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Acoustic communication ranges for northern elephant seals (*Mirounga angustirostris*)

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Abstract

Acoustic communication range estimates for four northern elephant seal (*Mirounga angustirostris*) vocalization types are presented for this species. Maximum signal detection ranges are determined using an integrated approach involving: field measurements of vocalization source levels and spectral characteristics, signal directivity patterns, natural ambient noise measurements, and previously collected laboratory audiometric data. Signals and masking noise were analyzed using two filter bandwidths believed to approximate the upper and lower limit of auditory filter widths for the northern elephant seal auditory system. Signal detection ranges are estimated for representative pup 'female attraction calls' (FAC), adult female 'pup attraction calls' (PAC), adult female 'threat calls' (AFT), and adult male 'clap threat calls' (AMCT) in each of three intensity categories for biotic noise, wave noise, and wind noise. Signal detection ranges in these nine natural masking noise conditions vary from 5–70 m for FAC, 10–105 m for PAC, 41–479 m for AFT, and 59–507 m for AMCT. The results demonstrate the extent to which communication ranges in the field can vary depending on call type, signal directivity, ambient noise conditions, and receiver capabilities. These data are also useful in considering natural constraints on acoustic communication in northern elephant seals, selective pressures on signal production and reception systems, and potential negative effects of anthropogenic noise.

Key words: pinnipeds, elephant seals, acoustics, communication, active space, signal detection, ambient noise, masking.

Introduction

Vocal communication plays a central role in the social and reproductive biology of northern elephant seals (*Mirounga angustirostris*). Animals of all sex and age classes produce aerial vocalizations under several different conditions that serve to attract or repel other individuals. Females and pups produce 'attraction' vocalizations during the 24–29 d lactation period to gain each other's attention and maintain mother-pup contact (Bartholomew & Colias, 1962; Le Boeuf *et al.*, 1972). The detection of these acoustic signals is believed to be critical to the pup's survival (Reiter *et al.*, 1981). Females also emit vocalizations during agonistic encounters, attempting to repel individuals who have entered the signaller's space and/or threaten their pup. Male northern elephant seals emit pulsed, low frequency vocalizations called 'clap threats' which function primarily to substantiate the outcomes of prior male-male agonistic encounters and repel subdominant males (Bartholomew & Colias, 1962; Le Boeuf, 1972; 1974). These processes are likely possible because the calls contain idiosyncratic and age-class-specific signal characteristics (Shipley *et al.*, 1981). In addition, males probably associate acoustic signals, as well as other sensory cues, with previous interactions to learn individual identities and dominance relationships (Schusterman *et al.*, 2001).

While types and functions of northern elephant seal vocalizations have been described, as well as structural aspects of the signals that likely affect discriminability (Insley, 1992), the maximum distance over which two seals can communicate vocally and how this distance might change for different call types and ambient noise conditions is unknown. The present study attempts to estimate northern elephant seal acoustic communication ranges by integrating field measurements of signals and natural noise with laboratory measurements of elephant seal hearing capabilities. These estimates will provide insight into how natural masking noise may constrain vocal communication for this species. Such constraints act as selective pressures on both signal production and reception systems (Schusterman *et al.*, 2000). Furthermore, understanding the effects of naturally occurring noise on

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elephant seal acoustic communication is useful in assessing the potential harmful effects of aerial anthropogenic noise (Richardson *et al.*, 1995; National Research Council, 2000).

A number of studies estimated the distances over which animal vocalizations are presumably detectable to conspecifics (e.g., Payne & Webb, 1971; Marten & Marler, 1977; Garstang *et al.*, 1995). However, only three studies quantify communicative ranges or 'active space' using empirical measurements of signal and noise parameters in conjunction with receiver processing characteristics. Brenowitz (1982) estimated the active space radius for one component of redwing blackbird (*Agelaius phoeniceus*) song to be 189 m, depending on ambient noise levels and relative wind condition. Brown (1989) indicated that the effective communicative ranges of blue monkey (*Cercopithecus mitis*) and grey-cheeked mangabey (*Cercocubus albigena*) vocalizations average about 870 m and 1800 m respectively, depending on call type. Janik (2000) demonstrated that the maximum underwater active space radius for unmodulated bottlenose dolphin (*Tursiops truncatus*) whistles ranges from 1.5–25.0 km, depending on sea state and the frequency band considered. Active space has not been documented for other marine mammals in which conspecific vocal signals are critical in reproductive interactions.

Two recent studies used hearing data on auditory filter characteristics to determine the appropriate analysis bandwidths in estimating detection ranges for inter-specific acoustic stimuli. Finneran *et al.*, (2000) estimated yellowfin tuna (*Thunnus albacares*) detection ranges for various sounds produced by dolphins, incorporating data on auditory filter bandwidths for other fish species. Similarly, Erbe & Farmer (2000) calculated zones around anthropogenic noise sources in which various auditory effects likely occur for beluga whales (*Delphinapterus leucas*), based on empirical measurements of beluga hearing capabilities.

Active space estimates require considerable field data on vocalization and masking noise parameters, as well as laboratory data on receiver auditory capabilities. Specifically needed are: vocalization source level and spectral characteristics, signal directivity patterns, signal transmission properties, ambient noise level and spectral characteristics, and absolute and masked hearing data. Averaged signal and noise parameters are typically compared in estimating average spatial ranges of signal detectability in variable masking conditions (e.g., Janik, 2000). Active space estimates require simplifying assumptions because of limited data on variables affecting signal detection as well as the infinite possible combinations of signal, noise, and receiver conditions experienced in the field.

Comprehensive, species-specific field and laboratory bio-acoustic data are rarely available. This is due to the difficulties of acquiring calibrated signal and ambient noise measurements, as well as the limited availability of trained laboratory subjects with which to obtain reliable hearing data. Recent research on northern elephant seals in both areas has significantly expanded available data in each of these areas. Aerial vocalization source levels, calibrated recordings of various call types, signal directivity patterns for male clap threats, signal propagation loss measurements, and calibrated ambient noise recordings are presented by Southall (2002) for northern elephant seals on breeding rookeries. Additionally, Kastak & Schusterman (1998; 1999) and R. Schusterman (unpubl. data) determined absolute, aerial hearing capabilities for one trained female northern elephant seal in the laboratory. Finally, Southall (2002) determined aerial critical masking ratios (the quietest tonal signals detectable on 50% of trials above broadband masking noise) and made direct measurements of critical bandwidths (auditory filters) using a band-narrowing procedure. The aerial critical ratios for this individual northern elephant seal were very similar to those determined for the same subject under water (Southall *et al.*, 2000). In both media, critical ratios generally increase monotonically with frequency at a rate of approximately 3 dB/octave, as occurs in most mammals tested (see Fay, 1988). The combined aerial and underwater masking data support the hypothesis that elephant seal auditory filters increase in absolute bandwidth gradually with increasing frequency and remain approximately constant as a function of centre frequency. The elephant seal auditory system appears to function in a manner consistent with a constant-Q model of frequency processing across a wide range of test frequencies.

In the current study, both field and laboratory data were incorporated to generate estimates of signal detection ranges of aerial northern elephant seal vocalizations for northern elephant seal receivers in breeding aggregations. Active space for four northern elephant seal vocalization types were calculated in nine different natural ambient noise conditions. Along the same lines as Erbe & Farmer (2000) and Finneran *et al.* (2000), this study took a species-specific approach to the analysis of signals and masking noise. Auditory masking data for one northern elephant seal are used to determine appropriate filter bandwidths for analyzing conspecific signals and natural masking noise. Results are discussed in the context of northern elephant seal acoustic communicative systems, reproductive biology, and anthropogenic noise impacts.

Materials and Methods

Measurements and recordings of northern elephant seal vocalization source levels, signal directivity characteristics, and ambient noise parameters were obtained in and around breeding rookeries at Año Nuevo State Reserve, 19 miles north of Santa Cruz, CA. This research was enabled by and conducted under the guidelines of a Long-term Use Agreement for Scientific Research between the University of California and the California Department of Parks and Recreation and was approved by State Parks officials at Año Nuevo State Reserve. Vocalizations were recorded opportunistically rather than being intentionally elicited from animals in the field.

Each of the four northern elephant seal call types for which signal detection ranges are estimated in this study are described in detail by Bartholomew & Colias (1962). These call types are: pup 'female attraction call' (FAC), adult female 'pup attraction call' (PAC), adult female 'threat' (AFT), and adult male 'clap threat' (AMCT). Shipley *et al.* (1981) differentiated between two types of threat calls, clap threats and burst threats, which differ primarily in the clustering of broadband impulses. This distinction was not made in this study.

Vocalizations were recorded in the field with a calibrated Neumann KMR 82i directional microphone (frequency response 20 Hz–20–kHz ± 1 dB) connected to a Sony DC-8 DAT recorder (sampling rate 32 kHz, frequency response 20 Hz–14.5 kHz ± 3 dB). Recordings analyzed for the active space estimates were obtained between approximately 2–8 m from vocalizing individuals at 0° orientations relative to the directional microphone. The microphone was positioned 1 m above the ground. Observers and vocalizing animals were generally on packed sand, with the seals' mouths typically positioned at or slightly below the elevation of the microphone. A total of 95 FACs (from seven nursing pups), 62 PACs (from five adult females), 81 AFTs (from eight adult females), and 163 AMCTs (from 15 adult males) were recorded and vocalization source levels were determined (Southall, 2002). Individual recordings for each of the four call types with the highest signal-to-noise ratios, and having source levels within 1 dB of the median value for each call type, were digitized using PC-based Spectra Plus software (resolution 16–bit, sampling rate 24 kHz, FFT size 8192 pts.). Analyses of these 'representative calls' were conducted using 1/3 and 1/12-octave analysis bandwidths. These bandwidths were selected because they represent the likely upper and lower limit of auditory filter bandwidths in northern elephant seal auditory systems, based on the available masking data for this species (Southall *et al.*, 2000; Southall, 2002). The infinite, linear averaging algorithm of the spectrum analyzer was used to provide 1/3 and 1/12-octave band levels that were stable averaged (i.e., not temporally weighted) for the entire duration of each call.

To estimate signal directivity characteristics, multiple vocalizations were recorded for animals calling at different orientations. Directivity analyses were conducted only for AMCT because of difficulty in obtaining sufficient samples at each orientation angle from individuals in other sex/age classes. Since the orientation angles were determined visually, several easily judged angles (90° left or right orientation, and 180° orientation) were used in addition to the head-on (0°) position (as in Gerhardt, 1975). Spectral analyses were conducted and relative differences in 1/3-octave band levels between orientations determined for calls from the same individual at the same range. These signal directivity characteristics at three discrete signaller orientations were used to demonstrate the active space asymmetry that likely occurs in certain environmental conditions.

A simple investigation of signal propagation loss in northern elephant seal breeding rookeries was conducted to assess the accuracy of a spherical spreading loss (20 logR) model for relatively short-range signal propagation. Pure tone signals at three frequencies predominant in elephant seal vocal signals (0.5, 1.0 and 2.0 kHz) were projected using a portable speaker and recorded at ranges of 1, 2, 4, and 8 m with the calibrated Neumann KMR 82i directional microphone. Playbacks were conducted after animals departed at the end of the breeding season in areas that had earlier been the centre of breeding rookeries. Additional important variables affecting long-range signal propagation are vertical thermal and wind gradients. These environmental factors can enhance signal propagation in conditions where signals are refracted toward the ground or exaggerate propagation loss in other conditions (Larom *et al.*, 1997). A very simple and limited analysis of thermal and wind gradients was conducted by measuring temperature and wind speed using an Extech Instruments 45118 thermo-anemometer. These variables were measured in various locations within and around breeding rookeries at 1 m increments from 0–4 m elevation.

Natural ambient noise on northern elephant seal breeding rookeries at Año Nuevo State Reserve is typically associated with one of the following sources: biotic activity (including sea bird calls, but predominately elephant seal vocalizations), wave activity, and wind activity. Thirty individual 1-min samples of each of these noise sources were recorded in three different intensity conditions. Efforts were made to obtain samples of each noise source independently of one another. For instance, wave noise was recorded away from breeding

rookeries in the lightest wind conditions possible. Low, moderate, and high intensity conditions for biotic and wave noise were qualitatively judged based on animal density and activity status, as well as tidal condition and wave height. For wind noise, the thremo-anemometer was used to determine low (<2.0 m/s), moderate (2.0–4.0 m/s), and high (>4.0 m/s) categories. For recordings of ambient noise resulting from wind activity, the wind-suppression system surrounding the directional microphone was removed. This was done to more closely represent the noise generated by wind at the ear of a seal than would likely be the case with this system engaged. Individual 'representative' noise samples in each of the nine conditions having the closest broadband noise level to the median level for that condition were selected and averaged over the 1 min duration of each sample. Average 1/3 and 1/12-octave band levels were also determined using the stable averaging function of the spectrum analyzer.

Communication ranges were estimated for each of the four signal types in each of the nine natural masking noise conditions based on relative differences between average representative root-mean-square (RMS) signal sound pressure levels and average representative RMS noise levels determined using identical analyses. The signal frequency band with the highest signal-to-noise ratio was considered to be detectable until this ratio decreased to 0 dB (as in Erbe & Farmer, 2000), provided that the noise level within this band exceeded the estimated unmasked detection threshold. This is a simplifying assumption made to allow reasonable calculations of average signal detection ranges based on the limited knowledge of pinniped processing of complex acoustic signals. The presence of multiple signal bands in vocalizations may increase detection in noise (see discussion). That a 0 dB signal-to-noise ratio within analysis bandwidths corresponds to the signal detection threshold is probably somewhat conservative, based on the relatively low critical masking ratios determined for one individual northern elephant seal (Southall *et al.*, 2000; Southall, 2002). Spherical spreading was assumed and atmospheric absorption ignored in estimating propagation loss. The maximum distance over which the frequency band containing the maximum signal-to-noise level could be detected was estimated as the range required for the signal band level to attenuate to the ambient noise band level.

Results

In all conditions, minimum signal-band levels assumed to be detectable exceeded absolute detection thresholds at similar frequencies for one individual of this species (R. Schusterman, unpubl. data). Acoustic communication in northern elephant seals thus appears to be constrained by the presence of natural masking noise rather than absolute hearing sensitivity.

Estimated active space generally decreased with increasing noise intensity, particularly for wave and wind noise, although there are some exceptions to this trend. Signal-detection ranges were larger in some cases in higher overall noise conditions because of the relative distribution of signal and noise energy in various frequency bands. This effect is most pronounced for biotic noise because it generally contains more tonal components than wind and wave noise. The largest communication ranges generally were estimated for each call type in low intensity wave noise conditions. The smallest communication ranges generally were estimated in high intensity wave noise.

For vocalizations containing the greatest signal energy in fairly narrow frequency bandwidths (attraction vocalizations), maximum signal-to-noise ratios tend to occur in relatively few frequency bands for all ambient noise conditions. For call types in which energy was more evenly spread across many bandwidths (threat vocalizations), maximum signal-to-noise ratios occurred in more frequency bands and depended primarily on the spectral distribution of noise energy.

The AMCT-directivity analyses and signal-propagation measurements are reported in detail elsewhere (Southall, 2002), but the most significant findings as they relate to this study are as follows. Overall signal strength was lower for AMCTs produced at off-axis orientation angles (90 and 180°) than those produced at 0° orientation angles. This effect was particularly pronounced at higher frequencies. Pure-tone signal attenuation roughly approximated (± 4 dB) theoretical losses based on a spherical model (20 log R) of geometrical spreading loss over short ranges (1–8 m). However, at the highest wind velocity, propagation losses were consistently less than expected when the wind was in the direction of signal propagation and greater than expected in the opposite condition. The vertical thermal and wind profiles relatively close to the ground (0–4 m elevation) indicated the presence of slight, variable thermal and wind gradients. These effects are certainly more pronounced over greater elevations and are likely very significant in terms of effective signal propagation (Larom *et al.*, 1997).

In calculating the PAC-active space in low intensity biotic noise (Fig. 1), the maximum signal-to-noise ratio using 1/3-octave band analyses was 26 dB, occurred in the 630 Hz band, and corresponded to a maximum detection range of approximately 20 m. For the 1/12-octave band analysis, the maximum signal-to-noise ratio was 29 dB, occurred

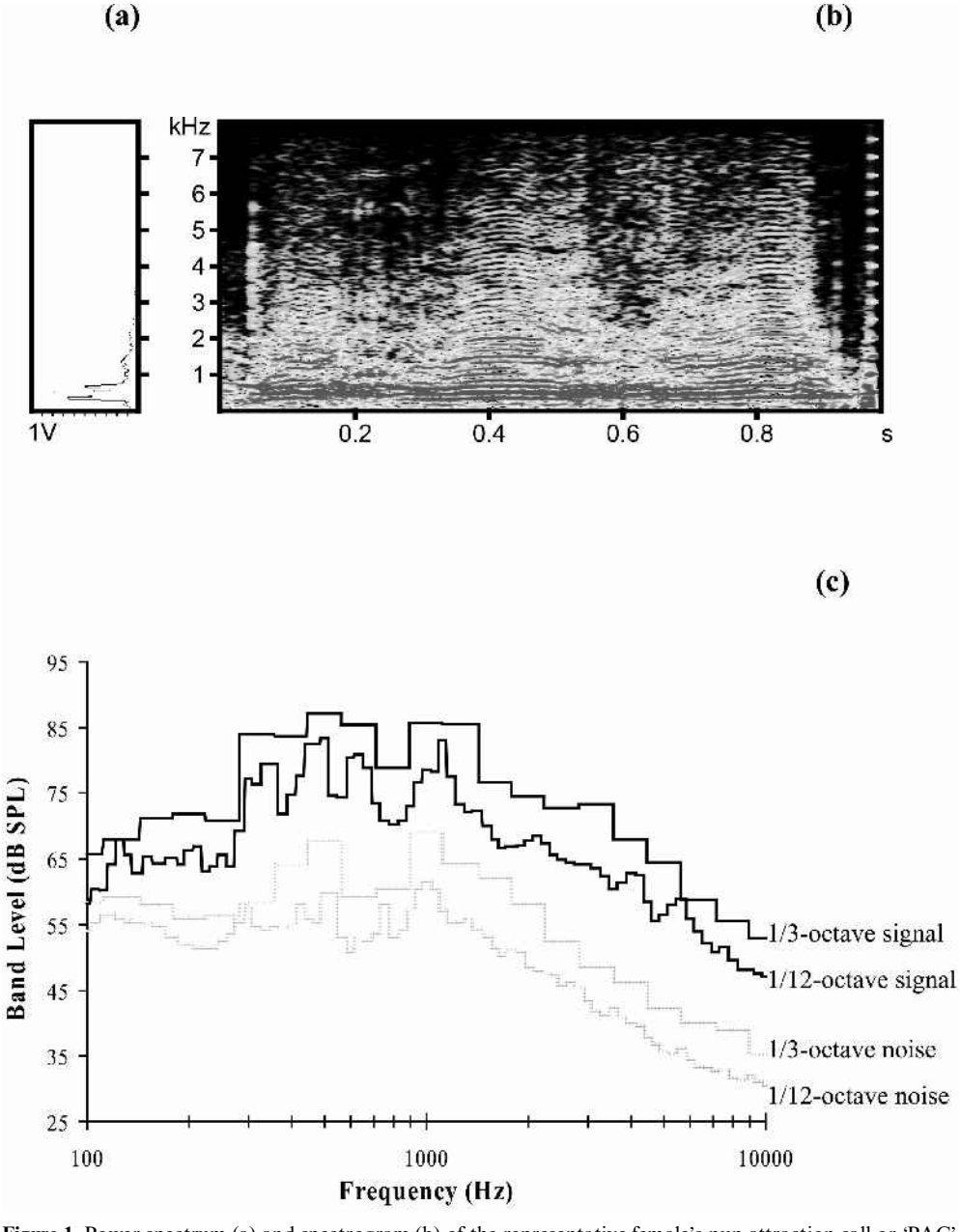

Figure 1. Power spectrum (a) and spectrogram (b) of the representative female's pup attraction call or 'PAC' (sampling rate 16 kHz, FFT size 512, analysis bandwidth 31 Hz, Blackman window, temporal resolution 1.5 ms). An example of 1/3 and 1/12-octave band analyses for this PAC (signal; solid curves) and the representative low intensity biotic noise sample (noise; grey curves) is shown in (c).

in the 600 Hz band, and corresponded to an estimated active space of approximately 30 m. Seventy-two signal and noise analyses conducted in this manner generate active space estimates for each call type in each masking noise condition using both analysis bandwidths (Figs. 2 and 3). Active space estimates for threat vocalizations were generally larger in identical masking noise conditions than those estimated for attraction vocalizations. Additionally, estimated maximum detection ranges

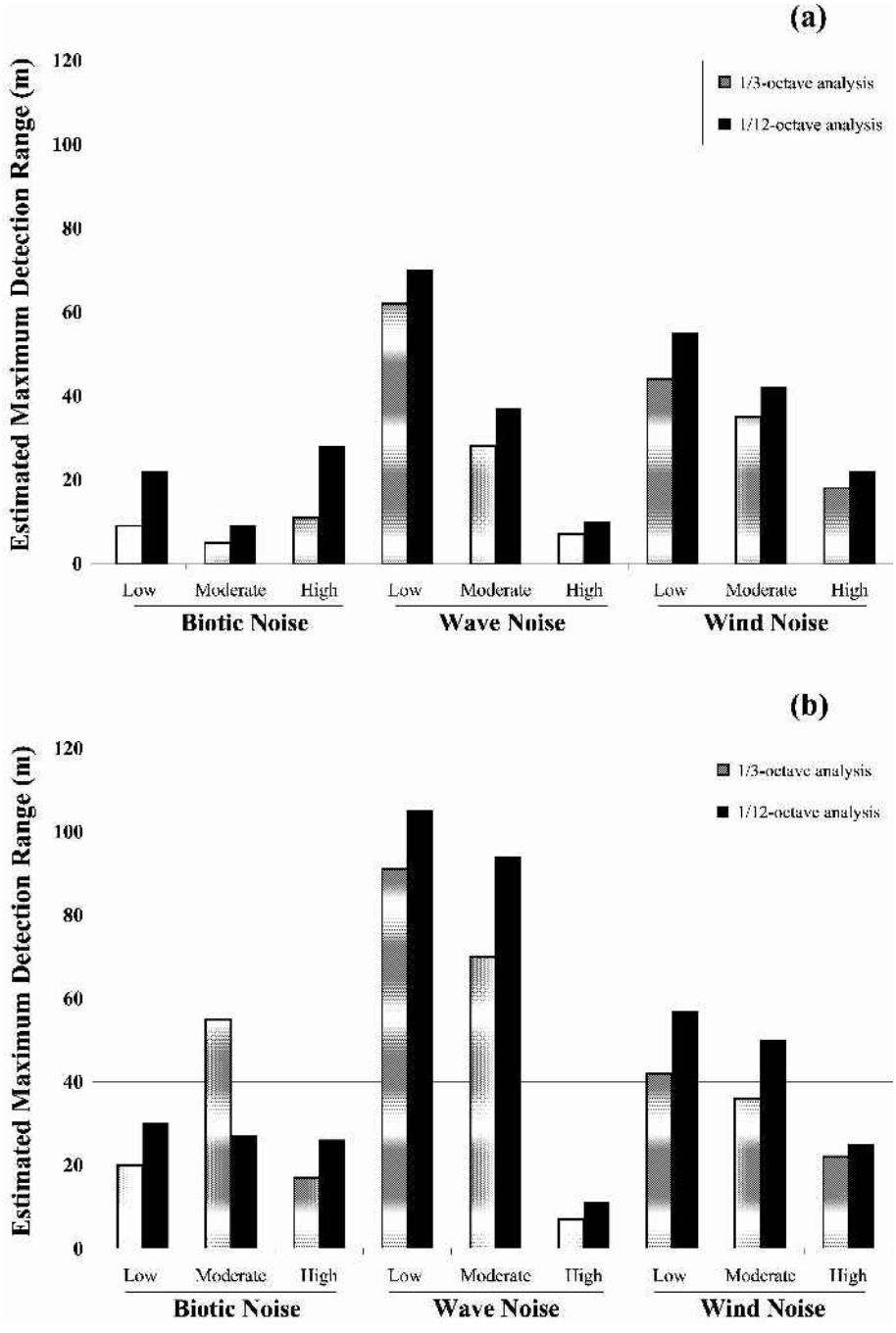

Figure 2. Estimated maximum detection range radii (m) for (a) representative pup 'female attraction call' or 'FAC' and (b) female 'pup attraction call' or 'PAC' in nine natural ambient noise conditions based on 1/3-octave (stipled bars) and 1/12-octave band (black bars) signal and noise analyses.

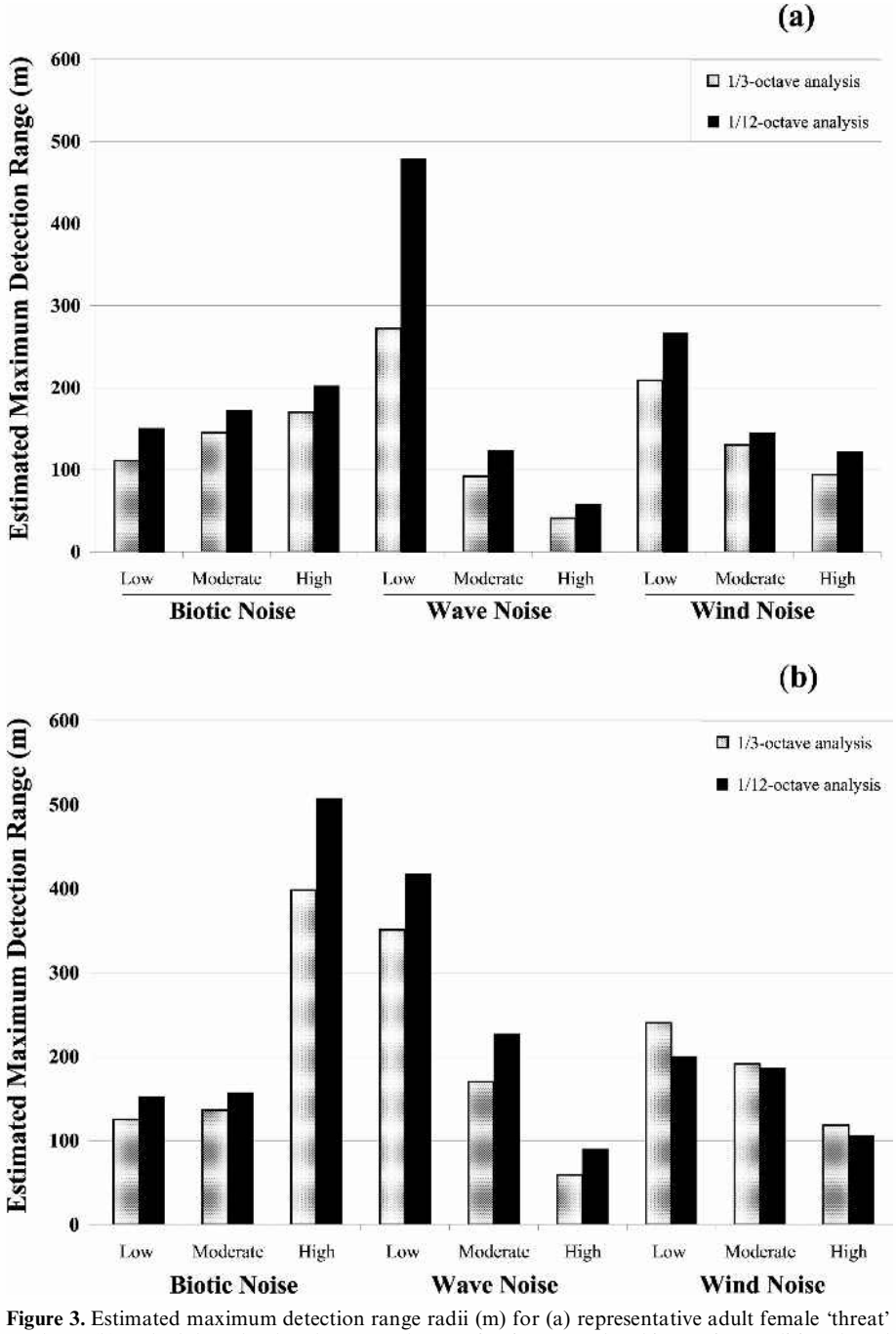

Figure 3. Estimated maximum detection range radii (m) for (a) representative adult female 'threat' or 'AFT' (b) and adult male 'clap threat' or 'AMCT' in nine natural ambient noise conditions based on 1/3-octave (stipled bars) and 1/12-octave band (black bars) signal and noise analyses. Note the difference in range scale from Figure 2.

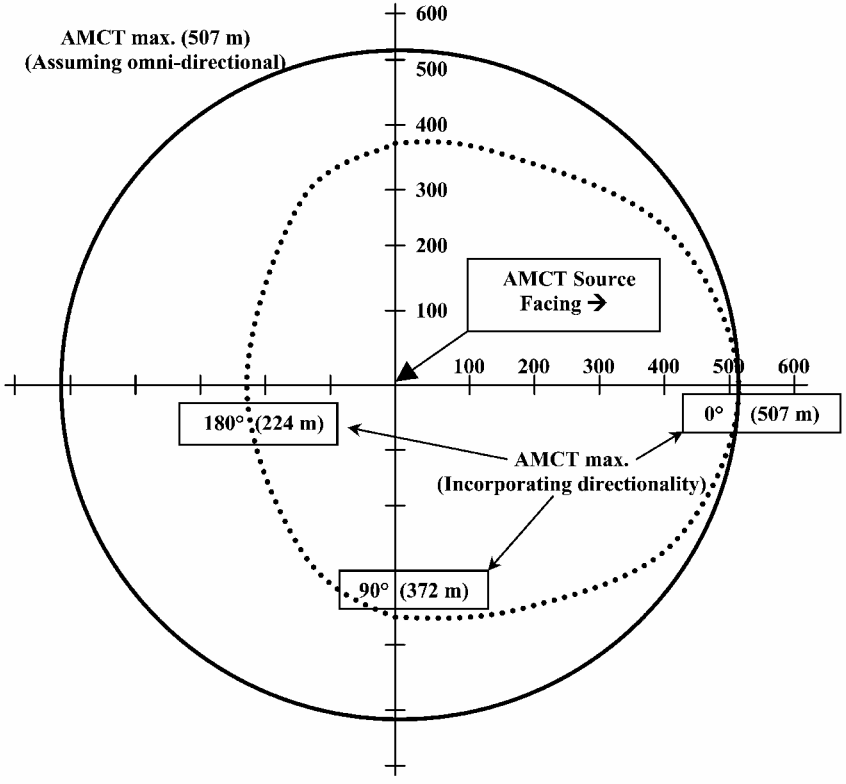

Figure 4. Two-dimensional spatial representation of the active space surrounding a vocalizing male northern elephant seal in high intensity biotic noise (1/3-octave band analysis), assuming AMCTs are omni-directional (solid) and incorporating empirical measurements of signal directivity patterns (dashed). Detection range maxima at three discrete signal orientations were used to estimate active space asymmetry. Detection ranges at intermediate angles were interpolated visually.

were larger in almost every noise condition based on 1/12 rather than 1/3-octave band analyses.

Two-dimensional spatial representations of the estimated AMCT-active space, assuming omni-directionality and incorporating signal-directivity characteristics, demonstrate the potential for asymmetry in the effective active space (Fig. 4). Detection range maxima at three discrete signal orientations (0, 90, and 180°) were used to generate the directional-beam pattern shown in Fig. 4. Detection ranges at intermediate angles were interpolated visually. For the 125 Hz band of the representative AMCT, 1/3-octave signal levels at 90 and 180° are 2.7 and 7.1 dB lower, respectively, than those recorded at the 0° orientation. The shape and overall volume of the active space is consequently substantially different when vocalization directivity characteristics are incorporated than when signals are assumed to be omni-directional.

Discussion

An integrated approach involving field measurements, auditory masking data, and species-specific analysis filter bandwidths was used to estimate acoustic communication ranges for northern elephant seals. The findings demonstrate that active-space dimensions are variable, depending on call type, signal directivity, ambient noise conditions, and receiver characteristics. Further, the results are useful in considering: (1) the significance of northern elephant seal acoustic communication in terms of reproductive biology, (2) selective pressures on signal production and processing systems, (3) the limitations of this kind of mathematical approach in estimating active space, and (4) potential impacts of anthropogenic noise.

The spatial relationships of most northern elephant seal breeding rookeries during the breeding season (generally tightly-clustered colonies) are

such that relatively long-range detection of vocalizations is not always critical. Masking noise is probably less likely to constrain northern elephant seal vocal communication than is probably the case for some otariid pinnipeds for whom signal detection over greater distances is essential in various social interactions (Schusterman, 1978). However, the active-space estimates for attraction vocalizations used by elephant seal females and pups to maintain contact with one another are as small as 5–7 m. Compromised ability to communicate vocally over relatively short ranges could decrease pup survival. Bartholomew & Colias (1962) observed that nursing pups separated from their mothers by as little as 2–3 m could become permanently separated and that greater separation distances increased the probability of separation. The consequence of permanent separation is death for approximately 70% of pups resulting from socially-induced trauma and/or starvation (Le Boeuf *et al.*, 1972). Particularly in loud natural ambient noise conditions, masking could sufficiently limit the effective communication ranges of attraction vocalizations to decrease the likelihood of mother–pup reunions.

Maximum signal detection ranges for northern elephant seal threat vocalizations are generally much greater than those for attraction vocalizations. This corroborates qualitative descriptions about the intense nature of threat signals and the relatively long ranges over which threat vocalizations are likely detectable (Bartholomew, 1952; Bartholomew & Colias, 1962). The large active spaces determined for the AMCT indicate that these signals may be detectable in certain conditions hundreds of meters from senders. Interestingly, maximum-signal-detection ranges for the AFT are of similar magnitude to those estimated for the AMCT. Thus, adult female threat vocalizations are also likely detectable by conspecifics over relatively large areas. One putative function of female threat vocalizations is to alert rival males to the approach and/or copulation attempts of other males and thus incite male-male competition (Cox & Le Boeuf, 1977). The AFT detection ranges obtained in this study indicate that female threat vocalizations are sufficiently intense to be detected by large numbers of surrounding males on breeding rookeries.

There appears to be a variety of sender and receiver characteristics which enable acoustic communication by northern elephant seals over fairly large distances in relatively high background noise levels. First, most elephant seal vocalizations are relatively loud (Southall, 2002). Additionally, calls are frequently redundant (Bartholomew & Colias, 1962), a signaller strategy believed to enhance the probability of signal detection in noisy conditions for pinnipeds (Schusterman, 1978). There also appears to be some receiver characteristics, based on laboratory audiometric data for one individual northern elephant seal, that increase signal detection ranges as well. Of foremost significance is that this test subject detects tonal signals quite well over simultaneous masking noise both in water (Southall *et al.*, 2000) and in air (Southall, 2002). Additionally, auditory-filter bandwidths (critical bandwidths) are relatively narrow (between 1/12 and 1/3-octave) for this seal based on direct measurements using a band-narrowing procedure and indirect estimates using critical ratio data (Southall, 2002). The consistently larger signal-detection ranges obtained using the narrower of these filter bandwidths in this study illustrates the potential advantages of narrow-band auditory filtering in terms of signal detection and noise suppression. This could reflect selective forces favouring relatively narrow critical bandwidths in pinnipeds. Based on a variety of field and laboratory bio-acoustic data, elephant seals and other pinnipeds appear generally able to communicate vocally despite frequently high natural ambient noise levels, presumably due to evolutionary pressures on both signal productive and receptive systems (Schusterman *et al.*, 2000).

There are a multitude of acknowledged limitations to the active space estimates presented in this study, many of which are the result of limited available data. Certain simplifying assumptions were made to provide average, first-order active space estimates without attempting to model every possible condition affecting signal propagation, signal and noise spectral and temporal relationships, and receiver operating characteristics. The seven major limitations of the model resulting from data constraints and the simplifying assumptions made in estimating active space are discussed below.

First, the assumption of spherical and non-frequency specific signal propagation over relatively large ranges is almost certainly invalid in some conditions. While the signal propagation measurements indicate that the spherical spreading model approximates propagation loss for tonal signals over short ranges on elephant seal breeding rookeries, long range propagation of animal vocalizations can vary tremendously in different environmental conditions (Larom *et al.*, 1997). Specifically, atmospheric variables, such as refraction caused by vertical thermal and kinematic gradients and wind speed/direction, play a critical role in determining propagation over long ranges in environments similar to elephant seal breeding rookeries (Garstang *et al.*, 1995; Larom *et al.*, 1997). Such variables are likely as significant as some sender and receiver characteristics (e.g., signal directivity patterns and receiver directional hearing characteristics) in determining effective communicative ranges.

However, receiver directional hearing properties likely does play a considerable role in determining signal detection ranges and the asymmetry of the active space in certain conditions. A second limitation to this study is that these receiver characteristics were not included in the active space estimates. How strongly receiver orientation affects detectability of conspecific vocalizations for northern elephant seals is unknown. However, Holt (2002) found that a northern elephant seal could discriminate broadband acoustic stimuli presented from different directions until the angle separating sound sources was reduced to approximately 5°. This demonstration of directional-hearing capabilities in an elephant seal supports the hypothesis that additional receiver characteristics than those included in the active space calculations affect signal detection. Directional properties of senders, receivers, and noise sources likely interact in complex ways to affect active space.

Third, the active space estimates are based on signal- and noise-band levels that are averaged over the entire duration of each representative sample. At any point in time, effective signal detection ranges may be considerably larger or smaller, depending on the specific timing of signal and noise elements. Along the same lines, it is possible, if not likely, that amplitude modulations of noise energy remote from the predominant signal band(s) can enhance signal detectability. Reduction in the amount of masking resulting from modulation of on- and off-frequency masking noise energy, referred to as comodulation masking release (CMR), has been extensively demonstrated in humans (see Hall & Grose, 1991 for a review). Each of the masking noise types considered in this study contains some amplitude modulation. Consequently, CMR for signal detection could occur in each of the noise conditions considered. The result of this would be an increase in the active space of unknown magnitude. Colony noise generally contains the most substantial amplitude modulations in masker bands most similar to the predominant signal bands. In humans, modulation of noise energy in bands close to, but outside of, signal frequency bands results in the greatest CMR (Cohen & Schubert, 1987). Thus, CMR might be largest for the detection of elephant seal vocalizations in masking noise resulting from conspecific vocalizations. Whether elephant seal auditory systems process acoustic signal and noise envelopes and experience CMR as humans do is unknown. However, the potential for these kinds of perceptual phenomena to enhance signal detectability to varying degrees is acknowledged.

Fourth, the signal and noise samples used in the active space estimates made in this study are representative samples. Individual differences in northern elephant seal vocalizations (Shipley *et al.*, 1981; Insley, 1992) and idiosyncrasies in masking noise conditions would produce somewhat different estimated detection ranges if alternative representative samples were selected.

Fifth, efforts were made to obtain noise samples that were as isolated from other kinds of noise as possible. This isolation of noise conditions rarely occurs on elephant seal breeding rookeries. Also, biotic noise samples were recorded at the periphery of breeding rookeries, where noise levels are almost certainly lower than those occurring within dense breeding aggregations. This almost certainly means that effective detection ranges for seals in the centre of breeding rookeries are less on average than those estimated in this study.

Sixth, the temporal integration time of the elephant seal auditory system is unknown. If this integration time is less than the duration of certain conspecific signals, the detectability and active space could be less than that assumed in the current study. This might be particularly true for the detection of the relatively brief and rapid-onset pulses contained in male CTs.

Finally, assuming that the maximum signal-to-noise ratio is exclusively responsible for signal detection may be an oversimplification. Certain frequency bands contain more information with respect to individual vocal differences. Masking of these frequencies might cause a greater reduction in detection and/or discrimination, despite higher signal-to-noise ratios existing in other frequency bands. Also, detectability of complex acoustic signals improves in humans in certain conditions as additional signal elements are available in multiple auditory filters (Green, 1958; Buus *et al.*, 1986). It is unknown whether auditory masking for complex acoustic signals is similar for northern elephant seals. Presuming this to be the case, detectability for each of the call types considered in this study would likely be enhanced because signal energy for each exists in multiple frequency bands. This would result in somewhat greater effective signal-detection ranges than those estimated based on the frequency band containing the greatest signal-to-noise ratio.

Despite these carefully considered constraints, we believe that the results presented in this study are reliable first-order approximations of active space for four northern elephant seal call types in nine natural masking noise conditions. The integration of source, path, and receiver data, as well as the use of species-specific analysis filter bandwidths, in generating these estimates represent important advancements in the study of pinniped acoustic communication. Further, the results of this study illustrate some important considerations with regards to anthropogenic noise. The fairly large signal detection ranges estimated for some northern

elephant seal vocalizations in loud natural masking noise conditions should not minimize concerns regarding potential anthropogenic noise impacts. The masking data for this species indicate that noise interference renders signals inaudible in a manner generally similar to other species. Introduction of anthropogenic noise into breeding rookeries will further reduce maximum detection ranges for communicative signals when anthropogenic noise-band levels exceed natural ambient noise levels. Additionally, regulatory agencies should not focus exclusively on low frequency anthropogenic noise with respect to potential masking. Certain elephant seal call types contain considerable energy in relatively high frequency bands, which likely contribute to their detectability in certain conditions.

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