Title

Auditory studies of spotted and ringed seals: Amphibious hearing and the effects of noise

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AUDITORY STUDIES OF SPOTTED AND RINGED SEALS: AMPHIBIOUS HEARING AND THE EFFECTS OF NOISE

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by

Jillian M. Sills

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AUDITORY STUDIES OF SPOTTED AND RINGED SEALS: AMPHIBIOUS HEARING AND THE EFFECTS OF NOISE

Jillian M. Sills

ABSTRACT

The auditory biology and acoustic behavior of Arctic seals are incompletely understood, in large part due to the significant challenges of studying ice-living seals in natural habitats. Consequently, many questions regarding their perception of acoustic cues in the marine environment, and the ways in which increasing anthropogenic noise may influence their ability to detect biologically relevant sounds, remain unanswered. This dissertation describes a series of behavioral studies conducted in the laboratory to characterize the auditory capabilities of trained spotted (*Phoca largha*, Pallas 1811) and ringed seals (*Pusa hispida*, Schreber 1775) in quiet conditions, in the presence of controlled noise, and in real-world listening scenarios. The first two chapters comprise a set of three standard audiometric studies for each species, including aerial audiograms, underwater audiograms, and critical ratio measurements in both media. The results presented in Chapter 1 are the first hearing data available for spotted seals, and provide insight into the acoustic ecology of this minimally studied species. The results presented in Chapter 2 are the most comprehensive hearing data available thus far for ringed seals, and offer an updated perspective on the auditory capabilities of this species relative to historical data.

Chapter 3 builds upon these standard examinations of hearing to investigate auditory performance in more complex acoustic environments—specifically, habitats altered by seismic noise from geophysical exploration. Taken together, these experiments provide fundamental knowledge about the sensory biology of spotted and ringed seals, which can be applied to management decisions for these species in an increasingly human-influenced Arctic environment.

DEDICATION

To my ice-living collaborators at the Pinniped Lab

Amak, Tunu, Natchek, and Nayak

without whom none of this research would have been possible.

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The body of work presented herein was made possible by the contribution of many, many individuals. First and foremost I would like to thank my husband, Ryan, for tolerating my long and often unpredictable hours at the lab, for reading every draft of every paper, for never getting tired of talking about critical ratios or reaction time data, and for being a constant source of calm and strength. I am incredibly lucky and incredibly grateful. Without his unwavering confidence and patient MATLAB help I could never have completed this dissertation. I thank my parents, Alyssa and William, for being my first and my biggest fans, for believing in me, and for always encouraging and enabling me to follow my dreams. I also thank my sisters Nicole, Cassandra, and Lauren; my stepmom Jackie; my grandparents Stan and Joanna Cutler, William and Frances Vitacco, and Steve Zappalla; and all the rest of my family, whether or not we are related by blood, for being my foundation and for contributing to my work in countless ways.

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Sills, J. M., Southall, B. L., and Reichmuth, C. 2015. Amphibious hearing in ringed seals (*Pusa hispida*): underwater audiograms, aerial audiograms, and critical ratio measurements. *The Journal of Experimental Biology* 218: 2250-2258. doi:10.1242/jeb.120972

Co-author Dr. Colleen Reichmuth directed and supervised the research that forms the basis for this dissertation. Co-author Dr. Brandon Southall provided technical expertise regarding experimental design and analysis. As the first author on both publications and the author of this dissertation, I (Jillian Sills) designed all experiments, collected and analyzed all experimental data, and was responsible for manuscript preparation.

GENERAL INTRODUCTION

Sensory systems are shaped to a large degree by the environments in which they operate. When the terrestrial ancestors of marine mammals entered the aquatic environment, selective pressures imposed by the fluid medium progressively modified their physiology, anatomy, and behavior. In terms of sensory biology, air-adapted sensory organs evolved to function under water. For ancestors of modern-day pinnipeds (seals, sea lions, and walruses of the order Carnivora), which began their transition to the marine environment more than 25 million years ago, this presented a particular evolutionary challenge. Modern pinnipeds are amphibious mammals that operate at the interface of land and sea, a lifestyle that demands sensory structures capable of receiving and processing information in both environments. This unique requirement makes the sensory biology of these animals particularly interesting from both an evolutionary and an ecological perspective.

With regard to the auditory sense, pinnipeds rely on sounds received both above and below the water's surface to support social interaction, navigation, foraging, predator avoidance, and other essential life functions. In order to efficiently utilize acoustic information in both media, the auditory systems of pinnipeds are adapted to function in these two vastly different physical environments. While it is likely that the air-filled ear functions in the same manner as a traditional terrestrial ear above water, phocid (true) seals in particular exhibit a range of anatomical adaptations that may support enhanced sound reception under water. These include the absence of external pinnae, muscular control of the external meatal openings, a layer of cavernous tissue lining the outer and middle ear, enlarged auditory bullae, and massive middle ear ossicles relative to those of their terrestrial counterparts (Wartzok and Ketten, 1999; Nummela, 2008). These derived morphological features may be the result of selective pressures for underwater hearing or, alternatively, they may have been shaped by a need to withstand pressure effects experienced during diving. Regardless, the consequences of these structural adaptations are reflected in what is known to date about the functional hearing of seals.

Phocid seals have retained acute sound reception capabilities in air despite their development of broad and highly sensitive underwater hearing (Reichmuth *et al.*, 2013). While their aerial hearing sensitivity rivals that of many terrestrial carnivores, seals also possess a unique ability to detect sound across an expanded range of frequencies in water. An examination of hearing in these amphibious seals can address important questions related to auditory structure, function, and evolution. However, prior to this dissertation, behaviorally obtained hearing profiles were available for only six (of 18) species in the Phocidae family, including four (of 10) species of northern seals in the Phocinae subfamily (see Erbe *et al.*, 2016). The northern seals comprise the ringed (*Pusa hispida*), Baikal (*Pusa sibirica*), Caspian (*Pusa caspica*), spotted (*Phoca largha*), harbor (*Phoca vitulina*), grey (*Halichoerus grypus*), ribbon (*Histriophoca fasciata*), harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*) and bearded seals (*Erignathus barbatus*), species which inhabit the North Pacific, the North Atlantic, and the circumpolar seas of the northern hemisphere, as well as some freshwater regions including Lake Baikal, Lake Ladoga, and Lake Saimaa. As knowledge of species-typical hearing in this group is limited to behavioral data from harbor (Møhl, 1968; Terhune, 1988, 1989, 1991; Thomas *et al.*, 1990; Kastak and Schusterman, 1998, 1999; Wolski *et al.*, 2003; Southall *et al.*, 2005; Kastelein *et al.*, 2009; Reichmuth *et al.*, 2013; Cunningham *et al.*, 2014a), harp (Terhune and Ronald, 1971, 1972), ringed (Terhune and Ronald, 1975a), and Caspian seals (Babushina, 1997) for absolute measures of hearing in quiet conditions, and to data from harbor (Renouf, 1980; Turnbull and Terhune, 1990), harp (Terhune and Ronald, 1971), and ringed seals (Terhune and Ronald, 1975b) for descriptions of hearing in the presence of noise, it is presently difficult to conduct comparative analyses across species or to evaluate their susceptibility to anthropogenic noise.

Methods for examining auditory capabilities include detailed anatomical investigations, evaluations of sound production, neurophysiological experiments, field (playback) studies, and behavioral studies of hearing. However, only two of these—neurophysiological methods and behavioral methods—provide direct information about auditory sensitivity. Neurophysiological investigations have been conducted in seals, but have not proven to be as reliable as behavioral methods (Ridgway and Joyce, 1975; Wolski *et al.*, 2003; Houser *et al.*, 2007; Reichmuth *et al.*, 2007; Tripovich *et al.*, 2011; Ruser *et al.*, 2014). While behavioral measurements of hearing are preferred, these types of psychophysical studies are typically time and resource intensive, making the attainment of audiometric data for all species prohibitively challenging.

In light of the current and expanding extent of human influence throughout the world's oceans (*e.g.*, McDonald *et al.*, 2006; Hildebrand, 2009), knowledge gaps concerning auditory biology and the effects of noise on hearing in seals are troublesome. Arctic seals may be especially vulnerable, as these minimally studied species inhabit some of the most rapidly changing marine environments. As the global climate warms, sea ice in the northernmost regions of the planet continues to diminish; such changes result in habitat losses for Arctic species, fundamental alterations in marine food webs, and increasing ambient noise levels in regions that were previously isolated from anthropogenic influence (Huntington, 2009). While the effects on marine animals are likely to be multi-faceted, appropriate management decisions require direct species-typical auditory data. Information needs include measures of auditory sensitivity and the potential effects of noise on life history events in Arctic species, including seals. The gaps in our current understanding of auditory biology leave regulators ill equipped to address management issues related to anthropogenic noise. Before we can broach such applied management questions, we must describe the capabilities of the auditory system and attempt to relate sensory biology to ecology and life history for Arctic seals.

This dissertation addresses key knowledge gaps by examining the auditory sense of two species of ice-living northern seals that inhabit sub-Arctic and Arctic regions. A series of studies was conducted to characterize the auditory capabilities of spotted and ringed seals in quiet conditions, in the presence of controlled noise, and in real-world listening scenarios. The first chapter of this dissertation details a set of experiments that describe spotted seal hearing abilities in air and under water. Psychophysical methods were employed to measure hearing sensitivity through the voluntary participation of seals trained to report their sensory perception of auditory cues. This type of behavioral approach was applied in all three chapters of this dissertation, as it has been demonstrated to be the most reliable and accurate method for investigating the reception and perception of auditory stimuli (see, *e.g.*, Wolski *et al.*, 2003; Hall, 2007; Mulsow *et al.*, 2011). The resulting hearing profiles include complete underwater audiograms (0.1 – 72.4 kHz), aerial audiograms (0.075 – 51.2 kHz), and critical ratio measurements (0.1 – 25.6 kHz) in both media. These are the first hearing data available for spotted seals, and indicate that their auditory sensitivity is similar to that of the closely related harbor seal and different from what has been reported previously for ice-living seals.

Chapter 2 focuses on amphibious hearing in ringed seals, and comprises a set of auditory profiles that are similar to those obtained for the spotted seals in Chapter 1. The results presented are the most comprehensive hearing data available for ringed seals, and provide an updated perspective on the sound reception capabilities of this species relative to historical data (Terhune and Ronald, 1975a, 1975b). Significantly, these new findings suggest that northern seals as a group may possess generally similar hearing capabilities. This is relevant not only in terms of understanding the evolutionary linkages between species in the Phocinae subfamily (and ultimately the larger Phocidae family), but also as it relates to the management of anthropogenic noise effects for marine mammals with similar hearing abilities. The National

Research Council (2000, 2005) first identified the usefulness of such groupings for identifying research priorities and informing management over a decade ago, and marine mammal noise exposure criteria (Southall *et al.*, 2007; Finneran and Jenkins, 2012) have subsequently utilized these so-called functional hearing groups in the development of noise exposure guidelines. The data provided in this dissertation finally allow us to begin an informed discussion of whether such a grouping is in fact appropriate for phocid seals.

In addition to audiometric measurements in quiet conditions, critical ratios were measured for both spotted and ringed seals as the difference (in dB) between the sound pressure level of a just-audible signal and the spectral density level of an octave-band noise masker centered at the signal frequency (Fletcher, 1940). Critical ratio measurements such as these provide information about how the ear operates across a range of frequencies in the presence of noise, and are commonly used to predict the degree of masking experienced by listeners exposed to different noise conditions (*e.g.*, Erbe and Farmer, 2000; Erbe, 2002; Jensen *et al.*, 2009; Dooling *et al.*, 2013; Cunningham *et al.*, 2014b). However, while masking predictions based on critical ratio data are appropriate for many types of flat-spectrum, continuous noise, it is unclear the extent to which such predictions are accurate when considering spectrally complex, time-varying noise.

In the case of Arctic seals, the expansion of seismic exploration for oil and gas makes an examination of masking by impulsive sounds especially relevant. In Chapter 3 of this dissertation, detection probabilities were calculated for trained seals listening for a low-frequency sound presented at different intervals within a background of seismic noise, which was recorded close to (< 1 km) or far from (> 30 km) an operational airgun array. This novel approach enables an experimental assessment of masking potential by impulsive noise, and aids in determining the extent to which standard laboratory data can be reasonably applied to estimate masking effects in realistic and ecologically relevant conditions.

Considered together, this series of auditory studies expands upon what is currently known about hearing in seals, beginning with a thorough characterization of amphibious hearing capabilities in ice-living seals, and moving on to examine the hearing of these species in simple and complex acoustic environments. This work improves current understanding of the auditory biology of spotted and ringed seals by characterizing the sensitivity of their auditory systems and the way they perform under various acoustic conditions. Additionally, the results of these studies point to future research directions and provide necessary information to improve management decisions for these species. Further work is necessary to describe the auditory sense of related species, and to continually refine the models used to predict the effects of noise on seals listening for biologically relevant sounds in the marine environment.

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CHAPTER 1

AMPHIBIOUS HEARING IN SPOTTED SEALS (*PHOCA LARGHA*): UNDERWATER AUDIOGRAMS, AERIAL AUDIOGRAMS AND CRITICAL RATIO MEASUREMENTS

Reprinted with permission from:

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ABSTRACT

Spotted seals (*Phoca largha*) inhabit Arctic regions that are facing both rapid climate change and increasing industrialization. While little is known about their sensory capabilities, available knowledge suggests that spotted seals and other ice seals use sound to obtain information from the surrounding environment. To quantitatively assess their auditory capabilities, the hearing of two young spotted seals was tested using a psychophysical paradigm. Absolute detection thresholds for tonal sounds were measured in air and under water over the frequency range of hearing, and critical ratios were determined using octave-band masking noise in both media. The behavioral audiograms show a range of best sensitivity spanning four octaves in air, from approximately 0.6 to 11 kHz. The range of sensitive hearing extends across seven octaves in water, with lowest thresholds between 0.3 and 56 kHz. Critical ratio measurements were similar in air and water and increased monotonically from 12 dB at 0.1 kHz to 30 dB at 25.6 kHz, indicating that the auditory systems of these seals are quite efficient at extracting signals from background noise. This study demonstrates that spotted seals possess sound reception capabilities different from those previously described for ice seals, and more similar to those reported for harbor seals (*Phoca vitulina*). The results are consistent with the amphibious lifestyle of these seals and their apparent reliance on sound. The hearing data reported herein are the first available for spotted seals and can inform best management practices for this vulnerable species in a changing Arctic.

INTRODUCTION

Recent environmental warming and diminishing sea ice are enabling increased human presence and industrialization in historically undisturbed Arctic regions. Over the past decade, the growth of offshore activities such as oil and gas exploration and commercial shipping has increased low-frequency ambient noise in some areas (Huntington, 2009; Moore *et al*., 2012). This anthropogenic noise—associated with ship traffic, seismic surveys and drilling—alters acoustic habitats and may disturb or harm marine life. As these activities transform Arctic environments, it is increasingly important to consider and quantify their behavioral and auditory effects on marine mammals.

Among the species of particular concern are ice-dependent (‘pagophilic’) seals that inhabit northern regions. Ice seals are characterized by a strong association with, and ecological dependence on, sea ice for many important life functions (Boveng *et al*., 2009; Cameron *et al*., 2010; Kelly *et al*., 2010). Although hearing is believed to be a primary sensory modality for all pinnipeds (seals, sea lions and walruses) (Richardson *et al*., 1995), and ice seals are known to vocalize under water (Wartzok and Ketten, 1999), little is directly known about their reliance on and use of sound in their environment. In terms of sound reception, some auditory data exist for harp (*Pagophilus groenlandicus*) (Terhune and Ronald, 1971; Terhune and Ronald, 1972) and ringed seals (*Pusa hispida*) (Terhune and Ronald, 1975a; Terhune and Ronald, 1975b), but there are few measurements below 1 kHz where industrial and shipping noises typically occur (Wenz, 1962; Richardson *et al*., 1995). The most comprehensive data exist for the closely related, but more temperate living, harbor seal (*Phoca vitulina*) (Møhl, 1968; Terhune, 1988; Terhune, 1991; Kastak and Schusterman, 1998; Wolski *et al*., 2003; Southall *et al*., 2005; Kastelein *et al*., 2009; Reichmuth *et al*., 2013). However, because the phylogenetic relationships among the 10 species of northern seals are incompletely resolved (Berta and Churchill, 2012), the validity of extrapolating hearing capabilities across species in this group remains unclear. Characterizing species-typical hearing in Arctic seals is thus important in order to understand their perception of the acoustic environment, their potential susceptibility to anthropogenic noise, and the similarities or differences among related species. To this end, we are conducting a series of audiometric studies to assess basic hearing capabilities and the effects of noise on hearing in ice seals. This paper presents detailed hearing profiles for one species, the spotted seal (*Phoca largha*, Pallas 1811).

Spotted seals inhabit sub-Arctic and Arctic waters including portions of the Beaufort, Chukchi, East Siberian, Bering, Okhotsk and Yellow Seas, and the Sea of Japan (Boveng *et al*., 2009). Their movements and habitat-use patterns are strongly influenced by the presence of seasonal sea ice, and many of their life history events occur within the transition zone between pack ice and open water (Lowry *et al*., 1998; Lowry *et al*., 2000). Because these seals spend much of their time in light-limited, high-latitude environments and forage under water in relatively dark conditions, it is likely that they depend on acoustic cues for orientation, communication, and predator and prey detection. However, no information is currently available regarding sound reception in this species. An examination of hearing in spotted seals can provide insight into their auditory sensitivity and vulnerability to noise exposure, and can inform comparative analyses of auditory anatomy, function and evolution.

The aim of this study is to quantify the hearing abilities of spotted seals above and below the water's surface. Because seals are amphibious, dividing time between land and sea, it is essential to examine their hearing in both media to completely characterize the auditory system. Consequently, underwater and aerial audiograms were measured for two trained subjects in quiet conditions across the frequency range of hearing. To directly quantify how noise affects their ability to perceive relevant sounds, hearing was also tested in the presence of controlled background noise. Finally, reaction time measurements were obtained throughout testing to further evaluate the perception of similar sounds detected in quiet and noisy backgrounds. Together, these data allow for meaningful comparisons across frequencies, media, individuals and species, and describe the basic hearing capabilities of spotted seals under different environmental conditions.

RESULTS

Underwater audiograms

The underwater hearing thresholds measured for two spotted seals are provided in Table I, along with corresponding false alarm rates and ambient noise levels. The mean false alarm rates were 0.15 and 0.20, suggesting that neither subject had an especially conservative response bias. Threshold-to-noise offsets in the testing pool were calculated as the difference between hearing threshold and ambient noise spectral density level at each test frequency. The amount by which thresholds exceeded background noise at a specific frequency was variable (15–74 dB), and greatest at high frequencies. Underwater audiograms and the associated ambient noise profile are shown along with some representative audiograms from related species in Fig. 1. The psychometric functions associated with these hearing thresholds are given in Figs S1, S2; these show the relationship between signal sound pressure level (SPL) and detection probability at each frequency, and can be used to infer hearing threshold at the 50% detection level and any other level of interest.

The hearing curves of the two individuals were very similar, with a mean difference of 2 dB between their thresholds at each frequency. The frequency of best sensitivity under water was 25.6 kHz for both seals, whose hearing thresholds at this frequency were 53 and 51 dB re 1 μPa. The frequency range of best sensitivity within 20 dB of the lowest measured threshold extended over more than seven octaves, from approximately 0.3 to 56 kHz for both subjects. Above this range, sensitivity declined by 40 dB within a half octave. Both audiograms exhibited a general U-shape, with sharper high-frequency roll-offs than those observed at low frequencies.

In-air audiograms

Aerial hearing thresholds are provided in Table II, along with corresponding false alarm rates, ambient noise levels and reaction times. The mean false alarm rates were 0.18 and 0.13, again suggesting that neither subject had a particularly conservative response bias. Threshold-to-noise offsets in the acoustic chamber were 22–52 dB at frequencies above and below the range of best sensitivity, and 10–25 dB within that range. The audiograms are plotted in Fig. 2, along with the in-air ambient noise profile and existing aerial audiograms for northern seals. The psychometric functions associated with these hearing thresholds are provided in Figs S3, S4.

The frequency of best sensitivity in air was 3.2 kHz for both seals, whose hearing thresholds at this frequency were -10 and -13 dB re 20 μPa. Their 20 dB bandwidth of best sensitivity was much narrower in air than in water, extending across approximately four octaves from 0.6 to 11 kHz. Above this range, sensitivity declined by 20 dB per octave, with a more gradual high-frequency roll-off than that observed for these individuals in water. Similar to their underwater audiograms, however, aerial sensitivity rolled off more sharply at high than at low frequencies. Also of note is the contour of the audiograms, which appear more V-shaped than the underwater curves. The particular shape of the base of the audiogram was confirmed by testing in half-octave increments to either side of 3.2 kHz; both seals showed nearly identical thresholds in this region.

Underwater and in-air critical ratios

Underwater and in-air critical ratios (CRs) for the two seals are given in Table III, along with masked hearing thresholds, masking noise spectral density levels, false alarm rates and reaction times for each frequency. Mean false alarm rates were 0.17 and 0.16. The CRs are plotted in Fig. 3 with available masking data for northern seals. CRs measured in this experiment increased monotonically with increasing frequency. Underwater CRs for the spotted seal *Amak* ranged from 14 dB at 0.2 kHz to 30 dB at 25.6 kHz. Aerial CRs for the spotted seal *Tunu* ranged from 12 dB at 0.1 kHz to 27 dB at 25.6 kHz. *Amak's* underwater CRs were not significantly different from *Tunu's* aerial CRs (t_8=1.77, P=0.11). Furthermore, *Tunu's* three underwater CRs (14, 20 and 26 dB at 0.2, 3.2 and 12.8 kHz, respectively) were not significantly different either from his own aerial CRs (t_2=1.63, P=0.24) or *Amak's* underwater CRs (t_2=0.49, P=0.68) at the same test frequencies.

Reaction times

Median reaction times obtained in air under quiet conditions are reported in Table II for each frequency at threshold, or 0 dB sensation level (SL), and 20 dB above threshold (20 dB SL). Response times near threshold were typically less than 600 ms, and varied with frequency. *Tunu's* overall median reaction time at threshold was 475 ms while *Amak's* was 380 ms. As expected, reaction times were shortest for the loudest sounds presented at a particular frequency. For signals whose levels exceeded threshold by 20 dB, *Tunu's* median reaction times stabilized at 234 ms and *Amak's* at 182 ms. Reaction times were different between subjects at both 0 dB SL (t_{14}=2.58, *P*=0.02) and 20 dB SL (t_{14}=3.29, *P*=0.01). The median reaction times obtained in the aerial masking experiment are reported in Table III for each frequency at 0 and 20 dB SL. As observed with the aerial audiogram data, reaction times at threshold were longer and more variable than those measured at the higher stimulus level. Under masked conditions, *Tunu's* reaction time to threshold-level stimuli was 403 ms, and at 20 dB SL his reaction time was 252 ms. The response times of this seal in the presence of masking noise were not significantly different from his response times obtained under quiet conditions, either at threshold (t_7=1.04, *P*=0.33) or at 20 dB SL (t_7=0.08, *P*=0.94).

DISCUSSION

Underwater hearing

The spotted seal underwater audiograms obtained in this study agree well with published thresholds for the harbor seal (Møhl, 1968; Terhune, 1988; Kastelein *et al.*, 2009; Reichmuth *et al.*, 2013). However, the spotted seal hearing thresholds are considerably lower than existing underwater data for other Arctic seals. Published thresholds for harp (Terhune and Ronald, 1972) and ringed seals (Terhune and

Ronald, 1975a) are elevated across most of the frequencies tested, although there is better agreement with the spotted seal audiograms at the highest frequencies. While this could indicate species differences, more recent auditory data suggest that the hearing capabilities of spotted and ringed seals are actually quite similar (J.M.S., unpublished). When compared with fully aquatic species such as bottlenose dolphins (*Tursiops truncatus*) or harbor porpoises (*Phocoena phocoena*) (Johnson, 1967; Kastelein *et al.*, 2002; Kastelein *et al.*, 2010), spotted seals hear nearly as well in water in their range of best sensitivity, although this range is shifted lower in frequency for the seals. While the cetaceans have higher upper-frequency limits, the seals hear considerably better below 10 kHz, suggesting that they may be more vulnerable to the effects of anthropogenic noise.

An important aspect of any psychoacoustic study is a thorough description of ambient noise in testing environments. Although the time-varying nature of background noise is difficult to characterize, the 50th percentile statistical method used in this experiment more accurately describes temporal variability in noise than do typical methods using L_{eq} values (equivalent continuous SPLs) (Mulsow and Reichmuth, 2010; Reichmuth *et al.*, 2013). Based on the critical ratios obtained for the subjects in this study, frequencies of concern for possible masking of underwater hearing thresholds are 3.2–36.2 kHz. Threshold-to-noise offsets of approximately one CR in this range suggest that masking noise may have marginally influenced these thresholds. Although ambient measurements were obtained in test-ready conditions, they do not represent the exact noise conditions concurrent with each signal presentation. Therefore, the combination of CRs and measured average noise conditions informs the interpretation of these underwater hearing data, but does not allow a definitive analysis given the difficulty of quantifying the effect of temporal fluctuations in noise on thresholds.

The absolute audiograms reported here provide information about the range of frequencies that are detectable by spotted seals, and that may be most relevant in terms of noise exposures. It is important to note that, even if masking of important stimuli is not occurring, the acoustic environment is still altered with the addition of background noise. Such changes may be ecologically significant for acoustically vigilant Arctic seals that utilize auditory cues to orient to features in their environment (Elsner *et al.*, 1989). The broad range of best sensitivity under water suggests that spotted seals may be attending to auditory stimuli across seven or more octaves. This expanded range—relative to the aerial hearing abilities of terrestrial carnivores, and extending upwards toward the high-frequency hearing limits of fully aquatic cetaceans—is likely related to the enhanced role of bone and tissue conduction under water and the operation of different constraints on hearing in each medium (Hemilä *et al.*, 2006; Nummela, 2008). High-frequency hearing supports localization abilities (Heffner and Heffner, 2008; Nummela and Thewissen, 2008), and may allow detection of relevant stimuli such as predator vocalizations. However, while high-frequency hearing sensitivity seems to be a derived characteristic of seals, the ecological and adaptive significance of their wide range of sensitive underwater hearing remains uncertain.

In-air hearing

The spotted seal aerial thresholds measured in this study are the lowest reported for any marine mammal. Compared with available data for seals, *Amak* and *Tunu's* thresholds are most comparable to those of harbor seals. The data reported in this experiment are similar to those measured previously for an adult harbor seal tested in the same acoustic chamber (Reichmuth *et al*., 2013), except at the frequency of best sensitivity, where the spotted seal thresholds are roughly 8 dB lower. The lower thresholds measured for the spotted seals at 3.2 kHz may be attributable to the age of these subjects, who were 15 years younger than the harbor seal at the time of testing. Existing harp seal thresholds (Terhune and Ronald, 1971) are substantially elevated across the frequency range of hearing relative to the thresholds measured in this study. While some have suggested that these thresholds were elevated by background noise (Moore and Schusterman, 1987; Watkins and Wartzok, 1985), they were more likely influenced by methodological factors. During testing, the harp seal's head was submerged immediately prior to each trial, which may have impeded the aerial sound conduction pathway (Terhune and Ronald, 1971).

Recent studies have shown that most previously reported hearing thresholds for seals—particularly aerial thresholds—were masked because of inadequate control of the ambient noise background in testing enclosures, leading to underestimates of sensitivity and confounding interpretations of amphibious hearing (Reichmuth *et al*., 2013). Based on the low aerial thresholds obtained in this study, combined with the CR data, there is some concern for potential masking from 1.6 to 6.4 kHz, where threshold-to-noise offsets are within a few dB of one CR. However, the ambient noise levels in the acoustic chamber approach the limit of detectability for the measurement instrumentation used; threshold-to-noise offsets are therefore conservative at frequencies from 0.8 to 20 kHz, making it difficult to rule out the influence of masking. Regardless, the extremely quiet testing conditions during this experiment enabled the measurement of very low aerial thresholds for both seals, which conservatively estimate hearing sensitivity for this species. In light of thresholds measured for pinnipeds generally that approach or fall below 0 dB re 20 µPa, and especially the spotted seal audiograms obtained in this experiment, it appears that the effects of airborne anthropogenic noise may be of particular concern for these species.

These results suggest that spotted seals have not lost their acute ability to perceive aerial sounds in their transition to a semi-aquatic lifestyle. In fact, the spotted seal thresholds reported herein describe hearing sensitivity comparable to that of terrestrial carnivores (*e.g.*, Heffner, 1983; Heffner and Heffner, 1985a; Heffner and Heffner, 1985b; Kelly *et al.*, 1986). Although the terrestrial species have higher upper-frequency limits and somewhat broader ranges of best sensitivity, at mid to low frequencies there is a high degree of similarity between the hearing of these marine carnivores and their terrestrial counterparts. For seals that forage at sea but remain tied to sea ice for activities such as whelping and molting, this is not unexpected.

Spotted seals are vigilant when hauled out on ice floes and are susceptible to acoustic disturbance (Boveng *et al*., 2009), which is supported by their sensitivity to airborne sounds.

Amphibious comparison

It is relevant to consider the extent to which the auditory systems of amphibious animals may be adapted for use in one medium or the other. To account for the acoustic impedance difference between media, a basic comparison can be made between underwater and in-air thresholds in terms of energy, given certain assumptions about plane wave propagation in small testing enclosures. An energetic comparison of best hearing sensitivity can be estimated from the measured pressure thresholds for the spotted seals as -131 dB re 1 W m^{-2} in water and -133 dB re 1 W m^{-2} in air. These spotted seal data are discussed in terms of pressure rather than intensity because the seal ear is thought to be sensitive primarily to sound pressure, as is true for most mammals; for further discussion of this issue see Kastak and Schusterman (Kastak and Schusterman, 1998), Finneran *et al*. (Finneran *et al*., 2002) and Reichmuth *et al*. (Reichmuth *et al*., 2013). Regardless of metrics, it is clear that these seals possess efficient sound reception pathways both in water and in air, allowing auditory capabilities comparable to those of hearing specialists in either environment.

Auditory masking

The finding that spotted seal CRs are consistent with those of harbor seals in both air and water (Southall *et al*., 2000; Southall *et al*., 2003) provides further evidence for similar hearing between the two species and supports the general trend of low CRs in seals (Reichmuth, 2012). It has been suggested that such low CRs might be an adaptation for detection of signals in relatively noisy marine environments (Southall *et al*., 2000). Although the spotted seal CRs increase with frequency at a rate similar to that of most mammals (Fay, 1988), their consistently lower CRs indicate that signal detection within background noise is an enhanced capability for these seals. In fact, the CRs measured in this study are among the lowest reported for mammals (Fay, 1988).

Significantly, the spotted seal CRs do not differ across media or subjects. Although underwater and aerial hearing sensitivity are quite different, this finding for CRs is expected and confirms earlier hypotheses. Because sound transmission through the medium and auditory pathway similarly influences signals and noise, CRs—which are based on relative differences between the two—are the same for seals listening above or below water (Renouf, 1980; Turnbull and Terhune, 1990; Southall *et al*., 2003).

When compared with masking data for other ice seals, these CRs are within 8 dB of those reported in air for one harp seal except at the highest frequency (Terhune and Ronald, 1971); the especially high CR at 8.6 kHz can be explained by the harp seal's behavior during testing (Terhune and Ronald, 1971). The spotted seal

CRs are also quite different from those obtained in water for two ringed seals (Terhune and Ronald, 1975b). These differences have implications for our understanding of auditory filtering in ice seals. Based on the CR equal power method (Richardson *et al*., 1995), estimated masking bandwidths are 2–16% of center frequency in this experiment, with one exception for one subject at 0.1 kHz (40%). Above 0.2 kHz, estimated auditory filter widths are roughly a constant percentage of center frequency. This finding of critical bandwidths of less than one-third of an octave is in contrast to the previous estimates for ice seals reviewed by Richardson *et al.* (Richardson *et al*., 1995). It is important to note that these indirect estimates often differ from direct critical bandwidth measurements (Richardson *et al.*, 1995; Southall *et al*., 2003). Regardless, these data suggest that critical bands in ice seals are narrower than previously believed. Future studies involving direct measurement of critical bandwidth are necessary to characterize auditory filter parameters in ice seals.

In addition to informing cross-species comparisons and providing insight into auditory processing, these CRs can be applied to management decisions. Masking data describe the efficiency with which individuals can extract meaningful signals from noise, as well as their susceptibility to increasing ambient noise levels. The CRs reported herein can be used to quantitatively estimate zones of masking for spotted seals exposed to relevant signals embedded within natural or anthropogenic noise. While these estimates do not account for release from masking due to spatial or other complex factors, they do delineate the outer bounds of masking surrounding a given sound source.

Response latency under different environmental conditions

Comparing reaction time measures across subjects and acoustic testing environments provides additional insight into auditory perception in quiet and noise. In contrast to the measured hearing thresholds, response latencies showed more individual variation. The difference in latencies for the two seals tested under identical conditions underscores the importance of within-individual comparisons when examining the influence of any factor (*e.g.*, background noise) on perception.

In this study, reaction time data for the same individual in the unmasked and masked experiments is a proxy for perceptual loudness under these different signal and noise conditions (Moody, 1970). During the masking experiment, the absolute level of the stimulus was considerably higher than during audiogram testing at the same frequency. Despite 20–50 dB differences in absolute SPL, however, latencies were no different for signals of the same SL across the two noise conditions. This is because sensation level relates the amplitude of the target stimulus to sensory threshold. The different test signals were perceptually equated by the presence of noise in the environment, as expected based on the CR data and confirmed by the equal response times in both cases. Thus it is clear that CRs and reaction times are different metrics for quantifying the same phenomenon: the effects of noise on perception. Both data sets indicate that the addition of anthropogenic noise requires that a relevant sound be of considerably higher amplitude to achieve the same perceptual loudness as a sound received in quiet conditions.

Conclusions

Little is known about the acoustic ecology of spotted seals, with no prior studies describing their hearing and few assessing their acoustic communication or behavior (Beier and Wartzok, 1979; Gailey-Phipps, 1984; Xiao-mei *et al*., 2012). The present study provides auditory profiles for two young spotted seals, addressing a significant knowledge gap. Comparisons of underwater and in-air data demonstrate acute sensitivity in each medium, suggesting a need to consider anthropogenic noise effects both above and below the water's surface for these amphibious animals. Furthermore, these data reveal hearing capabilities comparable to those of the closely related harbor seal, suggesting that the larger knowledge base available for the harbor seal may be applied as a good first approximation for spotted seal auditory processing and ecology. Of special relevance to the present study is the remarkable similarity in data obtained for the two subjects in matched conditions. The high degree of agreement between thresholds measured with young, well-trained animals in controlled conditions lends confidence to the conclusion that these data represent species-typical hearing in spotted seals. Finally, the auditory data presented in this paper support the claim that seals have not traded their aerial hearing capabilities for superior underwater sound reception (Reichmuth *et al*., 2013). Rather, these spotted seals have retained acute hearing sensitivity in both media, consistent with an amphibious existence.

As human presence at high latitudes increases, it is necessary to assess the capacity of northern species to cope with changing environments. Anthropogenic noise is one of many threats facing pagophilic seals, and the ultimate persistence of these seals will depend on resilience in the face of multiple simultaneous stressors. Effective conservation depends first on an understanding of the potential impacts. Careful assessments of hearing for individual species can quantify both perceptual capabilities and the potential effects of increasing noise levels. This psychoacoustic study thoroughly describes the amphibious hearing capabilities of spotted seals, and informs best management practices for this vulnerable species in a rapidly shifting environment.

MATERIALS AND METHODS

General experimental methods

Test Subjects

The subjects were two young male spotted seals, *Phoca largha*, identified as *Amak* (NOA0006675) and *Tunu* (NOA0006674). Both subjects were 1 year old at the start of testing. These seals stranded as pups and were subsequently transferred to

Long Marine Laboratory at the University of California at Santa Cruz. Neither seal had a known history of ear injury, exposure to ototoxic medication, or other complication that might affect their hearing capabilities. Their body masses at the start of testing were 42 and 34 kg, respectively, and their interaural distances were 15 and 14 cm. As true seals lack external pinnae, the interaural distance was measured as the curvilinear length between the meatal openings, measured dorsally.

The seals were housed outdoors at Long Marine Laboratory in free-flow seawater tanks with adjacent haul-out space. Both subjects were trained via operant conditioning methods using fish reinforcement to voluntarily participate in husbandry and research sessions. They underwent extensive training for the signal detection task prior to audiometric testing, which occurred from 2011 to 2013. Throughout this period, the seals received one- third to one-half of their daily diets (freshly thawed capelin) during experimental sessions. Their diets were established to maintain a healthy body mass and were not constrained for experimental purposes. Each seal generally participated in experimental sessions once per day for 5 days per week.

All research was conducted with the approval and oversight of the University of California at Santa Cruz Institutional Animal Care and Use Committee, with authorization from the Ice Seal Committee and the National Marine Fisheries Service of the United States (research permit 14535).

Test environments

Testing took place in two environments. The underwater environment comprised a circular, partially in-ground pool 1.8 m deep and 7.6 m in diameter. This concrete, epoxy-lined test pool was filled with seawater that ranged from 10 to 14°C. Aerial testing took place in a modified hemi-anechoic acoustic chamber (Eckel Industries, Cambridge, MA, USA) that contained a 3.3×2.3×2.2 m testing room with double-paneled stainless steel walls and ceiling lined with sound-attenuating, fiberglass-filled aluminum wedges. The solid floor of the acoustic chamber was covered with a 4 cm thick foam mat. The experiments were controlled remotely from an adjacent, sound-isolated room where the experimenter could monitor surveillance cameras in the test enclosure while remaining out of view.

Psychoacoustic procedures

Hearing thresholds were determined using similar behavioral methods for all experimental conditions. Each seal was trained to perform a go/no-go procedure with single-response audiometry, in which he touched a response target upon detecting an acoustic signal or withheld this response when he did not (Stebbins, 1970). To begin an experimental session, a trainer unaware of the individual trial conditions cued the subject to enter the test enclosure and place his head on a chin station positioned within a calibrated sound field. This station precisely controlled head position and ensured consistency across trials and sessions. A small light, placed in front of this station at eye level, was illuminated by the experimenter to define the 4-s duration of each individual trial. The response target—which the subject could press upon detection of a signal—was a PVC plate located 20 cm to the left of station. Each trial began when the subject was settled in the chin station and the trial light was turned on, and ended when the subject touched the response target or when the 4-s interval was complete and the light was extinguished.

Trials had two possible types—signal present or signal absent—and four possible outcomes. A correct detection occurred on signal-present trials when the subject touched the response target. A correct rejection occurred on signal-absent trials when the subject remained on station for the entire trial interval. Both correct responses were marked with a conditioned acoustic reinforcer (buzzer) triggered by the experimenter. The trainer, wearing a headset linked to the experimenter, was then instructed to deliver primary reinforcement (one fish) to the seal. Conversely, if the subject withheld a response when a signal was presented (miss) or touched the response target when no signal was generated (false alarm), he did not receive conditioned or primary reinforcement, and was allowed to progress to the subsequent trial. The trial sequence for each session was pseudorandomly predetermined according to a set ratio of signal-present to signal-absent trials. This sequence was constrained such that there were never more than four in a row of a given trial type; this further reduced the likelihood of the subject predicting the trial type over a typical Gellermann (Gellermann, 1933) series. Testing sessions included 40–60 trials. The frequencies for each experiment were tested successively in random order to avoid learning effects.

Two psychoacoustic procedures were used to determine hearing thresholds. An adaptive staircase method (Cornsweet, 1962) was used to estimate a preliminary threshold, followed by the method of constant stimuli (MCS) (Stebbins, 1970) for final threshold determination. Within a single testing session of either type, frequency was held constant while signal amplitude was varied. The absolute threshold at each frequency was defined as the SPL in dB_{rms} re 1 μPa (under water) or dB_{rms} re 20 μPa (in air) at which there was a 50% correct detection rate.

Adaptive staircase testing was conducted over multiple sessions at the start of each frequency to allow the subject to acclimate to the test signal and to establish the preliminary estimate of threshold. These sessions began with a signal level easily detected by the subject, after which the amplitude was decreased by 4 dB following each correct detection until the first miss. The experimenter would then adjust the signal amplitude up in 4 dB steps after each miss and down by 2 dB steps after each correct detection, until five descending misses within 6 dB of each other were obtained. These five misses made up the test phase. Finally, a cool-down phase concluded each session, consisting of four to six trials at a more salient level—approximately 20 dB above the estimated threshold—to ensure stimulus control on the signal detection task. Once testing performance had stabilized, the preliminary threshold was estimated as the mean of three individual session thresholds within 3 dB of one another.

Subsequent MCS testing served to determine the final hearing threshold and proceeded as follows. Five signal levels were selected in 2 dB increments centered on the preliminary threshold obtained from adaptive staircase testing [+4, +2, +0 (preliminary threshold), −2 and −4 dB]. Each SPL was presented five times per session, distributed evenly into randomized blocks to eliminate any effect due to predictable changes in level. Final threshold was calculated using probit analysis (Finney, 1971). This involved fitting the psychometric function to the proportion of correct responses obtained at each signal level, and using an inverse prediction to determine threshold at the 50% correct detection level. A minimum of two MCS sessions were used for this analysis, with additional sessions run until 95% confidence intervals were narrower than 4 dB.

Response bias was evaluated by monitoring false alarm rates, quantified as the percentage of signal-absent trials in which subjects reported a detection. To maintain a stable response bias (Schusterman, 1974), the proportion of signal-present trials was varied between 0.50 and 0.70 and the reinforcement ratio for correct detections to correct rejections was varied between 1:1 and 2:1[1]. Adjustment of these parameters occurred between but not within sessions. False alarm rates during each session's test phase were deemed acceptable if they were above 0 and below 0.3.

Stimulus generation and calibration

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[1] A 2:1 reinforcement ratio was used for *Amak* at 72.4 kHz under water. *Amak* exhibited a conservative response bias at this frequency, with a false alarm rate of 0 for five sessions with a 70:30 signal to catch ratio, until the reinforcement ratio was adjusted.

These experiments were conducted using the Hearing Test Program (HTP) virtual instrument (Finneran, 2003) built from LabVIEW software (National Instruments Corp., Austin, TX, USA). Signals were sent from HTP through an NI USB-6259 BNC M-series data acquisition module with an update rate of 500 kHz. For all experiments, test stimuli were 500 ms frequency-modulated sweeps with 10% bandwidth (±5% from the test frequency) and 5% rise and fall times on the signal. These narrowband sweeps were used rather than pure tones to minimize variability in the received sound field (Kastelein *et al*., 2002; Finneran and Schlundt, 2007). The outgoing test stimuli were bandpass filtered as an added measure to ensure signal integrity, using a Krohn-Hite 3364 anti-aliasing filter (Krohn-Hite, Brockton, MA, USA). Subsequently, signals were sent through a TDT PA5 digital attenuator (Tucker-Davis Technologies, Alachua, FL, USA) and, in some cases, a Hafler P1000 power amplifier (for underwater audiogram testing at 6.4 kHz and below, and for the masking experiment at all frequencies; Hafler Professional, Tempe, AZ, USA) prior to reaching the transducer.

Stimulus calibration was performed daily. Immediately prior to each session, calibration tones at the test frequency were generated at various levels and transmitted into the test enclosure. Received signals were returned from a hydrophone or microphone (see below) through the same filter, NI hardware and HTP software used for signal generation. The update rate on the incoming signal was 500 kHz. Calibration signals were measured, compared with expected SPLs and examined in the frequency domain using fast Fourier transform analysis to ensure that the subject was receiving clean signals without harmonics. Sound level calibrations were conducted at the listening station in the absence of the subject.

Ambient noise characterization

Ambient noise measurements were taken daily at the center position of the seal's head during testing, using a battery-powered Brüel & Kjær 2250 sound analyzer (Brüel & Kjær A/S, Nærum, Denmark) with a calibrated Reson TC4032 low-noise hydrophone (0.01–80 kHz, ±2.5 dB; Reson A/S, Slangerup, Denmark) under water and a calibrated Brüel & Kjær 4189 free- field microphone (0.006–20 kHz) in air. One-minute, unweighted noise samples were recorded prior to each session and percentile statistics of 1/3-octave band levels were calculated from 1 min L_{eq} values for frequencies from 0.04 to 20 kHz. For frequencies from 20 to 78 kHz under water, a battery-powered Fostex FR-2 Field Memory Recorder (Fostex Company, Tokyo, Japan) was used in conjunction with the Reson TC4032. These high-frequency noise measurements were made on several days under testing conditions. In air, equipment limitations prevented absolute noise measurements lower than 0 dB re 20 μPa above 20 kHz.

Underwater audiograms

Underwater auditory thresholds for the two subjects were measured across the hearing range at 13 frequencies: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 12.8, 25.6, 36.2, 51.2, 60.9 and 72.4 kHz.

Stimulus generation and calibration

In addition to the hardware described above, three underwater transducers were used to project stimuli into the test enclosure. These transducers were a Naval Undersea Warfare Center J-11 speaker (Newport, RI, USA) for 0.1–0.2 kHz signals, a Lubell Labs 1424 HP projector (Columbus, OH, USA) for 0.4–6.4 kHz, and an ITC 1042 projecting hydrophone (International Transducer Corporation, Santa Barbara, CA, USA) for 12.8–72.4 kHz. These transducers were decoupled from the underwater testing apparatus and suspended into the pool 5–6 m behind the subject, a distance that exceeded the theoretical near-field boundary (Siler, 1969) at all frequencies. The precise position of the transducer was frequency specific and based on spatial mapping of the received sound field. Prior to testing, mapping was conducted at each frequency to ensure acceptable variability (±3 dB) in the test stimulus recorded at 25 positions on a 14×14×14 cm grid centered at the daily calibration position (i.e. the depth of the seal's ears in the center of the head). We used the Reson TC4032 hydrophone with a Reson EC6073 input module, or a calibrated ITC 1042 hydrophone (0.01–100 kHz, ±2.5 dB), as a receiver for both mapping and calibration.

During mapping, the speaker was moved around the testing enclosure until criteria were met, which determined the speaker's testing location for each frequency.

The underwater experimental apparatus consisted of a water-filled PVC frame with a mounted chin cup designed to position each animal's ears at a depth of 1 m, 0.75 m from the edge of the pool. This apparatus was located in the same position for all testing configurations with all subjects.

In-air audiograms

Aerial auditory thresholds were measured across the hearing range at 15 frequencies: 0.075, 0.1, 0.2, 0.4, 0.8, 1.6, 2.3, 3.2, 4.5, 6.4, 12.8, 18.1, 25.6, 36.2 and 51.2 kHz.

Stimulus generation and calibration

In addition to the hardware described above, four aerial transducers were used to project stimuli. These speakers were the JBL 2245H (JBL Incorporated, Northridge, CA, USA) for 0.075, 0.1 and 0.8 kHz; the JBL 2123H for 0.2, 0.4 and 1.6–3.2 kHz; the Fostex FT96H for 4.5–36.2 kHz; and the Avisoft Vifa (Avisoft Bioacoustics, Berlin, Germany) for 51.2 kHz. A calibrated Josephson C550H microphone (0.02–20 kHz, ±2 dB; Josephson Engineering, Santa Cruz, CA, USA) or a calibrated Microtech MK301 microphone capsule (0.005–100 kHz, ±2 dB;

Microtech Gefell GmbH, Gefell, Germany) with an ACO Pacific 4016 preamplifier and PS9200 power supply (ACO Pacific Incorporated, Belmont, CA, USA) was used for stimulus calibration and sound field mapping. The speakers were mounted in the acoustic chamber 0.6–1.2 m directly in front of the subject, at a frequency-specific distance determined by spatial mapping of the sound field. The near-field boundary was exceeded at every test frequency (Siler, 1969). The received sound field was measured at each frequency at 11 positions within a 12×12×12 cm grid surrounding the position of the animal's head during testing, in order to ensure acceptable variability (±3 dB). The grid points included locations coincident with the seal's left and right auditory meatus. The daily calibration position depended on frequency and was at the position of the left or right meatus, based on which location had a higher received level during sound field mapping.

The in-air experimental apparatus consisted of a U-shaped chin station that positioned the seal's ears 0.3 m above the floor of the chamber. The station included a plexiglass latency switch that the animal was trained to depress with his nose to initiate each trial. This enabled the measurement of time between signal onset and release of the switch as the subject moved to touch the response target.

Underwater and in-air CRs

Underwater and aerial masked hearing thresholds were obtained in the presence of octave-band noise centered on the frequency of the test signal. CRs—

defined as the difference (in dB) between the SPL of the masked threshold and the spectral density level of the octave-band noise masker at the center frequency of the masking band (Fletcher, 1940; Scharf, 1970)—were obtained for each subject at nine frequencies: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 12.8 and 25.6 kHz. *Amak* completed testing at these nine frequencies under water, and *Tunu* completed the same testing in air. In addition, *Tunu* completed testing at three frequencies (0.2, 3.2 and 12.8 kHz) under water to cross-validate these data.

The masking task was similar to audiogram testing in each medium, the exception being that calibrated noise was paired with the duration of the trial light. Masking noise was presented only during the trial interval as a precaution to avoid loudness adaptation (Gelfand, 1981; Southall *et al*., 2000).

Stimulus generation and calibration

Test stimuli for the masking experiment were generated, calibrated and projected using the same hardware as that used for the audiograms. Noise stimuli were gated (500 ms rise time) octave-band white noise maskers, generated and filtered using AVS Audio Editor 7.1 (Online Media Technologies Limited, London, UK) or Adobe Audition CS6 (Adobe Systems Incorporated, San Jose, CA, USA) and analyzed using SpectraPLUS (Pioneer Hill Software LLC, Poulsbo, WA, USA). These maskers were produced (sampling rate 44.1 kHz, 16 bit resolution) and passed from the sound card of a computer to a Hafler P1000 power amplifier—where they were mixed with the test signals—prior to reaching the speaker. The only exception was the 25.6 kHz masker, which was generated and filtered using MATLAB (MathWorks, Natick, MA, USA) and transmitted from the computer through a Roland Quad-Capture USB 2.0 Audio Interface (sampling rate 192 kHz; Roland Corporation US, Los Angeles, CA, USA) and a Reson VP1000 voltage preamplifier (in air only) before reaching the amplifier. Test signals and masking noise were projected from the same speaker to avoid spatial release from masking (Terhune and Turnbull, 1989; Turnbull, 1994; Holt and Schusterman, 2007). For in-air CR determination, the speakers used were the same as for the in-air audiogram. For underwater testing, the J-11 was used at frequencies from 0.1 to 12.8 kHz and the ITC 1042 at 25.6 kHz.

The masking noise was filtered to ensure that spectral density levels were relatively flat (±3 dB in air; ±5 dB under water) across the central 1/3-octave band at the daily calibration position[2]. Noise stimuli were mapped prior to testing, across a subset of the mapping positions used for the test signals. Under water, 1 min noise samples were projected and received across nine positions in a 14×14 cm plane at the depth of the subject's ears. In air, 1 min noise samples were recorded across six positions in a 12×12 cm plane at the height of the subject's ears. Each of the three 1/3-octave band levels across the entire octave-band masker was measured at every

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[2] At the two highest frequencies under water—12.8 and 25.6 kHz—variability in spectral density levels was ±9 and ±7 dB, respectively. This resulted from narrowband peaks or troughs in the noise that were unable to be filtered. The primary 1/3-octave band criterion was met for both frequencies.

position, and acceptable variability was ±3 dB between all 1/3-octave bands across all positions in the mapping grid.

Before each testing session, both signal SPL and masking noise spectral density level were calibrated. The masker level was invariant throughout audiometric testing at a particular frequency. Masking noise spectral density levels [dB re $(1\ \mu\text{Pa})^2$/Hz underwater and dB re $(20\ \mu\text{Pa})^2$/Hz in air] were either 10 or 20 dB (determined by hardware limitations) above the hearing threshold measured for each frequency for the same subject. Because CRs are independent of masker level (Fay, 1988), this difference was unlikely to affect measurements. Noise stimuli were calibrated using SpectraPLUS to ensure that the 1/3-octave band centered on the test frequency was within 1 dB of the target level, and that the 1/3-octave bands above and below this central band were within 3 dB of the target level.

Reaction times

Reaction times (in ms, between tone onset and release of latency switch) were automatically recorded in HTP on all signal-present trials correctly detected during aerial testing, in both quiet and noisy conditions. Data from MCS testing only were pooled across sessions to generate latency–intensity functions at each frequency for each condition. A least-squares power function (Moody, 1970) was used to fit these data and to interpolate reaction times at threshold and 20 dB SL. A comparison of median latencies across subjects in quiet conditions was conducted using a paired t-test. A direct comparison was also made between *Tunu's* audiogram latencies at 0 and 20 dB SL and those obtained at the same frequencies and sensation levels during CR testing.

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	Amak		Tunu		Ambient noise
Frequency (kHz)	Threshold (dB re 1 μPa)	FA rate	Threshold (dB re 1 μPa)	FA rate	Power spectral density [dB re (1 μPa)^2/Hz]
0.1	93	0.15	92	0.25	74
0.2	76	0.13	75	0.17	58
0.4	71	0.07	68	0.23	48
0.8	66	0.12	65	0.16	44
1.6	63	0.16	62	0.24	41
3.2	56	0.11	52	0.25	37
6.4	56	0.18	54	0.20	33
12.8	60	0.14	51	0.20	31
25.6	53	0.14	51	0.10	30
36.2	57	0.26	56	0.24	28
51.2	63	0.24	64	0.19	28
60.9	81	0.17	80	0.25	29
72.4	102	0.10	101	0.10	28

TABLE I. Underwater hearing thresholds obtained with psychophysical methods for two spotted seals. Fifty percent detection thresholds are reported for each test frequency with corresponding noise levels in the test pool. Noise levels are shown in units of power spectral density determined from 1/3-octave band measurements that included each test frequency. False alarm (FA) rates during the testing phase (pooled across all method of constant stimuli sessions) are also given for each frequency (N≥20). For both subjects, 95% confidence intervals were less than 4 dB for all reported thresholds. The psychometric functions associated with each threshold are provided in Figs S1 and S2.

	Amak				Tunu				Ambient noise
Frequency (kHz)	Threshold (dB re 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	Threshold (dB re 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	Power spectral density [dB re (20 μPa)^2/Hz]
0.075	47	0.16	289	216	42	0.16	527	230	20
0.1	41	0.28	363	260	39	0.14	565	251	14
0.2	25	0.19	302	182	29	0.20	475	301	−2
0.4	13	0.14	494	185	15	0.13	485	243	−14
0.8	3	0.03	502	306	6	0.08	507	229	−19
1.6	−1	0.03	439	141	−3	0.09	472	265	−20
2.3	0	0.17	421	133	−1	0.12	512	216	−22
3.2	−10	0.25	697	160	−13	0.09	605	282	−23
4.5	−7	0.28	293	171	−8	0.07	529	222	−24
6.4	−1	0.27	409	205	−3	0.21	449	234	−22
12.8	14	0.19	380	196	8	0.07	442	242	−28
18.1	21	0.10	411	227	24	0.03	247	195	−28
25.6	35	0.22	206	150	37	0.21	435	302	–
36.2	44	0.21	204	142	45	0.22	248	191	–
51.2	57	0.19	243	140	57	0.13	367	215	–

TABLE II. In-air hearing thresholds obtained with psychophysical methods for two spotted seals. Fifty percent detection thresholds are reported for each test frequency with corresponding ambient noise levels in the acoustic chamber. Noise levels are shown in units of power spectral density determined from 1/3-octave band measurements that included each test frequency. False alarm (FA) rates during the testing phase (pooled across all method of constant stimuli sessions) are also given for each frequency (N≥20). Median reaction times are shown at threshold (0 dB SL) and 20 dB above threshold (20 dB SL) for each frequency. For both subjects, 95% confidence intervals were less than 4 dB for all reported thresholds. The psychometric functions associated with each threshold are provided in Figs S3 and S4.

	Underwater critical ratios				In-air critical ratios					
Frequency (kHz)	Masked threshold (dB re 1μPa)	Masker level [dB re $(1\ \mu\text{Pa})^2$/Hz]	Critical ratio (dB)	FA rate	Masked threshold (dB re 20 μPa)	Masker level [dB re $(20\ \mu\text{Pa})^2$/Hz]	Critical ratio (dB)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)
0.1	119	103	16	0.06	61	49	12	0.10	414	248
0.2	99	86	14	0.22	63	49	14	0.17	367	222
0.4	96	81	15	0.26	50	35	15	0.16	367	279
0.8	92	76	16	0.12	42	26	16	0.17	622	373
1.6	90	73	18	0.13	36	17	19	0.19	489	308
3.2	87	66	21	0.21	26	7	18	0.06	387	256
6.4	90	66	24	0.16	41	17	24	0.18	586	182
12.8	96	70	27	0.14	55	31	24	0.26	392	162
25.6	93	73	30	0.19	74	47	27	0.16	–	–

TABLE III. Underwater and in-air masked hearing thresholds and critical ratios obtained in the presence of octave-band noise for two spotted seals at nine frequencies. Underwater critical ratios were obtained with *Amak* and in-air critical ratios were obtained with *Tunu*. Also reported for each frequency are corresponding masker spectral density levels and test phase false alarm (FA) rates (pooled across method of constant stimuli sessions, N≥20). For the in-air data, median reaction times at threshold (0 dB SL) and 20 dB above threshold (20 dB SL) are also provided.

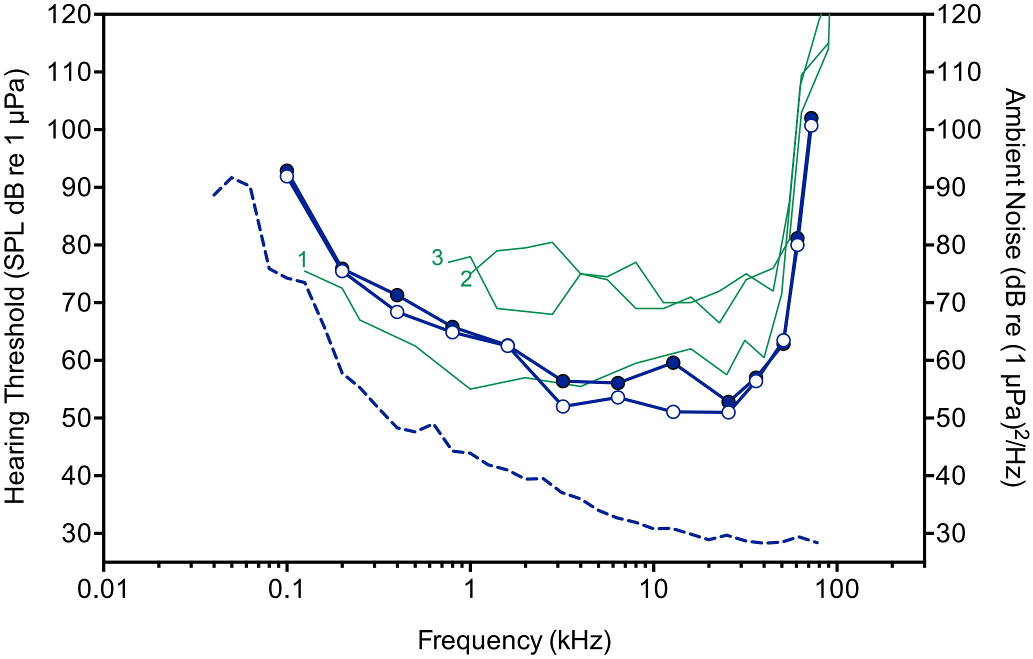

FIG 1. Underwater audiograms for two spotted seals, *Amak* (filled circles) and *Tunu* (open circles), obtained using psychophysical methods. Ambient noise in the underwater testing enclosure is plotted as a dashed line corresponding to the right-hand y-axis. The ambient noise profile comprises power spectral density levels [in dB re (1 μPa)^2/Hz] calculated from the median of 1/3-octave band 50th percentile levels measured across all sessions. For comparison, behavioral audiograms are also shown for harbor seals [1, N=2 (Kastelein *et al*., 2009)], ringed seals [2, N=2 (Terhune and Ronald, 1975a)] and harp seals [3, N=1 (Terhune and Ronald, 1972)]. SPL, sound pressure level.

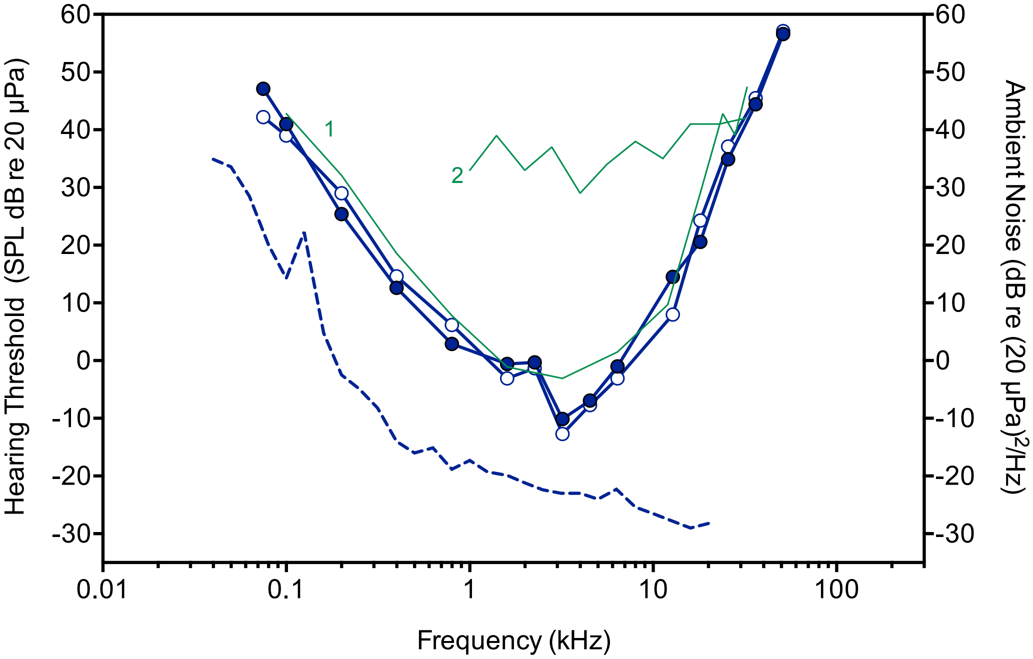

FIG 2. Aerial audiograms for two spotted seals, *Amak* (filled circles) and *Tunu* (open circles), obtained using psychophysical methods. Ambient noise in the acoustic testing chamber is plotted as a dashed line corresponding to the right-hand y-axis. The noise profile comprises power spectral density levels [in dB re (20 µPa)^2/Hz] calculated from the median of 1/3-octave band 50th percentile levels measured across all sessions. Previously published thresholds are shown for harbor seals [1, N=1 (Reichmuth *et al*., 2013)] and harp seals [2, N=1 (Terhune and Ronald, 1971)]. SPL, sound pressure level.

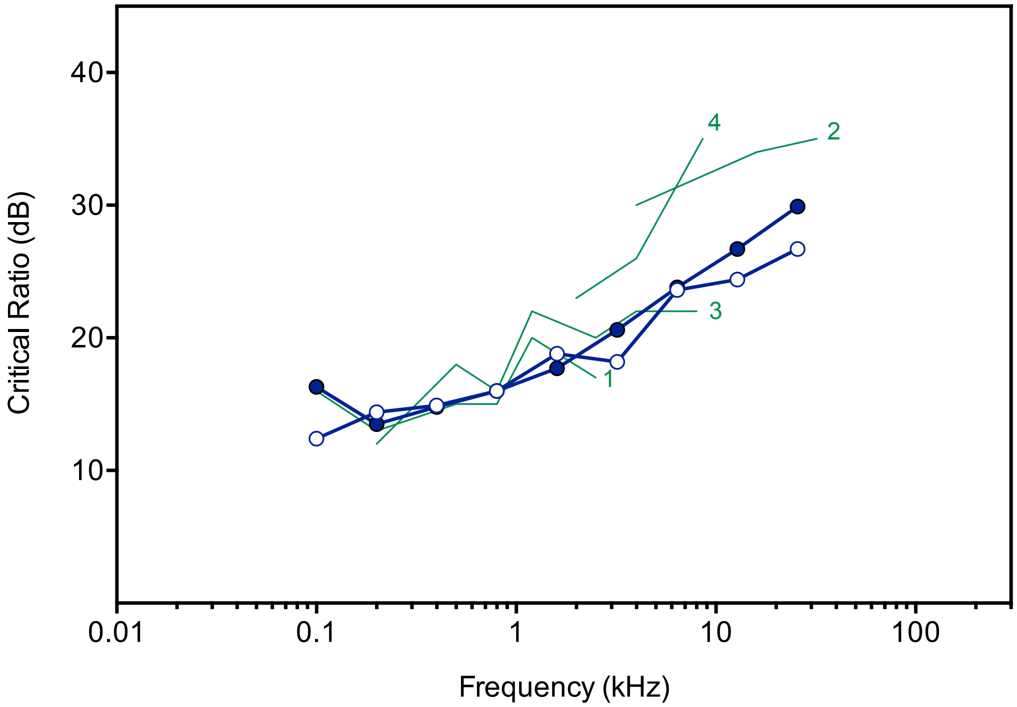

FIG 3. Underwater and in-air critical ratios for two spotted seals measured in the presence of octave-band masking noise. Underwater critical ratios are shown for *Amak* (filled circles) and in-air critical ratios are shown for *Tunu* (open circles) at nine frequencies. Also plotted are underwater critical ratios for harbor [1, N=1 (Southall *et al*., 2000)] and ringed seals [2, N=2 (Terhune and Ronald, 1975b)], and aerial critical ratios for harbor [3, N=1 (Southall *et al*., 2003)] and harp seals [4, N=1 (Terhune and Ronald, 1971)].

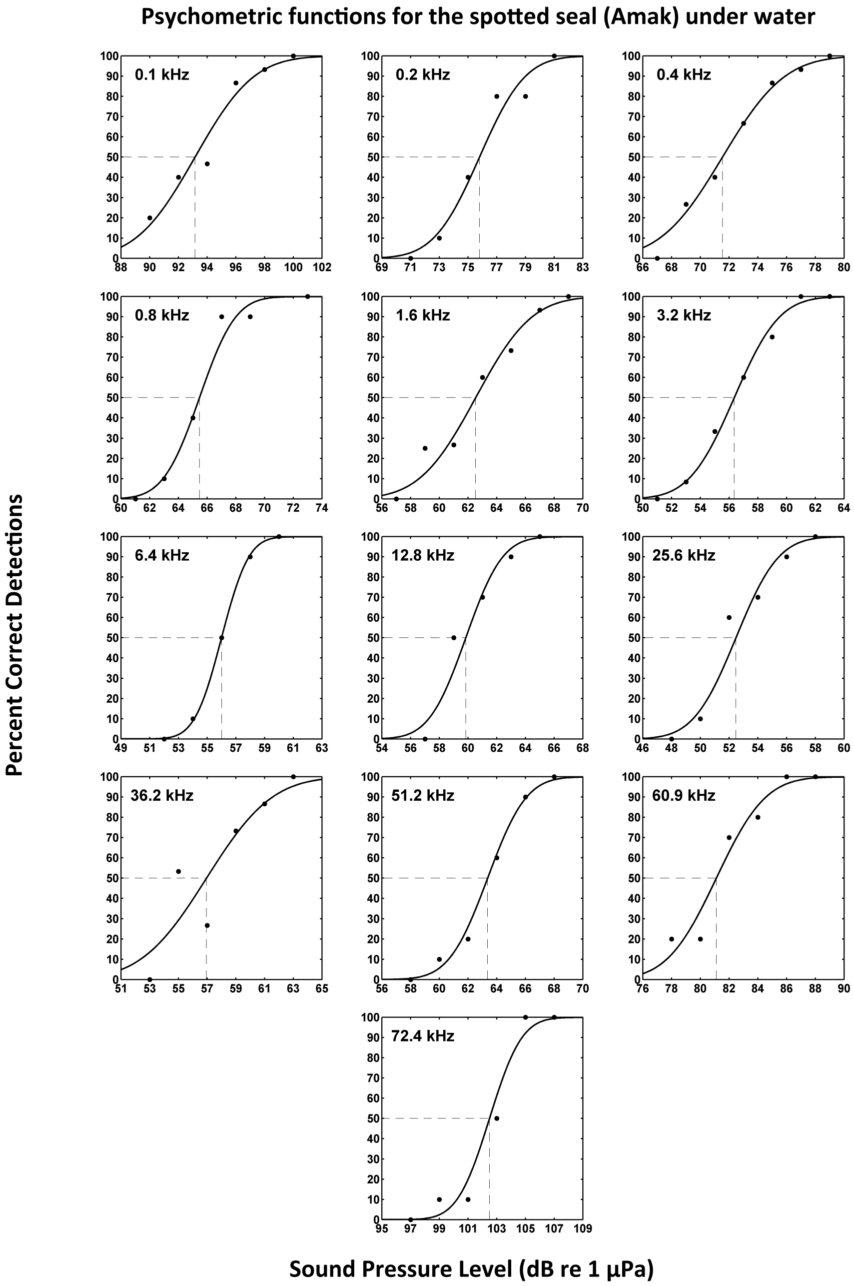

FIG S1. The psychometric function obtained at each frequency underwater for the spotted seal *Amak*. On all plots, the x-axis represents sound pressure level in dB re 1 µPa while the y-axis shows percent correct detection on signal-present trials. Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Threshold, defined at the 50% correct detection rate and indicated on these plots by the dashed lines, was determined using an inverse prediction (not shown).

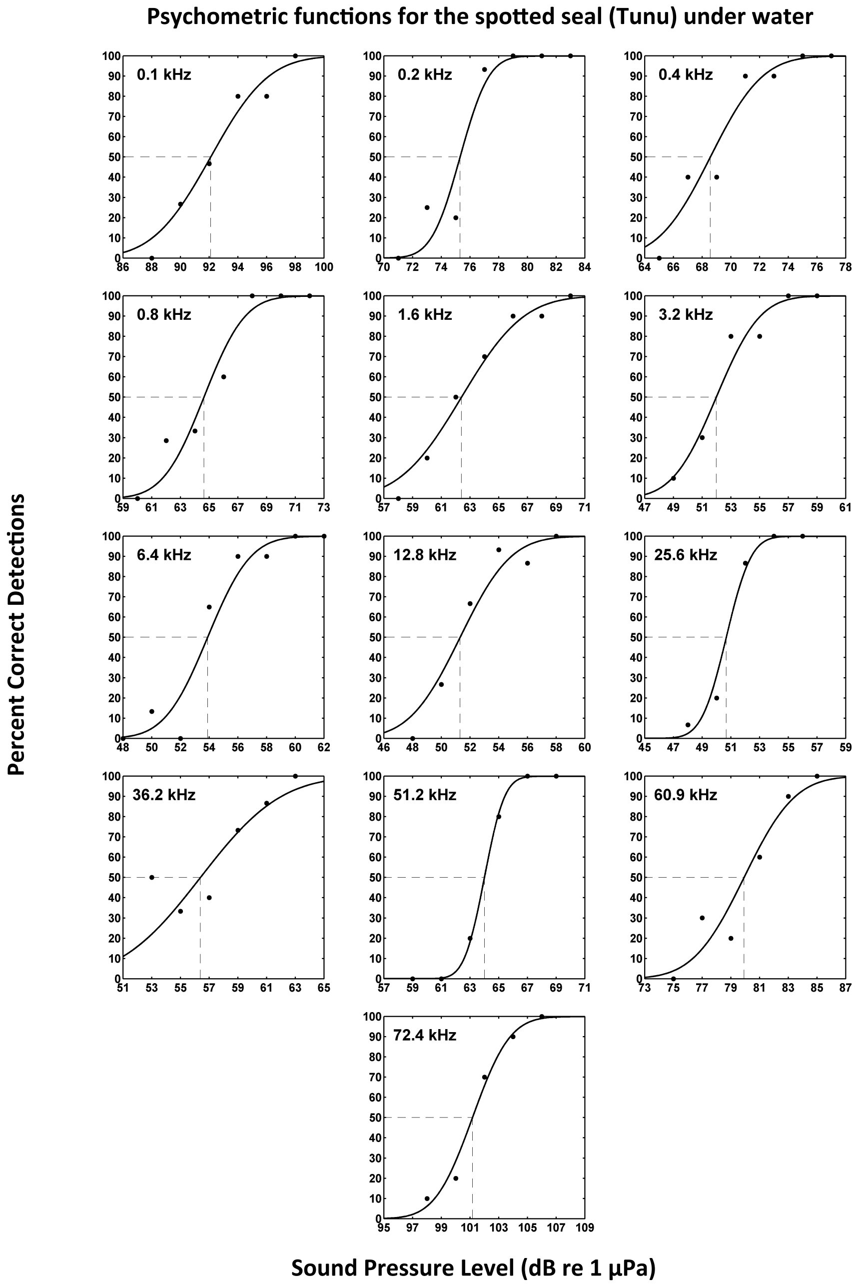

FIG S2. The psychometric function obtained at each frequency underwater for the spotted seal *Tunu*. On all plots, the x-axis represents sound pressure level in dB re 1 µPa while the y-axis shows percent correct detection on signal-present trials. Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Threshold, defined at the 50% correct detection rate and indicated on these plots by the dashed lines, was determined using an inverse prediction (not shown).

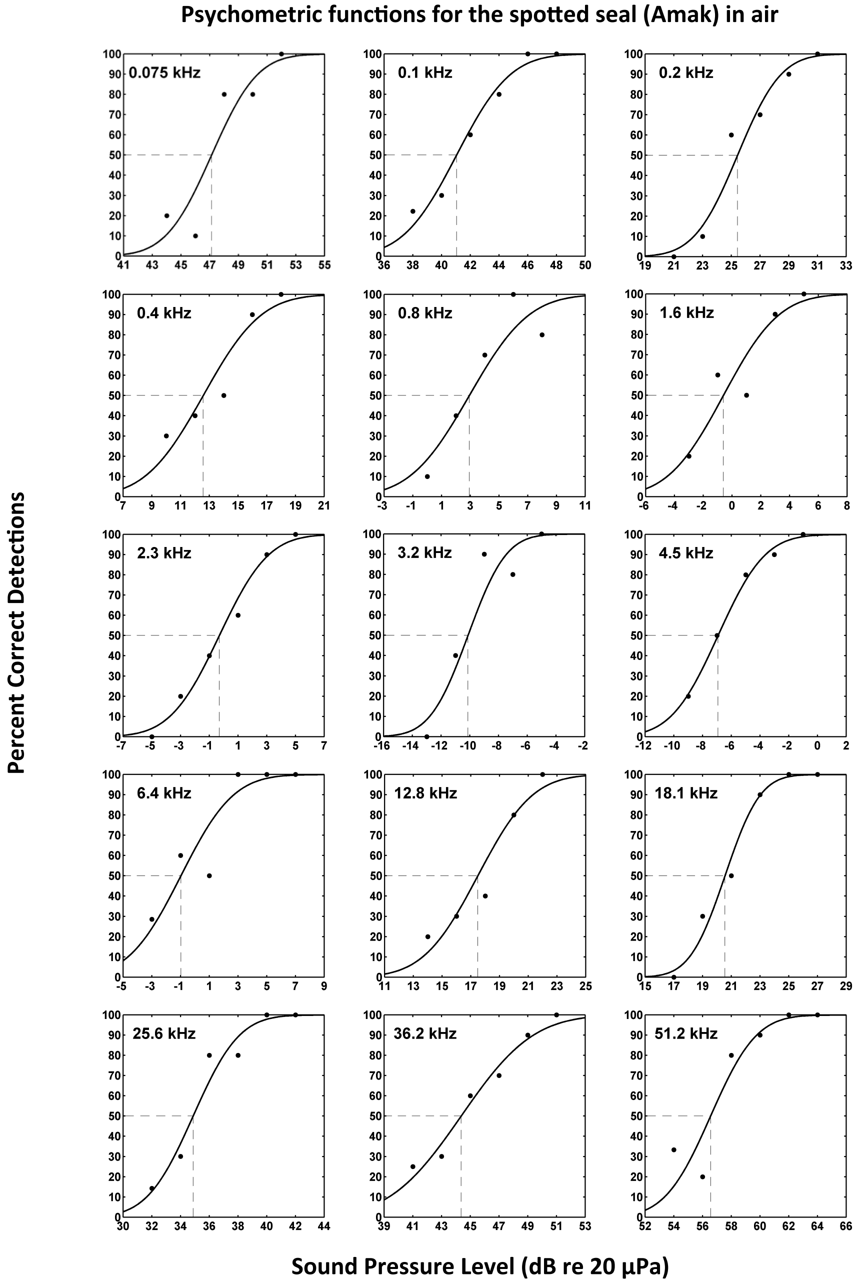

FIG S3. The psychometric function obtained at each frequency in air for the spotted seal *Amak*. On all plots, the x-axis represents sound pressure level in dB re 20 µPa while the y-axis shows percent correct detection on signal-present trials. Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Threshold, defined at the 50% correct detection rate and indicated on these plots by the dashed lines, was determined using an inverse prediction (not shown).

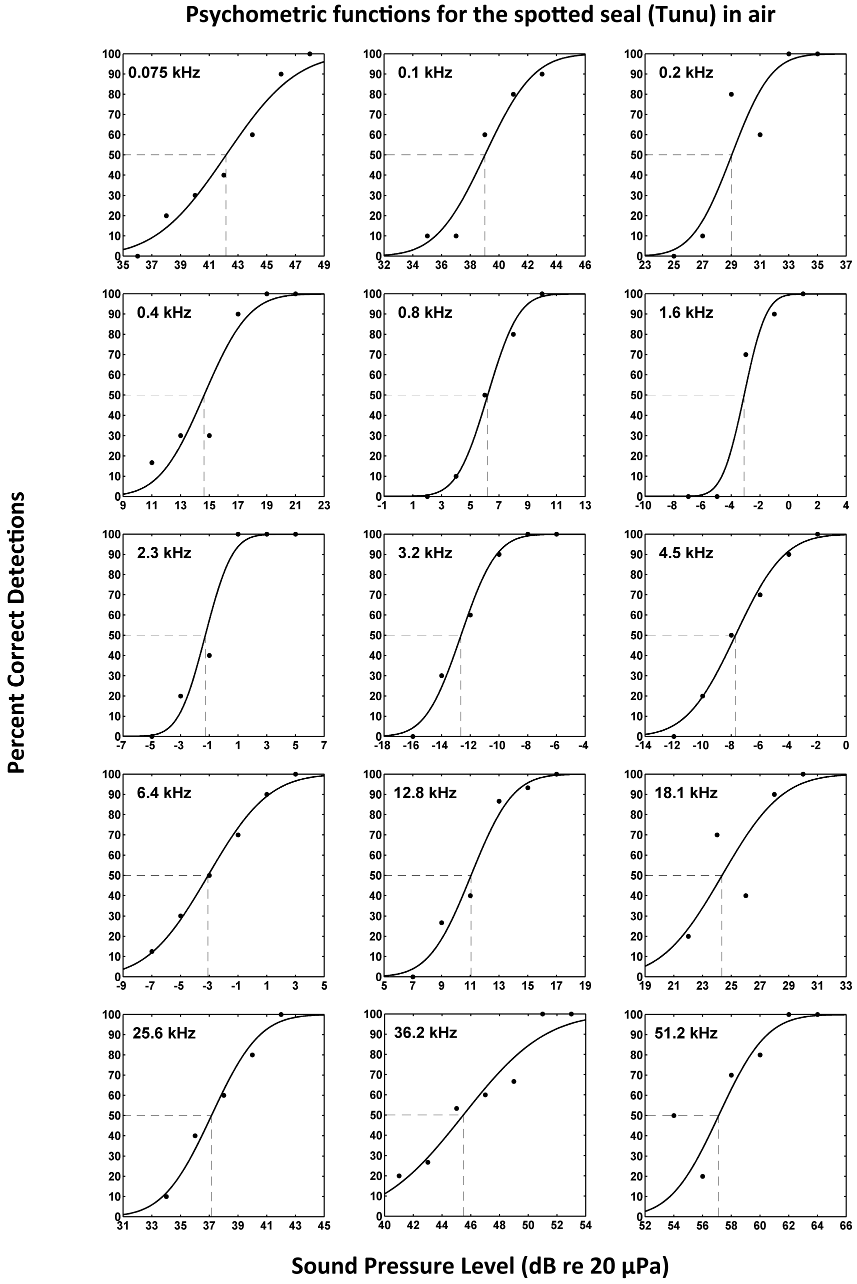

FIG S4. The psychometric function obtained at each frequency in air for the spotted seal *Tunu*. On all plots, the x-axis represents sound pressure level in dB re 20 µPa while the y-axis shows percent correct detection on signal-present trials. Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Threshold, defined at the 50% correct detection rate and indicated on these plots by the dashed lines, was determined using an inverse prediction (not shown).

CHAPTER 2

AMPHIBIOUS HEARING IN RINGED SEALS (*PUSA HISPIDA*): UNDERWATER AUDIOGRAMS, AERIAL AUDIOGRAMS AND CRITICAL RATIO MEASUREMENTS

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ABSTRACT

Ringed seals (*Pusa hispida*) are semi-aquatic marine mammals with a circumpolar Arctic distribution. In this study, we investigate the amphibious hearing capabilities of ringed seals to provide auditory profiles for this species across the full range of hearing. Using psychophysical methods with two trained ringed seals, detection thresholds for narrowband signals were measured under quiet, carefully controlled environmental conditions to generate aerial and underwater audiograms. Masked underwater thresholds were measured in the presence of octave-band noise to determine critical ratios. Results indicate that ringed seals possess hearing abilities comparable to those of spotted seals (*Phoca largha*) and harbor seals (*Phoca vitulina*), and considerably better than previously reported for ringed and harp seals (*Pagophilus groenlandicus*). Best sensitivity was 49 dB re 1 µPa (12.8 kHz) in water, and -12 dB re 20 µPa (4.5 kHz) in air, rivaling the acute hearing abilities of some fully aquatic and terrestrial species in their respective media. Critical ratio measurements ranged from 14 dB at 0.1 kHz to 31 dB at 25.6 kHz, suggesting that ringed seals—like other true seals—can efficiently extract signals from background noise across a broad range of frequencies. The work described herein extends similar research on amphibious hearing in spotted seals recently published by the authors. These parallel studies enhance our knowledge of the auditory capabilities of ice-living seals, and inform effective management strategies for these and related species in a rapidly changing Arctic environment.

INTRODUCTION

Ringed seals (*Pusa hispida* or alternatively, *Phoca hispida* Schreber 1775) live throughout the Arctic in close association with sea ice (Kelly *et al*., 2010). These small seals construct, maintain and defend breathing holes and subnivean lairs in seasonally ice- covered waters. Although little is known about their sensory biology, it is probable that—like other pinnipeds (seals, sea lions, walruses)—ringed seals rely on acoustic cues for vital behaviors including foraging, communication, orientation and predator detection in often light-limited conditions. Although they remain tied to sea ice for biological activities such as whelping and molting, ringed seals breed and forage in water. Their amphibious lifestyle suggests a role for hearing both above and below the water's surface. Measurements of hearing in ringed seals provide information about the characteristics of their auditory system and improve understanding of their acoustic ecology. Ringed seals are of particular interest because of their importance as a subsistence resource, their ecological role as primary prey for polar bears (*Ursus maritimus*), and their vulnerability to the effects of climate change, including loss of sea ice and rapid industrialization.

Laboratory studies on hearing have provided information about the auditory capabilities of some species of phocid (true) seals, but there is a lack of comprehensive data for many species. The northern seals (subfamily Phocinae) include the ringed, Baikal (*Pusa sibirica*), Caspian (*Pusa caspica*), spotted (*Phoca largha*), harbor (*Phoca vitulina*), grey (*Halichoerus grypus*), ribbon (*Histriophoca* *fasciata*), harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*) and bearded seals (*Erignathus barbatus*). Among these species, hearing thresholds are currently available for spotted (Sills *et al*., 2014), harbor (Møhl, 1968a; Terhune, 1988, 1991; Kastak and Schusterman, 1998; Wolski et al., 2003; Southall *et al*., 2005; Kastelein *et al*., 2009; Reichmuth *et al*., 2013), Caspian (Babushina, 1997), harp (Terhune and Ronald, 1972) and ringed seals (Terhune and Ronald, 1975a). Of note relative to the present study, however, is that sensitivity data for ringed, harp and Caspian seals do not extend to the low frequencies, and ringed seal hearing has only been studied in water. Based on available information, it is difficult to determine the extent to which the hearing of these related species is similar or different. Other researchers have proposed the existence of so-called 'functional hearing groups' of species with comparable auditory capabilities, which is useful for those tasked with managing the effects of noise on a wide range of species (Southall *et al*., 2007). For example, observed similarities in the audiograms of the otariid pinnipeds (sea lions and fur seals) have led to the suggestion of a functional hearing group for these 14 species (Mulsow *et al*., 2012). Currently, there are insufficient data to determine whether a similar grouping is appropriate for the Phocidae family (18 spp.) or the Phocinae subfamily (10 spp.). Additional descriptions of auditory sensitivity are necessary for seals.

Here, we describe a series of behavioral experiments that characterize species-typical hearing in ringed seals by testing individuals in controlled acoustic settings. This includes measurement of hearing sensitivity for two seals above and below the water’s surface, in quiet conditions and in the presence of noise. Results comprise aerial and underwater audiograms to describe absolute (unmasked) hearing sensitivity, and underwater critical ratio measurements that can be used to evaluate frequency tuning and auditory masking. With these standardized and quantitative descriptions of auditory sensitivity, direct comparisons can be made across individuals, frequencies, noise conditions, media and species.

This study with ringed seals parallels and complements a set of experiments recently conducted with spotted seals (Sills *et al*., 2014) as part of a larger effort to describe hearing, and the effects of noise on hearing, in ice-living seals. The methods and testing environments used for the two species were nearly identical. Considered together, these studies inform understanding of how the auditory systems of these Arctic seals are adapted for an amphibious existence, and enable relevant intra- and inter-specific comparisons of auditory performance.

RESULTS

Underwater audiograms

Underwater hearing thresholds are reported for a 16-year-old male ringed seal (*Natchek*) and a 2-year-old female ringed seal (*Nayak*), with measures of response bias (false alarm rates) and ambient noise (Table I). The corresponding audiograms and environmental noise floor are shown alongside representative data for northern seals (Fig. 1). The psychometric functions associated with these hearing thresholds are provided as Fig S1.

False alarm rates were measured as the proportion of signal-absent trials in the psychophysical task on which subjects incorrectly reported detection of a signal. Mean false alarm rates were 0.16 and 0.19 for *Natchek* and *Nayak*, respectively, and response bias remained stable across frequencies and between seals. Threshold-to-noise offsets were calculated at each test frequency as the difference between measured hearing threshold and ambient noise spectral density level (50th percentile level) in the testing pool. This offset ranged from a minimum of 15 to a maximum of 88 dB, and was greatest at high frequencies. The audiograms of both seals exhibited a general U-shape, with sharper roll-offs in sensitivity at the high relative to the low frequency end. The frequency of best hearing was 12.8 kHz for *Natchek* and 25.6 kHz for *Nayak*, with measured thresholds of 49 and 50 dB re 1 µPa, respectively. At low to mid frequencies, hearing sensitivity was similar for the two subjects, with an average threshold difference of 3 dB for frequencies between 0.1 and 25.6 kHz. However, at higher frequencies (>25.6 kHz), the hearing of the young, female ringed seal was markedly superior. The frequency range of best sensitivity—within 20 dB of lowest measured threshold, as in Reichmuth *et al.* (2013)—extended from approximately 0.4 to 32 kHz for *Natchek* and 0.3 to 52 kHz for *Nayak*. Although it began at a lower frequency for *Natchek*, the slope of the high-frequency roll-off was similarly steep for both subjects, with thresholds increasing by approximately 36 dB over a quarter octave span.

In-air audiograms

In-air hearing thresholds for the two ringed seals are reported with false alarm rates, ambient noise levels and reaction time data (Table II). The audiograms and environmental noise floor are shown alongside representative data for other northern seals (Fig. 2). The psychometric functions associated with these thresholds are provided as Fig S2.

Mean false alarm rates were 0.17 for *Natchek* and 0.18 for *Nayak*. Threshold-to-noise offsets in the acoustic chamber ranged from 12 to 61 dB, and were lowest between 0.8 and 6.4 kHz. The aerial audiograms were narrow and more V-shaped than their underwater counterparts, with more gradual high-frequency roll-offs. Similar to the underwater curves, however, sensitivity declined faster at high relative to low frequencies. Although comparable overall, hearing sensitivity varied somewhat between subjects, with a mean threshold difference of 7 dB. The frequency of most sensitive hearing in air was 3.2 kHz for *Natchek* and 4.5 kHz for *Nayak*, with thresholds of -6 dB re 20 μPa and -12 dB re 20 μPa, respectively. The 20 dB bandwidth of best sensitivity ranged from 0.7 to 11 kHz for *Natchek* and 0.6 to 12 kHz for *Nayak*, with sensitivity rolling off above this range. Rather than increasing with a fixed slope, the high-frequency thresholds for both subjects exhibited an apparent reduction in slope in the region near 18 kHz. At the highest frequencies

(>25.6 kHz), as observed in water, *Natchek* showed a considerable reduction in sensitivity relative to *Nayak*.

To supplement auditory thresholds, interpolated reaction times at threshold (0 dB sensation level, SL) and 20 dB above threshold (20 dB SL) are provided for each subject at each test frequency (Table II). While these response latencies varied with frequency, they were typically less than 500 ms for signals near threshold. Across all frequencies, the median reaction times at threshold and 20 dB SL were 359 and 181 ms for *Natchek*, and 428 and 177 ms for *Nayak*. In general, while supra-threshold reaction times (20 dB SL) were similar for all frequencies, reaction times near threshold exhibited more frequency dependence and were higher at low frequencies for both subjects.

Underwater critical ratio measurements

Underwater critical ratios (CRs), masked thresholds, noise spectral density levels and false alarm rates are reported for both seals (Table III). These data are shown along with aerial and underwater CR measurements for related species (Fig. 3). Mean false alarm rate was 0.20 for each subject. CRs for *Natchek* ranged from 16 dB at 0.1 kHz to 31 dB at 25.6 kHz, whereas CRs for *Nayak* ranged from 14 dB at 0.1 kHz to 31 dB at 25.6 kHz. Overall, CRs increased at a rate of approximately 2 dB per octave.

DISCUSSION

Underwater hearing

Underwater thresholds obtained for two ringed seals show greater than expected hearing sensitivity for this species, and are considerably lower than previously reported for both ringed (Terhune and Ronald, 1975a) and harp seals (Terhune and Ronald, 1972) at most frequencies. The audiograms for the two subjects are in good agreement from 0.1 to 25.6 kHz, above which the adult male (*Natchek*) exhibits apparent high-frequency hearing loss. The thresholds of the young female (*Nayak*) are quite similar to those reported recently for harbor (Kastelein *et al*., 2009; Reichmuth *et al*., 2013) and spotted seals (Sills *et al*., 2014) across the hearing range. In contrast to historical data, these ringed seal audiograms are consistent with the hypothesis of a functional hearing group for northern seals.

To assess how well underwater audiograms reflect absolute hearing sensitivity, it is important to consider the potential influence of ambient noise on the measured thresholds. Threshold-to-noise offsets at each frequency can be compared with CRs to determine whether thresholds may have been constrained by background noise in the testing environment. Based on the CRs obtained for the subjects in this study, threshold-to-noise offsets were approximately one CR between 0.8 and 36.2 kHz, indicating that ambient noise may have influenced thresholds within this range.

At higher and lower frequencies, background noise was sufficiently low (threshold-to-noise offset>one CR) to confirm the measurement of absolute thresholds. Despite rigorous noise measurement and analysis using percentile statistics, it remains difficult to accurately characterize the relationship between temporally fluctuating background noise and signal detectability. Given these constraints, the reported thresholds can be considered accurate or somewhat conservative for these ringed seals.

When considering the biological relevance of species-typical hearing, there is often a presumed correlation between the frequency range of sensitive hearing and the frequency range of vocalizations. This predicted tuning between signal and receiver (Endler, 1992) has been demonstrated in some vertebrate species (*e.g.*, Dooling *et al*., 1971; Ryan and Wilczynski, 1988; Esser and Daucher, 1996; Ladich and Yan, 1998). Ringed seal underwater vocalizations have been hypothesized to support the maintenance of social structure around breathing holes in winter and spring (Stirling, 1973; Stirling *et al*., 1983). The typical energy of these calls is between 0.1 and 5 kHz (Stirling, 1973; Stirling *et al*., 1983; Cummings *et al*., 1984; Jones *et al*., 2014). While this frequency span is largely encompassed by the 20 dB bandwidth of best hearing in water, the range of best hearing in ringed seals extends more than three octaves above the upper limit of dominant vocal energy. This suggests that selective pressures other than those associated with conspecific communication have influenced hearing capabilities. Seals may listen for auditory cues to aid in predator avoidance, prey detection, or passive orientation in the environment (Schusterman *et* *al*., 2000). Ice-living seals may use the local soundscape to find breathing holes or the ice edge in low-light conditions (Elsner *et al*., 1989; Wartzok *et al*., 1992; Miksis-Olds and Madden, 2014). Additionally, the extended high-frequency hearing range of seals in water may support their ability to localize sounds (Heffner and Heffner, 2008; Nummela and Thewissen, 2008). Finally, it is important to note that species-typical hearing is not only the outcome of auditory adaptations; enhanced underwater hearing may also be related to physiological traits for a semi-aquatic existence, such as modifications to the ear for withstanding high pressures while diving.

In-air hearing

The audiograms obtained in this study demonstrate acute aerial hearing sensitivity for ringed seals that is comparable to that of spotted (Sills *et al*., 2014) and harbor seals (Reichmuth *et al*., 2013). Although they forage and travel extensively at sea, ringed seals rely on sea ice as a substrate for resting, whelping and molting, and experience terrestrial predation pressure from polar bears. Retention of sensitive aerial hearing in addition to enhanced underwater sound reception reflects the truly amphibious nature of these seals.

Recent findings suggest that many published hearing thresholds for seals in air are masked by environmental noise (Reichmuth *et al*., 2013). As with the underwater data, aerial thresholds should be considered relative to CRs and typical noise conditions to evaluate the possibility of masking. In this study, threshold-to-noise offsets were approximately equal to one CR between 0.8 and 6.4 kHz, indicating that noise may have limited threshold measurements in this range, but not at higher or lower frequencies. However, because the quiet conditions in the testing chamber approached the measurement limits of the equipment (Brüel & Kjær 2250 sound analyzer; Brüel & Kjær A/S, Nærum, Denmark), masking by background noise can neither be confirmed nor entirely ruled out between 0.8 and 6.4 kHz. Regardless, the in-air thresholds measured for these ringed seals are among the lowest reported for marine mammals.

When compared with available data for ice-living seals, these ringed seal audiograms—along with recent data for spotted seals (Sills *et al.*, 2014)—show significantly better sensitivity to airborne sounds than measured previously for one harp seal (Terhune and Ronald, 1971). While others have suggested that the harp seal thresholds were elevated as a result of noise (Watkins and Wartzok, 1985; Moore and Schusterman, 1987), the reported ambient noise levels and CRs (Terhune and Ronald, 1971) suggest that masking was not a relevant factor. We conducted a separate experiment to reconcile these differences in reported hearing sensitivity between studies and species. The findings showed that, while the elevated thresholds reported for the harp seal could be replicated for one ringed seal tested in a similar experimental configuration, the results could not be explained by masking at the test frequency. See Appendix for details.

The aerial audiograms of the two ringed seals have several features that differ from the underwater audiograms obtained for the same individuals. Among the expected differences is a narrower frequency range of hearing in air that is more similar to the hearing range of some terrestrial carnivores (Heffner, 1983; Heffner and Heffner, 1985a,b; Kelly *et al.*, 1986). Another difference is the shallower slope observed on the high-frequency roll-off for these seals in air compared with the steeper roll-offs on their underwater audiograms, as previously described for other seals (Reichmuth *et al*., 2013). Two additional features are particularly notable in the aerial curves. First, both ringed seals exhibited best sensitivity around 3–5 kHz, with significantly lower thresholds in this region relative to adjacent frequencies. This 'notch' of increased sensitivity was also observed for two spotted seals tested under the same conditions (Sills *et al*., 2014). Second, both ringed seals showed an apparent change in slope in the aerial high-frequency roll-off, around 20–30 kHz. Neither of these features is reflected in the underwater audiograms of these individuals. Hence, they may be related to the frequency selectivity of peripheral auditory structures (*e.g*., resonances), which almost certainly operate differently in air and water. Anatomical studies are needed, and should be combined with these psychoacoustic data to inform models of auditory form and function for seals.

The measured response latencies obtained for the ringed seals listening in air provide valuable information about perceptual loudness. For both subjects, response time changed less with increasing amplitude at high relative to low frequencies. This suggests that at higher frequencies there is less of a perceptual difference between just-audible sounds and supra-threshold stimuli. Conversely, at lower frequencies, there is apparently a more gradual perceptual transition between quiet (0 dB SL) and supra-threshold (20 dB SL) sounds. Measures of response time complement the threshold values obtained at each frequency by providing a useful metric for determining the equivalence of signals of various frequencies and levels.

Observed differences in hearing between subjects

Although the two ringed seals' hearing curves are generally similar, *Natchek* showed reduced sensitivity relative to *Nayak* at a range of frequencies in air, and at high frequencies in water. In fact, the juvenile female *Nayak's* thresholds for airborne sounds were more similar to those measured for two young male spotted seals (Sills *et al.*, 2014) than for the adult male ringed seal (*Natchek*), revealing greater observed differences in hearing with age than across sex or species.

Differences in auditory sensitivity between individuals can be explained by a range of variables including age-related hearing loss (presbycusis), congenital deficits, disease processes, prior exposure to noise, medication history and inherent individual differences (Yost, 2000). Although the occurrence of presbycusis is not well documented in seals, it is possible that, at 16 years old, *Natchek* had hearing loss related to his age. Alternatively, *Natchek's* brief exposures to ototoxic medication could have contributed to his elevated thresholds. Aminoglycoside antibiotics—including Amikacin, which *Natchek* received for 5 days between 1996 and 2003—are known to cause degeneration of sensory hair cells in the cochlea, with hearing loss initially observable at high frequencies (see, *e.g.*, Yost, 2000; Huth *et al.*, 2011).

Conductive hearing loss may also explain *Natchek's* apparent reduction in hearing sensitivity (see below). While it is beyond the scope of this manuscript to resolve this issue definitively, the differences in hearing observed between seals in this study underscore the importance of testing multiple individuals in behavioral studies of sensory biology, to ensure that measured capabilities are representative of best sensitivity for the species.

Mechanisms of amphibious hearing

The hearing data presented herein highlight the incredible dual function of the auditory system of seals in air and water. Despite their need to detect sound in these very different physical environments, ringed seals are able to hear nearly as well (in terms of best sensitivity) as fully aquatic and fully terrestrial mammals in their respective media. The mechanisms by which the seal ear operates efficiently in both media are not well understood. The seal ear likely functions in the same manner as a traditional terrestrial ear above water, with energy transmitted from the air-filled spaces of the outer ear to the fluid within the cochlea via the middle ear ossicles, which compensate for the impedance mismatch between the two media. It has been suggested that, when submerged, expansion of cavernous tissue in the external meatus and/or middle ear cavity creates a functionally 'fluid-filled' ear that more closely matches the impedance of the surrounding fluid environment (see Møhl, 1967, 1968b; Ramprashad, 1975; Møhl and Ronald, 1975). The enhanced role that bone and tissue conduction are thought to play in sound detection under water (Møhl, 1968b; Repenning, 1972; Ramprashad, 1975; Nummela, 2008) may further explain some of the observed differences in hearing between subjects in this study. The ringed seal *Natchek's* reduced sensitivity at lower frequencies in air, but not in water, may be the result of conductive damage to peripheral auditory structures that function differently in each medium. The contribution of bone and tissue conduction could explain why the underwater audiogram does not also suggest conductive loss. Conversely, it is more likely that *Natchek's* significant high-frequency hearing loss (>25.6 kHz) is cochlear in origin, because of its expression in both media. While the results of the present study provide some clues, the auditory pathways that support amphibious hearing remain unresolved.

When considering the hearing of amphibious seals, one feature of theoretical and practical interest is the expanded frequency range of hearing in water relative to in air. Comparing the slopes of the high-frequency sensitivity roll-offs for the ringed seals enables consideration of the constraints that limit hearing in each medium. In water, the roll-offs not only occur at higher frequencies, but are also considerably steeper than the lower and more gradual roll-offs observed in air for the same subjects. This pattern, which is reported for other true seals (Reichmuth *et al.*, 2013; Sills *et al.*, 2014), supports the idea that different mechanisms determine the high-frequency hearing limits in air and water. The frequency limit of hearing in air may be constrained by inertia of the dense ossicular bones (Hemilä *et al.*, 2006), for example, or perhaps the hearing range is expanded in water because of alternative energy-transmission pathways. We suggest that fine-scale audiometric data, including the amphibious thresholds reported here, can be combined with theoretical models of auditory function to improve understanding of the unique hearing abilities of seals.

Auditory masking

Underwater CRs were similar between subjects and to those reported for harbor (Southall *et al*., 2000, 2003) and spotted seals (Sills *et al*., 2014) in air and water, providing additional evidence for similar hearing capabilities across these species. Despite the male ringed seal's reduction in absolute sensitivity at some frequencies, his ability to detect signals within noise over the broad frequency range tested (0.1–25.6 kHz) has apparently not been diminished by age, ototoxic exposure or any other factor. The CRs measured in this study were 3–10 dB lower than previously reported for ringed seals (Terhune and Ronald, 1975b). Our results indicate that, like other phocids, ringed seals possess a refined ability to extract signals from background noise relative to many terrestrial mammals (Fay, 1988). CRs were measured over the full vocal range and did not show any correlation with the frequencies of ringed seal vocalizations. Therefore, these seals possess a general ability for enhanced signal detection in noise across a range of frequencies.

While CRs were measured in water, they can be applied to quantify masking by both underwater and airborne noise (for further discussion, see Renouf, 1980; Turnbull and Terhune, 1990; Southall *et al.*, 2003; Sills *et al*., 2014). To predict masking in real environments, ambient and anthropogenic noise conditions in either medium can be assessed relative to measured absolute audiograms and CRs. Such an analysis provides a good (conservative) approximation for understanding the effects of noise on hearing (see Dooling *et al.*, 2013), but does not consider the potential for masking release due to complex stimulus features (Branstetter *et al.*, 2013). To accurately quantify the extent of masking experienced by seals exposed to realistic noise sources, more data about auditory performance under different signal and noise scenarios are required (Cunningham *et al*., 2014).

Conclusions

While the effects of climate change and industrialization on Arctic marine mammals are multi-faceted, the gaps in current understanding of hearing in Arctic species—including seals—leave regulators poorly equipped to address management issues related to anthropogenic noise. Appropriate decision-making requires direct measurements of hearing, and the effects of noise on hearing and fitness, in Arctic seals. To this end, we must begin by characterizing the auditory system and acoustic ecology of species of concern.

Recent data for harbor, spotted and now ringed seals collectively support the notion of similar hearing capabilities in all northern seals (subfamily Phocinae) and the characterization of these 10 species as a functional hearing group. However, data for additional species are necessary to fully resolve this issue. In particular, audiograms are needed for species such as bearded seals that are more phylogenetically distant or ecologically divergent from the species whose capabilities are known. Ultimately, informed identification of one or more functional hearing groups will be significant in improving understanding of evolutionary biology and developing broad, practical approaches for resource management.

The auditory profiles reported here provide a thorough evaluation of the basic auditory capabilities of ringed seals, and inform analyses of functional hearing, auditory anatomy, conservation, ecology and evolution. This work demonstrates the value of testing multiple species in the same facilities using similar methodology, and enables a comparative assessment of hearing capabilities across phylogenetic groups. These data indicate that the amphibious lifestyle of these ice-living marine carnivores has favored the evolution of acute hearing both in air and under water. Along with harbor and spotted seals, ringed seals have retained the ability to perceive extremely quiet airborne sounds despite adaptations related to aquatic hearing. Although the mechanisms that support these dual, seemingly contradictory abilities remain unresolved, careful comparisons of hearing sensitivity across frequencies and media can contribute to the ongoing discussion of amphibious hearing and auditory pathways in seals.

MATERIALS AND METHODS

General experimental methods

This study was conducted as part of an ongoing effort to describe hearing in Arctic seals. The methods used were similar to those described in detail for a parallel study with spotted seals (Sills *et al*., 2014).

Test subjects

Subjects were two ringed seals, one adult male identified as *Natchek* (NOA0005618) and one juvenile female identified as *Nayak* (NOA0006783). At the start of testing *Natchek* was 16 years old and weighed 46 kg, and *Nayak* was 2 years old and weighed 21 kg. The interaural distances of these seals, measured dorsally as the curvilinear length between meatal openings, were 13 and 12 cm respectively. *Natchek* participated in this study while on loan from SeaWorld San Diego, and was transferred to Long Marine Laboratory (LML) at the University of California Santa Cruz in December 2010. *Natchek* was an apparently healthy adult seal. He had previously been treated with small amounts of ototoxic medication, including an aminoglycoside antibiotic, but these exposures were below levels considered harmful to auditory structures (T. Schmitt and D. Casper, personal communication). *Natchek's* hearing had not been evaluated prior to this study; however, he previously failed to show a spontaneous behavioral response to a 69 kHz underwater pinger (Bowles *et al*., 2010). The female ringed seal *Nayak* stranded in Alaska as a neonate in 2011, and was transferred to LML in May 2012. She had no known history of ear injury or exposure to ototoxic medication.

Both seals were housed outdoors at LML, in free-flow seawater tanks with adjacent haul-out space. The seals were trained with operant conditioning methods and positive reinforcement to voluntarily participate in the auditory signal detection task. Training occurred over several months and continued until performance was highly reliable at a wide range of sound frequencies and amplitudes. Audiometric testing took place from 2012 to 2014. Typically, the seals received one-third to one-half of their daily diets (freshly thawed capelin and herring) for participation in experimental sessions, and their diets were not constrained for experimental purposes. Subjects participated in one to two research sessions per day, 5 days per week.

Research was conducted with the approval and oversight of the University of California Santa Cruz Institutional Animal Care and Use Committee, with permission from the Ice Seal Committee and the National Marine Fisheries Service of the United States (marine mammal research permit 14535).

Test environments

Audiometric measurements were obtained in one of two environments: a circular, partially in-ground pool of 1.8 m depth and 7.6 m diameter, or a modified hemi-anechoic acoustic chamber (Eckel Industries, Cambridge, MA, USA) for in-air testing. Ambient noise measurements were taken daily under water and at least once per week in the acoustic chamber, at the center position of the seal's head during experimental sessions. Further details regarding test environments, apparatus and ambient noise characterization procedures are given by Sills *et al.* (2014).

Psychoacoustic procedures

Hearing thresholds were measured for each experimental condition using similar behavioral methods. The task was an auditory go/no-go procedure. To start a session, the seal entered the test environment and placed its head on a cupped chin station positioned within a calibrated sound field. Within a 4-s listening interval delineated by a trial light, the subject was trained to touch a response target upon detection of an acoustic signal (correct detection) and withhold this response when it did not (correct rejection). Both correct trial types were rewarded with primary (fish) reinforcement. Misses (remaining on station when a signal was presented) and false alarms (reporting a detection when no signal was presented) were never reinforced. Within a testing session, frequency was held constant while signal amplitude was adjusted. Signal frequencies were tested to completion in random order. At the end of each experiment, the first test frequency was re-checked to eliminate the possibility of a practice effect.

An adaptive staircase procedure (Cornsweet, 1962) was used to estimate hearing thresholds. Sessions began with a signal level easily detected by the subject, after which the amplitude was progressively decreased by 4 dB after each correct detection until the first miss. An asymmetrical step-size was then used—4 dB increases in signal amplitude after misses and 2 dB decreases after correct detections—to maintain stimulus control with these relatively naïve animals by minimizing errors following misses. Five consecutive descending misses within 6 dB of one another made up the test phase of each session, which was followed by a series of easily detectable trials to complete the session. Once individual performance had stabilized (when the average level of these misses varied by less than 3 dB across sessions), data collected over three sessions contributed to threshold determination.

When measuring masked thresholds to calculate CRs, initial adaptive staircase sessions were followed by additional testing using the method of constant stimuli (MCS) (Stebbins, 1970). Five signal levels were selected in 2 dB increments surrounding the masked threshold obtained with adaptive staircase testing. Each of these sound pressure levels (SPLs) was presented five times per session, distributed evenly into randomized blocks. Over the course of two to four MCS sessions, the proportion of correct responses at each signal level was obtained. While this more rigorous method of adaptive staircase followed by MCS is preferred, MCS was not used for audiogram testing because of time constraints. However, in practice, thresholds measured using adaptive staircase testing are often compared to those obtained with MCS methods.

For all experiments, the final threshold at each frequency was calculated using probit analysis (Finney, 1971) and was defined as the SPL in $\mathrm{dB_{rms}}$ re 1 μPa (in water) or $\mathrm{dB_{rms}}$ re 20 μPa (in air) at which there was a 50% correct detection rate. For either testing method (staircase or MCS), the psychometric function was fit to the proportion of correct detections obtained at each signal level, and an inverse prediction was applied to calculate threshold at the 50% correct detection level. Threshold criteria were met when 95% confidence intervals were less than 4 dB.

A similar response bias was maintained within and between subjects across testing conditions by adjusting the relative amount of signal-present and signal-absent trials in each session. The proportion of signal-present trials varied between 0.50 and 0.70, and was typically 0.55 for both seals. The reinforcement ratio for correct detections to correct rejections was always 1:1. The false alarm rate during a session's test phase (which excluded initial and terminal supra-threshold trials) was deemed acceptable if it was above 0 and below 0.3.

Signal generation and calibration

Experiments were conducted using Hearing Test Program (HTP) (Finneran, 2003), custom LabVIEW-based software (National Instruments Corp., Austin, TX, USA). Test stimuli were 500 ms frequency-modulated sweeps with 10% bandwidth (±5% from center frequency) and 5% rise and fall times. Outgoing stimuli were sent from HTP through an NI USB-6259 BNC M-series data acquisition module with an update rate of 500 kHz, were subsequently band-pass filtered with a Krohn-Hite 3364 anti-aliasing filter (Krohn-Hite, Brockton, MA, USA), and were sent through a TDT PA5 digital attenuator (Tucker-Davis Technologies, Alachua, FL, USA) prior to reaching the projector. In some cases, a Hafler P1000 power amplifier (Hafler Professional, Tempe, AZ, USA) was also in line before the projector. For all experiments, the sound field was mapped prior to testing at each frequency to ensure minimal variability in received signals and noise. Daily calibration and analysis of signal structure took place immediately prior to each experimental session. Except where noted below, mapping and calibration procedures and experimental apparatuses were identical to those described previously (Sills *et al*., 2014).

Underwater audiograms

Hearing thresholds were obtained in water at frequencies from 0.1 to 25.6 kHz, in octave steps. Because of differences in auditory capabilities at high frequencies, testing above 25.6 kHz varied between the two subjects. *Natchek* was tested at 36.2 and 43.1 kHz, whereas *Nayak* completed testing at 36.2, 51.2, 60.9 and 72.4 kHz.

Three underwater transducers were used during testing: a Naval Undersea Warfare Center J-11 (Newport, RI, USA) or a Lubell Labs 1424 HP (Columbus, OH, USA) for signals from 0.1 to 12.8 kHz and an ITC 1042 projecting hydrophone (International Transducer Corporation, Santa Barbara, CA, USA) for signals from 12.8 to 72.4 kHz. For sound field mapping and daily stimulus calibration, a Reson TC4032 hydrophone (0.01–80 kHz, ±2.5 dB; Reson A/S, Slangerup, Denmark) with a Reson EC6073 input module or an ITC 1042 hydrophone (0.01–100 kHz, ±2.5 dB) was used as a receiver. A nominal sensitivity of -170 dB re 1 μPa/V was used for the Reson TC4032 during testing; following data collection, the hydrophone was recalibrated and a frequency-specific correction was applied to the measured thresholds. As the transducers used for testing sometimes varied between subjects, *Natchek* completed testing at 1.6 kHz with both the J-11 and the Lubell Labs 1424 HP; results confirmed that threshold did not vary based on the projector used.

In-air audiograms

Hearing thresholds were obtained in air at 0.075, 0.1, 0.2, 0.4, 0.8, 1.6, 2.3, 3.2, 4.5, 6.4, 12.8, 25.6 and 36.2 kHz. For both subjects, testing increments were smallest surrounding the frequency of best sensitivity (3.2 and 4.5 kHz for *Natchek* and *Nayak*, respectively). To achieve finer resolution in the region of his high-frequency roll-off, *Natchek* was also tested at 9.1 kHz. Because of her greater sensitivity to high frequencies, *Nayak* completed additional testing at 51.2 kHz. Four aerial projectors were used: the JBL2245H (JBL Incorporated, Northridge, CA, USA) for 0.075, 0.1 and 0.8 kHz; the JBL 2123H for 0.2, 0.4 and 1.6–3.2 kHz; the Fostex FT96H (Fostex Company, Tokyo, Japan) for 4.5–36.2 kHz; and the Avisoft Vifa (Avisoft Bioacoustics, Berlin, Germany) for 51.2 kHz. For sound field mapping and daily stimulus calibration, a Josephson C550H microphone (0.02–20 kHz, ±2 dB; Josephson Engineering, Santa Cruz, CA, USA) or a Microtech MK301 microphone capsule (0.005–100 kHz, ±2 dB) with an ACO Pacific 4016 preamplifier and PS9200 power supply (ACO Pacific Incorporated, Belmont, CA, USA) was used.

The experimental apparatus included a latency switch that the seal was trained to depress with his nose to initiate each trial. Reaction times (in ms)—from signal onset to release of the latency switch as the subject moved to touch the response target—were automatically recorded in HTP on all correctly detected signal-present trials. Latencies measured at a range of sensation levels ($N \geq 8$) at each frequency were used to generate latency-intensity curves with a least-squares power function (Moody, 1970). Only data from final staircase sessions (three per frequency) were used for this analysis. Reaction times were interpolated at threshold (0 dB SL) and at 20 dB above threshold (20 dB SL).

Underwater critical ratios

Masked hearing thresholds were obtained in water for both subjects at nine frequencies (0.1–25.6 kHz in octave steps) in the presence of white masking noise that was spectrally flattened by amplitude compensation. The J-11 transducer was used to project both signals and noise from 0.1 to 6.4 kHz and the ITC 1042 projecting hydrophone was used for 12.8–25.6 kHz. CRs were measured as the difference (in dB) between the SPL of the masked threshold and the spectral density level [dB re $(1\ \mu\text{Pa})^2/\text{Hz}$] of the surrounding 1/3-octave-band noise (Fletcher, 1940; Scharf, 1970). The signal detection task was the same as for audiogram testing, the exception being that calibrated noise was paired with the 4-s duration of each trial interval. The target level of this masking noise was always 10 or 20 dB (determined by equipment limitations) above the hearing threshold measured for the same subject, and was invariant during testing at a particular frequency. The masker was calibrated just prior to each session to ensure that the center 1/3-octave band was within 1 dB of this target level, and that the other two 1/3-octave bands were within 3 dB of this target level. Further details about masking noise generation, calibration and projection are given by Sills *et al*. (2014).

APPENDIX

In-air sensitivity following submergence

A preliminary experiment was conducted with one ringed seal (*Nayak*) to examine the residual effects of submergence on aerial hearing sensitivity. Prior research examining the in-air hearing sensitivity of harp seals (Terhune and Ronald, 1971) yielded high detection thresholds relative to newer data for northern seals (Reichmuth *et al.*, 2013; Sills *et al*., 2014; this study). Whereas these recent data exhibit a steep roll-off in sensitivity at high frequencies, the harp seal thresholds are substantially elevated across the frequency range tested (1–32 kHz, Fig. 2). This offset in reported sensitivity may be related to several factors, such as methodological differences between studies or the effects of masking due to inadequate control of the ambient noise background. In the previous harp seal study, the subject was submerged and swimming immediately prior to each hearing trial, a factor which may have hindered the aerial sound conduction pathway (Terhune and Ronald, 1971). The present study sought to resolve this discrepancy and revisit the conceptual model of how the seal ear operates in air and water (Møhl, 1968b), using direct measures of auditory sensitivity obtained under different conditions.

This pilot experiment was conducted at 12.8 kHz to examine whether in-air hearing is affected when audiometric trials are preceded by brief submergence. The Fostex FT96H transducer was used to project the signals, as for the aerial audiogram. The young ringed seal, *Nayak*, was trained to perform the signal detection task while in the water in the testing pool, with her head—including the auditory meatus—positioned above the surface. An inter-trial interval of 10 s preceded each listening trial, during which the subject would remain still at either a submerged station (ears at 1 m water depth) for the experimental condition, or at a nearby surface station (ears 20 cm above water) for the control condition. After performance stabilized over several training sessions, one testing session was conducted in each condition under near-optimal environmental conditions. The resulting thresholds were compared with each other and with *Nayak's* 12.8 kHz threshold obtained in the acoustic chamber. Ambient noise measurements were taken prior to each session in test-ready conditions, in the center position of *Nayak's* head during testing.

The resulting thresholds were 43 dB re 20 µPa in both the submerged and the surface inter-trial interval testing conditions. Whether *Nayak* was under water for 10 s prior to the hearing trial or at the surface of the water for those 10 s did not have a measurable effect on subsequent hearing sensitivity. False alarm rates were 0.22 and 0.11 for the submerged and surface inter-trial interval conditions, respectively. When compared with *Nayak's* measured sensitivity in the acoustic chamber (9 dB re 20 μPa, false alarm rate 0.23), her threshold was elevated by 34 dB in both outdoor conditions. The threshold-to-noise offset in the outdoor environment was 60 dB on average in the 1/3-octave band surrounding 12.8 kHz.

If one had been observed, a difference in thresholds across inter-trial interval conditions in this experiment could have been attributed to the methodology of having *Nayak* submerged immediately before having her in-air hearing sensitivity measured. In theory, the seal's ear could be partially fluid-filled upon surfacing, which would impede the aerial sound-conduction pathway. However, although *Nayak's* thresholds were elevated in the outdoor environment relative to her audiogram threshold, the results showed no sensitivity difference across the two inter-trial interval conditions. While we were able to replicate the threshold elevation observed for the harp seal tested in a similar configuration (Terhune and Ronald, 1971), the reason for these reductions in sensitivity remains unclear. The threshold-to-noise offset of approximately 60 dB at 12.8 kHz indicates that the measured thresholds were not limited by background noise; in fact, based on repeated measurements, *Nayak* theoretically should have been able to detect signals as quiet as her absolute threshold of 9 dB re 20 μPa. Therefore, energetic masking does not seem to explain the elevated thresholds in either case. Possible relevant factors include the role of informational masking, auditory or visual distractions, or anticipatory physiological changes in the middle ear related to diving. While additional work is needed to understand the significance of these factors and to better describe hearing mechanisms in seals, the aerial audiograms measured in the acoustic chamber in the current study can be considered representative of best hearing in this species. When combined with recent hearing studies in seals (Reichmuth *et al.*, 2013; Sills *et al.*, 2014), these data suggest that other Arctic seal species might hear equally well when tested under sufficiently quiet conditions.

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	Natchek		Nayak		Ambient noise
Frequency (kHz)	Threshold (dB re 1 μPa)	FA rate	Threshold (dB re 1 μPa)	FA rate	PSD [dB re 1(μPa)^2 /Hz]
0.1	88	0.16	91	0.28	68
0.2	76	0.14	74	0.23	54
0.4	69	0.16	68	0.14	46
0.8	61	0.19	59	0.14	44
1.6	60	0.21	59	0.14	41
3.2	58	0.22	52	0.20	36
6.4	59	0.14	54	0.16	31
12.8	49	0.16	52	0.28	32
25.6	53	0.14	50	0.14	28
36.2	77	0.11	54	0.17	26
43.1	114	0.14	–	–	26
51.2	–	–	65	0.17	24
60.9	–	–	101	0.23	24
72.4	–	–	104	0.15	26

TABLE I. Underwater hearing thresholds obtained for two ringed seals using psychophysical methods. The 50% detection thresholds are reported for each test frequency, along with false alarm (FA) rates during the testing phase (pooled across the three test sessions at each frequency, N≥20), and corresponding ambient noise levels in the test pool. Noise levels are shown in units of power spectral density (PSD), calculated from the median of unweighted, 1/3-octave band 50th percentile measurements (L50) that included each test frequency. For both subjects, 95% confidence intervals were narrower than 4 dB for all reported thresholds. The psychometric functions associated with these hearing thresholds are provided as Fig. S1.

	Natchek				Nayak				Ambient noise
Frequency (kHz)	Threshold (dB re 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	Threshold (dB re 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	PSD [dB re (20 μPa)^2/Hz]
0.075	47	0.22	419	182	41	0.18	518	194	20
0.1	42	0.13	448	181	36	0.15	449	186	14
0.2	29	0.15	412	212	23	0.15	652	127	−2
0.4	19	0.19	353	203	14	0.23	438	211	−14
0.8	12	0.08	588	322	2	0.10	573	211	−19
1.6	0	0.29	405	181	0	0.09	417	167	−20
2.3	0	0.24	281	190	0	0.11	317	141	−22
3.2	−6	0.26	359	180	−7	0.17	476	228	−23
4.5	−2	0.17	367	165	−12	0.16	417	201	−24
6.4	1	0.08	264	184	−9	0.23	401	179	−22
9.1	3	0.21	277	166	–	–	–	–	−26
12.8	25	0.23	384	156	9	0.23	355	146	−28
18.1	33	0.12	224	150	31	0.20	340	141	−28
25.6	36	0.19	270	155	38	0.22	265	135	–
36.2	57	0.15	236	160	42	0.17	438	175	–
51.2	–	–	–	–	64	0.16	–	–	–

TABLE II. In-air hearing thresholds obtained for two ringed seals using psychophysical methods. The 50% detection thresholds are reported for each of 16 frequencies, along with false alarm (FA) rates during the testing phase (pooled across the three test sessions at each frequency, N≥20), interpolated reaction times at threshold (0 dB SL) and 20 dB SL, and corresponding ambient noise levels in the acoustic chamber. Noise levels are shown in units of power spectral density (PSD), calculated from the median of unweighted, 1/3-octave band 50th percentile measurements (L50) that included each test frequency. For both subjects, 95% confidence intervals were narrower than 4 dB for all reported thresholds. The psychometric functions associated with these hearing thresholds are provided in Fig. S2.

	Natchek				Nayak			
Frequency (kHz)	Masked threshold (dB re 1 μPa)	Masker level [dB re 1 μPa^2/Hz]	Critical ratio (dB)	FA rate	Masked threshold (dB re 1 μPa)	Masker level [dB re 1 uPa^2/Hz]	Critical ratio (dB)	FA rate
0.1	125	109	16	0.15	118	104	14	0.22
0.2	106	89	17	0.20	104	88	16	0.17
0.4	102	82	20	0.12	97	81	16	0.20
0.8	93	74	19	0.23	93	72	20	0.16
1.6	93	74	19	0.29	93	72	20	0.20
3.2	95	71	24	0.19	88	64	23	0.15
6.4	93	72	21	0.22	89	67	22	0.20
12.8	90	61	29	0.10	90	64	26	0.23
25.6	96	64	31	0.29	103	71	31	0.28

TABLE III. Underwater critical ratio measurements obtained for two ringed seals at nine frequencies. In addition to the critical ratio at each frequency, also provided are the spectral density level for each flat-spectrum, octave-band masker; masked hearing threshold; and false alarm (FA) rate (pooled across method of constant stimuli sessions, N≥40). For both subjects, 95% confidence intervals were narrower than 4 dB for all masked thresholds.

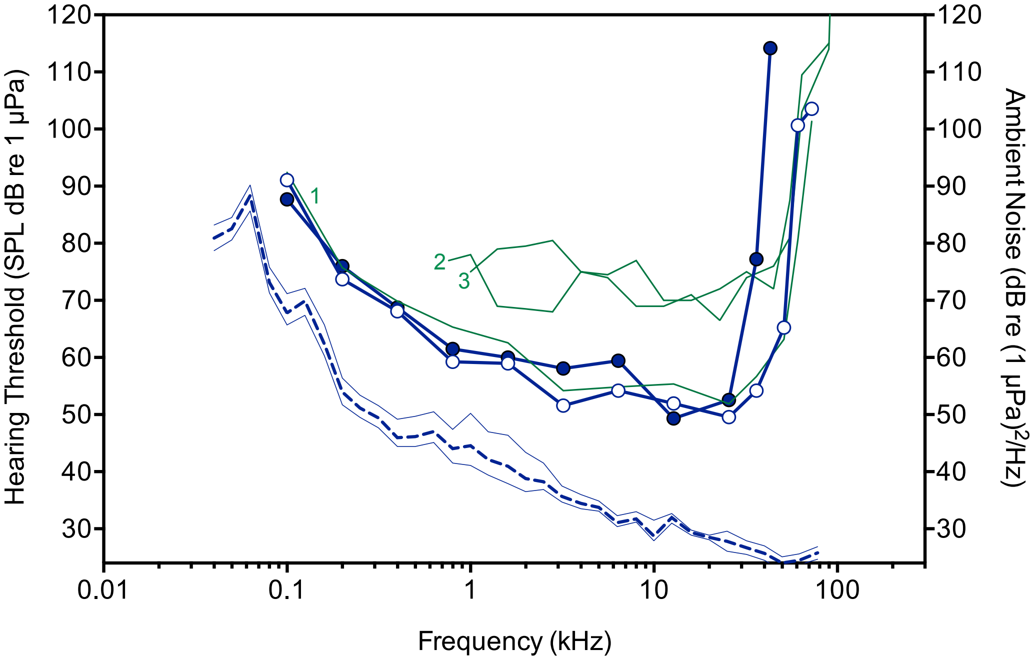

FIG 1. Underwater audiograms for two ringed seals, *Natchek* (filled circles) and *Nayak* (open circles). The 50% detection thresholds obtained using psychophysical methods are shown for 14 frequencies from 0.1 to 72.4 kHz. Ambient noise levels measured in the underwater testing pool [power spectral density, dB re (1 µPa)^2/Hz] are plotted as a dashed line corresponding to the right-hand y-axis. Noise levels were calculated from the median of unweighted1/3-octave band 50th percentile levels (L50) measured throughout the testing period, and are shown here bracketed by lines representing the 10th (above) and 90th (below) percentile levels (L10 and L90, respectively) to demonstrate variance in the distribution of ambient noise. For comparison, behavioral audiograms are shown for spotted seals [1, N=2 (Sills *et al.*, 2014)], harp seals [2, N=1 (Terhune and Ronald, 1972)] and ringed seals [3, N=2 (Terhune and Ronald, 1975a)].

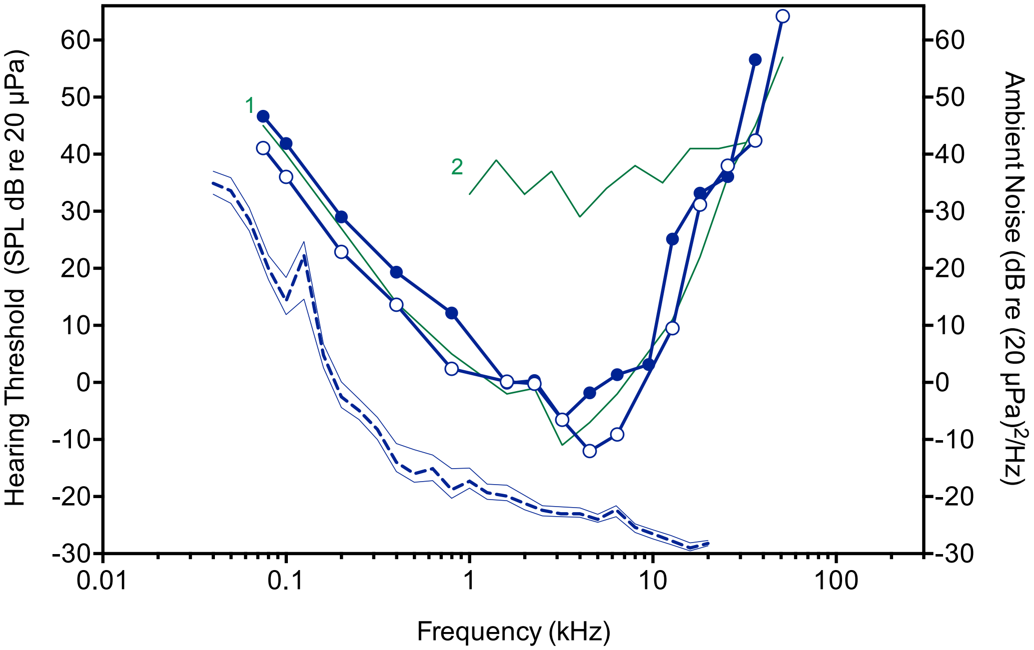

FIG 2. In-air audiograms for two ringed seals, *Natchek* (filled circles) and *Nayak* (open circles). The 50% detection thresholds obtained using psychophysical methods are shown for 16 frequencies from 0.075 to 51.2 kHz. Ambient noise levels measured in the acoustic chamber [power spectral density, dB re (20 µPa)^2/Hz] are plotted as a dashed line corresponding to the right-hand y-axis. Noise levels were calculated from the median of unweighted 1/3-octave band 50th percentile levels (L50) measured throughout the testing period, and are shown here bracketed by lines representing the 10th (above) and 90th (below) percentile levels (L10 and L90, respectively) to demonstrate variance in the distribution of ambient noise. For comparison, behavioral audiograms are shown for spotted seals [1, N=2 (Sills *et al.*, 2014)] and harp seals [2, N=1 (Terhune and Ronald, 1971)].

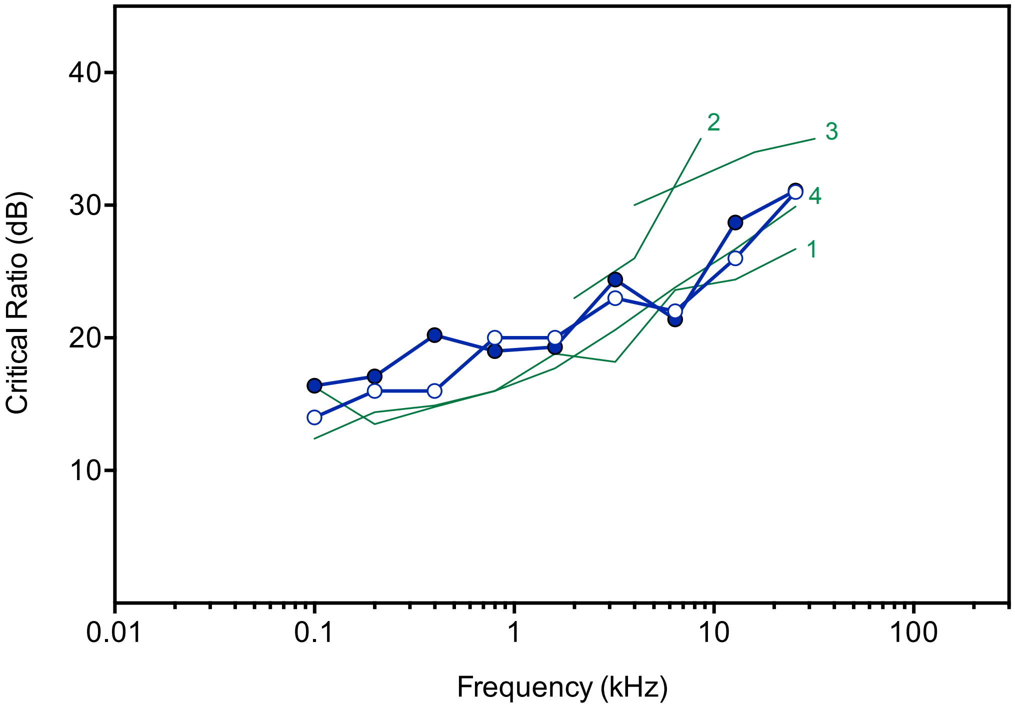

FIG 3. Underwater critical ratios measured for two ringed seals. *Natchek* (filled circles) and *Nayak* (open circles). Critical ratios were measured at nine frequencies (0.1 to 25.6 kHz) as the difference (dB) between the sound pressure level of the masked threshold and the spectral density level of the surrounding octave-band noise. Also shown are aerial critical ratios for spotted [1, N=1 (Sills *et al*., 2014)] and harp seals [2, N=1 (Terhune and Ronald, 1971)] and underwater critical ratios for ringed [3, N=2 (Terhune and Ronald, 1975b)] and spotted seals [4, N=1 (Sills *et al*., 2014)].

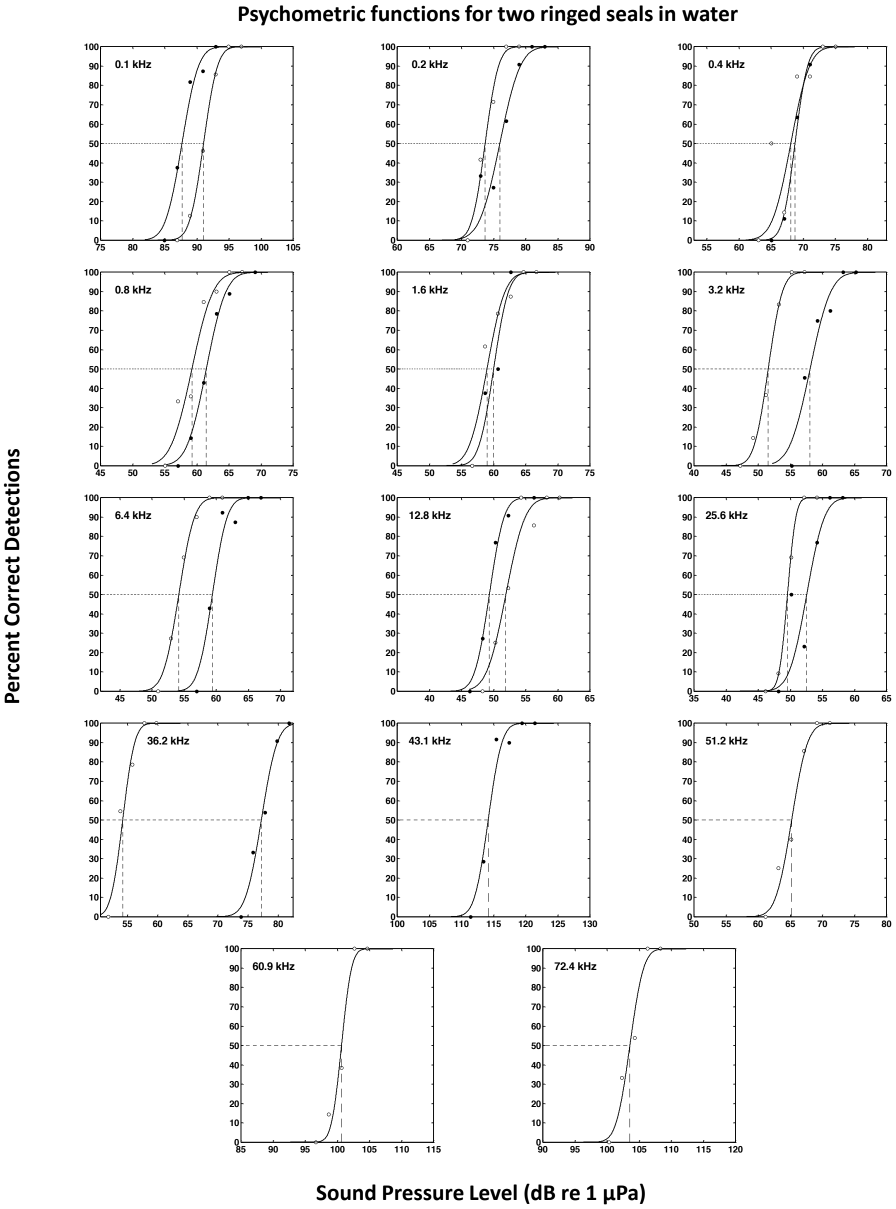

FIG S1. Psychometric functions obtained at each frequency under water for two ringed seals: *Natchek* (filled circles) and *Nayak* (open circles). Percent correct detection on signal-present trials (y-axis) is shown as a function of sound pressure level in dB re 1 μPa (x-axis). Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Thresholds were measured using an inverse prediction (not shown), and are indicated on each plot by the dashed line at the level corresponding to 50% correct detection.

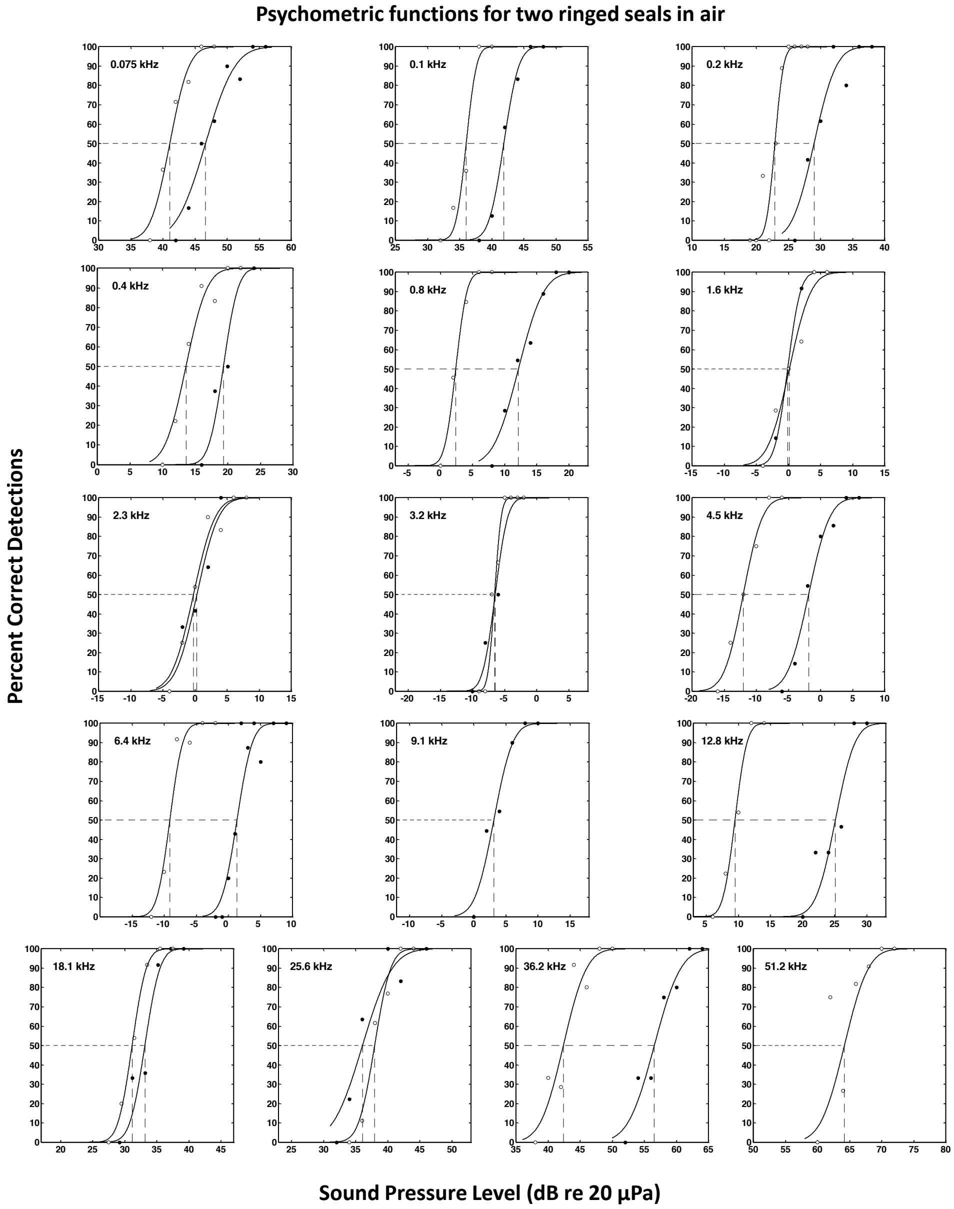

FIG S2. Psychometric functions obtained at each frequency in air for two ringed seals: *Natchek* (filled circles) and *Nayak* (open circles). Percent correct detection on signal-present trials (y-axis) is shown as a function of sound pressure level in dB re 20 μPa (x-axis). Probit analysis was used to fit these psychometric functions to the proportion of correct detections at each stimulus level presented during MCS testing. Thresholds were measured using an inverse prediction (not shown), and are indicated on each plot by the dashed line at the level corresponding to 50% correct detection.

CHAPTER 3

SIGNAL DETECTION IN COMPLEX ACOUSTIC ENVIRONMENTS: THE INFLUENCE OF TEMPORALLY VARYING SEISMIC NOISE ON HEARING IN SPOTTED AND RINGED SEALS

ABSTRACT

When considering the effects of noise on hearing, standard audiometric data are often applied to predict how noise will influence an individual or species. In the case of auditory masking, critical ratios—obtained from subjects in the laboratory using tonal signals and flat-spectrum maskers—can be combined with spectrum levels derived from 1/3-octave band noise levels to predict signal amplitudes required for detection. However, the efficacy of this *conventional model of masking* varies based on the signal and noise in question. For ice-living seals, the ability to quantify masking by seismic noise is relevant due to widespread geophysical exploration in Arctic regions. To address this, captive spotted and ringed seals were trained to detect low-frequency signals within seismic pulses recorded 1 and 30 km from an airgun array. The conventional model of masking accurately predicted the extent of masking only in some cases. When noise varied significantly in time, it became necessary to consider whether higher signal-to-noise ratios occurred within time windows shorter than the full signal duration. This study evaluates when it is appropriate to use average noise levels and critical ratios to predict masking, and informs management practices for ice-living seals in an increasingly industrialized Arctic.

INTRODUCTION

Marine mammals rely on the efficient reception and processing of sound to obtain information about their underwater environment. An increase in background noise can result in masking of biologically significant sounds, thereby interfering with an individual's ability to effectively orient and navigate, forage, communicate with conspecifics, or detect and avoid predators. While hearing can be limited by both natural and anthropogenic noise, auditory masking of sounds by anthropogenic sources is of particular concern for marine mammals. Human activities—including commercial shipping, military operations, and oil and gas development—have increased in recent decades throughout many of the world's oceans (*e.g.*, McDonald *et al.*, 2006; Hildebrand, 2009). In the face of continued human expansion into marine environments, the ability to accurately predict the extent of masking experienced by marine mammals exposed to noise-generating activities is needed to inform effective management practices.

Critical ratios obtained using narrowband signals and continuous, spectrally flattened noise provide a useful first approximation for understanding the effects of noise on hearing. Critical ratios are measured from subjects in the laboratory as the difference (in dB) between the sound pressure level of a just-audible tonal signal and the spectral density level of a broadband, flat-spectrum noise masker centered at the signal frequency (Fletcher, 1940). Historically, critical ratios have been used to infer frequency-processing characteristics of auditory systems. However, while they have been applied to estimate the frequency bandwidths of auditory filters (*i.e.* critical bandwidths), this approach has been shown to be inaccurate in many cases (*e.g.*, Fletcher, 1940; Southall *et al*., 2003; Yost and Shofner, 2009). Although critical ratios apparently cannot be used to directly determine critical bandwidths, they do describe the frequency tuning of the auditory system and its ability to extract sounds embedded within noise.

In practice, critical ratios are often used to predict the extent to which a noise source masks detection of a biologically relevant sound (see Erbe *et al.*, 2016). By adding the critical ratio at a particular frequency to the noise spectral density level determined from the surrounding 1/3-octave band, one can estimate the quietest level at which a target signal can be detected. This approach—derived from the power spectrum model of masking (Moore, 1993)—will be referred to in this paper as the *conventional model of masking*. The model relies on the assumptions that 1) the auditory periphery behaves as a series of linear bandpass filters, with sound detection driven by the output of a single auditory filter, 2) this auditory filter has a functional bandwidth that is approximately 1/3-octave wide, and 3) fine-scale spectral and temporal variations in noise can be largely ignored. This type of model has been applied to predict the degree of masking in a range of natural and anthropogenic noise conditions, with varying degrees of success (*e.g.*, Erbe and Farmer, 2000; Erbe, 2002; Jensen *et al.*, 2009; Dooling *et al.*, 2013; Cunningham *et al.*, 2014).

In realistic listening scenarios, marine mammals often encounter spectrally complex, time-varying noise sources that deviate markedly from the continuous, flat-spectrum noise used to measure critical ratios in the laboratory (Erbe *et al.*, 2016). For Arctic seals, the prevalence of seismic exploration for oil and gas makes an evaluation of masking by impulsive sounds particularly relevant. However, the acoustic features of airgun pulses and the complexity of their propagation make a description of masking effects difficult. Sounds received from airgun operations vary dramatically depending on the characteristics of the seismic array, the distance from the source, and a range of environmental parameters (Greene and Richardson, 1988). Seismic airguns are typically considered to be transient noise sources (Richardson *et al.*, 1995), but at distances of tens to thousands of kilometers seismic noise can significantly influence overall ambient noise levels, even during the intervals between pulses (Greene and Richardson, 1988; Guerra *et al.*, 2011; Nieukirk *et al.*, 2012; Guan *et al.*, 2015; Nowacek *et al.*, 2015). At this time, despite awareness of the masking potential of impulsive noise, the extent to which laboratory studies of hearing can be reasonably applied to estimate masking probabilities in the presence of seismic surveys remains unclear.

Starting from a foundation of standard auditory masking research with ice-living seals (Sills *et al.*, 2014; 2015), and informed by the advances of recent experiments using complex signals and maskers (*e.g.* Branstetter *et al.*, 2013; Dooling *et al.*, 2013; Cunningham *et al.*, 2014), we examined the influence of time-varying seismic noise on auditory detection in Arctic seals. In particular, we sought to address the question: *how well can critical ratio data and the conventional model of masking predict the extent of masking in the temporally fluctuating noise background* *produced by seismic airguns?* 1/3-octave band signal-to-noise ratios required for detection were measured behaviorally with one spotted seal (*Phoca largha*) and one ringed seal (*Pusa hispida*) listening for low-frequency signals embedded within seismic noise. The experimental approach involved parsing the noise from a single airgun pulse into multiple time intervals, and considering these as distinct maskers with different masking potential and thus, different signal-to-noise ratios required for sound detection. Measured signal-to-noise ratios at threshold within these different time intervals were compared to predictions based on critical ratio data obtained previously with the same two seal subjects. The results of this experimental paradigm provide insight into the importance of signal timing within a dynamic noise background, as well as the validity of applying audiometric data to characterize masking experienced by seals in complex acoustic environments.

METHODS

In this study, auditory detection thresholds were measured for 100 Hz test signals presented at different intervals within a background of seismic noise. To capture the spectral and temporal differences between airgun pulses received at various distances, testing was conducted with maskers recorded both 1 and 30 km from an operational airgun array. Behavioral testing using an auditory go/no-go procedure took place with two trained subjects between March 2014 and November

2015. The measured signal-to-noise ratios (SNR) required for detection across six testing conditions were compared with predictions based on critical ratio data reported previously for the same subjects. Fine-scale time window analyses were performed to examine the influence of the temporally fluctuating composition of the noise on detection of the 100 Hz signal.

Subjects and testing environment

The subjects for this experiment were one male spotted seal identified as *Tunu* (NOA0006674) and one female ringed seal identified as *Nayak* (NOA0006783). At the start of testing both seals were 4 years old. The subjects had prior experience participating in psychoacoustic experiments (*e.g.*, Sills *et al.*, 2014; 2015), and neither had known history of ear injury or exposure to ototoxic medication. During data collection each subject typically ran one session per day, five days per week. The seals' diets were established to maintain healthy body weights and were not constrained for experimental purposes.

All testing took place at Long Marine Laboratory in Santa Cruz, California. The underwater testing enclosure was a circular, partially in-ground pool 1.8 m deep and 7.6 m in diameter, filled with natural seawater ranging from 11 to 18°C. The experimental apparatus comprised a water-filled PVC frame with a mounted chin cup—referred to as the listening station—that positioned each subject's ears precisely and reliably at 1 m depth, 0.75 m from the edge of the pool, within a calibrated sound field. A small underwater light was placed 40 cm in front of the station at eye level, and was illuminated by the experimenter to define each 4-s trial interval. The response target, which the subject could press upon detection of a test signal, was a PVC plate located 20 cm to the left of the station. The listening station also included a plexiglass switch that the seal was trained to depress with his nose to initiate each test trial. This enabled the measurement of response latencies, calculated as the time (in ms) between signal onset and release of the switch as the subject moved to touch the response target.

Experiments were conducted remotely from a sound-isolated room adjacent to the test enclosure. The experimenter had visual access to the subject via an underwater surveillance camera, but was out of sight of the seal and the trainer during testing. The trainer—wearing a headset linked to the experimenter—cued the subject to dive to the listening station at the start of each trial and delivered primary (fish) reinforcement when instructed to do so, but was blind to specific trial conditions.

Test signals and seismic masking noise

Target signals were 500 ms frequency-modulated upsweeps centered on 100 Hz, with 10% bandwidth (95-105 Hz) and 5% linear rise and fall times (25 ms ramps). Signals were synthesized using MATLAB (MathWorks, Natick, MA). Masking noise was recorded during calibrated measurements of a seismic survey in the Chukchi sea (for details, see Patterson *et al.*, 2007); the survey was conducted in relatively shallow water (~40 m) using an operational three-string airgun array (24 Bolt airguns, 3147 in^3, 2000 psi). Representative 6-s samples containing single airgun shots were selected at two recording distances from the array: approximately 1 km away to exemplify the impulsive condition close to the source, and approximately 30 km away to represent a more distant condition with significant propagation effects. While the 1 km masker was spectrally broadband and characterized by a rapid rise/fall time (Fig. 1, Panel A), the 30 km masker was considerably longer in duration and contained frequency-modulated downsweeps (Fig. 1, Panel B), likely as a result of multipath propagation and reverberation in shallow water (Urick, 1983; Guerra *et al.*, 2011). Pulse duration—defined as the time interval between the arrival of 5% and 95% of the total energy in the pulse—was 0.25 s for the 1 km exemplar and 0.98 s for the 30 km exemplar. Over this duration, the received broadband sound pressure levels (SPL) measured in the field was 190 $\mathrm{dB_{peak}}$ re 1 μPa and 181 $\mathrm{dB_{rms}}$ re 1 μPa for the 1 km pulse, with a corresponding sound exposure level (SEL) of 175 dB re 1 μPa^2 s; for the 30 km pulse, broadband SPL was 154 $\mathrm{dB_{peak}}$ re 1 μPa and 142 $\mathrm{dB_{rms}}$ re 1 μPa, with 142 dB re 1 μPa^2 s SEL.

Both noise samples were saved as 6-s WAV files, with the onset (5% time) of the airgun pulse positioned 2 s into the WAV file in each case. During testing these files were projected to surround each 4-s trial interval, so that the start and end of the noise fell 1 s before and 1 s after each test trial, and the onset of the airgun pulse occurred 1 s into the trial. Each masker had a 50 ms linear rise time, which did not affect the rise time of the impulse itself. As demonstrated in Fig. 1, the received noise stimuli measured in the reverberant environment of the testing enclosure (panels C and D) retained the key spectrotemporal features of the actual airgun stimuli.

Generation and calibration of acoustic stimuli

100 Hz signals and masking noise were combined at particular SNRs in Adobe Audition (Adobe Systems Inc., San Jose, CA, USA) to form the final acoustic stimuli used during testing. These SNRs were defined in terms of the 100 Hz 1/3-octave band level of the signal relative to the 100 Hz 1/3-octave band level of the noise, measured over the full duration of the signal. The 100 Hz signal could occur within one of three 500 ms intervals during each 4 s trial: at the onset of the projected airgun pulse (*onset interval*), one second later (*intermediate interval*), or two seconds later (*terminal interval*). To achieve the desired SNR, the signal amplitude was varied while the masker amplitude remained constant. For the two different masking conditions (1 and 30 km airgun noise), a set of merged WAV files was created for each signal interval (onset, intermediate, and terminal), with SNRs spanning a range of at least 15 dB in 3 dB increments. The 100 Hz 1/3-octave band SNR of each merged WAV file (measured during the appropriate 500 ms interval) was verified in MATLAB.

Outgoing stimuli were sent from a custom LabVIEW virtual instrument (National Instruments Corp., Austin, TX, USA) through an NI USB-6259 BNC M-series data acquisition module (with update rate of 500 kHz), a TDT PA5 digital attenuator (Tucker-Davis Technologies, Alachua, FL, USA), and a Hafler P1000 power amplifier (Hafler Professional, Tempe, AZ, USA) prior to reaching the Naval Undersea Warfare Center J-11 transducer (Newport, RI, USA) that projected these stimuli into the test pool. The J-11 was suspended into the pool from a metal cable 5.3 m behind the subject, at a depth of 1.6 m. Stimuli were received at the listening station with a Reson TC4032 hydrophone (0.01–80 kHz, ±2.5 dB; Reson A/S, Slangerup, Denmark) and a Reson EC6073 input module before being passed through a Roland Quad-Capture USB 2.0 Audio Interface (sampling rate 192 kHz; Roland Corporation US, Los Angeles, CA, USA) to a battery-powered PC laptop. SpectraPlus software (Pioneer Hill Software LLC, Poulsbo, WA) was used to visualize the received spectrum and to measure the received SPL in the 1/3-octave band encompassing 100 Hz.

The sound field surrounding the listening station was mapped prior to testing to ensure that there was minimal variability in received stimuli. The seismic maskers and several merged test stimuli (specifically, the WAV file with the highest SNR for each signal interval) were projected and received at 9 positions in a 14 x 14 cm plane at the depth of the subject's ears. Additionally, the 100 Hz test signal was measured at 24 positions in a 14 x 14 x 14 cm grid surrounding the listening station. In all cases, acceptable variability in received SPL was +/- 3 dB across the measured positions in the 100 Hz 1/3-octave band.

To confirm that the masking noise received at the position of the subject's head in the reverberant enclosure was similar to the noise sent to the J-11 projector, the relative 100 Hz 1/3-octave band levels of each stimulus were compared. Sliding analysis windows (50 ms duration, 10 ms step size) were used to measure the noise over the entire 4-s trial duration (Figure 1, panels E and F; note that the shaded regions mark the onset, intermediate, and terminal signal intervals of each masker). The projected and received stimuli had similar temporal patterns in the relevant 100 Hz frequency band, with an average difference between projected and received stimuli of 3 dB for the 1 km masker and 4 dB for the 30 km masker.

Sound field calibration took place at the listening station just prior to each session, in the absence of the subject. The masker to be used for testing was projected and received using the hardware chain described above, and the Hafler P1000 power amplifier was adjusted until the 100 Hz 1/3-octave band SPL was within 1 dB of target level (128 dB_{rms} re 1 μPa for the 1 km masker and 125 dB_{rms} re 1 μPa for the 30 km masker) over the 6-s duration of the masker. This corresponded to average 100 Hz 1/3-octave band levels of 127, 91, and 86 dB_{rms} re 1 μPa for the onset, intermediate, and terminal intervals of the 1 km masker, respectively, and levels of 124, 103, and 100 dB_{rms} re 1 μPa for the onset, intermediate, and terminal intervals of the 30 km masker. These levels were chosen to ensure that the quietest portion of the masking noise was louder than the median 50th percentile 1/3-octave band level of the ambient noise in the testing enclosure at 100 Hz (82 dB_{rms} re 1 μPa). While the absolute noise levels varied across the three testing intervals for each of the two maskers, the use of SNRs allowed relative comparisons to be made across all conditions. For reference, the corresponding broadband SPLs of the received stimuli are provided in Figure 1;

dB_{peak} values were measured using SpectraPlus software (as described above), while the remaining values were measured using the same hardware chain and a custom LabVIEW virtual instrument.

Psychoacoustic procedures

The experimental task was an auditory go/no-go behavioral procedure with single response audiometry, during which the subject was trained to press the response target when he detected the 100 Hz signal and withhold this response when he did not (Cornsweet, 1962). Each trial began once the subject had settled in the listening station and the experimenter had illuminated the trial light, and subsequently ended either when the subject touched the response target or when the 4-s trial interval was complete and the light was extinguished.

Seismic masking noise was presented on every trial at fixed amplitude and, within a session, was always drawn from the same distance condition (1 or 30 km). However, the target signal was only present on 50% of trials during a particular test session. A correct detection occurred on these *signal-present trials* when the subject touched the response target, while a correct rejection occurred on *signal-absent trials* when the subject remained in the listening station for the entire 4-s trial duration. Both correct trial types were marked with a conditioned acoustic reinforcer (buzzer) triggered by the experimenter, followed by primary reinforcement (one piece of fish) given by the trainer at the water's surface. The reinforcement ratio for the two trial types was always 1:1. Alternatively, if the subject withheld a response on a signal-present trial (*miss*) or reported a detection on a signal-absent trial (*false alarm*), no reinforcement was provided and the subject was allowed to begin the next trial after a brief period at the surface. The trial sequence for each testing session was pseudorandomly predetermined, and constrained in a modified Gellerman series (Gellerman, 1933) such that there were never more than four in a row of a given trial type.

Following an initial training period, final thresholds were estimated using the method of constant stimuli (Stebbins, 1970). Testing was completed for the 30 km distance condition before data collection began with the 1 km condition. Sessions included 40 to 60 trials. They began with a warm-up phase of approximately 10 trials with SNRs easily detected by the subject, and finished with a cool-down phase of another 4-6 easily detectible trials to complete the session and ensure stimulus control on the signal detection task. The majority of each session fell between these two phases and comprised the test phase, during which the signal timing (interval) and the SNR presented on each signal-present trial were shuffled. The number of presentations of each timing/SNR combination (encoded in the different WAV files) was balanced over blocks of 30 signal-present trials, and was not necessarily balanced during every testing session. Within the onset, intermediate, and terminal signal intervals, there were ultimately five to six possible SNRs that ranged from detectable to undetectable. Sessions were run until there were at least 10 presentations of each of these SNRs within a given time interval. Response bias was evaluated by monitoring false alarm rates during the test phase of each session, with this rate defined as the number of false alarms out of the total number of signal-absent trials during the test phase of the session. Usable sessions had test phase false alarm rates >0% and <30%.

Threshold was calculated for a given interval using probit analysis (Finney, 1971), and defined as the SNR in the 100 Hz 1/3-octave band (dB_{rms} re 1 μPa) resulting in a 50% correct detection rate. The psychometric function was fit to the proportion of correct detections obtained for each SNR within a time interval, and an inverse prediction was used to determine threshold at the 50% correct detection level. The proportion of correct detections for each interval was pooled across multiple testing sessions (13-36) for each masker distance. Data were considered converged when the 95% confidence interval for the threshold was less than 4 dB. Thresholds were measured for a total of six testing conditions for each subject, within the three signal intervals of the two different masker distances.

In addition to measuring detection thresholds, reaction times were used as a secondary measure of auditory performance. Reaction times were automatically calculated in the LabVIEW virtual instrument for all correct detections throughout testing. Response latencies were pooled across sessions within a testing condition (*e.g.* the 1 km onset interval) and were used to generate latency-intensity curves with least-squares fits to a power function (Moody, 1970). Reaction times at threshold were interpolated from this function.

Threshold predictions

Signal-to-noise ratio at threshold was predicted for each subject from previously measured critical ratio data at 100 Hz, using the conventional model of masking. These critical ratio data (Sills *et al*., 2014; 2015) had been obtained using the same testing enclosure and acoustics equipment and similar testing methodology as that applied in this seismic masking experiment. Typically, to generate a masked threshold prediction in terms of SPL (dB_{rms} re 1 μPa), the critical ratio is added to the masking noise spectral density level at the same frequency (dB_{rms} re 1 $\mu Pa^2/Hz$). This spectral density level can be approximated from the measured 1/3-octave band level by subtracting 10log(*B*), where *B* is the 1/3-octave bandwidth. To normalize across testing conditions and enable easier performance comparisons, 1/3-octave band SNRs required for detection can be calculated by subtracting the 1/3-octave band level of the noise from these predicted SPLs. This process is numerically equivalent to the method applied here. To generate masked threshold predictions for this experiment in terms of 100 Hz 1/3-octave band SNR, the previously measured critical ratios were converted to 1/3-octave band levels by subtracting 10log(*B*) to account for bandwidth. For all six testing conditions, the measured 100 Hz critical ratios of 12 dB (*Tunu*) and 14 dB (*Nayak*) minus 10log(23) yielded predicted SNRs at threshold of -1 dB and 0 dB for *Tunu* and *Nayak*, respectively (calculated using unrounded critical ratios).

To determine whether there was a difference between predicted and measured SNR, the offset between the two values was calculated for each testing condition as the measured SNR at threshold minus the predicted SNR at threshold. These sensitivity offsets provided a measure of masking release or masking increase observed relative to that predicted by the conventional model of masking. Negative offsets indicated greater sensitivity than predicted (masking release) and positive offsets indicated poorer sensitivity than predicted (masking increase).

Time window analysis of signals and noise

In order to characterize the time-varying nature of the masking noise—and thus the SNR—across the entire trial and within each signal interval, time window analysis was conducted on recordings made at the listening station on three separate testing days. This analysis aimed to describe noise and SNR patterns in time and investigate whether temporal variation influenced the predictive capability of the conventional model of masking. Replicate recordings were made of the two maskers, the 100 Hz test signals used to create each merged WAV file, and the final testing stimuli. The outgoing and incoming equipment chains and measurement software were identical to those used during testing, and recordings were subsequently analyzed in MATLAB.

For the merged testing files, 100 Hz 1/3-octave band SNR was measured in the appropriate interval over sliding, overlapping time windows ranging from 50 to 500 ms in duration (in 50 ms increments). In each case, there was a 10 ms time increment between the start of adjacent windows. For the individual signal and noise recordings, the same procedure was applied to measure SPL over these various analysis windows. Signal and noise SPL data for the same interval were then used to calculate SNRs. The SNRs computed directly from merged testing files were consistent with those calculated after separately measuring the SPL of received signals and maskers; given this, the measured SNRs were averaged across all replicate recordings (n = 7 - 10). A 50 ms time window was chosen to represent the noise and to be the minimum SNR analysis length because this duration should fall well below the temporal integration time for seals at this frequency (Terhune, 1988; Holt *et al.*, 2004; Kastelein *et al.*, 2010; Reichmuth *et al.*, 2012).

100 Hz 1/3-octave band noise was also compared—in terms of both the SPL range (ρ) and the SPL variance (σ^2) measured for 50 ms analysis windows—to the offset between measured and predicted SNRs at threshold within the same interval. The aim of these comparisons was to determine whether certain amplitude-based features of the noise correlated with the performance of the conventional model of masking. Ordinary least squares regressions were calculated to predict SNR offset (averaged across subjects) based on SPL range or variance, and determine the strength of the associated correlations.

RESULTS

Threshold performance

Measured SNRs at threshold are reported for the spotted seal and the ringed seal across six testing conditions (TABLE I). Predicted SNR at threshold is also provided for each subject. SNR offsets are shown for each testing condition as the difference between measured and predicted SNR. In the initial portion of the pulse for both the 1 km and the 30 km masker (*i.e.*, the onset interval), sensitivity was much greater than predicted for both subjects (average SNR offsets of -23 dB for 1 km and -9 dB for 30 km). In contrast, sensitivity was well predicted (SNR offsets of +/- 2 dB) for the two subjects in the latter intervals of these maskers. The only case in which the performance of the two subjects diverged was for the female ringed seal listening for signals in the 30 km intermediate interval; her sensitivity in this interval was much poorer than predicted (SNR offset 9 dB).

Both subjects exhibited a stable and similar response bias throughout all testing conditions. *Tunu's* false alarm rate was 0.18 for each of the three 1 km conditions and 0.17 for each 30 km condition, while *Nayak*'s false alarm rate was 0.17 for all six testing conditions. Both subjects showed greater variability in measured thresholds than in previous experiments with flat-spectrum maskers. The average standard deviation (SD) for *Tunu* was 4.0 dB (range 3.1 to 6.0) in this study, compared to 2.6 dB (range 1.8 to 3.4 dB) in the prior experiment (Sills *et al.*, 2014). *Nayak's* average SD was 3.4 dB (range 2.5 to 4.7 dB) compared to 2.5 dB (range 1.7 to 3.6 dB) during previous testing (Sills *et al.*, 2015).

Interpolated response latencies at threshold are given alongside the SNR values for each testing condition (TABLE I). Response times were longest near threshold and typically less than ~500 ms—*Tunu's* median response time at threshold was 506 ms and *Nayak's* was 432 ms—and varied based on testing condition. While there was no clear overall pattern in these data, latencies for both individuals in the 1 km onset condition were notably longer (>600 ms at threshold) than for the other five conditions tested.

Time window analysis of signals and noise

The upper panels (A and B) of Figure 2 show the relative 100 Hz 1/3-octave band amplitude of the received 1 km and 30 km maskers, respectively, across the 4-s trial interval. These noise curves—which correspond to moving averages over 50 ms sliding, overlapping time windows—are the same as those provided in panels E and F of Figure 1. These curves reflect the amplitude fluctuations of the noise across the entire trial duration (a 54 dB range for the 1 km masker and a 46 dB range for the 30 km masker). A notable feature is that noise does not return to background (pre-impulse) levels by the end of the 4-s trial in either case. Amplitude variation is most substantial in the onset interval of each masker; when comparing across distances, the 1 km onset interval shows greater variation in amplitude over time than does the 30 km onset interval. Within a particular interval, SNR offset at threshold could be predicted from the 100 Hz 1/3-octave band SPL range (ρ) of the noise by the following formula, obtained via linear regression (Fig. 3): SNR offset (dB) = $0.70\rho - 5.6$, $R^2 = 0.82$, $p = 0.013$; similarly, offset could be predicted from 1/3-octave band

SPL variance (σ^2) by the formula: SNR offset (dB) = $0.12\sigma^2 + 1.1$, $R^2 = 0.93$, $p = 0.002$. Additionally shown within the onset, intermediate, and terminal intervals are received noise SPLs when measured instead over non-overlapping analysis windows of 50, 250, and 500 ms (Fig. 2, horizontal bars in panels A and B). These different measurement windows greatly affect the measured noise values, especially when the noise varies considerably within a given interval.

The lower panels (C and D) of Figure 2 provide an overview of time window analysis when applied to the testing files for 1 and 30 km, respectively. The plotted data points reflect the variation in SNR across each time interval, and demonstrate the variability in this measured SNR as a result of analysis window duration (50 – 500 ms). Note that the 500 ms SNR is the nominal SNR at threshold, as reported for the seismic masking experiment (see Table I); this point is shown in the center of each 500 ms (shaded) interval. Specifically, these plots show a snapshot of SNRs at threshold for the spotted seal subject, *Tunu*, across the three signal intervals, measured over durations of 50, 250, and 500 ms. However, SNR patterns over time are identical for both subjects, and any differences in *Nayak's* thresholds would be reflected simply as a shift in these data points on the Y-axis.

Additional detail is provided for both maskers in Figure 4, with SNR at threshold shown in separate subplots for each of the six testing conditions for analysis durations of 50 to 500 ms (in 50 ms increments). These plots represent how the auditory scene is changing in time when the subject is at sensory threshold. The horizontal dotted line visible on each subplot marks *Tunu's* predicted SNR at threshold based on 100 Hz critical ratio data. As can be seen in this figure, measured SNR crosses this line in all cases for a subset of the analysis durations.

To complement the graphical representations of noise variation over time, Table II presents the maximum 100 Hz 1/3-octave band SNR received at threshold (for *Tunu*) when measured over analysis windows of 100 to 500 ms. Again, the 500 ms column represents the nominal SNR, measured over the full duration of the signal interval. In the case of the 1 and 30 km onset intervals in particular, there is considerable variation in received SNR when measured over these successively longer time windows. Comparison of these values against predicted SNR at threshold (-1 dB) demonstrates that the predicted level is exceeded in all testing conditions for at least one measurement duration.

DISCUSSION

This study aimed to evaluate how airgun pulses limit the detection of low-frequency sounds by ice-living seals, and how well standard audiometric data can predict the extent of masking these seals experience in the real world. To incorporate the influence of propagation on the spectral and temporal characteristics of the received noise, we quantified the masking of acoustic signals at different time intervals within seismic noise received by seals “close to” and “far from” an operational airgun array. The results of this work demonstrate that, even in complex masking scenarios, a conventional model of masking is sometimes sufficient to predict hearing in noise. In the case of seismic noise, this simple approach works surprisingly well when considering the reverberant portion of the received airgun stimulus. Only when the noise background fluctuates more rapidly—closer to the onset of the airgun pulse—do predictions based on critical ratios consistently diverge from observed threshold performance. The application of time window analyses to explain this finding demonstrates the importance of fine-scale temporal structure when considering signal detection against time-varying noise.

Detection of low-frequency signals embedded within seismic noise

Masked thresholds were measured across six noise conditions to enable an experimental assessment of masking by seismic noise received at different spatial and temporal intervals relative to the source. For both the 1 and 30 km noise maskers, clear patterns emerged across time from the onset interval of the pulse to the terminal interval: the conventional model of masking provided poor estimates of sensitivity in the onset intervals of both maskers, with better predictions in the reverberant portion of the airgun noise.

The auditory performance of the subjects in this experiment suggest that—in cases when sensitivity offsets from predicted are large—the conventional model of masking overestimates the extent of masking. However, it is important to note that this paradigm only considers the reliable detection of a target signal, and that signal discrimination, recognition, and comfortable communication are also necessary for meaningful information transfer. In the same noise conditions, these perceptual metrics require progressively higher signal amplitudes than that needed for detection alone (Lohr *et al.*, 2003; Franklin *et al.*, 2006; Dooling *et al.*, 2009a, 2009b; Dooling and Blumenrath, 2014), which must be considered when using masking models to estimate the effects of anthropogenic noise. Furthermore, the results of this study represent the abilities of well-trained, highly experienced animal subjects. Both seals participated in several months of preparation for this task; their performance improved significantly between the initial training sessions and the start of data collection. When assessing masking with wild seals attempting to receive and process relevant sounds in the marine environment, it is important to consider that 1) they likely require larger SNRs to support functional hearing than those measured at the 50% detection level, and 2) based on prior experience, individuals may have varying degrees of practice ignoring particular noise sources and focusing on specific target signals, which will affect their ability to hear relevant signals in background noise. Additionally, the unpredictable nature of seismic noise in the real world—the result of factors including distance from the noise source, water depth and other environmental parameters, and precise signal timing and character—could reduce signal detectability relative to what was demonstrated here using predictable masking noise from trial to trial. When extending these laboratory results to wild populations, it must be recognized that within- and between-individual variability may be greater for real-world sounds than for the simpler, controlled test stimuli often used in audiometric testing. This assertion is supported by the higher standard deviations reported for this experiment, relative to those obtained for the same seals in studies with flat-spectrum noise maskers.

When considering possible explanations for the poor performance of the conventional model of masking in the initial (onset) intervals of the seismic noise, response latencies may provide a clue. In particular, the relatively long latencies measured for signals in the onset interval of the 1 km masker indicate that, at threshold, the subjects took longer than expected to perceive the target stimulus. Similar results (not reported here) were obtained for the seals at supra-threshold levels (20 dB sensation level, or 20 dB above threshold), with markedly longer response latencies observed in the 1 km onset interval than in the other five test intervals. Since response time can be considered a proxy for perceptual loudness (Moody, 1970), latencies at a particular sensation level should be consistent across conditions. It is possible that, in this case, the subjects may have experienced complete masking during the impulse, for the first ~200 ms, and then perceived the signal only during the latter portion of the interval, resulting in longer measured reaction times. Combined with the large SNR offsets for this condition—with both subjects demonstrating much greater sensitivity than predicted—this result suggests that predictions based on average signal and noise levels over the 500 ms duration of the signal may sometimes be misleading. SNRs calculated across different time windows within a given signal interval may reveal that the relevant listening period is sometimes shorter than the full signal duration; when this is the case, fine-scale temporal analyses may yield improvements in the predictive capability of conventional masking models.

Insights provided by time window analysis

Studies examining human auditory perception have used “glimpsing” models to explain how human listeners are able to understand brief snippets of speech in noisy backgrounds (*e.g.* Miller and Licklider, 1950; Howard-Jones and Rosen, 1993; Buss *et al.*, 2003; Assmann and Summerfield, 2004; Holt and Carney, 2005; Cooke, 2006). These models are based on the auditory system’s ability to process multiple, brief “looks” at the target signal within fluctuating noise (Viemeister and Wakefield, 1991; Erbe, 2008). The response latency data in this seismic masking experiment suggest that, similarly, the spotted and ringed seal subjects may have been attending to certain portions of the target signal while other portions remained masked. In essence, within-valley or “dip” listening (Buus, 1985) could have allowed detection of the signal within the quieter portions of the amplitude-modulated masking noise. This may have been the case particularly when the masker amplitude varied considerably over the duration of the 500 ms signal.

The results of time window analysis suggest that the fluctuating noise background produced by the airgun maskers enabled the subjects in this experiment to detect the target signal even when longer-term SNR averages indicated that detection was improbable. Examination of SNR at threshold over windows of different duration (Fig. 4) revealed that the predicted threshold was exceeded in all cases over a subset of the analysis windows used. For the onset intervals of both masker distances—which exhibited considerable variation in 100 Hz 1/3-octave band SPL range—the large SNR offsets observed could be reconciled with the conventional model of masking simply by measuring SNR over shorter time windows (< 200 to300 ms). Glimpses of the signal afforded to the subjects due to variations in noise amplitude were apparently sufficient to allow signal detection. These results are consistent with a dip-listening hypothesis, with detection driven by variations in local rather than global SNR. For the intermediate and terminal intervals of the seismic masker, on the other hand, the comparatively minimal temporal variability in the noise is reflected in SNR measurements that are less dependent on the particular analysis window used. This observation corresponds well with the improved performance of the conventional model of masking in these intervals, relative to the onset interval of the noise. When there is less variation in noise—and thus SNR—over time, longer-term amplitude averages yield reasonable predictions of masking.

Time window analysis performed with these seismic noise stimuli addressed the methodological question: *when do standard, averaged noise measurements work and when do they not?* Clearly, amplitudes averaged over the entire signal are most useful for predicting the detectability of signals embedded within less variable noise (*i.e.*, during the reverberant portion of an airgun impulse). When noise variation is significant, a smaller analysis window can improve predictive ability. The relevant time window for detection likely depends upon the particular features of the noise in question, as well as on the temporal processing capabilities of the receiver. However, regression analyses demonstrated that two amplitude-based measures of noise variation (1/3-octave band SPL range and variance) were correlated with the offset between measured and predicted SNRs at threshold: increased amplitude variation in noise within an interval consistently led to increased offset between measured and predicted threshold values, even when temporal processing was not taken into account.

While we focused here on amplitude variation in the two maskers within the 1/3-octave band containing the target signal—which seemed to be driving threshold performance—many other factors likely influenced signal detection in this case. These include the shape and bandwidth of auditory filters, the role of frequency modulation in the maskers, the relevance of different measurement metrics (*e.g.*, peak SPL or SEL versus rms SPL values), and a more detailed consideration of temporal processing capabilities. The accuracy of hearing predictions may be improved by including such factors into masking models (Erbe *et al.*, 2016).

An example: estimating seismic masking in realistic conditions

The conventional model of masking, informed by the results of this study, can be applied to real-world scenarios of signal detection in the presence of noise. The seismic noise values used in the following example are based on the 1 and 30 km exemplars from this experiment, combined with data reported in Patterson *et al.*

(2007) and adjusted for ambient noise (measured ~1 s before the impulse in each case). Note that this simplified analysis assumes that spotted seal vocalizations are the same duration as the test signals in this study (500 ms).

Consider a spotted seal vocalizing in relatively shallow water in the Chukchi Sea. The 100 Hz component of his vocalization is approximately 110 $\mathrm{dB_{rms}}$ re 1 μPa at 1 m (Sills, unpublished data). In sea state 4 conditions, we can assume that the 100 Hz spectrum level of ambient noise is ~60 dB re 1 $\mu\mathrm{Pa}^2/\mathrm{Hz}$, which falls more than a critical ratio below the hearing threshold of spotted seals at this frequency (hearing threshold 89 dB re 1 μPa, critical ratio 12 dB for the spotted seal *Tunu*; Sills *et al.*, 2014). Therefore, if detection is based simply on sensory threshold in this case, and we assume that idealized 10log*R*[3] spreading occurs in the shallow water environment, a second spotted seal should theoretically be able to detect the vocalizing individual at a distance of approximately 125 m. However, if these seals were located 1 km from an operational airgun array, 100 Hz received spectrum levels would be approximately 155, 117, and 107 dB re 1 $\mu\mathrm{Pa}^2/\mathrm{Hz}$ for seismic noise in the onset, intermediate, and terminal intervals, respectively, as defined in this experiment. Adding *Tunu's* critical ratio at 100 Hz to these values, and then adjusting for the offset results reported in the seismic masking study (TABLE I), received SPLs required for the detection of this vocalization would be 144, 130, and 119 $\mathrm{dB_{rms}}$ re 1 μPa for these three intervals. The

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[3] The use of 10log*R* here is a simplification, which assumes that only cylindrical spreading occurs. However, considering that spherical spreading will likely occur near the vocalizing individual, 15log*R* may be a more realistic approximation. The true spreading loss will depend on local conditions between the vocalizing individual and the listener.

call would be completely masked at the vocalizing individual in each of these cases. Conversely, if these seals were 30 km from the same airgun array, the 100 Hz received spectrum levels would be approximately 119, 100, and 95 dB re 1 μPa^2/Hz for noise received in the onset, intermediate, and terminal intervals. This would correspond to signal detection levels of 121, 114, and 105 dB$_{rms}$ re 1 μPa, suggesting that the call could only be detected if it was received 2 or more seconds after the pulse, and then only within a distance of about 3 m. Extending this analysis further in time would allow an estimate of the total extent of masking between successive pulses, and a practical and dynamic sense of how seismic noise constrains hearing in seals.

Of course, there are several caveats associated with this example. First, note that spotted seal underwater breeding vocalizations are ~4 s in duration(Sills, unpublished data), which would presumably increase their detectability over the 500 ms call considered in this example. On the other hand, the estimates provided represent 50% detection levels, meaning that signal levels required for certain detection, discrimination, recognition, or comfortable communication would all be higher than those discussed here. Another relevant consideration is the relationship between airgun received levels and ambient noise. Based on the particular airgun samples used in this example, 100 Hz noise levels returned to ambient within ~7 s of the pulse received at 1 km, and within ~10 s of the pulse received at 30 km. It is important to note that the time at which airgun received levels fall below background noise will vary greatly based on the source array, distance to the receiver, environment, current ambient conditions, and other factors, and in some cases there may not be a complete return to background levels between pulses (Guerra *et al.*, 2011; Nieukirk *et al.*, 2012; Guan *et al.*, 2015; Nowacek *et al.*, 2015). In this example, ambient noise levels were defined based on received levels ~1 s before the impulse; if reverberation consistently elevated noise levels between consecutive pulses, these values provide an overestimate of ambient noise and a resulting underestimate of the extent of masking caused by the impulse. Nonetheless, this simplified example underscores the importance of considering detection probability for signals received at different times within a temporally varying noise background, rather than using typical methods to average noise levels. Although the corrections applied in this example were based on experimentally measured offsets from predicted thresholds for this particular noise source, corrections could be similarly derived for other cases by assessing the fluctuating composition of the noise relative to the target signal and considering SNR over different analysis durations. Furthermore, our data suggest that, while the dominant portion of the airgun impulse (< ~300 ms close to the source and < 1 s at distances of ~ 30 km) requires such special consideration, a conventional masking model can be reasonably applied to the remainder of the inter-pulse interval without a correction factor.

CONCLUSIONS

When extending laboratory results obtained with trained animals to predict auditory masking in complex listening scenarios, one must consider the many sources of variability inherent in natural environments and how they may result in deviation from predicted values. Measuring critical ratios alone cannot accomplish this. The empirical methods developed in this study provide a new way to consider masking from the perspective of the listener—taking into account differences in the auditory scene experienced by an animal as a result of distance from the noise source and timing of the target signal relative to the noise exposure. For noise sources that are relatively stable in time (*e.g.*, certain types of shipping noise, reverberant noise in the inter-pulse intervals of seismic surveys)—at least when combined with tonal signals—a conventional model generates reasonable estimates of masking. However, for noise sources that vary significantly in space and time (*e.g.*, airgun impulses generated during seismic exploration), factoring physical distance and signal timing into masking models can enable more accurate estimates of masking probability. Furthermore, considering variation in SNR over analysis windows shorter than the full signal duration can provide insight into the time-varying soundscape that the listener experiences. Quantifying these SNR "snapshots" can yield improved masking predictions, even when using simple models.

While the recorded seismic noise used as a masker in this study represents a specific stimulus that might be encountered by seals in the Arctic, this study was conducted with narrowband audiometric signals that fell entirely within a single critical band. Future work using signals extending across multiple auditory filters, and ultimately a representative signal like a conspecific vocalization, would illuminate whether the patterns observed in this simpler case apply in even more realistic listening scenarios. While working with increasingly complex stimuli would improve our understanding of masking, additional research conducted with simple, controlled stimuli is also needed. For example, an experiment with a pure tone signal embedded within a frequency-modulated downsweep masker—reminiscent of the propagation effects observed in distant airgun recordings—would help to characterize the impact of a changing frequency-modulated background, independent of amplitude modulation. Alternatively, the role of amplitude modulation could be more thoroughly examined by using synthesized noise with different modulation rates (*e.g.*, Buss *et al.*, 2009; Vélez *et al.*, 2011), to see how long of a glimpse within fluctuating noise is required for signal detection. Investigations of temporal processing in seals and other marine mammals would complement this type of work. With continued research and an improved understanding of the mechanisms underlying auditory masking, we can work toward more accurate predictions of zones of masking for marine mammals around specific noise sources in their environment, including seismic airguns.

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Testing Condition		Tunu				Nayak			
		Predicted SNR at threshold (dB)	Measured SNR at threshold (dB)	SNR offset (measured – predicted, dB)	Response latency at threshold (ms)	Predicted SNR at threshold (dB)	Measured SNR at threshold (dB)	SNR offset (measured – predicted, dB)	Response latency at threshold (ms)
1 km	onset	-1	-24	-23	666	0	-22	-23	648
	intermediate	-1	0	1	523	0	0	0	426
	terminal	-1	-1	0	450	0	-1	-1	437
30 km	onset	-1	-11	-10	489	0	-8	-8	280
	intermediate	-1	1	2	537	0	9	9	468
	terminal	-1	-3	-2	472	0	-1	-1	404

TABLE I. Signal-to-noise ratios (SNR) at threshold obtained for one spotted and one ringed seal using psychophysical methods. The SNRs required for 50% correct detection were measured as the 100 Hz 1/3-octave band level of the signal relative to the 100 Hz 1/3-octave band level of the noise over the full 500 ms duration of the signal. These levels are reported for each testing condition, along with predicted SNRs at threshold, offsets between measured and predicted levels, and interpolated reaction times at threshold. For both subjects, 95% confidence intervals were narrower than 4 dB in all cases. Predicted SNR at threshold was constant for each subject across all six conditions, based on previously measured critical ratio data at 100 Hz and a conventional model of masking.

Testing Condition		Max 100 Hz 1/3-octave band SNR at threshold, measured over different window durations (dB re 1 μPa)				
		100 ms	200 ms	300 ms	400 ms	500 ms
1 km	onset	5	3	-8	-19	-24
	intermediate	2	1	0	0	0
	terminal	2	2	1	0	-1
30 km	onset	5	4	3	-5	-11
	intermediate	2	4	3	3	1
	terminal	7	4	2	0	-3

TABLE II. Maximum received 100 Hz 1/3-octave band signal-to-noise ratios (SNR) at threshold for the spotted seal *Tunu*. The maximum SNR for each of the six testing conditions is reported for measurement durations of 100 to 500 ms. These values can be compared to *Tunu's* predicted SNR at threshold of -1 dB re 1 μPa in the 100 Hz 1/3-octave band. This predicted level is met or exceeded in all cases over shorter analysis windows, even when the maximum SNR measured over the entire signal duration (500 ms) is well below that predicted for detection.

FIG 1. Comparison of projected and received 1 and 30 km airgun maskers during the 4-s trial duration. The left side of this figure portrays data for the 1 km airgun masker while the right side of this figure corresponds to the 30 km airgun masker. The top panels show the normalized waveform and spectrogram for the original recordings made 1 km (panel A) and 30 km (panel B) from the operational airgun array. Panels C and D represent the same for the 1 km and 30 stimuli, respectively, when projected in the testing enclosure and received at the listening station. For the 1 km masker, the broadband received sound pressure levels throughout testing were 161 $\mathrm{dB_{peak\text{-}peak}}$ re 1 μPa, 155 $\mathrm{dB_{peak}}$ re 1 μPa, and 134 $\mathrm{dB_{rms}}$ re 1 μPa, with a corresponding sound exposure level of 141 dB re 1 $\mu\mathrm{Pa}^2$-s. For the 30 km masker, the broadband received sound pressure levels throughout testing were 158 $\mathrm{dB_{peak\text{-}peak}}$ re 1 μPa, 152 $\mathrm{dB_{peak}}$ re 1 μPa, and 134 $\mathrm{dB_{rms}}$ re 1 μPa, with 142 dB re 1 $\mu\mathrm{Pa}^2$-s sound exposure level. Spectrogram analysis settings were as follows: sampling rate 44.1 kHz; Hann window; FFT size 2048 (filter bandwidth 31 Hz); overlap 90%. The bottom panels depict the normalized 100 Hz 1/3-octave band amplitude of the projected (dashed lines) versus received (solid lines) 1 km (panel E) and 30 km (panel F) maskers during each test trial. Amplitude is normalized for each curve to the maximum measured 1/3-octave band level of that stimulus, to allow for direct comparison of projected and received maskers. These curves correspond to moving averages over 50 ms sliding windows, with a step size of 10 ms. Also visible in panels E and F are shaded gray regions representing the three intervals during each test trial during which a signal may be present (onset, intermediate, and terminal intervals).

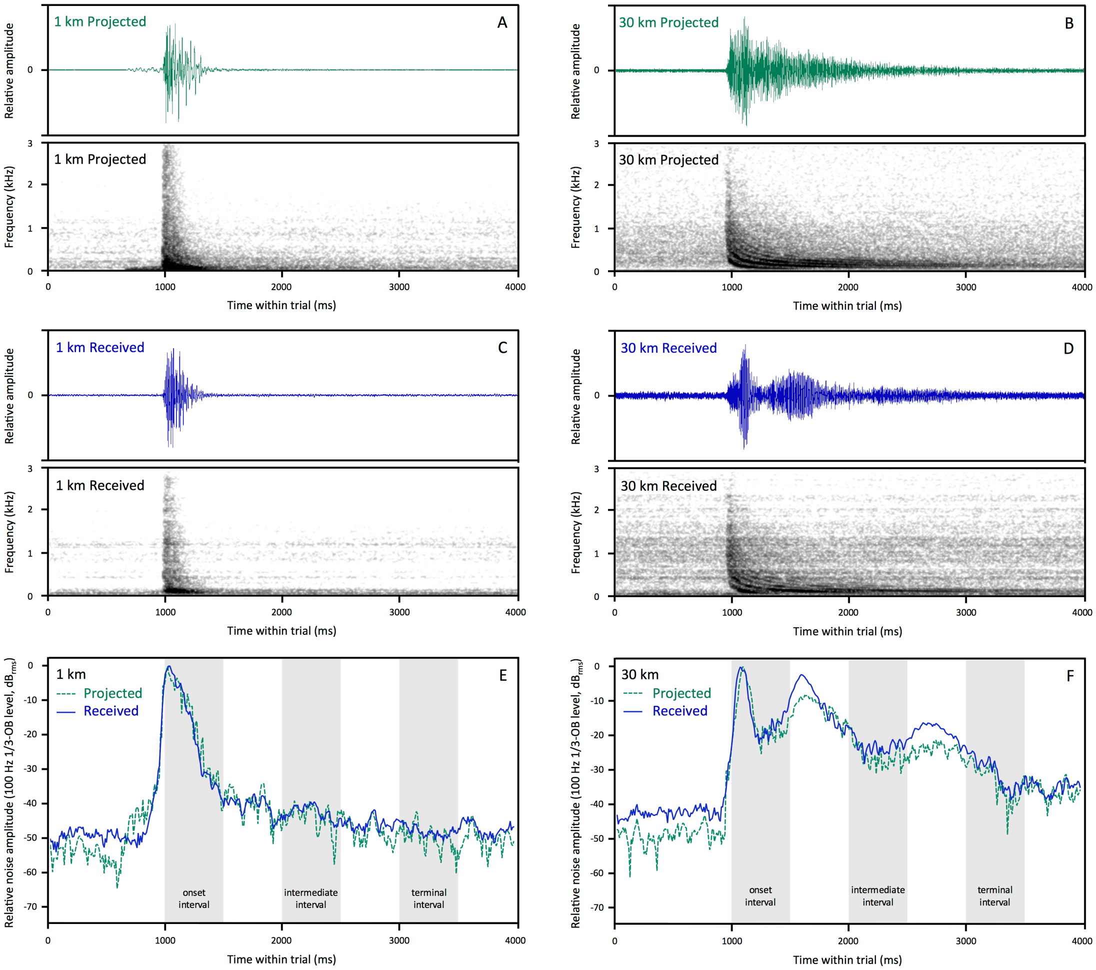
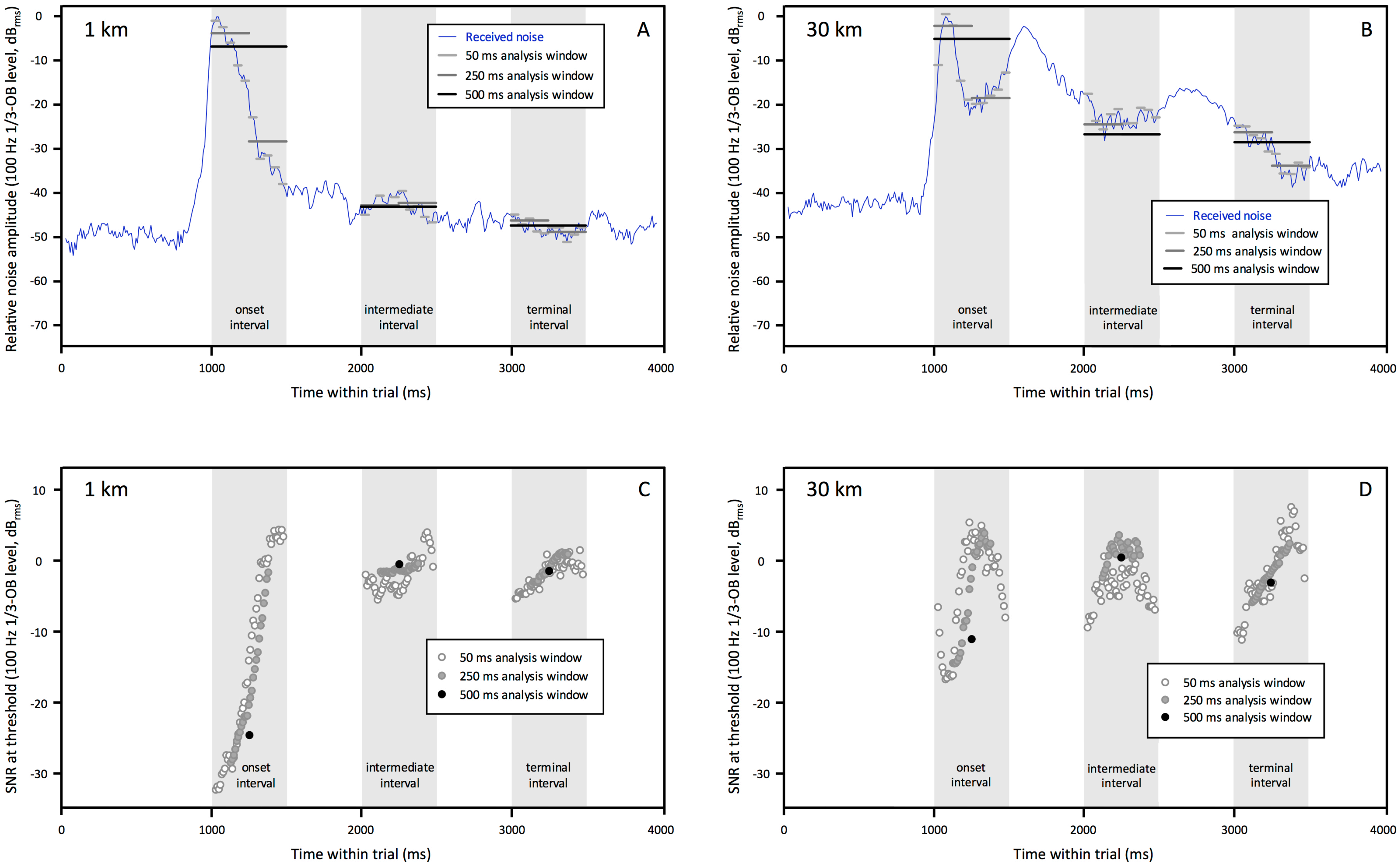

1 km Projected
A
Relative amplitude
0
30 km Projected
B
1 km Projected
Frequency (kHz)
3
2
1
0
1000
2000
3000
4000
Time within trial (ms)
30 km Projected
1 km Received
C
30 km Received
D
1 km Received
30 km Received
1 km
Projected
Received
E
Relative noise amplitude (100 Hz 1/3-OB level, dBrms)
-10
-20
-30
-40
-50
-60
-70
onset interval
intermediate interval
terminal interval
30 km
F

FIG 2. Overview of time window analysis with the 1 km masker (left side of figure) and 30 km masker (right side of figure). The upper panels show the normalized 100 Hz 1/3-octave band amplitude of the received 1 km (panel A) and 30 km (panel B) maskers across the 4-s trial duration. These received noise curves are the same as those described and plotted in the bottom panels of Figure 1. Additionally, within the three signal intervals (denoted by shaded gray regions) are plotted the normalized noise levels when measured over non-overlapping analysis windows of 50, 250, and 500 ms. The horizontal lines denote the specific windows over which noise was measured in each case. The lower panels show—for the 1 km (panel C) and 30 km (panel D) airgun maskers—the 100 Hz 1/3-octave band signal-to-noise ratios over the same three signal intervals, measured across overlapping time windows of 50, 250, and 500 ms (step size 10 ms). Each data point is plotted in the center of the time window over which it was calculated (*i.e.* the data point for the window from 1000 to 1500 ms is plotted as a single point at 1250 ms). These signal-to-noise ratios correspond to received levels at threshold for the spotted seal subject, *Tunu*. Additional detail is provided in Figure 4.


1 km
A
Received noise
50 ms analysis window
250 ms analysis window
500 ms analysis window
onset interval
intermediate interval
terminal interval
Relative noise amplitude (100 Hz 1/3-OB level, dB$_{rms}$)
0
-10
-20
-30
-40
-50
-60
-70
0
1000
2000
3000
4000
Time within trial (ms)
30 km
B
C
D
SNR at threshold (100 Hz 1/3-OB level, dB$_{rms}$)
10
0
-10
-20
-30

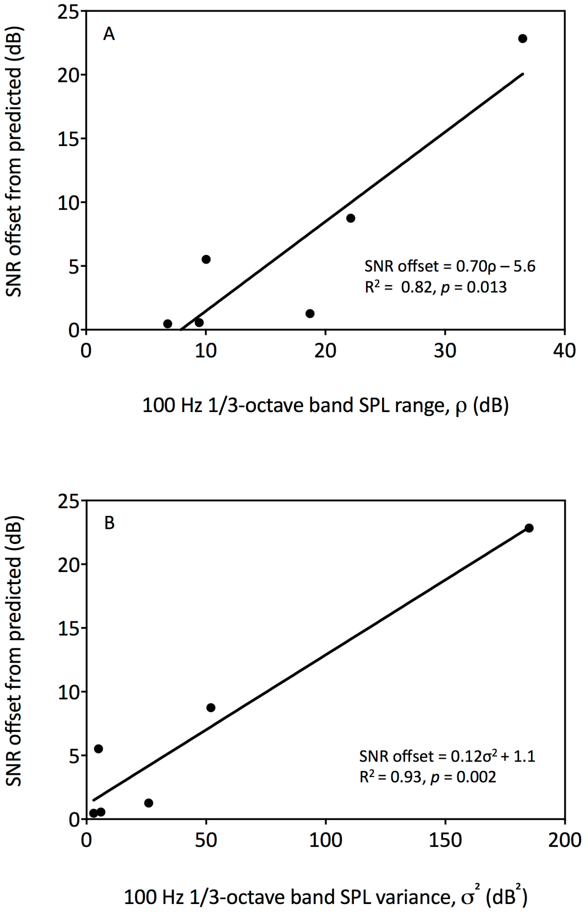
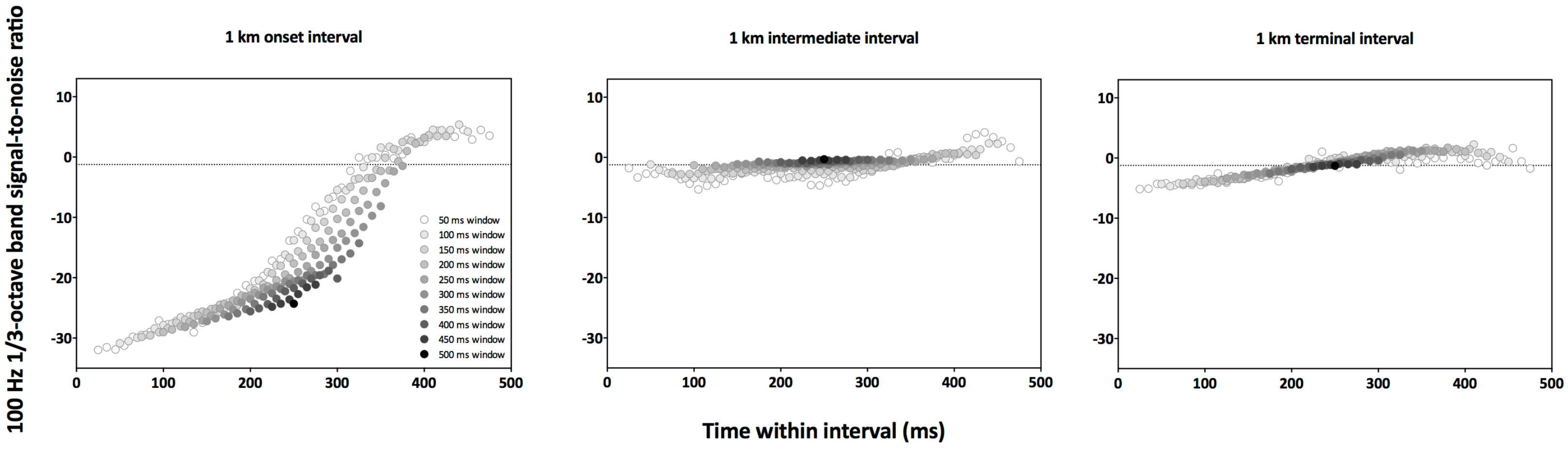
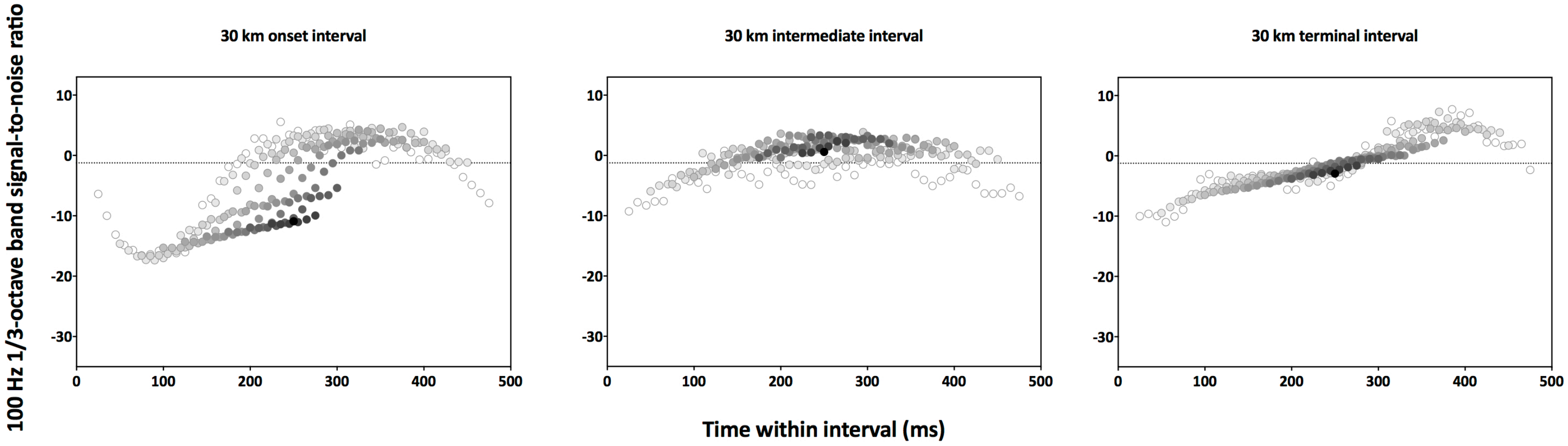


FIG 3. Ordinary least squares regression analyses calculated to predict SNR offset at threshold from the 100 Hz 1/3-octave band SPL range (panel A) or SPL variance (panel B) of the masking noise. For each of the six data points shown per panel—corresponding to the six different testing conditions—the offset between measured and predicted SNR at threshold was averaged for the two test subjects. These offsets were compared to noise variation measured over 50 ms analysis windows within the corresponding signal intervals. The resulting regression line in each case is shown along with its regression equation, R^2, and p-value.

FIG 4. 100 Hz 1/3-octave band signal-to-noise ratios measured across each signal interval at threshold for the spotted seal subject, *Tunu*. The upper three subplots show (from left to right) signal-to-noise ratio data for the onset, intermediate, and terminal intervals, respectively, of the 1 km masker. The lower three subplots show the same for the 30 km masker. Signal-to-noise ratios are plotted in each case for durations ranging from 50 to 500 ms, in 50 ms increments. These signal-to-noise ratios were calculated for overlapping time windows with a 10 ms step size. Also shown is a horizontal dotted line at the level of *Tunu's* predicted 1/3-octave band signal-to-noise ratio at threshold (-1 dB), based on critical ratio data obtained previously for the same subject and the conventional model of masking.


1 km onset interval
1 km intermediate interval
1 km terminal interval
100 Hz 1/3-octave band signal-to-noise ratio
10
0
-10
-20
-30
0
100
200
300
400
500
50 ms window
100 ms window
150 ms window
200 ms window
250 ms window
300 ms window
350 ms window
400 ms window
450 ms window
500 ms window
Time within interval (ms)


30 km onset interval
30 km intermediate interval
30 km terminal interval
100 Hz 1/3-octave band signal-to-noise ratio
10
0
-10
-20
-30
0
100
200
300
400
500
Time within interval (ms)

SUMMARY

This dissertation builds upon a strong foundation of audiometric research conducted with trained seals over the past five decades, beginning with the harbor seal hearing work done by Møhl (1968a, 1968b). The air-water comparisons made here for spotted and ringed seals extend many thoughtful characterizations and discussions of amphibious hearing by others (*e.g.*, Møhl 1968a, 1968b; Terhune and Ronald, 1971, 1972; Turnbull and Terhune, 1990; Terhune, 1991; Schusterman *et al.*, 1972; Schusterman, 1974; Moore and Schusterman, 1987; Babushina *et al.*, 1991; Kastak and Schusterman, 1998, 1999; Southall *et al.*, 2003; Reichmuth *et al.*, 2013). By replicating and significantly expanding on earlier studies, the high-resolution behavioral experiments reported herein fill key knowledge gaps related to auditory biology in seals and enable mitigation of anthropogenic noise effects for these species.

Chapters 1 and 2 of this dissertation thoroughly describe the basic hearing abilities of spotted and ringed seals in air and under water. The hearing profiles of these species demonstrate acute auditory sensitivity in both media, a finding that diverges from historical data for ice-living phocids but is consistent with what is known about the amphibious existence of these seals. Despite their need to receive and process sound in two very different physical environments, spotted and ringed seals are able to hear nearly as well (in terms of best sensitivity) as fully aquatic and fully terrestrial mammals in their respective media. While the detailed mechanisms supporting such sensitive amphibious hearing in these species remain incompletely resolved, their demonstrated auditory abilities emphasize the need to assess and mitigate noise effects both above and below the water's surface.

In addition to the measures of absolute hearing sensitivity obtained in air and water, the masked (noise-limited) hearing measurements provided in Chapters 1 and 2 allow for detailed comparisons across frequencies, media, individuals, and species. Prior to this dissertation, some measures of auditory masking were available to describe how seals detect acoustic signals in elevated noise conditions. Here, critical ratios—measured in air and in water, and across a significant frequency range—are reported for spotted and ringed seals listening for tonal signals in the presence of spectrally flattened, octave-band noise. These critical ratio data clarify the quantitative relationship between sound frequency and masking effect (see Erbe *et al.*, 2016) and provide insight into how the ears of seals operate to filter and process environmental sounds. Importantly, these data improve the capacity of scientists and regulators to predict the simultaneous effect of many types of anthropogenic noise on hearing in seals.

Chapter 3 extends the classic audiometric work conducted in the first two chapters of this dissertation in order to investigate hearing and masking in more realistic acoustic environments. Focusing on a pervasive source of noise in the Arctic—seismic airguns used for geophysical exploration—experiments with trained spotted and ringed seals revealed that a conventional model of masking could accurately predict the extent of masking only under certain conditions. Specifically, combining critical ratio data with spectrum levels of coincident noise (derived from average 1/3-octave band noise levels) produced reasonable estimates of sensitivity when noise was relatively stable in time, but poor estimates of sensitivity when the noise background was significantly amplitude modulated. Estimates of the extent of masking induced by seismic impulses were improved by considering signal-to-noise ratios measured over analysis windows shorter than the duration of the target signal. The results presented in this chapter indicate that it is necessary to consider temporal as well as spectral features of received auditory stimuli to better understand masking outside the laboratory. However, this work also demonstrates the power of classical behavioral methods to address timely and applied questions related to auditory perception. Additional behavioral studies with trained animals can help researchers further understand the ability of seals to detect relevant sounds in complex marine environments.

Beyond this dissertation, additional work is needed to describe the auditory capabilities of marine mammal species for which no data are presently available. Such efforts, while time and resource intensive, would expand available knowledge concerning sensory biology in semi-aquatic and fully aquatic animals, and enable new comparative evaluations of functional hearing, auditory anatomy, and evolutionary biology. For the amphibious seals, sea lions, fur seals, and walruses, in particular, continued investigations of auditory biology will serve to reveal the abilities and mechanisms that supported the transformation of these previously terrestrial carnivores into modern pinnipeds uniquely suited to amphibious living. In addition to these and other fundamental scientific gains, our ability to manage wild marine mammal populations will improve as more hearing data become available. Identification and resolution of functional hearing groups, for example, will inform and streamline the regulatory process. The similarities observed in hearing between the spotted and ringed seals tested here, combined with recently published data for harbor seals (Kastelein *et al.*, 2009; Reichmuth *et al.*, 2013), suggest that the 10 species of northern seals (subfamily Phocinae) can be characterized as a single functional hearing group. Although additional work is needed to confirm this assertion—*e.g.*, auditory measurements for more distantly related species within the subfamily—it is clear that extrapolations can reasonably be made at least between spotted, harbor, and ringed seals, and their close relatives.

While many details of their acoustic behavior remain to be discovered, the improved characterization of auditory biology provided herein offers new insight into the amphibious lives of Arctic seals. Broadly sensitive underwater hearing, which extends several octaves above the upper limits of their dominant vocal energy, suggests that these seals are receiving other sounds in addition to the calls of their conspecifics. In the seasonally ice-covered waters of the northern hemisphere, spotted and ringed seals likely attend to auditory cues across a wide range of frequencies to support predator avoidance, prey detection, and under-ice orientation in often light-limited environments. In summary, the research conducted as part of this dissertation—which describes the auditory capabilities of spotted and ringed seals in quiet conditions, in the presence of controlled noise, and in realistic acoustic environments—provides new information about the acoustic ecology of ice-living seals, and improves our ability to manage noise pollution in an increasingly industrialized Arctic.

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