

RESEARCH ARTICLE

Amphibious hearing in ringed seals (*Pusa hispida*): underwater audiograms, aerial audiograms and critical ratio measurements

Jillian M. Sills^{1,*}, Brandon L. Southall^{2,3} and Colleen Reichmuth²

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. Best sensitivity was 49 dB re. 1 μ Pa (12.8 kHz) in water, and –12 dB re. 20 μ Pa (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.

KEY WORDS: Ringed seal, Amphibious, Audiogram, Hearing, Arctic, Noise

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, walrus) – 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 (*Histiophoca 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 (Möhl, 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.,

¹Department of Ocean Sciences, University of California Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA. ²Institute of Marine Sciences, Long Marine Laboratory, University of California Santa Cruz, Santa Cruz, CA 95060, USA. ³SEA, Inc., 9099 Soquel Drive, Suite 8, Aptos, CA 95003, USA.

*Author for correspondence (jmsills@ucsc.edu)

Received 19 February 2015; Accepted 12 May 2015

List of symbols and abbreviations

CR	critical ratio
FA	false alarm
HTP	Hearing Test Program [NI LabVIEW-based software (Finneran, 2003)]
MCS	method of constant stimuli
PSD	power spectral density
SL	sensation level
SPL	sound pressure level

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 1). 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 supplementary material 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 μ Pa, 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 2). 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 supplementary material 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 μ Pa and –12 dB re. 20 μ Pa, 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.

Table 1. Underwater hearing thresholds obtained for two ringed seals using psychophysical methods

Frequency (kHz)	Natchek		Nayak		Ambient noise
	Threshold (dB re. 1 μ Pa)	FA rate	Threshold (dB re. 1 μ Pa)	FA rate	PSD [dB re. (1 μ Pa) ² Hz ⁻¹]
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

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, $N \geq 20$), 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 supplementary material Fig. S1.

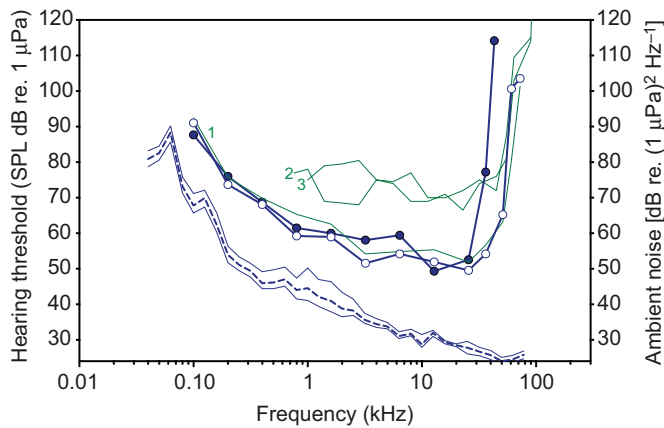


Fig. 1. Underwater audiograms for two ringed seals. Natchek (filled circles) and Nayak (open circles). The 50% detection thresholds obtained using psychophysical methods are shown for 14 frequencies from 0.1 to 72.4 kHz. Ambient noise levels measured in the underwater testing pool [power spectral density, dB re. $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$] 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)], harp seals [2, $N=1$ (Terhune and Ronald, 1972)] and ringed seals [3, $N=2$ (Terhune and Ronald, 1975a)].

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 2). 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 3). 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

Table 2. In-air hearing thresholds obtained for two ringed seals using psychophysical methods

Frequency (kHz)	Natchek			Nayak			Ambient noise PSD [dB re. $(20 \mu\text{Pa})^2 \text{Hz}^{-1}$]		
	Threshold (dB re. $20 \mu\text{Pa}$)	FA rate	Latency (ms) at 0 dB SL	Latency (ms) at 20 dB SL	Threshold (dB re. $20 \mu\text{Pa}$)	FA rate		Latency (ms) at 0 dB SL	Latency (ms) at 20 dB SL
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	-	-	-

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, $N \geq 20$), 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 as supplementary material Fig. S2.

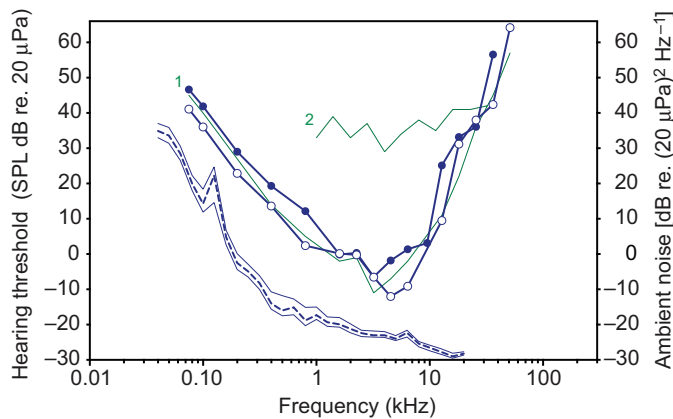


Fig. 2. In-air audiograms for two ringed seals. Natchek (filled circles) and Nayak (open circles). The 50% detection thresholds obtained using psychophysical methods are shown for 16 frequencies from 0.075 to 51.2 kHz. Ambient noise levels measured in the acoustic chamber [power spectral density, dB re. $(20 \mu\text{Pa})^2 \text{Hz}^{-1}$] 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)].

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 & Kjør 2250 sound analyzer; Brüel & Kjør A/S, Nærum, Denmark), masking by background noise can neither be confirmed nor entirely ruled out

Table 3. Underwater critical ratio measurements obtained for two ringed seals at nine frequencies

Frequency (kHz)	Natchek				Nayak			
	Masked threshold (dB re. $1 \mu\text{Pa}$)	Masker level [dB re. $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$]	Critical ratio (dB)	FA rate	Masked threshold (dB re. $1 \mu\text{Pa}$)	Masker level [dB re. $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$]	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

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, $N \geq 40$). For both subjects, 95% confidence intervals were narrower than 4 dB for all masked thresholds.

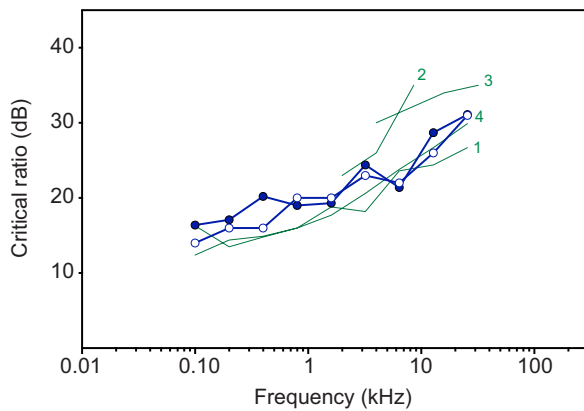


Fig. 3. Underwater critical ratios measured for two ringed seals. Natchek (filled circles) and Nayak (open circles). Critical ratios were measured at nine frequencies (0.1 to 25.6 kHz) as the difference (dB) between the sound pressure level of the masked threshold and the spectral density level of the 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)].

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; Ramprasad, 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; Ramprasad, 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, 1975a). 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 dB_{rms} re. 1 μ Pa (in water) or dB_{rms} re. 20 μ Pa (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 ($\pm 5\%$ 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 National 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 μ Pa V^{-1} 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 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 (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. $(1 \mu\text{Pa})^2 \text{ Hz}^{-1}$] of the surrounding 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.

Acknowledgements

We thank the Alaska SeaLife Center and SeaWorld San Diego for providing access to the ringed seals in this study, J. Finneran (US Navy Marine Mammal Program) for providing access to the HTP software, and J. Terhune (University of New Brunswick)

for contributions to design and analysis. This work was made possible by the entire team at the Pinniped Cognition and Sensory Systems Laboratory, especially J. Lofstrom, C. Casey, K. Cunningham, S. Knaub, A. Ghoul, A. Rouse, R. Nichols, P. Cook and R. King. We thank R. Sills, J. Terhune and an anonymous reviewer for helpful comments on this manuscript. Portions of this research were presented at the 164th Meeting of the Acoustical Society of America and the 3rd International Conference on the Effects of Noise on Aquatic Life.

Competing interests

The authors declare no competing financial interests.

Author contributions

J.M.S. was involved in all aspects of this study and responsible for data collection and manuscript preparation. B.L.S. was involved with experimental design and provided technical expertise. C.R. was involved in all aspects and responsible for funding and animals.

Funding

Funding provided by the International Association of Oil and Gas Producers, through their E&P Joint Industry Programme on Sound and Marine Life [award 22-07-23].

Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.120972/-DC1>

References

- Babushina, E. S.** (1997). Audiograms of the Caspian seal under water and in air. *Sens. Syst.* **11**, 67–71.
- Bowles, A. E., Graves, S. K., Shane, M. and Denes, S. L.** (2010). Harbor seals (*Phoca vitulina*) respond with aversion to 69-kHz pings: implications for weighting procedures for marine mammal noise metrics. *J. Acoust. Soc. Am.* **127**, 1803.
- Branstetter, B. K., Trickey, J. S., Bakhtiari, K., Black, A., Aihara, H. and Finneran, J. J.** (2013). Auditory masking patterns in bottlenose dolphins (*Tursiops truncatus*) with natural, anthropogenic, and synthesized noise. *J. Acoust. Soc. Am.* **133**, 1811–1818.
- Cornsweet, T. N.** (1962). The staircase-method in psychophysics. *Am. J. Psychol.* **75**, 485–491.
- Cummings, W. C., Holliday, D. V. and Lee, B. J.** (1984). Potential impacts of man-made noise on ringed seals: vocalizations and reactions. *Outer Continental Shelf Environmental Assessment Program, Final Report. OCS Study MMS 86-0021; NTIS PB87-107546*. Anchorage, AK: NOAA.
- Cunningham, K. A., Southall, B. L. and Reichmuth, C.** (2014). Auditory sensitivity of seals and sea lions in complex listening scenarios. *J. Acoust. Soc. Am.* **136**, 3410–3421.
- Dooling, R. J., Mulligan, J. A. and Miller, J. D.** (1971). Auditory sensitivity and song spectrum of the common canary (*Serinus canarius*). *J. Acoust. Soc. Am.* **50**, 700–709.
- Dooling, R. J., Blumenrath, S. H., Smith, E. and Fristrup, K.** (2013). Evaluating anthropogenic noise effects on animal communication, Noise-Con 2013, Denver, CO, August 26–28, 2013, pp. 1–6.
- Elsner, R., Wartzok, D., Sonafank, N. B. and Kelly, B. P.** (1989). Behavioral and physiological reactions of arctic seals during under-ice pilotage. *Can. J. Zool.* **67**, 2506–2513.
- Endler, J. A.** (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153.
- Esser, K.-H. and Daucher, A.** (1996). Hearing in the FM-bat *Phyllostomus discolor*: a behavioral audiogram. *J. Comp. Physiol. A.* **178**, 779–785.
- Fay, R. R.** (1988). *Hearing in Vertebrates: A Psychophysics Databook*. Winnetka, IL: Hill-Fay Associates.
- Finneran, J. J.** (2003). *An Integrated Computer-Controlled System for Marine Mammal Auditory Testing*. San Diego, CA: SPAWAR Systems Center.
- Finney, D. J.** (1971). *Probit Analysis*, 3rd edn. Cambridge: Cambridge University Press.
- Fletcher, H.** (1940). Auditory patterns. *Rev. Mod. Phys.* **12**, 47–65.
- Heffner, H. E.** (1983). Hearing in large and small dogs: absolute thresholds and size of the tympanic membrane. *Behav. Neurosci.* **97**, 310–318.
- Heffner, R. S. and Heffner, H. E.** (1985a). Hearing range of the domestic cat. *Hear. Res.* **19**, 85–88.
- Heffner, R. S. and Heffner, H. E.** (1985b). Hearing in mammals: the least weasel. *J. Mamm.* **66**, 745–755.
- Heffner, H. E. and Heffner, R. S.** (2008). High-frequency hearing. In *Handbook of the Senses: Audition* (ed. P. Dallos, D. Oertel and R. Hoy), pp. 55–60. New York, NY: Elsevier.
- Hemilä, S., Nummela, S., Berta, A. and Reuter, T.** (2006). High-frequency hearing in phocid and otariid pinnipeds: an interpretation based on inertial and cochlear constraints. *J. Acoust. Soc. Am.* **120**, 3463–3466.
- Huth, M. E., Ricci, A. J. and Cheng, A. G.** (2011). Mechanisms of aminoglycoside ototoxicity and targets of hair cell protection. *Int. J. Otolaryngol.* **2011**, 937861.
- Jones, J. M., Thayre, B. J., Roth, E. H., Mahoney, M., Sia, I., Mercuri, K., Jackson, C., Zeller, C., Clare, M., Bacon, A. et al.** (2014). Ringed, bearded, and ribbon seal vocalizations north of Barrow, Alaska: seasonal presence and relationship with sea ice. *Arctic* **67**, 203–222.
- Kastak, D. and Schusterman, R. J.** (1998). Low-frequency amphibious hearing in pinnipeds: methods, measurements, noise, and ecology. *J. Acoust. Soc. Am.* **103**, 2216–2228.
- Kastelein, R. A., Wensveen, P. J., Hoek, L., Verboom, W. C. and Terhune, J. M.** (2009). Underwater detection of tonal signals between 0.125 and 100 kHz by harbor seals (*Phoca vitulina*). *J. Acoust. Soc. Am.* **125**, 1222–1229.
- Kelly, J. B., Kavanagh, G. L. and Dalton, J. C. H.** (1986). Hearing in the ferret (*Mustela putorius*): thresholds for pure tone detection. *Hear. Res.* **24**, 269–275.
- Kelly, B. P., Bengtson, J. L., Boveng, P. L., Cameron, M. F., Dahle, S. P., Jansen, J. K., Logerwell, E. A., Overland, J. E., Sabine, C. L., Waring, G. T. et al.** (2010). *Status Review of the Ringed Seal (Phoca hispida)*. NOAA Technical Memorandum NMFS-AFSC-212. Washington, DC: US Department of Commerce.
- Ladich, F. and Yan, H. Y.** (1998). Correlation between auditory sensitivity and vocalization in anabantoid fishes. *J. Comp. Physiol. A. Sens. Neural. Behav. Physiol.* **182**, 737–746.
- Miksis-Olds, J. L. and Madden, L. E.** (2014). Environmental predictors of ice seal presence in the Bering Sea. *PLoS ONE* **9**, e106998.
- Møhl, B.** (1967). Seal ears. *Science* **157**, 99.
- Møhl, B.** (1968a). Auditory sensitivity of the common seal in air and water. *J. Aud. Res.* **8**, 27–38.
- Møhl, B.** (1968b). Hearing in seals. In *The behaviour and physiology of pinnipeds* (ed. R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice and R. J. Schusterman), pp. 172–195. New York, NY: Appleton-Century-Crofts.
- Møhl, B. and Ronald, K.** (1975). The peripheral auditory system of the harp seal, *Pagophilus groenlandicus* (Erleben, 1777). *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **169**, 516–523.
- Moody, D. B.** (1970). Reaction time as an index of sensory function. In *Animal Psychophysics: The Design and Conduct of Sensory Experiments* (ed. W.C. Stebbins), pp. 227–302. New York, NY: Appleton-Century-Crofts.
- Moore, P. W. B. and Schusterman, R. J.** (1987). Audiometric assessment of northern fur seals, *Callorhinus ursinus*. *Mar. Mamm. Sci.* **3**, 31–53.
- Mulsow, J., Houser, D. S. and Finneran, J. J.** (2012). Underwater psychophysical audiogram of a young male California sea lion (*Zalophus californianus*). *J. Acoust. Soc. Am.* **131**, 4182–4187.
- Nummela, S.** (2008). Hearing in aquatic mammals. In *Sensory Evolution on the Threshold: Adaptations in Secondary Aquatic Vertebrates* (ed. J. G. M. Thewissen and S. Nummela), pp. 211–224. Berkeley, CA: University of California Press.
- Nummela, S. and Thewissen, J. G. M.** (2008). The physics of sound in air and water. In *Sensory Evolution on the Threshold: Adaptations in Secondary Aquatic Vertebrates* (ed. J. G. M. Thewissen and S. Nummela), pp. 175–181. Berkeley, CA: University of California Press.
- Ramprasad, F.** (1975). Aquatic adaptations in the ear of the harp seal *Pagophilus groenlandicus* (Erleben, 1777). *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **169**, 102–111.
- Reichmuth, C., Holt, M. M., Mulsow, J., Sills, J. M. and Southall, B. L.** (2013). Comparative assessment of amphibious hearing in pinnipeds. *J. Comp. Physiol. A.* **199**, 491–507.
- Renouf, D.** (1980). Masked hearing thresholds of harbour seals (*Phoca vitulina*) in air. *J. Aud. Res.* **20**, 263–269.
- Repenning, C. A.** (1972). Underwater hearing in seals: functional morphology. In *Functional Anatomy of Marine Mammals*, Vol. 1 (ed. R. J. Harrison), pp. 307–331. London: Academic Press.
- Ryan, M. J. and Wilczynski, W.** (1988). Coevolution of sender and receiver: effect on local mate preference in cricket frogs. *Science* **240**, 1786–1788.
- Scharf, B.** (1970). Critical bands. In *Foundations of Modern Auditory Theory*, Vol. 1 (ed. J. V. Tobias), pp. 159–202. New York, NY: Academic Press.
- Schusterman, R. J., Kastak, D., Levenson, D. H., Reichmuth, C. J. and Southall, B. L.** (2000). Why pinnipeds don't echolocate. *J. Acoust. Soc. Am.* **107**, 2256–2264.
- Sills, J. M., Southall, B. L. and Reichmuth, C.** (2014). Amphibious hearing in spotted seals (*Phoca largha*): underwater audiograms, aerial audiograms and critical ratio measurements. *J. Exp. Biol.* **217**, 726–734.
- Southall, B. L., Schusterman, R. J. and Kastak, D.** (2000). Masking in three pinnipeds: underwater, low-frequency critical ratios. *J. Acoust. Soc. Am.* **108**, 1322–1326.
- Southall, B. L., Schusterman, R. J. and Kastak, D.** (2003). Auditory masking in three pinnipeds: aerial critical ratios and direct critical bandwidth measurements. *J. Acoust. Soc. Am.* **114**, 1660–1666.
- Southall, B. L., Schusterman, R. J., Kastak, D. and Reichmuth, C.** (2005). Reliability of underwater hearing thresholds in pinnipeds. *Acoust. Res. Lett. Online* **6**, 243–249.

- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E. et al.** (2007). Marine mammal noise exposure criteria: initial scientific recommendations. *Aquat. Mamm.* **33**, 411-414.
- Stebbins, W. C.** (1970). Principles of animal psychophysics. In *Animal Psychophysics: The Design and Conduct of Sensory Experiments* (ed. W. C. Stebbins), pp. 1-19. New York, NY: Appleton-Century-Crofts.
- Stirling, I.** (1973). Vocalization in the ringed seal (*Phoca hispida*). *J. Fish. Res. Board Can.* **30**, 1592-1594.
- Stirling, I., Calvert, W. and Cleator, H.** (1983). Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high Arctic. *Arctic* **36**, 262-274.
- Terhune, J. M.** (1988). Detection thresholds of a harbour seal to repeated underwater high-frequency, short-duration sinusoidal pulses. *Can. J. Zool.* **66**, 1578-1582.
- Terhune, J. M.** (1991). Masked and unmasked pure tone detection thresholds of a harbour seal listening in air. *Can. J. Zool.* **69**, 2059-2066.
- Terhune, J. M. and Ronald, K.** (1971). The harp seal, *Pagophilus groenlandicus* (Erleben, 1777). X. The air audiogram. *Can. J. Zool.* **49**, 385-390.
- Terhune, J. M. and Ronald, K.** (1972). The harp seal, *Pagophilus groenlandicus* (Erleben, 1777). III. The underwater audiogram. *Can. J. Zool.* **50**, 565-569.
- Terhune, J. M. and Ronald, K.** (1975a). Underwater hearing sensitivity of two ringed seals (*Pusa hispida*). *Can. J. Zool.* **53**, 227-231.
- Terhune, J. M. and Ronald, K.** (1975b). Masked hearing thresholds of ringed seals. *J. Acoust. Soc. Am.* **58**, 515-516.
- Turnbull, S. D. and Terhune, J. M.** (1990). White noise and pure tone masking of pure tone thresholds of a harbour seal listening in air and underwater. *Can. J. Zool.* **68**, 2090-2097.
- Wartzok, D., Elsner, R., Stone, H., Kelly, B. P. and Davis, R. W.** (1992). Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals. *Can. J. Zool.* **70**, 1712-1722.
- Watkins, W. A. and Wartzok, D.** (1985). Sensory biophysics of marine mammals. *Mar. Mamm. Sci.* **1**, 219-260.
- Wolski, L. F., Anderson, R. C., Bowles, A. E. and Yochem, P. K.** (2003). Measuring hearing in the harbor seal (*Phoca vitulina*): comparison of behavioral and auditory brainstem response techniques. *J. Acoust. Soc. Am.* **113**, 629-637.
- Yost, W. A.** (2000). *Fundamentals of Hearing: An Introduction*, 4th edn. San Diego, CA: Academic Press.