Masking in three pinnipeds: Underwater, low-frequency critical ratios

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

Behavioral techniques were used to determine underwater masked hearing thresholds for a northern elephant seal (*Mirounga angustirostris*), a harbor seal (*Phoca vitulina*), and a California sea lion (*Zalophus californianus*). Octave-band white noise maskers were centered at five test frequencies ranging from 200 to 2500 Hz; a slightly wider noise band was used for testing at 100 Hz. Critical ratios were calculated at one masking noise level for each test frequency. Above 200 Hz, critical ratios increased with frequency. This pattern is similar to that observed in most animals tested, and indicates that these pinnipeds lack specializations for detecting low-frequency tonal sounds in noise. However, the individual pinnipeds in this study, particularly the northern elephant seal, detected signals at relatively low signal-to-noise ratios. These results provide a means of estimating zones of auditory masking for pinnipeds exposed to anthropogenic noise sources. © *2000 Acoustical Society of America.* [S0001-4966(00)02509-1]

I. INTRODUCTION

Many pinnipeds (seals, sea lions, and walruses) use low-frequency, broadband acoustic signals under water for intraspecific communication (Schusterman, 1978; Watkins and Wartzok, 1985). In addition to detection of conspecific signals, passive listening to other natural sounds may also be biologically significant for pinnipeds in localization of predators or prey, or in spatial orientation and navigation (see Schusterman *et al.*, 2000). Since they spend considerable time in coastal environments where noise levels from natural sources such as wind, waves, and biologics are frequently high (Urick, 1983), hearing in the presence of interfering noise is very important for pinnipeds. Additional sources of noise, however, have resulted from the industrialization of marine environments, greatly increasing overall noise levels, particularly at low frequencies, in many areas (see Ross, 1976). The inundation of new noise sources, such as large vessels, petroleum exploration and recovery efforts, and low-frequency military sonar systems, is likely to adversely impact some pinniped species either by displacing individuals from important foraging or reproductive areas or by interfering with hearing (Richardson *et al.*, 1995; Kastak and Schusterman, 1998; Kastak *et al.*, 1999).

One way noise can compromise hearing is by masking a signal. The magnitude of interference depends upon signal and noise frequency and is greatest when they are similar. The lowest signal-to-noise ratio at which a subject can detect a tonal signal over broadband masking noise is called the critical ratio (Fletcher, 1940). Critical ratios (CRs) are calculated as the ratio of the sound pressure level of a just-audible tonal signal (dB *re*: 1μPa) to that of the masking noise sound pressure level at the center frequency of the masking band, calculated from the measured masker spectral density level (dB *re*: 1 μPa^2/Hz). While the CR method of investigating auditory masking appears to be of little use in predicting critical bandwidth and auditory filter shape, it does provide simple measures of signal-to-noise ratios required for detection (Scharf, 1970). In nearly all mammals, CRs increase gradually with frequency, except at very low frequencies (see Fay, 1988). In contrast, some mammals have markedly lower CRs at specific frequencies. For instance, the horseshoe bat (*Rhinolophus ferrumequinum*) has dramatically lower CRs near 83 kHz, the constant frequency component of its echolocation signal (Long, 1977). Obtaining CRs within a range of frequencies prevalent in species-typical vocalizations is one of several methods used to determine if specific frequencies are processed particularly efficiently. Anatomical analyses of some mammals with such processing specializations have revealed relatively shallow stiffness gradients in certain regions of the basilar membrane (see Echteler *et al.*, 1994).

Despite the fact that the majority of pinniped vocalizations, as well as the natural background noise over which they must be detected, contain considerable energy at low frequencies, most studies of pinniped masked hearing have been conducted at or above 2000 Hz. Individuals of four species have been tested: the harp seal, *Phoca groenlandica* [Terhune and Ronald, 1971 ($n=1$)], ringed seal, *Phoca hispida* [Terhune and Ronald, 1975 ($n=2$)], harbor seal, *Phoca vitulina* [Renouf, 1980 ($n=2$); Turnbull and Terhune, 1990 ($n=1$); Terhune, 1991 ($n=1$)], and northern fur seal, *Callorhinus ursinus* [Moore and Schusterman, 1987 ($n=2$)]. Of these, only Terhune (1991) investigated masking below 2000 Hz. In general, pinniped CRs appear similar in form across frequencies to those of unspecialized mammals in that they increase gradually with frequency. Northern fur seal, harbor seal, and harp seal CRs are similar in magnitude to those of humans and some odontocete cetaceans, but are somewhat lower than those of the ringed seal (Terhune and Ronald, 1975) and some terrestrial mammals (see Fay, 1988).

The general lack of knowledge about low-frequency pinniped hearing and the effects of noise has prompted research

in response to concerns regarding anthropogenic noise pollution in marine environments. There has been recent emphasis on obtaining low-frequency absolute hearing thresholds (e.g., Kastak and Schusterman, 1998). However, the relevance of unmasked thresholds to problems involving animals in environments dominated by low-frequency noise is questionable. In such contexts, knowledge of masked hearing capabilities is needed to understand noise impacts. While absolute hearing thresholds are basic in predicting when masking will occur, masked hearing thresholds are necessary for determining the degree of masking. Thus both measures are required to adequately assess signal detection in noise.

This study investigated auditory masking at six frequencies between 100 and 2500 Hz in a northern elephant seal (*Mirounga angustirostris*), a California sea lion (*Zalophus californianus*), and a harbor seal (*Phoca vitulina*). Combined with the absolute thresholds measured using similar techniques for the same individuals by Kastak and Schusterman (1998), the masking data of this study will provide some basis for evaluating low-frequency anthropogenic noise impacts on free-ranging pinnipeds.

II. METHODS

Subjects

The subjects were a 4-year-old female northern elephant seal (Burnyce), a 9-year-old male harbor seal (Sprouts), and a 12-year-old female California sea lion (Rio). They were housed at Long Marine Laboratory in Santa Cruz, California in free-flow saltwater pools and adjacent haul-out space. Subjects received 20%–50% of their daily allotment of fish during experimental sessions.

Each of the subjects had extensive experience performing behavioral audiometric tasks; no deficits or abnormalities were apparent in their absolute, low-frequency audiograms (see Kastak and Schusterman, 1998).

Apparatus

The testing enclosure was a circular 7.5-m diameter, 2.5-m deep, concrete pool. A testing apparatus was placed in a fixed position on the pool edge for each experimental session. The apparatus comprised a 1-in PVC frame on which a chin station, a movable opaque door, and a square, plastic response paddle were mounted. The chin station was located 1.4 m from the surface of the water, 1.2 m from the side of the pool, and 0.4 m from the response paddle.

Test stimuli and masking noise

Test stimuli were 500-ms pure tones (40-ms rise/fall time) generated with Stanford Research Systems (SRS) Arbitrary Waveform Composer software and triggered from a SRS DS345 function generator. Signals were fed to a Hewlett-Packard 350C stepwise attenuator and then to a Realistic MPA-20 power amplifier. The output of this amplifier was connected to either a J-9 or a J-11 Naval Undersea Warfare Center (NUWC) underwater transducer. The transducer was suspended into the test pool by a PVC harness and could be moved along a steel support. It was placed in the same position, approximately 5 m from the testing apparatus, for all sessions at each test frequency.

The masking stimuli consisted of octave-band white noise centered at each test frequency, although a slightly wider band was used at 100 Hz. Noise pressure spectral density levels (dB *re*: 1 μPa^2/Hz) were 20 dB above directly measured or interpolated absolute hearing thresholds (i.e., 20 dB sensation level) determined by Kastak and Schusterman (1998). Since CRs obtained using bands of noise have been shown to be independent of masker level for most of the dynamic range in other mammals (see Fay, 1988), masked thresholds were obtained at a single masker level.

Gaussian white noise was generated with CoolEdit® software (Syntrillium) and identical 6-s intervals were recorded onto audio tapes. For each trial, one interval of masking noise was played back on a Technics RS-686 tape recorder and filtered with a Krohn-Hite 3550 bandpass filter. The output of this filter was connected to the input of the amplifier that drove the transducer. Thus signals and masking noise were mixed before being amplified and projected from the same source.

Signal and masking noise levels were calibrated at the chin station of the test apparatus before and after each experimental session. A NUWC H-56 hydrophone was mounted on the test apparatus so that its acoustic center was in approximately the same position as the center of the animal's head during testing. The hydrophone output was monitored on either a Hitachi V202 or a Kikusui cos 5041 oscilloscope, as well as on a real-time PC-based spectrum analyzer (SpectraPlus®, Pioneer Hill). Using the spectrum analyzer, narrow-band analysis (2.7-Hz analysis bandwidth) was performed and the noise pressure spectral density level was measured at the masking noise band center frequency. However, in order to more accurately represent the average noise levels in a slightly wider band surrounding each test frequency, masking noise spectral density levels were calculated from measured 1/3-octave levels. Calculated levels from the 1/3-octave measurement were generally within 1 dB of directly measured values at the center frequency of the noise band.

Careful calibration procedures and strict criteria on variability in signal and noise fields were employed in this study (see Moore and Schusterman, 1987). The acoustic response of the testing enclosure to low-frequency pure tones had previously been mapped (Kastak and Schusterman, 1998). Additional mapping was conducted to measure: (1) the distribution of noise energy within masker bands, (2) variation in received signal and noise levels at the chin station and many other positions around it, and (3) how these levels fluctuated over time. Large variations in received masker levels within noise bands (up to ±20 dB) were obtained when white noise was projected. To compensate for this, masking noise was digitally filtered prior to recording intervals onto analog tape. This adjustment resulted in received noise levels that were relatively flat (within ±3 dB) across the entire band. Masking noise was calibrated before and after each experimental session to ensure that this criterion was achieved when noise was projected into the testing enclosure. Large fluctuations in

received signal and noise levels (up to ±10 dB) were also initially measured within a few cm from the chin station. Transducer positions were selected for each test frequency that minimized signal and noise variability at and around the chin station. To ensure maximum uniformity in signal and noise fields, signal and noise levels were calibrated at 26 positions within a $20 \times 20 \times 20$ cm region centered at the chin station and encompassing all reasonable positions of the subject's head during testing. Values at each position were maintained within ±3 dB of central calibration position measurements. Additionally, temporal variation in received levels was measured; transducer positions were selected so that these fluctuations were within ±3 dB at all calibration positions.

Procedure

Before each trial, a trainer signaled the subject to swim to the test apparatus and place its muzzle in the chin station. A trial began when the apparatus door was raised. Noise was presented for the duration of each 6-s trial and was terminated with the closing of the apparatus door; no noise was presented during inter-trial intervals. Noise alone was presented on 50% of trials while a signal and noise were presented on the remaining trials. A go/no-go procedure was used in which the sequence of noise and signal plus noise trials was pseudorandom (Moore and Schusterman, 1987). A subject indicated that it detected a signal by pressing the response paddle with its nose (go response) and indicated that it did not detect a signal by remaining stationed (no-go response). Correct responses were rewarded with fish; incorrect responses were not reinforced.

Each experimental session consisted of an 8–10 trial warm-up phase in which signal levels were constant and clearly audible over masking noise. This was followed by a threshold phase of 40–60 trials in which signal levels varied. Finally, a cool-down phase of six to eight trials was run in which signal levels were again constant and clearly audible. Warm-up and cool-down phases were used to evaluate subject motivation and stimulus control over responding.

Two different psychophysical procedures were used in the threshold phase. Initially a staircase method (Cornsweet, 1962) was used in which signal levels were attenuated 4 dB following each signal detection until the subject failed to detect a signal (miss). Adjustments were then made in 2-dB steps (increased following a miss, decreased following signal detection). Between 2 and 10 staircase sessions were conducted at each test frequency to provide a preliminary estimate of masked hearing thresholds. Subsequently, a method of constant stimuli procedure (Stebbins, 1970) was used in which five to seven discrete signal levels, separated by 4 dB and bracketing the estimated masked hearing threshold, were randomly presented. Masked hearing thresholds were determined to be the signal level corresponding to 50% correct detection using probit analysis (Finney, 1971). Between three and six method of constant stimuli sessions were conducted until 95% confidence limits of calculated thresholds fell within ±3 dB. False alarm rates, defined as the percentage of noise trials on which go responses occurred, were

TABLE I. Underwater masked hearing thresholds and critical ratios obtained from test sessions using the psychophysical method of constant stimuli. For each pinniped species listed, a single individual was tested.

Species	Frequency (Hz)	Masker Level (dB re: 1 μPa^2/Hz)	Masked threshold (dB re: 1 μPa)	Critical ratio (dB)
N. elephant seal	100	110	124	14
Harbor seal	100	115	131	16
N. elephant seal	200	93	103	10
Harbor seal	200	104	117	13
Calif. sea lion	200	112	130	18
N. elephant seal	500	98	111	13
Harbor seal	500	98	113	15
Calif. sea lion	500	107	127	20
N. elephant seal	800	95	109	14
Harbor seal	800	100	115	15
Calif. sea lion	800	94	122	18
N. elephant seal	1200	96	111	15
Harbor seal	1200	94	114	20
Calif. sea lion	1200	97	119	22
N. elephant seal	2500	95	112	17
Harbor seal	2500	97	114	17
Calif. sea lion	2500	86	108	22

measured in method of constant stimuli sessions to obtain estimates of response bias.

Test frequencies were selected based on the ability to generate adequate test signals and masking noise that did not exceed our *a priori* maximum allowable variance in the area surrounding the chin station. Underwater masked hearing thresholds were obtained for all subjects at 200, 500, 800, 1200, and 2500 Hz. The elephant seal and harbor seal were also tested at 100 Hz where a relatively wider band of noise (50–200 Hz) was used to ensure coverage of the entire critical bandwidth. It was not possible to test the sea lion at 100 Hz because of this subject's higher absolute threshold at this frequency and limitations of the equipment. Critical ratios were calculated as the ratio (in dB) between the masked hearing threshold and the masking noise sound-pressure level at the center frequency of the masking band, calculated from the measured masker spectral density level.

III. RESULTS

Standard deviations for masked hearing thresholds were <1 dB and false alarm rates were <20% for all subjects at all frequencies. Table I shows the principal results of our study which include masked hearing thresholds and CRs for each subject representing three species of pinniped. The CRs of the pinnipeds in this study are graphically depicted in Fig. 1 so they may be compared with those of selected marine and terrestrial mammals. As Table I and Fig. 1 show, all subjects of this study displayed the general mammalian trend of increasing CRs with frequency, except at very low frequencies. Calculated CRs were slightly lower for the harbor seal than the California sea lion and were lower still in the elephant seal, whose values are similar to the lowest reported mammalian values (see Fay, 1988). These inter-individual differences were small, but consistent at all test frequencies.
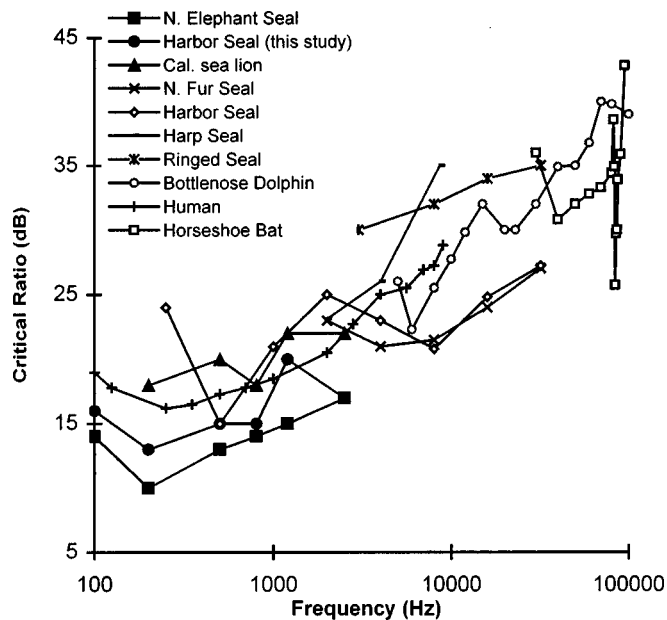
FIG. 1. Critical ratios for a northern elephant seal, a harbor seal, and a California sea lion shown with data from: northern fur seal (Moore and Schusterman, 1987), harbor seal (combined data from Turnbull and Terhune, 1990; Terhune, 1991), harp seal (Terhune and Ronald, 1971), ringed seal (Terhune and Ronald, 1975) bottlenose dolphin (Johnson, 1968), human (Hawkins and Stevens, 1950), and horseshoe bat (Long, 1977).

IV. DISCUSSION

Across a range of low frequencies, the CRs of the pinnipeds in this study are similar in form to those of most mammals tested. The apparent lack of specialization for enhanced detection of specific tonal signals is consistent with the fact that most pinniped vocalizations and other biologically significant sounds, such as incidental noise associated with schooling prey, are broadband and/or frequency modulated. This has probably limited the selective advantage of specialization for enhanced detection of specific frequency sounds and favored similar detection efficiency across frequencies.

The pinniped CRs in this study are somewhat lower in average magnitude than most other animals tested at similar frequencies (see Fay, 1988). Generally similar results have been obtained in other marine mammals with the exception of the ringed seal (see Richardson *et al.*, 1995). Low CRs in marine mammals might be a signal processing adaptation, facilitating detection in naturally noisy marine environments. Signal production strategies also thought to serve this purpose, such as signal redundancy, have been noted in pinnipeds (see Schusterman, 1978). With the caveat that auditory masking studies have been conducted with very few species and individuals, most of the available data indicate pinnipeds hear signals relatively well in noise. However, more masking studies, as well as additional research on pinniped cochlear mechanics and auditory neurophysiology with respect to frequency resolution, are needed to determine if this is in fact characteristic of pinnipeds. Additionally, more research on masking for individuals both in air and under water is needed to corroborate Turnbull and Terhune's (1990) conclusion that CRs should not differ between the two media. Future studies should contain adequate controls of spatiotemporal variability in signal and noise fields.

Unfortunately, the numerous methodological differences among studies of auditory masking in pinnipeds and other mammals and the generally small sample sizes limit comparisons between species. One potentially important variable in CR measurements that has received little attention is the duty cycle of masking noise presentation. In some mammalian masking studies, including ours, noise exposure was limited to the duration of each trial. However, in other studies noise was presented continuously during the entire experimental session, while still others fail to specify if masking noise was gated or continuous. In human subjects, continuous monaural exposure to moderate level (40–70 dB SPL) bands of noise changed a subject's perceived loudness of dichotically presented tonal signals in the same ear relative to a comparison signal in the "rested" ear by 2.3 to 9.9 dB in approximately 1 min. (Carterette, 1956). This effect is known as loudness adaptation and the change in perceived loudness of a signal following noise exposure is likely related to central neural processes (Gelfand, 1981). We are unaware of research on the potential effects of loudness adaptation on CR measurements obtained when masking noise was presented continuously and binaurally in humans or other animals. If adaptation occurs but affects both the masker and signal similarly, there should be no difference in the CRs obtained. However, since this is unknown, it is possible that loudness adaptation has some confounding effect on CR measures when masking noise is not gated for each trial. In order to avoid this possibility, intermittent masker presentation was used in this study.

Recent data on low-frequency absolute hearing (Kastak and Schusterman, 1998), temporary threshold shift (Kastak *et al.*, 1999), and auditory masking (this study) in pinnipeds are particularly relevant in considering noise impacts on free-ranging pinnipeds. This is because these studies involve frequencies produced by most anthropogenic noise sources and contained in most biologically significant signals, particularly conspecific vocalizations. The results of this study provide measures for estimating zones of auditory masking caused by specific anthropogenic noise sources such as large ships, as in the following, very simplified example. The 200-Hz component of a male harbor seal underwater call should be detectable by another harbor seal at a distance of approximately 160 m based on the calculated CR of 12.9 dB and assuming the following: the 200-Hz component of the call has a spectrum level of 105 dB (re: 1 μPa @ 1 m), $10 \log R$ spreading occurs because both animals are assumed to be in shallow water, and sea state four conditions [the 200-Hz spectrum level of resulting ambient noise would be approximately 70 dB (re: 1 μPa)]. If a supertanker 10 km away and in much deeper water were generating noise in which the 200-Hz spectrum level was 160 dB (re: 1 μPa @ 1 m), the audible distance between the two seals would be reduced to approximately 8.1 m, assuming ship noise propagation loss based on $20 \log R$ spreading for the first 5 km and $10 \log R$ for the final 5 km. An assumption made in this example is that CRs at a particular frequency do not differ for different masker levels. In other masking studies using

wideband noise, measured masking effects generally increased directly with increasing effective masker level across most of the dynamic range (see Fay, 1988). However, studies using tonal maskers have shown that more remote masking occurs with higher masker levels, particularly at frequencies above the masker, in both human (Ehmer, 1959) and bottlenose dolphin subjects (Johnson, 1971). If this is true for pinnipeds as well, the above example must be further qualified. While the CR at a particular frequency will likely remain the same in different noise levels, the degree of remote masking may differ, changing the perception of other frequency components of the salient signal.

While the majority of available data on masking indicate low CRs in pinnipeds and other marine mammals, this trend is contradicted by results obtained in a single study with one ringed seal (Terhune and Ronald, 1975). However, the finding that some pinnipeds hear signals well in noise should not be construed as an indication that anthropogenic noise is in some way innocuous to pinnipeds. Indeed, such sensory processing capabilities would in fact underscore the importance of effective hearing in pinnipeds and reiterate concerns regarding anthropogenic noise. Further, the masking effects of loud noise sources may still be very great even if individuals of a species are assumed to have low CR values. Regulatory agencies estimating zones of auditory masking for wild pinnipeds should opt for conservative estimates based on the upper limits of the range of CR values until additional data are available.

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