

Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements

Brandon L. Southall,^{a)} Ronald J. Schusterman,^{b)} and David Kastak
Long Marine Laboratory, University of California at Santa Cruz, 100 Shaffer Road, Santa Cruz,
California 95060

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This study expands the limited understanding of pinniped aerial auditory masking and includes measurements at some of the relatively low frequencies predominant in many pinniped vocalizations. Behavioral techniques were used to obtain aerial critical ratios (CRs) within a hemianechoic chamber for a northern elephant seal (*Mirounga angustirostris*), a harbor seal (*Phoca vitulina*), and a California sea lion (*Zalophus californianus*). Simultaneous, octave-band noise maskers centered at seven test frequencies (0.2–8.0 kHz) were used to determine aerial CRs. Narrower and variable bandwidth masking noise was also used in order to obtain direct critical bandwidths (CBWs). The aerial CRs are very similar in magnitude and in frequency-specific differences (increasing gradually with test frequency) to underwater CRs for these subjects, demonstrating that pinniped cochlear processes are similar both in air and water. While, like most mammals, these pinniped subjects apparently lack specialization for enhanced detection of specific frequencies over masking noise, they consistently detect signals across a wide range of frequencies at relatively low signal-to-noise ratios. Direct CBWs are 3.2 to 14.2 times wider than estimated based on aerial CRs. The combined masking data are significant in terms of assessing aerial anthropogenic noise impacts, effective aerial communicative ranges, and amphibious aspects of pinniped cochlear mechanics. © 2003 Acoustical Society of America. [DOI: 10.1121/1.1587733]

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I. INTRODUCTION

A considerable amount is known about certain aspects of acoustic communication and auditory processing in pinnipeds [seals, sea lions, and walruses] (see Ketten and Watzok, 1999). Basic research in pinniped bioacoustics is frequently motivated by the importance of vocal signaling. Of additional interest is the fact that most of these amphibious marine mammals produce and detect both airborne and underwater sounds in environments that favor the use of acoustic communicative signals (Kastak and Schusterman, 1998; Tyack, 1998; Schusterman *et al.*, 2000). Potential interference with these processes by increasing anthropogenic noise levels in some marine environments (see Andrew *et al.*, 2002) is providing impetus for expanding the limited knowledge of the effects of noise on pinniped hearing (Richardson *et al.*, 1995; National Research Council, 2000). Significant interest has focused on the harmful effects of underwater noise (e.g., noise-induced temporary and permanent threshold shifts). Several recent studies have provided data bearing on these issues (Kastak *et al.*, 1999; Schlundt *et al.*, 2000; Finneran *et al.*, 2002). However, we still lack critical data on the effects of airborne sounds, including the potential for anthropogenic noise to mask the relatively low (<2 kHz) frequencies typically contained in many pinniped communicative signals (Richardson *et al.*, 1995; Southall *et al.*, 2000).

Therefore, this study focuses on the effects of airborne noise on aerial hearing for a wide range of frequencies, including low frequencies.

An observation from studies involving a variety of mammals is that tonal signals are almost exclusively masked by noise in a narrow band of similar frequencies (Wegel and Lane, 1924; Fletcher, 1940; Scharf, 1970), which Fletcher (1940) refers to as the critical band and its bandwidth as the critical bandwidth (CBW). Based largely on the results of auditory masking studies, mammalian auditory systems are typically viewed as segregating acoustic signals into their constituent frequencies in a manner analogous to the operation of overlapping bandpass filters. Auditory masking is quantified as the critical ratio (CR), which is the difference (in dB) between the masked hearing threshold and the masking noise spectral power density level (Fletcher, 1940; Scharf, 1970). A low CR at a particular frequency indicates relatively efficient extraction of signals from noise compared to a higher CR and, theoretically, a relatively narrower critical CBW. According to Fletcher (1940), the power of a signal at the masked hearing threshold is equal to the total noise power within the critical band. For a particular frequency the CBW may be estimated indirectly as $10^{(CR/10)}$, a method referred to as the critical ratio equal power (CR/EqP) method (as in Richardson *et al.*, 1995). However, studies using a variety of techniques to directly measure auditory filter parameters in human subjects have demonstrated that the CR/EqP method may be of limited accuracy in estimating CBWs (Egan and Hake, 1950; Schafer *et al.*, 1950; Hamilton, 1957; Zwicker *et al.*, 1957; Patterson, 1976).

There are many similarities in mammalian auditory

^{a)}Current address: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Acoustics Program, Silver Spring, MD 20910.

^{b)}Electronic mail: rjschust@cats.ucsc.edu

masking because cochlear mechanics are similar among non-specialized species (Echteler *et al.*, 1994). There is generally a linear relationship between the masking noise level and effective masking, so that CRs at each frequency are independent of masker level in most conditions (Hawkins and Stevens, 1950; Watson, 1963; Gourevitch, 1965; Johnson, 1968; Ehret, 1976). Additionally, relative auditory filter widths are an approximately constant percentage of center frequency (constant Q) but absolute CBWs increase with frequency, resulting in a gradual increase in CRs with frequency (~ 3 dB/octave).

While these trends are consistent among most mammals, and the relative differences in CR magnitudes are relatively small (see Fay, 1988), certain taxa tend to have somewhat lower CRs on average. For instance, humans, nonhuman primates, and most marine mammals generally have relatively lower CRs than many terrestrial vertebrates tested (Southall *et al.*, 2000). There are also species differences in the relationship between indirectly estimated and directly measured CBWs. In humans, indirect estimates are approximately 2.5 times smaller than directly measured CBWs, a difference that is fairly consistent for many frequencies (see Scharf, 1970). However, studies of nonhuman mammals indicate that this relationship is not found in all species (Seaton and Trahiotis, 1975; Ehret, 1976; Au and Moore, 1990; Turnbull and Terhune, 1990; Niemiec *et al.*, 1992).

Aerial or underwater CRs for individuals from six of the 34 pinniped species have been obtained experimentally (Terhune and Ronald, 1971, 1975; Renouf, 1980; Moore and Schusterman, 1987; Turnbull and Terhune, 1990; Terhune, 1991; Southall *et al.*, 2000). Pinniped CRs are generally low when compared to most other mammals, indicating relatively good hearing in noise. Aerial and underwater pinniped CRs are often directly compared despite the fact that aerial and underwater absolute hearing generally differs. Such comparisons are based on the notion that CRs are related to cochlear processes and that both signals and masking noise should be similarly affected by outer- and middle-ear filtering effects (Renouf, 1980; Turnbull and Terhune, 1990). Indeed, this hypothesis has been confirmed by data for one individual harbor seal, suggesting that there is no difference between pinniped CRs obtained in air and in water (Turnbull and Terhune, 1990). Moreover, these investigators found that critical bandwidths measured directly for the same individual harbor seal were consistently narrower than predicted with the CR/EqP method, became narrower with increasing frequency, and were similar in air and water.

The purpose of the present study was to provide in-air CRs and direct CBW measurements for individuals from three pinniped species: northern elephant seal (*Mirounga angustirostris*), harbor seal (*Phoca vitulina*), and California sea lion (*Zalophus californianus*). Aerial CRs are compared with underwater values for the same individuals obtained in a previous study (Southall *et al.*, 2000). Indirect filter bandwidth estimates are compared with direct CBWs.

II. METHODS

A. Subjects and testing enclosure

The subjects of the aerial auditory masking experiments were an 8-year-old female northern elephant seal (Burnyce), a 13-year-old male harbor seal (Sprouts), and a 16-year-old female California sea lion (Rio). All subjects had many years of experience in audiometric tasks prior to this study (Kastak and Schusterman, 1998; Kastak *et al.*, 1999; Schusterman, unpublished data). None of the subjects had been administered aminoglycoside antibiotics and no permanent hearing losses were known to have occurred. The elephant seal developed a chronic otitis externa in one ear prior to relocation at Long Marine Laboratory. This condition, while intermittently recurrent, is not thought to significantly impact absolute aerial or underwater hearing (see Kastak and Schusterman, 1998).

The animals were housed at Long Marine Laboratory in Santa Cruz, California in seawater-filled pools and adjacent haul-out space. Subjects received 25%–75% of their daily allotment of fish during one to three experimental sessions, 5 to 7 mornings per week between October 2001 and January 2002. The experiments were conducted under National Marine Fisheries Service (NMFS) permit 259-1481-00 and were approved by the University of California, Santa Cruz Chancellor's Animal Research Committee.

A hemianechoic chamber (Eckel Industries) mounted on a semi-isolated cement foundation served as the testing enclosure. The chamber consisted of a $3.3 \times 2.3 \times 2.2$ -m test room and an adjacent 1.3×3.3 -m experimental control room. The outside walls of the entire chamber were double-paneled, 8-gauge stainless steel, providing 40–60-dB of noise attenuation. The inside walls and ceiling of the test room were lined with fiberglass-filled, aluminum-covered anechoic wedges that limited acoustic reflection within the testing room. The cement floor of the test room was covered with several 2.6-cm-thick neoprene mats. The inside walls of the control room were lined with sound-absorptive foam panels. Equipment cable ducts between the test and control rooms were lined with sound-absorptive foam.

A floor-mounted convex section of polyvinyl chloride (PVC) served as a chin station for experimental sessions. An acoustically sealed, sliding PVC feeding tube allowed fish reinforcement to be delivered to the subjects from the control room during sessions. Animal responses were observed via a closed-circuit video system. A square plastic response paddle was located 0.3 m in front of and to the left of the chin station. The chin station was positioned in the same location for each individual, approximately 1 m in front of one of several projecting speakers, to ensure consistent placement of subjects within and between sessions.

B. Test stimuli and masking noise

Test stimuli were pure tones at seven frequencies between 0.2 and 8.0 kHz with either 20- or 40-ms rise/fall times and 500-ms overall duration. Two hardware and software configurations were used to generate these signals. The initial system was identical to that previously used for underwater auditory masking experiments (Southall *et al.*, 2000).

For some of the test conditions, including the entire band-narrowing experiment, signals were generated using custom-built software (LABVIEW) and a 6070E multifunction board mounted in a PXI-1010 chassis (National Instruments). For both configurations, signals were projected using either a JBL 2245H (0.2 kHz) JBL 2123H (0.5, 0.8, and 1.2 kHz), or JBL 2123H/J (2.5, 4.0, and 8.0 kHz) speaker.

Variable bandwidth masking noise was generated using COOL EDIT software (Syntrillium). Identical 6-s noise intervals were produced for each experimental trial using the sound card of a personal computer (sampling rate 22 050 Hz, 16-bit resolution, FFT size 512). The sound card output was fed through a Krohn-Hite 3550 bandpass filter, a Hewlett Packard stepwise attenuator, and into another input channel of the power amplifier, which drove the projecting transducer. Test signals and masking noise were projected from the same source to avoid reduced masking resulting from angular separation between signal and masker sources (Turnbull, 1994). Masking noise was presented only for the duration of each experimental trial was to prevent any confounding effects resulting from loudness adaptation (see Southall *et al.*, 2000).

At each frequency a single masking noise level was used, based on subject's minimum audible field hearing threshold measured in the anechoic chamber (Schusterman *et al.*, unpublished data). It was not possible to use the same relative noise levels for every frequency, due to limitations of the equipment and the fact that absolute aerial thresholds often varied greatly between subjects. Masking noise at each frequency and noise bandwidth had an average spectral density level [$\text{dB re: } (20 \mu\text{Pa})^2/\text{Hz}$] approximately 5–20-dB above each subject's hearing threshold. Masking noise was digitally filtered so that received masking noise spectral density levels were relatively flat (± 3 dB) across the entire masker band.

Signal sound-pressure levels ($\text{dB re: } 20 \mu\text{Pa}$) and masking noise spectral density levels [$\text{dB re: } (20 \mu\text{Pa})^2/\text{Hz}$] were calibrated before and after each session. An Etymotic ERC-7 clinical probe microphone with an internal reference calibration, a Tectronix TDS 420A digital oscilloscope, and SPECTRA PLUS software were used to analyze signal and noise characteristics. In addition to calibrating signal and masking noise levels at a central position corresponding to the center of the subject's head during testing, signal and noise fields were mapped at multiple nearby positions (as in Moore and Schusterman, 1987; Southall *et al.*, 2000). Mapping was conducted at 27 positions within a $10 \times 10 \times 10$ -cm region around the chin station by: (1) measuring received signal and masker levels; (2) analyzing the distribution of noise energy within masker bands; and (3) observing how these parameters varied within or between masker intervals. Signal and masking noise band average spectral density levels at each position were maintained within 3-dB of the average levels measured at the central calibration position both within and between multiple masker intervals.

C. Procedure

The psychophysical procedures employed were similar to those used by Kastak and Schusterman (1998) and

Southall *et al.* (2000). The use of experienced test subjects resulted in little additional training for the aerial masking experiments. Once subjects stationed appropriately, masking noise was engaged and a trial light placed near the projecting speaker was illuminated for the 6-s duration of each experimental trial. Masking noise alone was presented on either 25% or 50% of the trials (catch trials). Signals in addition to masking noise were projected on the remaining trials (signal trials). Either a 75:25 or 50:50 signal-to-catch trial ratio was used in to maintain appropriate subject response criteria. The order of signal and catch trials varied between sessions based on computer-generated 60-trial pseudorandom sequences. A go/no-go psychophysical response paradigm was used. Subjects reported detecting a signal by leaving the chin station and pressing the response paddle with their muzzle; they reported not detecting a signal by withholding this response. Fish reinforcement was delivered following correct responses [responding on a signal trial (hit) or not responding on a catch trial (correct rejection)]. Subjects restationed without reinforcement following incorrect responses [not responding on a signal trial (miss) or responding on a catch trial (false alarm)].

Each session consisted of an 8–20-trial warm-up phase in which signals were clearly audible, a 20–40-trial threshold phase, and a terminal 4–6-trial cool-down phase with clearly audible signals. The warm-up and cool-down phases were used to assess subject motivation and to maintain stimulus control over behavioral responses.

Two psychophysical techniques were used in determining masked hearing thresholds. First, three to eight sessions using the staircase method (Cornsweet, 1962) were conducted to obtain an initial estimate of the masked hearing threshold at each frequency. Signal levels were initially attenuated by 4-dB following each hit and were then adjusted in 2-dB steps in the threshold phase (increased following a miss, decreased following a hit), which consisted of nine reversals between sequences of hits and misses. Subsequently, five to seven discrete signal levels separated by 2-dB were selected, based on the staircase data, and randomly presented during three to five method-of-constant-stimuli sessions (Stebbins, 1970). Masked hearing thresholds were determined by pooling results from all method-of-constant-stimuli sessions and calculating the 50%-correct detection point using probit analysis (Finney, 1971). When a threshold's 95%-confidence limits fell within 3-dB of the calculated masked hearing threshold, testing at a particular frequency was ended.

1. Aerial critical ratio procedure (octave-band noise)

Aerial masked hearing thresholds were determined in the presence of octave band noise (OBN) maskers centered at test frequencies of 0.2, 0.5, 0.8, 1.2, 2.5, 4.0, and 8.0 kHz. The sequence of testing was randomized with respect to test frequency, but the same order was used for each test subject.

Critical ratios were calculated as the difference (in dB) between the masked hearing threshold sound-pressure level and the masking noise sound-pressure level at the center frequency of the masking band, corresponding to the measured masker spectral density level [$\text{dB re: } (20 \mu\text{Pa})^2/\text{Hz}$]

TABLE I. Aerial auditory masking data obtained using octave-band noise (70.7% of center frequency) for individual subjects from three pinniped species tested in a hemianechoic chamber. Data were obtained using the psychophysical method of constant stimuli.

Species	Frequency (kHz)	Masker level (dB <i>re</i> : 20 μ Pa ² /Hz)	Masked threshold (dB <i>re</i> : 20 μ Pa) & (std dev)	False-alarm rate (%)	Critical ratio (dB)
N. elephant seal	0.2	45.0	57.1 (1.0)	5.6	12
Harbor seal	0.2	41.0	53.3 (1.1)	12.8	12
California sea lion	0.2
N. elephant seal	0.5	31.0	44.4 (1.2)	5.9	13
Harbor seal	0.5	31.0	49.2 (0.8)	21.0	18
California sea lion	0.5	38.0	58.3 (0.8)	11.9	20
N. elephant seal	0.8	42.7	56.6 (1.3)	15.0	14
Harbor seal	0.8	33.8	49.6 (0.9)	13.3	16
California sea lion	0.8	45.4	62.6 (0.9)	9.8	17
N. elephant seal	1.2	37.5	55.4 (0.9)	18.2	18
Harbor seal	1.2	28.0	49.9 (0.9)	11.8	22
California sea lion	1.2	33.0	52.7 (1.1)	19.2	20
N. elephant seal	2.5	35.0	54.7 (0.9)	19.4	20
Harbor seal	2.5	20.0	40.4 (1.0)	17.6	20
California sea lion	2.5	27.0	45.7 (1.9)	8.3	19
N. elephant seal	4.0	40.0	62.1 (0.8)	18.8	22
Harbor seal	4.0	17.0	38.8 (0.8)	17.8	22
California sea lion	4.0	35.0	60.1 (1.3)	10.5	25
N. elephant seal	8.0	40.0	63.5 (0.8)	12.5	24
Harbor seal	8.0	25.0	46.7 (1.3)	6.3	22
California sea lion	8.0	25.0	51.2 (1.7)	11.5	26

(Fletcher, 1940; Scharf, 1970). The CRs obtained using octave band masking noise were used to indirectly estimate CBWs and additionally served as the initial broadband measurement for direct CBW measurements (described below).

2. Direct aerial critical bandwidth procedure (variable bandwidth noise)

Following the OBN masking experiments, two or three additional method-of-constant-stimuli sessions were conducted for five relatively narrower masker bandwidths. This procedure was conducted at the three highest frequencies (2.5, 4.0, and 8.0 kHz) to minimize the potential for audible interactions between tonal signals and narrow-band noise maskers (Bos and de Boer, 1966). Critical ratios were calculated in the same manner described above for masking noise with bandwidths of 3%, 6%, 12%, 18%, and 24% of each test frequency. All sessions for each masker bandwidth were conducted sequentially, but the testing order for each relative masker bandwidth was varied between frequencies. Critical bandwidths were estimated at each frequency based on CRs for different masker bandwidths. Specifically, CBWs as a percentage of center frequency were estimated as the intersection of the least-squares estimates functions for the fairly constant CRs (within 1-dB of CRs determined using OBN) at wide noise bandwidths and for the relatively lower CRs (more than 1-dB below the OBN value) at narrower masker bandwidths (as in Seaton and Trahiotis, 1975; Au and Moore, 1990; Niemic *et al.*, 1992).

III. RESULTS

A. Aerial critical ratios

For each of the three pinniped species tested, the aerial masked hearing thresholds as well as the CRs obtained using OBN for each test frequency are shown in Table I. Along with these values, the percentage of false alarms pooled for all method-of-constant-stimuli sessions is given for each animal. The aerial CRs for these three pinnipeds are quite similar to those determined by Southall *et al.* (2000) at overlapping frequencies under water (Fig. 1). For each subject, CRs generally increase gradually with frequency.

For the northern elephant seal, aerial CRs range from 12-dB at 0.2 kHz to 24-dB at 8.0 kHz and are not significantly different than underwater CRs at overlapping test frequencies. For the harbor seal, aerial CRs range from 12-dB at 0.2 kHz to 22-dB at 4.0 kHz and are not significantly different than underwater CRs at overlapping test frequencies. For the California sea lion, aerial CRs range from 17-dB at 0.8 kHz to 26-dB at 8.0 kHz and are not significantly different than underwater CRs at overlapping test frequencies.

False-alarm rates reflect subject response bias. High false-alarm rates indicate a relatively liberal response criterion, and low false-alarm rates indicate a conservative response criterion. We adjusted the relative percentage of signal and catch trials as necessary to ensure fairly consistent false alarm rates (between approximately 5%–20%) across test frequencies (Table I). Subjects who adopted response criteria that were either too liberal (>25% false-alarm rates on more than three consecutive sessions) or too conservative (0% false-alarm rates on more than three consecutive sessions) generally responded rapidly and appropriately to re-

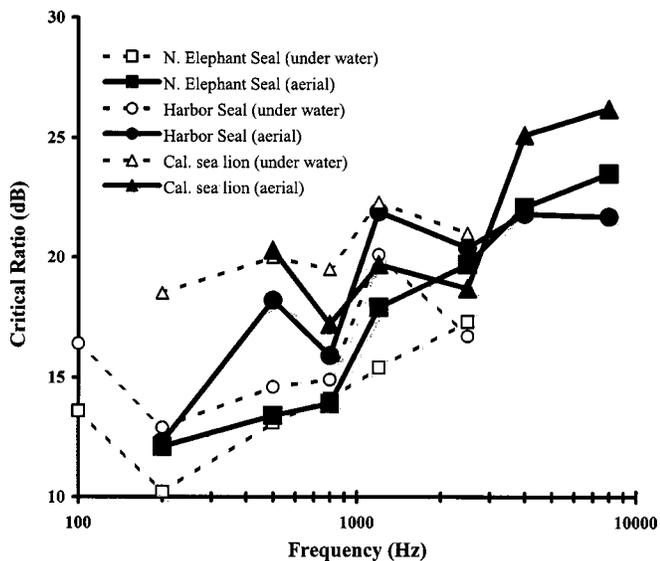


FIG. 1. Critical ratios versus frequency for aerial (this study) and underwater auditory masking (Southall *et al.*, 2000) for a northern elephant seal, a harbor seal, and a California sea lion.

spective decreases or increases in the relative signal-to-catch trial ratio.

B. Direct aerial critical bandwidths

Critical ratios at relatively wide masking noise bandwidths are very similar to those obtained using OBN, while lower CRs occur for relatively narrow masking noise bandwidths. At each test frequency, directly measured aerial CBWs are much wider than indirect estimates based on the aerial CRs obtained with OBN (Fig. 2). However, there are no consistent relationships across the three frequencies tested, between direct and indirect CBWs for any of the test subjects. For the northern elephant seal, direct aerial CBWs are 6.6, 3.9, and 4.6 times wider than the indirect estimates

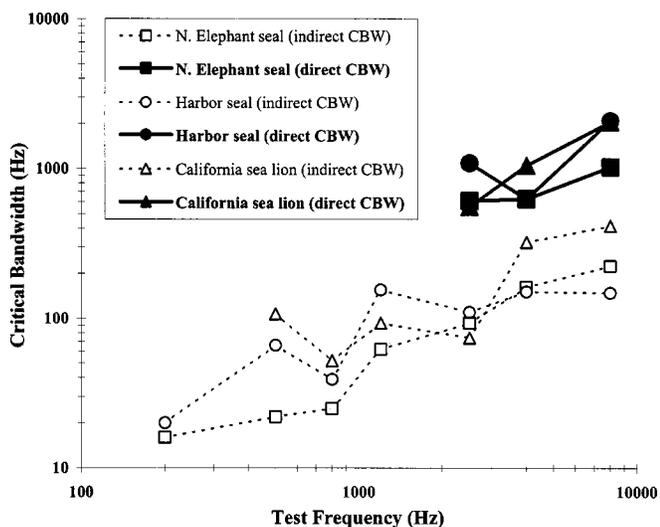


FIG. 2. Critical bandwidths (CBW) vs test frequency obtained in air (this study) and under water (Southall *et al.*, 2000) based on indirect estimates (CR/EqP method) and direct measurements obtained with a band-narrowing technique for a northern elephant seal, a harbor seal, and a California sea lion.

based on aerial CRs at 2.5, 4.0, and 8.0 kHz, respectively. The direct CBWs for this individual are 24.4%, 15.8%, and 12.9% of these test frequencies. For the harbor seal, direct aerial CBWs are 9.9, 4.2, and 14.2 times wider than the indirect estimates and equal 43.6%, 16.0%, and 26.3% of the respective test frequencies. For the California sea lion, direct aerial CBWs are 7.6, 3.2, and 4.9 times wider than the indirect estimates and equal 22.4%, 26.3%, and 25.8% of the respective test frequencies.

As in the CR measurements using OBN, pooled false-alarm rates in the critical bandwidth study were generally between 5%–20% across test frequencies. Interestingly though, for each subject, false alarms occurred in some cases during the first several catch trials using the two narrowest bandwidth maskers. This was generally not observed during the initial presentations of relatively wider masker bands. False alarms on the first few catch trials with the narrow-band maskers probably occurred because narrow-band noise is qualitatively more similar to test stimuli than wide bands of noise. After a few trials this behavior generally ceased, as subjects rapidly learned the distinctions between test signals and narrow-band noise.

IV. DISCUSSION

Aerial CRs obtained in the present study are comparable to underwater values for the same individuals (Southall *et al.*, 2000). This replication of Turnbull and Terhune's (1990) findings provides additional evidence that the masking effects of noise are similar in air and water. Because aerial and underwater CRs are similar for these particular species, which have quite different amphibious hearing characteristics and life histories (see Kastak and Schusterman, 1998), this trend likely applies for most, if not all, other pinniped species. Additionally, these results suggest that pinniped cochlear mechanisms are similar in air and water. This finding suggests that direct comparisons of aerial and underwater masked hearing capabilities between aquatic, amphibious, and terrestrial species may be appropriate (as in Southall *et al.*, 2000). However, comparative aerial and underwater masking data for a greater number of species with variable life history characteristics are needed to more fully address the validity of such comparisons.

While the differences are fairly small, the aerial CRs measured in this study are relatively low in magnitude compared to most terrestrial mammals (see Fay, 1988). This trend is also observed in most other pinnipeds [except the ringed seals tested thus far (Terhune and Ronald, 1975)] and the odontocete cetaceans tested thus far (see Richardson *et al.*, 1995; Southall *et al.*, 2000). It is reasonable to speculate that acoustic signal production and reception in typically noisy marine environments has led to selection for enhanced ability to detect signals in noise (Schusterman *et al.*, 2000). However, additional data are needed, including further research on ringed seals, to comprehensively assess this hypothesis.

Also evident in this study and consistent with previous results is that CRs increase monotonically with frequency. Thus, pinnipeds do not appear to be specialized to detect specific tonal signals, including those predominant in most

pinniped vocalizations. The aerial CRs increase at a similar rate as in most other mammals (see Fay, 1988), supporting the notion that pinnipeds are hearing generalists with respect to frequency processing (Southall *et al.*, 2000).

The presence of critical bands in the pinniped subjects of this study provides further indication that pinniped cochlear processes are similar to those occurring in other generalist mammals. Direct CBWs obtained in this study were much wider than indirect estimates. This finding is similar to data obtained using the band-narrowing technique in humans (e.g., Hamilton, 1957) and a bottlenose dolphin (Au and Moore, 1990), but opposite the relationships determined for chinchillas using the band-narrowing method (Niemic *et al.*, 1992) and a harbor seal using tonal maskers (Turnbull and Terhune, 1990). As observed in other marine mammals for which direct CBWs have been determined (Au and Moore, 1990; Turnbull and Terhune, 1990), there were not consistent quantitative relationships across test frequencies between direct and indirect CBWs for the pinniped subjects in this study. However, direct CBWs did not become relatively narrower with increasing frequency. The direct CBWs were roughly similar (~13%–44% of test frequencies) to those determined for humans (~15%–22%) using band narrowing (Hamilton, 1957; Greenwood, 1961; van den Brink, 1964), corresponding to approximately 1/3-octave bands. However, the indirect aerial CBW estimates were generally much narrower for these pinnipeds (~3%–9% of test frequencies), because of the relatively low CRs from which they are calculated, corresponding to approximately 1/12-octave bands.

There are several methodological limitations in utilizing the band-narrowing technique for direct CBW measurements. Since masking noise is concentrated in a relatively narrow bandwidth, subjects may detect unintended harmonics of tonal signals occurring outside the noise band, called off-frequency listening. Also, when the masking band becomes particularly narrow, where the most important measurements are made, there can be perceptible interactions between signal and masker as a result of audible amplitude fluctuations occurring in narrow-band noise (Bos and de Boer, 1966). Additionally, CBWs determined using the band-narrowing method depend on the slope of the least-squares estimate through the variable CRs obtained in relatively narrow-band noise, which may be determined by as few as two data points. Despite these limitations, however, Scharf (1970) and Seaton and Trahiotis (1975) asserted that the band-narrowing method provides fairly accurate CBWs for humans, noting the similarity of CBWs determined using band narrowing (Hamilton, 1957; Greenwood, 1961; van den Brink, 1964) with the generally accepted results that Zwicker *et al.* (1957) obtained using the loudness summation technique. Additional methods of directly measuring CBWs (e.g., notched and/or rippled noise maskers) should be used in future studies of pinniped masking in order to more fully understand auditory filter bandwidths and shapes (as in Halpern and Dallos, 1986; Niemic *et al.*, 1992).

The combined aerial and underwater masking data provide much needed information on the simultaneous effects of noise on hearing for pinnipeds at frequencies contained in

many acoustic communicative signals. The masking data will be useful to researchers, regulatory or military agencies, and environmental groups interested in generating quantitative estimates of communication ranges in natural or anthropogenic noise conditions. Further, filter bandwidth measurements, as well as the comparative aerial and underwater CRs, clarify cochlear processes in these amphibious mammals. Finally, the estimated CBWs may be used to define biologically significant filter bandwidths for analyzing communicative signals as well as the effects of natural or anthropogenic noise (Southall *et al.*, in press).

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- Andrew, R. K., Howe, B. M., Mercer, J. A., and Dzieciuch, M. A. (2002). "Ocean ambient sound: Comparing the 1960s with the 1990s for a receiver off the California coast," *ARLO* **3**, 65–70.
- Au, W. W. L., and Moore, P. W. B. (1990). "Critical ratio and critical bandwidth for the Atlantic bottlenose dolphin," *J. Acoust. Soc. Am.* **88**, 1635–1638.
- Bos, C. E., and de Boer, E. (1966). "Masking and discrimination," *J. Acoust. Soc. Am.* **39**, 708–715.
- Clack, T. D. (1966). "Effect of signal duration on the auditory sensitivity of humans and monkeys (*Macaca mulatta*)," *J. Acoust. Soc. Am.* **40**, 1140–1146.
- Cornsweet, T. N. (1962). "The staircase method in psychophysics," *Am. J. Psychol.* **75**, 485–491.
- Echteler, S. M., Fay, R. R., and Popper, A. N. (1994). "Structure of the mammalian cochlea," in *Comparative Hearing: Mammals*, edited by R. R. Fay and A. N. Popper (Springer, New York), pp. 134–171.
- Egan, J. P., and Hake, W. (1950). "On the masking pattern of a simple auditory stimulus," *J. Acoust. Soc. Am.* **22**, 622–630.
- Ehret, G. (1976). "Critical bands and filter characteristics in the ear of the housemouse (*Mus musculus*)," *Biol. Cybern.* **24**, 35–42.
- Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook* (Hill-Fay, Winnetka, IL).
- Finneran, J. J., Schlundt, C. E., Dear, R., Carder, D. A., and Ridgway, S. H. (2002). "Temporary shift in masked hearing thresholds in odontocetes after exposure to single underwater impulses from a seismic watergun," *J. Acoust. Soc. Am.* **111**, 2929–2940.
- Finney, D. J. (1971). *Probit Analysis*, 3rd ed. (Cambridge University Press, Cambridge).
- Fletcher, H. (1940). "Auditory patterns," *Rev. Mod. Phys.* **12**, 47–65.
- Gourevitch, G. G. (1965). "Auditory masking in the rat," *J. Acoust. Soc. Am.* **37**, 439–443.
- Greenwood, D. D. (1961). "Auditory masking and the critical band," *J. Acoust. Soc. Am.* **33**, 484–502.
- Halpern, D. L., and Dallos, P. (1986). "Auditory filter shapes in the chinchilla," *J. Acoust. Soc. Am.* **80**, 765–775.
- Hamilton, P. M. (1957). "Noise masked thresholds as a function of tonal duration and masking noise bandwidth," *J. Acoust. Soc. Am.* **29**, 506–511.
- Hawkins, Jr., J. E., and Stevens, S. S. (1950). "The masking of pure tones and of speech by white noise," *J. Acoust. Soc. Am.* **22**, 6–13.

- Johnson, C. S. (1968). "Masked tonal thresholds in the bottlenosed porpoise," *J. Acoust. Soc. Am.* **44**, 965–967.
- Kastak, D., Schusterman, R. J., Southall, B. L., and Reichmuth, C. J. (1999). "Underwater temporary threshold shift in three species of pinniped," *J. Acoust. Soc. Am.* **106**, 1142–1148.
- 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.
- Ketten, D., and Wartzok, D. (1999). "Marine mammal sensory systems," *The Biology of Marine Mammals*, edited by J. E. Reynolds III and S. A. Rommel (Smithsonian Institution Press, Washington), pp. 117–175.
- Moore, P., and Schusterman, R. J. (1987). "Audiometric assessment of northern fur seals (*Callorhinus ursinus*)," *Marine Mammal Sci.* **3**, 31–53.
- National Research Council. (2000). *Marine Mammals and Low-Frequency Sound: Progress since 1994* (National Academy Press, Washington D.C.).
- Niemiec, A. J., Yost, W. A., and Shofner, W. P. (1992). "Behavioral measures of frequency selectivity in the chinchilla," *J. Acoust. Soc. Am.* **92**, 2636–2649.
- Patterson, R. D. (1976). "Auditory filter shapes derived with noise stimuli," *J. Acoust. Soc. Am.* **59**, 640–654.
- Renouf, D. (1980). "Masked hearing thresholds of harbour seals (*Phoca vitulina*) in air," *J. Aud Res.* **20**, 263–269.
- Richardson, J. W., Greene, C. R., Malme, C. I., and Thomson, D. H. (1995). *Marine Mammals and Noise* (Academic, New York).
- Schafer, T. H., Gales, R. S., Shewmaker, C. A., and Thompson, P. O. (1950). "The frequency selectivity of the ear as determined by masking experiments," *J. Acoust. Soc. Am.* **22**, 490–496.
- Scharf, B. (1970). "Critical bands," in *Foundations of Modern Auditory Theory*, edited by J. V. Tobias (Academic, New York), Vol. 1, pp. 159–202.
- Schlundt, C. E., Finneran, J. J., Carder, D. A., and Ridgway, S. H. (2000). "Temporary shift in masked hearing thresholds (MTS) of bottlenose dolphins, *Tursiops truncatus*, and white whales, *Delphinapterus leucas*, after exposure to intense tones," *J. Acoust. Soc. Am.* **107**, 3496–3508.
- Schusterman, R. J. (1978). "Vocal communication in pinnipeds," in *Behavior of Captive Wild Animals*, edited by H. Markowitz and V. J. Stevens (Nelson-Hall, Chicago), pp. 247–308.
- Schusterman, R. J. (unpublished data).
- 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.
- Seaton, W. H., and Trahiotis, C. (1975). "Comparison of critical ratios and critical bands in the monaural chinchilla," *J. Acoust. Soc. Am.* **57**, 193–199.
- Southall, B. L., Schusterman, R. J., and Kastak, D. **in press**. "Acoustic communication ranges in northern elephant seals," *Aquat. Mamm.*
- 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.
- Stebbins, W. C. (1970). "Principles of animal psychophysics," in *Animal Psychophysics: The Design and Conduct of Sensory Experiments*, edited by W. C. Stebbins (Appleton-Century-Crofts, New York), pp. 1–19.
- Terhune, J. M. (1991). "Masked and unmasked pure tone thresholds of a harbor seal listening in air," *Can. J. Zool.* **69**, 2059–2066.
- Terhune, J., and Ronald, K. (1971). "The harp seal, *Pagophilus groenlandicus* (Erxleben 1777). The air audiogram," *Can. J. Zool.* **49**, 385–390.
- Terhune, J. M., and Ronald, K. (1975). "Masked hearing thresholds of ringed seals," *J. Acoust. Soc. Am.* **58**, 515–516.
- Turnbull, S. D. (1994). "Changes in masked thresholds of a harbor seal (*Phoca vitulina*) associated with angular separation of signal and noise sources," *Can. J. Zool.* **72**, 1863–1866.
- Turnbull, S. D., and Terhune, J. (1990). "White noise and pure tone masking of pure tone thresholds of a harbor seal listening in air and under water," *Can. J. Zool.* **68**, 2090–2097.
- Tyack, P. L. (1998). "Acoustic communication under the sea," in *Animal Acoustic Communication*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer, Berlin), pp. 163–220.
- van den Brink, G. (1964). "Detection of tone pulses of various durations in noise of various bandwidth," *J. Acoust. Soc. Am.* **36**, 1206–1211.
- Watson, C. S. (1963). "Masking of tones by noise for the cat," *J. Acoust. Soc. Am.* **35**, 167–172.
- Wegel, R. L., and Lane, C. E. (1924). "The auditory masking of one pure tone by another and its probable relation to the dynamics of the inner ear," *Phys. Rev.* **2**, 266–285.
- Zwicker, E., Flottorp, G., and Stevens, S. S. (1957). "Critical bandwidth in loudness summation," *J. Acoust. Soc. Am.* **29**, 548–557.