*. (2014) for both of the experiments in this study. This includes the stimuli characteristics, the procedure for calibrating stimuli and controlling spatial variability in the received sound field, and the calculation of 50% correct-detection thresholds using probit analysis. These prior studies should be consulted for details on these aspects of the experimental methodology.

The equipment chain used to project, receive, and calibrate signals was the same in both experiments. Outgoing signals were generated using custom software on a PC (HTP, Finneran, 2003). From the PC, signals were sent to a NI USB-6259 data acquisition system for digital-to-analog conversion (500 kHz sampling rate, National Instruments Corp., Austin, TX), attenuated using a TDT PA5 programmable attenuator (Tucker-Davis Technologies, Alachua, FL), and amplified using a Hafler P1000 amplifier (Hafler Professional, Tempe, AZ). Depending on frequency, signals were projected either from an ITC 1042 (International Transducer Corp., Santa Barbara, CA), or a Reson 4013 projector (Teledyne-RESON A/S, Slangerup, Denmark) and received by either a Reson 4032 or a Reson 4014 receiver.

Because this study deals with sounds at relatively high SPLs projected in an enclosed pool, extra care was taken to ensure signal fidelity in both time and frequency domains. This included visual inspection of digitized signals on a PC prior to each experimental session, as well as post-hoc analyses of temporal variability and additional inspection of recorded signals for artifacts or distortion. The details of these analyses are presented in Appendix B.

A. Sensitivity

The goal of the first experiment was to measure pinniped underwater auditory sensitivity in the 50-180 kHz range. To this end, 50% correct-detection thresholds were measured in quiet conditions for three pinniped subjects: one 6-year-old female California sea lion (*Ronan,* NOA0006602), one 26-year-old male harbor seal (*Sprouts,* NOA0001707), and one 4-year-old male spotted seal (*Tunu,* NOA0006674). The subjects were experienced in behavioral auditory testing and their hearing sensitivity had been previously measured under water at frequencies extending to 43 kHz for the sea lion (Reichmuth et al., 2013), and to 72.4 kHz for the harbor seal and spotted seal (Reichmuth et al., 2013, Sills et al., 2014).

The test signals were narrowband FM sweeps (10% bandwidth) of 500 ms duration presented within a 4 s trial window. Narrowband FM sweeps were used in favor of pure tones to reduce the spatial variability of signal SPL in the reverberant test environment (Kastelein *et al.*, 2002; Finneran & Schlundt, 2007). The hearing sensitivity of each subject was initially tested at signal frequencies 50, 80, 100, 140, and 180 kHz in a mixed order. The sea lion subject was tested at two additional frequencies—36 and 40 kHz—in order to fully capture the steep-slope portion of the audiogram. Additional hearing thresholds were obtained in quiet conditions for the harbor seal subject at 40, 50, 60, 70, 80, 90, 100, 120, and 140 kHz within 4 months of initial testing as part of the masking portion of this study (see section II.B). Therefore, at frequencies that were tested twice for this subject, final thresholds were determined by taking the average of the two measurements. Testing for the sensitivity experiment took place between April 2014 and January 2015.

B. Masking

An additional masking experiment was conducted with a single subject—the harbor seal—in order to determine BM excitation patterns for a pinniped exposed to an ultrahigh frequency noise. For this experiment, 50% detection thresholds were measured at a total of nine signal frequencies in a mixed order (40, 50, 60, 70, 80, 90, 100, 120, 140 kHz), first in quiet conditions, and then in the presence of narrowband, 140 kHz masking noise. At each frequency, testing was fully completed in quiet conditions before testing in masked conditions began.

The masking noise used for this experiment was narrowband, flat-spectrum noise centered at 140 kHz and extending to +/- 5% of the center frequency (133-147 kHz). This noise was generated in MATLAB (MathWorks, Natick, MA), sent to a NI PCI-6251 DAQ data acquisition system (500 kHz sampling rate, National Instruments Corp., Austin, TX), and then to a Behringer XENYX 502 mixer (MUSIC Group Co., Las Vegas, NV), where the signal and noise were mixed prior to amplification and projection from a single Reson 4013 projector. The SPL of the masking noise was kept constant across all treatments at 143 dB re 1 μPa, equivalent to a sensation level

(SL) of 13 dB[b] for this subject. A narrowband masking noise was used in order to stimulate a narrow region of the BM while minimizing the presence of acoustic beats (Egan and Hake, 1950), thereby producing a masking pattern representative of BM excitation in response to140 kHz sound. Similar methods have been used to study BM excitation patterns at frequencies within the normal hearing range in humans (Moore, 1993), and to study the excitation patterns generated by an ultrasonic masker delivered via a bone vibrator (Nishimura *et al.*, 2003).

To ensure that SPL measurements taken at the calibration position were representative of the sound field encountered by the subject, the spatial variability of the masker was determined by measuring the SPL at 24 locations on a 7 cm x 7 cm x 7 cm, cubic grid centered around the location that was to be occupied by the subject's head during testing (as in Sills *et al.*, 2014). The SPL of the masking noise was within +/- 3 dB of the calibration position at all 24 locations. The gradual onset of the masking noise (0.5 s ramp) began approximately 2 s before the start of the 4 s listening interval of the trial, and the offset occurred after the end of the listening interval. Testing for the masking experiment took place between September 2014 and December 2014.

Following completion of auditory testing, a masking model was built to test the hypothesis that the observed peak masking frequency (i.e., the frequency at which the threshold was most elevated by the presence of the masking noise) was

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[b] The original intent was to have the masker at 15 dB SL, but subsequent threshold measurements at 140 kHz indicated that the actual sensation level was slightly less.

determined by the end of the tonotopic map of the subject's BM (i.e., the highest frequency encoded by the BM). This model is described in full detail in Appendix A.

III. RESULTS

A. Sensitivity

The absolute detection thresholds for signals from 36 to 180 kHz are given for each subject in Table I. Thresholds ranged from a minimum of 64 dB re 1 μPa (spotted seal, 50 kHz) to a maximum of 148 dB re 1 μPa (sea lion, 180 kHz). The 95% confidence intervals for all thresholds were less than 3 dB at each frequency, and all standard errors were less than 0.6 dB. The false alarm rates (rate of response on signal-absent trials) ranged from 10-26% across all frequencies. Each high-frequency sensitivity curve obtained for each subject exhibited two distinct slope-regions: a steep slope-region followed by a shallow slope-region. The average rate of sensitivity decrease in the steep slope-region across all three subjects was 320 dB/decade, compared to 70 dB/decade in the shallow slope-region. Fig. 2 depicts the high-frequency thresholds measured in this study for each subject, along with the most recent audiogram data for the same individual animal, and the published psychophysical audiograms for other individuals of the same species. For comparison purposes, Fig. 3 depicts the extended audiograms (data from this study merged with previous subject data) for all three subjects in a single plot.

B. Masking

The amount of masking induced in the harbor seal subject by a 140 kHz, 13 dB SL masking noise at nine signal frequencies (40-140 kHz) is depicted in Fig. 4 (panel A). Masking amounts ranged from 0.6-4.4 dB, with peak masking occurring at 90 kHz. Masking increased monotonically with frequency from 40-90 kHz before decreasing sharply at 100 kHz and remaining low up to 140 kHz. Fig. 4 (panel B) shows the masking pattern predicted by a masking model developed for this study—the details of which are presented in Appendix A—along with the empirical measurements from the harbor seal. This model was built on the assumptions that (1) the tonotopic map of the harbor seal subject's BM ends at 95 kHz, and (2) sound energy at frequencies beyond 95 kHz stimulates the very basal tip of the BM. The root-mean-square (RMS) error between the model and the experimental data was 0.4 dB; the coefficient of determination (R^2) was 0.98.

IV. DISCUSSION

This study confirms that pinniped underwater audiograms exhibit two distinct slope-regions on the high-frequency end: an initial region of steep slope, followed by a region of much shallower slope. This was true for all subjects tested, representing three species and two families (Otariidae and Phocidae). This two-slope phenomenon explains the ability of all subjects to detect signals at 180 kHz, well above their presumed individual high-frequency hearing limits (Kastelein *et al.*, 2009; Møhl, 1968b; Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013; Sills *et al.*, 2014). When considered together, the three extended audiograms show that the transition point between the steeper and shallower slope-regions occurs at higher frequencies for subjects with better high-frequency hearing. The general shapes of the curves, however, are strikingly similar (Fig. 3). This suggests that similar physical mechanisms are determining sensitivity at high and ultrahigh frequencies in all three species, though different mechanisms may be active in the two different slope-regions.

The maximum amount of masking measured for the harbor seal subject exposed to 140 kHz noise occurred at 90 kHz. In typical masking scenarios—i.e. those not using an ultrahigh-frequency masker—maximum masking occurs at the frequency where signal and noise energy overlap the most (Fletcher, 1940). This would have resulted in peak masking at 140 kHz, more than ½-octave higher than the observed peak at 90 kHz. A possible explanation for this discrepancy is that the tonotopic map of the subject's BM ends somewhere between 90-100 kHz. If this were the case, the sudden decrease in masking above 90 kHz could be explained by the fact that no region of the BM is tuned to these ultrahigh frequencies, and hence the cochlear amplifier is inactive (Robles & Ruggero, 2001). The model used in this study was built specifically to test this hypothesis. The good agreement between the modeled masking patterns and the experimental data suggests that the active region of the cochlear amplifier—and presumably the tonotopic map of the BM—ends somewhere between 90-100 kHz for the harbor seal subject.

The hypothesis that the cochlear amplifier is active up to 90 kHz in the harbor seal subject runs contrary to the hypothesis that cochlear constraints limit underwater high-frequency hearing in pinnipeds (Hemilä *et al*., 2006). If cochlear constraints were limiting high-frequency hearing, and if the cochlear amplifier were active up to 90 kHz, one would expect the rapid decrease in hearing sensitivity to begin around this frequency. Instead, the harbor seal audiogram shows that sensitivity begins to decrease sharply approximately one octave below 90 kHz. Further, if cochlear constraints were the cause of the steep-slope region of the audiogram, it is unclear why there would be a second, shallower slope region at even higher frequencies. A better explanation of these results is that the efficiency of the primary bone conduction mechanism mediating the transmission of acoustic energy to the cochlea rapidly decreases beyond a certain frequency limit, resulting in a sharp decrease in sensitivity and therefore a steep slope. The two-slope phenomenon can then be explained by the presence of a second bone conduction mechanism that is able to operate more effectively at higher frequencies. This hypothesis is supported by studies of bone conduction in humans and other terrestrial mammals showing the existence of different bone conduction mechanisms (or modes) that operate more or less effectively in different frequency ranges (Stenfelt, 2011). While some hypotheses exist as to how bone conduction may be enhanced by certain derived characteristics in the auditory peripheries of pinnipeds (Repenning, 1972), the precise bone conduction mechanisms involved in pinniped underwater hearing are presently unknown.

The idea that pinniped underwater high-frequency hearing is constrained by the limits of a conductive mechanism is analogous to the hypothesis that the middle ear constrains aerial high-frequency hearing in humans. Human aerial audiograms exhibit a characteristic steep slope around 14-20 kHz. The presence of a single steep-slope region means that sound quickly becomes inaudible beyond a certain frequency, and that the high-frequency hearing limits of individuals tend to be well defined. This has led to the designation of sounds above 20 kHz as ultrasonic, i.e. inaudible to humans. The rapid loss of sensitivity at high frequencies is often attributed to the frequency response characteristics of the middle ear (Pumphrey, 1950; Hemilä, 1995; but see Ruggero and Temchin, 2002). This hypothesis is supported by the fact that humans *can* detect ultrasound in conditions where the stimulus is directly coupled to the head, such as via a bone vibrator (Corso, 1963), or via immersion in liquid media—as when listening underwater (Deatherage *et al*., 1954). Presumably, ultrasound is detectable in these situations because a bone-conducted pathway that bypasses the middle ear is available. The observation that human bone-conducted sensitivity patterns and pinniped underwater sensitivity patterns both exhibit two slope-regions near the high-frequency hearing limit has lead to the suggestion that similar mechanisms may be operating in both listening scenarios (Schusterman, 1972; Cunningham, 2014).

The bypassing of the middle ear is not the only possible explanation for the human ability to detect bone-conducted sound above 20 kHz. It has been proposed that ultrasound may be demodulated to lower frequencies by a non-linear process inherent to the bone-conducted energy pathway along which it travels (Lenhardt, 2003). Such a phenomenon could account for both the ability to detect ultrasound, and the fact that ultrasound is generally perceived as having a pitch in the high-audio range (Dieroff and Ertel, 1975; Kono *et al.*, 1985). Hypotheses as to the precise bone-conducted pathway that could lead to demodulation are scarce. Lenhardt (2003) proposed that ultrasonic energy is demodulated as it travels from the brain tissue, to the cerebrospinal fluid, to the cochlear aqueduct, to the scala tympani. According to this hypothesis, the frequency to which ultrasound is demodulated is determined by the size of the brain, and hence should vary inversely with head size. Therefore, the peak masking frequency resulting from an ultrasonic masker should also vary inversely with head size. By Lenhardt's (2003) calculations, the resonant frequency for a cat brain is around 40 kHz. Given that the brain of a harbor seal is larger than that of a cat, it would be reasonable to predict that, if a brain-demodulation mechanism were active for the harbor seal subject, the peak masking frequency would be less than 40 kHz. The observed peak masking frequency of 90 kHz, therefore, contradicts this hypothesis for the harbor seal.

Pitch perception and frequency discrimination studies provide additional insight into the frequency limits of the tonotopic map of the BM. In humans, it has been shown that pitch discrimination of bone-conducted ultrasonic tones is limited to frequencies below approximately 16-17 kHz, only slightly higher than the pitch discrimination limit for air-conducted sound (Corso and Levine, 1965). This upper-limit of frequency discrimination has been interpreted as marking the upper-frequency limit of the tonotopic map of the BM. Pinnipeds similarly show an upper limit, with the frequency discrimination ability of a California sea lion limited to about 40 kHz (Schusterman and Moore, 1978), versus about 60 kHz in a ringed seal and a harbor seal (Møhl, 1967; Terhune and Ronald, 1976). These results have led to speculation that tonotopic map of the BM ends around 40 kHz in otariids, while the phocid map ends around 60 kHz (Schusterman and Moore, 1978). The upper-frequency discrimination limit of 60 kHz is somewhat less than the 90-100 kHz limit of the tonotopic map indicated by the present study. However, comparing frequency discrimination data from these single subject studies with the masking data reported here for a harbor seal is problematic, as individual high-frequency hearing is likely variable.

It should be emphasized that interpreting the ultrahigh frequency masking data from this study is difficult given that only one subject was tested. More information is needed to determine the physiological mechanisms governing the shape of the pinniped audiogram at high frequencies. Future studies should focus on similar masking experiments with other subjects, and on expanding frequency discrimination and pitch perception data at ultrahigh frequencies. The measurement of psychophysical tuning curves near the high-frequency hearing limit could be particularly useful in determining whether the sharp tuning thought to be a product of the cochlear amplifier is present in these frequency regions. Until such studies are conducted, it can not be assumed that pinniped underwater high-frequency hearing is limited by cochlear constraints.

While uncertainty remains as to the precise mechanisms supporting pinniped underwater hearing, the sensitivity curves from this study, combined with measurements from earlier studies (Møhl, 1968b; Schusterman *et al*., 1972; Kastelein, 2009), demonstrate that pinniped audiograms are characterized by two distinct slope-regions on the high-frequency end. This explains the surprising abilities of seals and sea lions to detect sounds that are well above their nominal underwater high-frequency hearing limits. For example, the sea lion subject in this study could detect sounds at 180 kHz, two full octaves above the traditional California sea lion high-frequency hearing limit of 36-40 kHz (Mulsow, 2012; Reichmuth, 2013). Because of this, the two-slope phenomenon must be taken into account when evaluating the potential effects of high-frequency, high-energy marine technologies such as commercial sonars and recreational fish finders—an issue that will only become more relevant as these technologies progress and proliferate.

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APPENDIX A

A masking model based on BM displacement was created for this study to test the hypotheses that (1) the harbor seal subject's tonotopic map ends between 90-100 kHz, and (2) sound energy beyond the range of the tonotopic map stimulates the basal tip of the BM without activating the cochlear amplifier. The model compares estimated BM displacement for tonal signals and a 140 kHz noise masker in order to predict masking amounts. For signals, BM displacement was modeled as a function of signal SPL and frequency:

$$D_s(p,f) = p \cdot \frac{m(f)}{2} + D_0 \text{ (1),}$$

Where D_s is BM displacement in dB re d_Δ, and $m(f)$ is the rate of growth of displacement per unit pressure (in dB/dB) as a function of signal frequency. The factor of ½ associated with the growth function is included so that linear growth occurs at $m(f) = 1$ dB/dB, given that pressure is modeled in terms of SPL (dB re 1 μPa), which is determined by the square of the RMS pressure. The reference displacement, d_Δ, is the smallest detectable displacement such that when the signal SPL equals the pressure corresponding to the detection threshold ($p = p_T$), the BM displacement is 0 dB. Using this fact, Eq. 1 can be solved for D_0 at $p = p_T$:

$$D_0 = -p_T \cdot \frac{m(f)}{2} \text{ (2).}$$

The rate of growth of BM displacement—($m(f)$)—depends on whether the center frequency of the BM location being considered is the same as the frequency of the signal. If the signal is stimulating a region of the BM tuned to the signal frequency, BM displacement will grow at a slower-than-linear rate with increasing pressure due to a well-known compressive nonlinearity within the BM response thought to be the result of an active mechanism known as the cochlear amplifier. When the center frequency of the BM location being considered is distant from the frequency of the stimulating signal, the cochlear amplifier is considered to be inactive and displacement grows linearly with pressure (Robles and Ruggero, 2001).

For each signal considered in the masking model, the BM region of interest is where the maximum displacement occurs. For signals at frequencies within the range represented on the tonotopic map, maximum displacement occurs at the BM location tuned to the signal center frequency. Because the center frequency of the BM region of interest (i.e., the region where displacement is being modeled) equals the signal frequency, displacement will grow at a less-than-linear rate due to the cochlear amplifier. However, signals at frequencies higher than the highest frequency encoded by the subject's BM are assumed to cause maximum displacement at the very basal tip of the BM (where the highest frequencies are encoded). As a result, the BM region of interest for such signals is tuned to a lower center frequency than that of the stimulating signal, and displacement is assumed to grow at a linear rate. Hence, the growth-rate function—($m(f)$)—should be less than linear for signals at frequencies within the range of the tonotopic map and should transition to a linear rate once the end of the tonotopic map has been reached. This was achieved by modeling the growth function as a function of signal frequency using Eq. 3:

$$m(f) = m_{NL} + \frac{m_L - m_{NL}}{1 + e^{-(f - f_{end})}} \text{ (3),}$$

where m_{NL} is the non-linear rate of displacement growth for a BM location tuned to the frequency of the signal, and m_L is the linear growth rate for a BM location not tuned to the frequency of the stimulating signal. The function is a simple logistic curve that rapidly transitions from m_{NL} to m_L at the frequency corresponding to the end of the tonotopic map, f_{end}. Based on studies of the compressive non-linearity in multiple mammalian species (compiled in Robles and Ruggero, 2001), the value for m_{NL} was set to 0.3 dB/dB, and m_L was set to 1 dB/dB (linear growth with pressure). To test the hypothesis that the sharp drop-off in masking amount observed in this study between 90-100 kHz is caused by the end of the tonotopic map, the value of f_{end} was set to 95 kHz.

Because the energy in the 140 kHz masking noise was at frequencies above the assumed highest BM center frequency of 95 kHz, BM displacement due to the masker was modeled using the assumption that maximum displacement would occur at the very basal tip of the BM. As the displacement spreads apically, it was assumed to gradually decrease until it reached a magnitude that would not result in masking, i.e. d_Δ. Hence, BM displacement as a function of BM center frequency was modeled as a logistic function of the form:

$$d_m(F) = \frac{A \cdot d_\Delta}{1+e^{-k(F-F_0)}} + d_\Delta \text{ (4),}$$

where F is constrained to values less than or equal to 95 kHz, and $d_m(F)$ is in linear units of length.

In order to compare Eq. 4 to Eq. 1 (i.e., in order to compare the displacement caused by the signal to the displacement caused by the masker), Eq. 4 must be expressed in dB re d_Δ, which gives Eq. 5:

$$D_m(F) = 10 \log\left(\frac{d_m(F)}{d_\Delta}\right) \text{ (5).}$$

Then, comparing the difference in signal displacement and noise displacement to a threshold value gives:

$$T < D_s(p, f) - D_m(F) \text{ (6).}$$

The threshold T was set to 0 dB, i.e., the point at which displacement due to the signal equals the displacement due to the masker. Masked thresholds were subsequently modeled by combining Eqs. 1, 5, and 6, and solving for pressure, p.

The model was then fit to the experimental data by choosing the values for the three parameters determining the shape of the BM displacement—A, k, and, F_0—that minimize the RMS error between the model and the experimental data. The calculated values were $A = 0.2$, $k = 0.1$, and, $F_0 = 62\ Hz$; Fig. A.1 shows the resultant BM displacement. Using these parameters, the RMS error was 0.4 dB and the coefficient of determination (R^2) was 0.98.

APPENDIX B

When conducting underwater hearing experiments in an enclosed environment such as a test pool, acoustic reflections from the sides of the enclosure and from the air/water interface can create unwanted spatial and temporal variability in received signals. Because of this, special care was taken to ensure signal fidelity. As previously mentioned, signal spatial variability was controlled for in this experiment by requiring that the received SPL for all projected sounds was within 3 dB for 24 positions in a cubic grid surrounding the calibration position before testing could begin. Temporal variability in received SPL was also accounted for. For timescales greater than the signal duration (trial-to-trial timescales), temporal variability was quantified by measuring received SPL at the calibration position for 25 projections of the same signal over a 25-30 second period, and then calculating the standard deviation. For signals in the 50-180 kHz range, standard deviations increased slightly with increasing frequency, starting at 0.1 dB re 1 μPa at 50 kHz, and reaching a maximum of 0.5 dB re 1 μPa at 180 kHz. These measurements indicate that for all signals in this frequency range, received SPLs for different signal trials should be within +/- 1 dB of the desired level 95% of the time.

Temporal variability was also quantified on timescales shorter than the duration of a test signal (500 ms). This was achieved using custom MATLAB functions to measure the SPL of one thousand random samples, each 50 ms long, from recorded signals. The maximum SPL across all samples was then compared to the SPL over the full duration of the signal (the calibration level). For signals in the 50-180 kHz range, maximum SPLs for 50 ms samples were 1-2 dB higher than the full-duration SPLs. These measurements indicate that within-signal temporal variability was not a major factor in determining the audibility thresholds.

The relatively high SPLs employed in this study further complicated the acoustic situation and made it necessary to carefully inspect signals for low-frequency distortion. In addition to visual inspection of signals prior to each experimental session, signals were recorded for analysis using a low-noise, battery powered Fostex FR2 digital field recorder connected to the Reson 4014 located in the daily calibration position. Signals were projected at 80, 100, 140, and 180 kHz and outgoing voltages were adjusted to obtain a received SPL of 140 dB re 1 μPa. The maximum sampling rate of the FR2 was 192 kHz, limiting recordings to frequencies below 96 kHz, a range sufficient to capture any low-frequency signal distortion that may have been detectable by the subjects (at frequencies greater than 96 kHz, the subjects' detection thresholds were high enough that any audible distortion would have been clearly apparent during visual inspection).

For comparative purposes, recordings of ambient noise in the test environment (received sound at the calibration position in the absence of a projected signal) were taken using the same procedure. Custom MATLAB functions were then used to measure the average power spectral density (PSD) across 1/3-octave bands centered at frequencies ranging from 0.18-80 kHz. For each signal, 20 samples were measured. One hundred 500 ms samples of ambient noise were also measured (a duration of 500 ms was chosen to match the signal duration). The results of this analysis (Table B.I) show no evidence of any low-frequency distortion, indicating that subjects were responding to energy at the signal frequency and not distortion or artifacts.

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FREQUENCY (kHz)	THRESHOLD (dB re 1 µPa)		
	California sea lion	harbor seal	spotted seal
36	85		
40	110	75	
50	116	97	64
60		115	
70		117	
80	128	116	110
90		119	
100	132	120	113
120		125	
140	136	130	122
180	148	140	136

TABLE I. Fifty-percent auditory detection thresholds, measured under water in quiet conditions, for one California sea lion, one harbor seal, and one spotted seal. False alarm rates—calculated for each animal subject at each test frequency—ranged from 10-26%. Standard errors for all measurements were less than 0.6 dB.

1/3-Octave Bin Freq. (kHz)	Power Spectral Density (dB re 1 µPa^2/Hz)				
	Ambient (n=100)	80 kHz Signal (n=20)	100 kHz Signal (n=20)	140 kHz Signal (n=20)	180 kHz Signal (n=20)
0.18	65	64	64	65	64
0.20	62	61	61	63	61
0.25	59	58	58	58	58
0.32	57	56	56	54	56
0.40	54	55	54	54	53
0.50	53	53	53	53	53
0.63	52	51	51	52	51
0.80	51	51	51	52	51
1.25	50	50	51	50	50
1.58	50	50	50	50	50
2.00	50	50	50	50	50
2.50	50	50	49	50	49
3.15	49	50	49	50	49
4.00	49	49	49	50	49
5.00	50	50	50	50	50
6.30	49	49	49	49	49
8.00	49	49	49	49	49
10.0	48	48	48	48	48
12.5	48	48	48	48	48
16.0	48	48	48	48	48
20.0	48	48	48	48	48
25.0	48	48	48	48	48
32.0	48	48	48	48	48
40.0	48	48	48	48	48
50.0	48	48	48	48	48
63.0	48	48	48	48	48
80.0	48	97	50	48	48

TABLE B.I. Average PSD levels for 1/3-octave bands ranging from 0.18-80 kHz for four signals and ambient noise in the testing environment. Note that the PSD measurements are similar for treatments with signals and for ambient noise, indicating that no low-frequency distortion is present in the signals. The one exception is the 80 kHz 1/3-octave bin in the 80 kHz signal condition, which is expected.

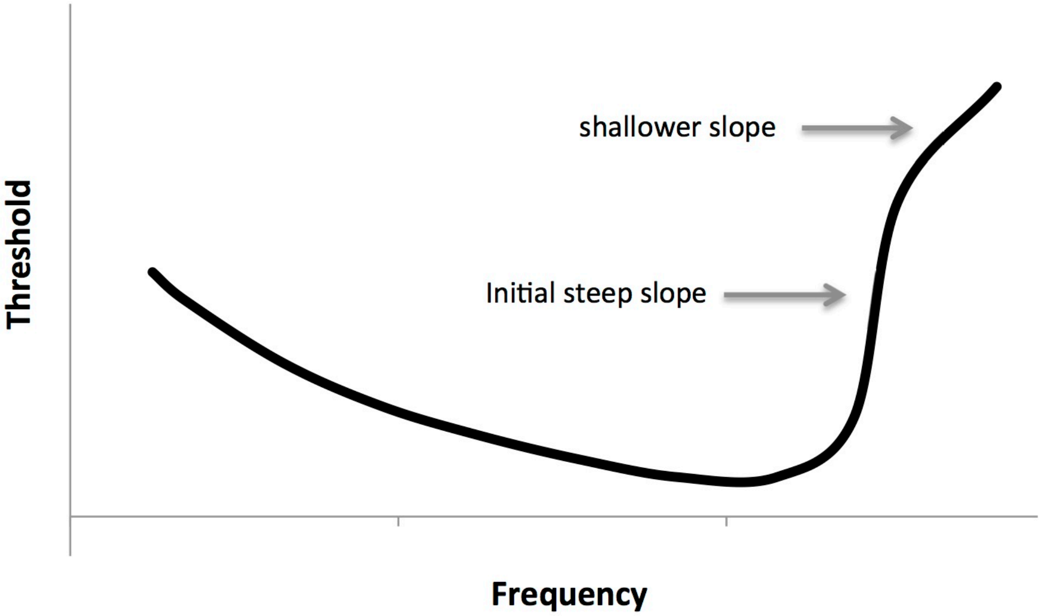

FIG 1. Illustration of the two slope-regions that have been observed on the high-frequency end of pinniped underwater audiograms. Both California sea lions and harbor seals have been shown to exhibit a similar pattern of an initial steep slope near the high-frequency hearing limit, followed by a shallower slope at ultrahigh frequencies. Note that this illustration does not represent a particular dataset and is only intended to depict the general curve-shape seen on the high-frequency end of some pinniped underwater audiograms.

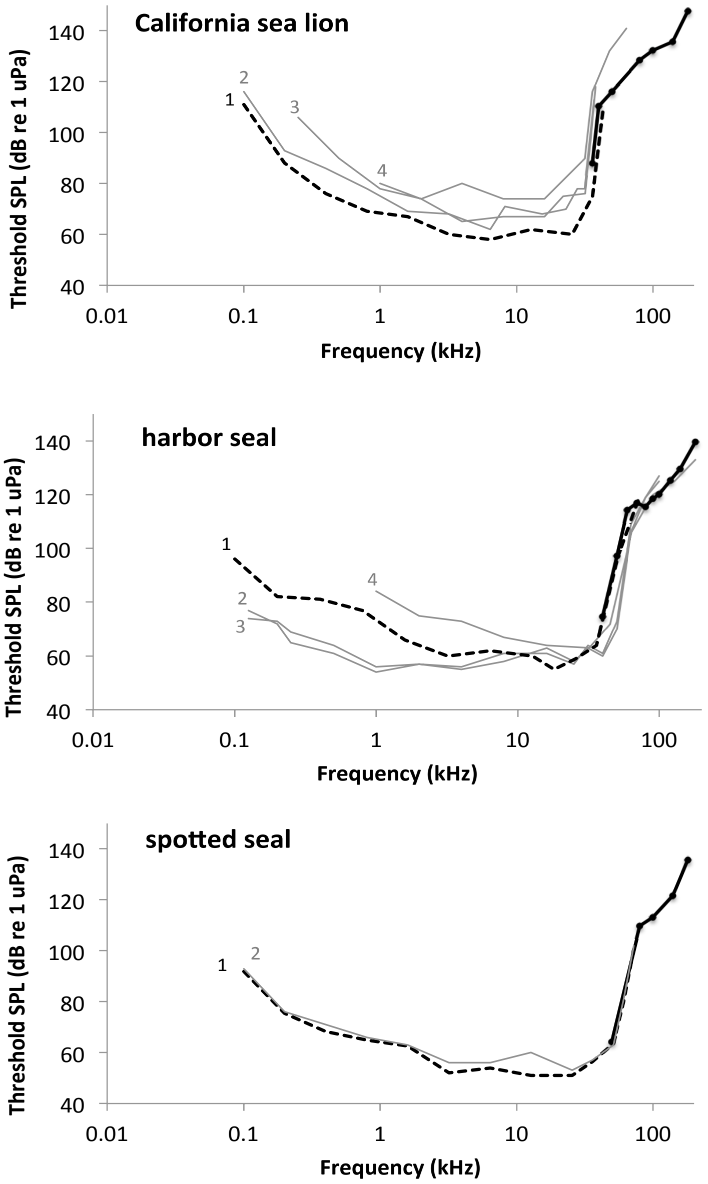

FIG 2. High-frequency auditory detection thresholds measured in this study for three pinniped subjects (solid lines), along with previously published audiogram data for the same individuals (dashed lines), and data from other individuals of the same species (light gray lines). Note the presence of two distinct slope-regions on the high-frequency end of the audiogram for all three subjects. California sea lion: 1 (Reichmuth *et al*., 2013), 2 (Schusterman *et al*., 1972), with 50% thresholds calculated in Reichmuth and Southall (2011), 3 (Reichmuth and Southall, 2011), 4 (Mulsow *et al*., 2012). Harbor seal: 1 (Reichmuth *et al*., 2013), 2 & 3 (Kastelein *et al*., 2009), 4 (Møhl, B., 1968a). Spotted seal: 1 & 2 (Sills *et al*., 2014).

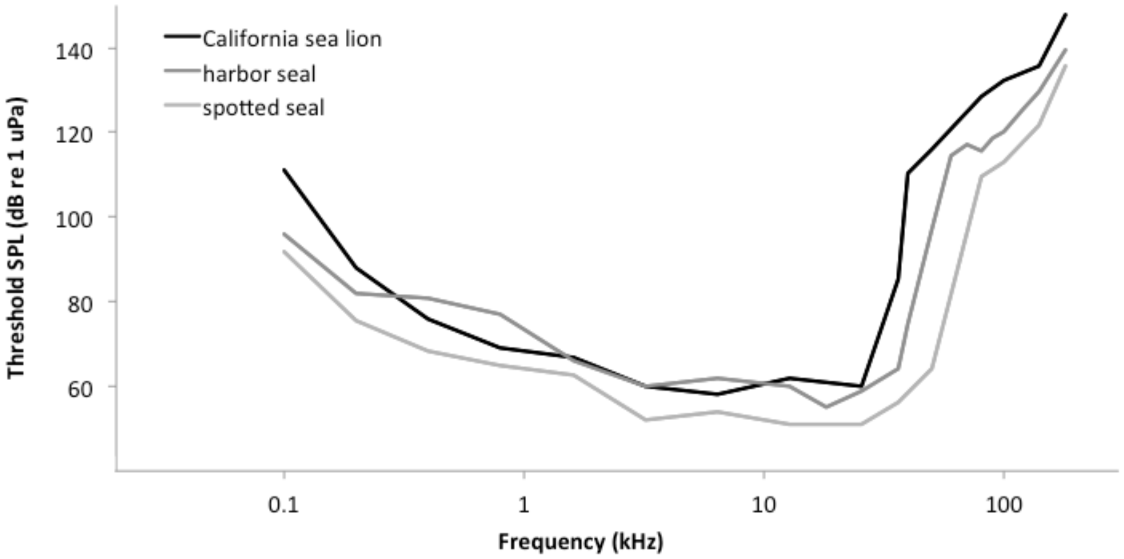

FIG 3. Extended audiograms for three pinniped subjects. Audiograms are composites of previously published data for the same animals (California sea lion and harbor seal: Reichmuth *et al*., 2013; spotted seal: Sills *et al*., 2014) and high-frequency data from this study. Note that, while the different animals have different hearing ranges, all three exhibit two distinct slope-regions on the high-frequency end.

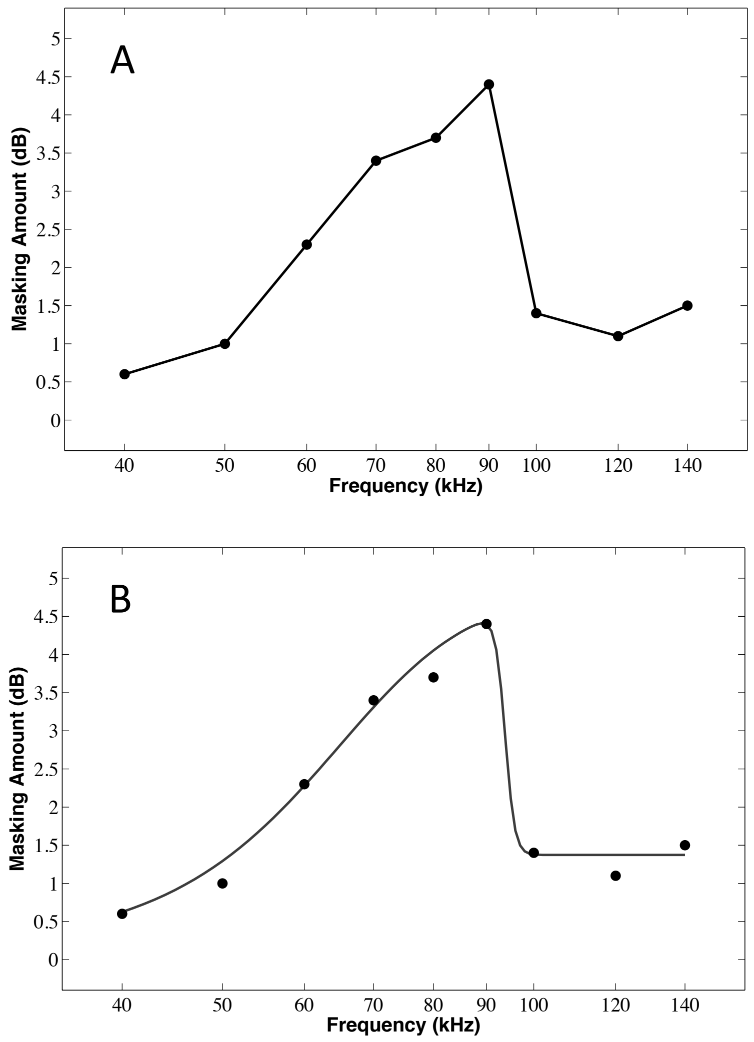

FIG 4. Masking amounts for a harbor seal subject exposed to a narrowband masking noise centered at 140 kHz at a sensation level of 13 dB. Panel A depicts the amount of masking for tonal signals in the 40-140 kHz range. Amount of masking is calculated as the difference between the detection threshold with and without the masker present. Panel B depicts the masking amount predicted by a model based on BM displacement (solid line) plotted over the experimental data (points). The model assumed that the tonotopic map of the harbor seal's BM ended at 95 kHz and that signals at higher frequencies stimulated the very basal tip of the BM.

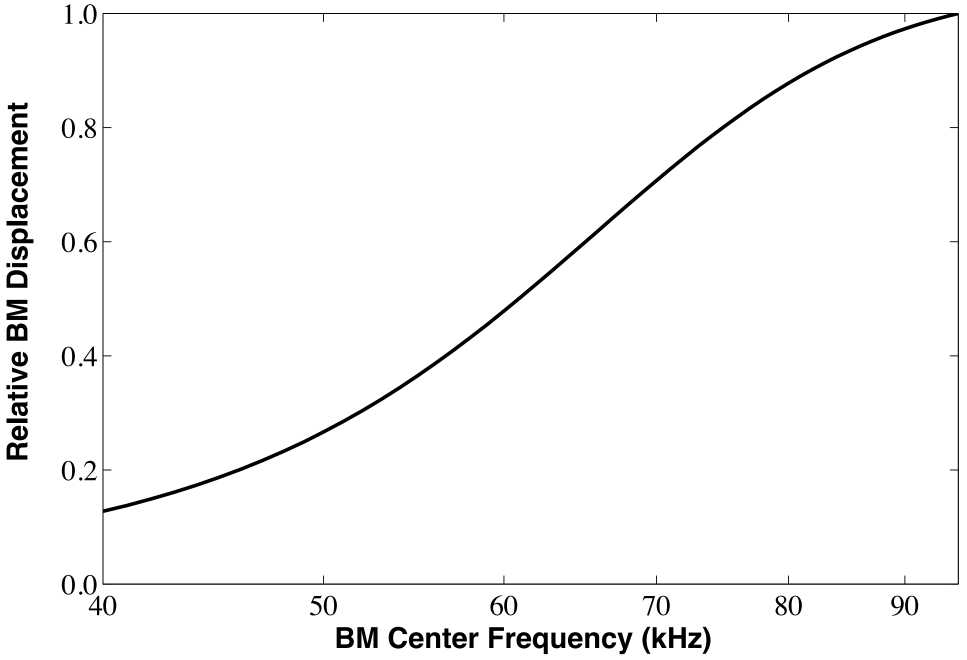

FIG A.1. Model of BM displacement caused by a 140 kHz narrowband masker. Displacement as a function of BM center frequency was modeled as a sigmoidal function, the parameters of which were determined by fitting the entire masking model to the empirical data using the minimum RMS error. Note that the end of the tonotopic map is assumed to occur at 95 kHz in the model used here.

SUMMARY

The experiments described in this dissertation were designed to address two major data gaps in pinniped auditory research, thereby improving understanding of how increasing levels of marine anthropogenic noise will affect wild pinnipeds. Specifically, this body of work was aimed at (1) expanding understanding of how effectively laboratory hearing data can be used to predict pinniped auditory performance in natural listening scenarios, and (2) extending measures of pinniped underwater hearing sensitivity to high and ultrahigh frequencies. The data generated as a part of this effort improve the ability of researchers to predict the effects of anthropogenic noise on pinnipeds, and hence improve the ability of regulators to effectively manage noise-generating human activities.

The results presented here demonstrate that traditional laboratory hearing data collected using simple stimuli do not accurately predict auditory sensitivity in certain listening scenarios involving complex sounds. Lower-than-predicted auditory detection thresholds measured as part of Chapter 2 indicate that the auditory systems of pinnipeds have evolved to exploit common complex features found in natural sounds. Specifically, the presence of multiple harmonics in acoustic signals enhanced detectability in both quiet and noisy conditions, while the presence of comodulation and/or frequency modulation enhanced detectability in noisy conditions only. These effects are likely related to higher-order processes in the auditory systems of pinnipeds that compare information across multiple auditory filters and extract temporal properties from amplitude envelopes. The enhanced detectability of complex signals is problematic for regulators attempting to predict the effects of noise on wild pinnipeds using baseline laboratory hearing data that do not account for the enhanced detectability of certain complex sounds. As such, the research described here should be expanded in order to inform improved auditory models that incorporate the effects of the complex acoustic features of natural sounds.

Future research efforts in this area should focus on improving auditory models without increasing complexity to the point of impracticality. The experimental results described in Chapter 2 clearly suggest certain future research directions. First, studies should be conducted to determine how the separability of signal and noise affect detectability in noisy conditions. While the findings presented in Chapter 2 support the hypothesis of Nelken *et al*. (1999) that inseparable signals may be more easily extracted from separable noise, an in-depth effort is necessary to determine the degree to which separability affects detectability and whether or not such an effect can be parameterized for inclusion in auditory models. Similarly, further work must be done to quantify how harmonic structure affects the detectability of signals in both quiet and noisy conditions so that this can also be accounted for in models.

The high-frequency sensitivity measurements presented in Chapters 1 & 3 confirm previous, preliminary observations of two-slope regions on the high-frequency end of pinniped underwater audiograms (Møhl, 1968b; Schusterman *et al.*, 1972; Kastelein *et al.*, 2009; Cunningham *et al.*, 2014). This two-slope phenomenon makes defining underwater high-frequency hearing limits of pinniped species difficult. This can lead to confusion over what types of high-frequency sounds may be audible to wild pinnipeds, as demonstrated in Chapter 1. This is an important consideration for regulators given the rapid proliferation of high-energy acoustic marine technologies operating in the 80-200 kHz frequency range, such as commercial and recreational sonars and fish-finders. Further, the two-slope phenomenon and the results of the masking study presented in Chapter 3 are inconsistent with the prominent hypothesis that pinniped underwater hearing is limited by cochlear constraints (Hemilä *et al.*, 2006), suggesting instead that the primary constraint on high-frequency hearing is the frequency range over which energy can be efficiently transferred to the cochlea via bone conduction.

Considerable further work is needed to fully understand underwater hearing in pinnipeds at high and ultrahigh frequencies. The high-frequency sensitivity measurements presented in Chapter 3, combined with measurements from previous studies, provide considerable evidence in support of the presence of two slope-regions near the high-frequency hearing limit. Uncertainties over the mechanism behind this phenomenon, however, remain. While the masking study in Chapter 3 suggests that the high-frequency hearing limit in pinnipeds does not have a cochlear origin, it should be emphasized that this was a single study conducted with a single individual, and so the results must be verified. Future work should focus on identifying the physical processes that give rise to the steep-slope region of pinniped audiograms near the high-frequency hearing limit, possibly through the measurement of psychophysical tuning curves at high and ultrahigh frequencies.

In addition to providing new knowledge of hearing capabilities in pinnipeds, the data collected as part of this dissertation are intended to aid regulators charged with mitigating the potential effects of anthropogenic noise on marine wildlife. The experiments described herein focused on filling prominent gaps in understanding of underwater hearing in pinnipeds. The acoustic environments of the world's oceans will no doubt continue to change as marine technologies advance and proliferate. Because of this, an in-depth understanding of pinniped auditory sensitivity is needed to ensure that important life functions mediated by sound are not disrupted in wild animals.

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