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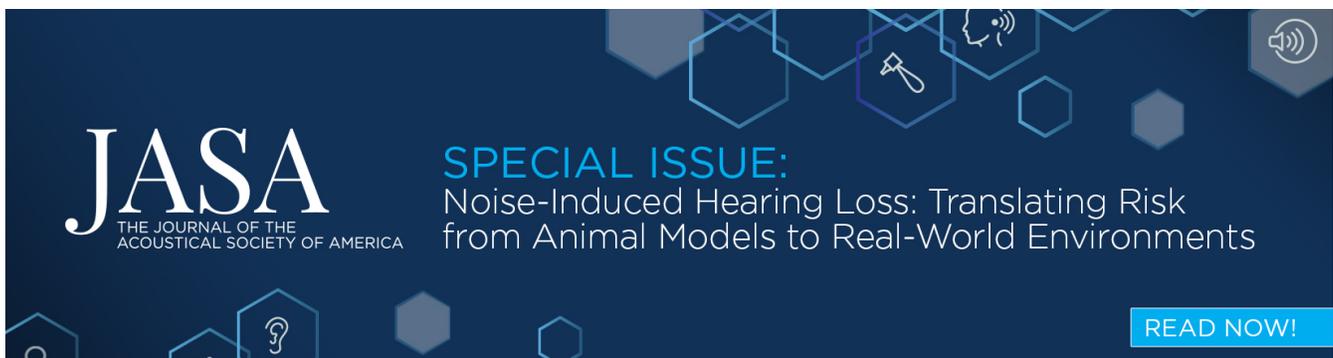
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# High-amplitude vocalizations of male northern elephant seals and associated ambient noise on a breeding rookery

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Northern elephant seals (*Mirounga angustirostris*) are massive, land-breeding marine mammals that produce loud, stereotyped calls during annual breeding seasons. To determine vocalization source levels emitted by competing males on a mainland breeding rookery, aerial calls were measured on-axis at 1 m from adult males using three different sound pressure level metrics. Time-averaged (1 min) ambient noise was also measured under variable environmental and social conditions. Results indicate that male northern elephant seals emit high amplitude airborne calls with little variation in call amplitude. Mean source levels ranged from 98 to 114 dB re: 20  $\mu$ Pa [root-mean-square (rms) -fast], 102–116 dB re: 20  $\mu$ Pa (rms-impulse), and 120–131 dB re: 20  $\mu$ Pa (peak) and average standard deviations for all metrics were <2.3 dB. Further, these seal rookeries exhibit high variability in ambient noise (in terms of both spectrum and amplitude) from biotic and environmental sources. Finally, males sampled did not adjust call amplitude to compensate for higher background noise levels and thus did not exhibit a Lombard effect. These findings reinforce the view that the remarkable vocalizations of male northern elephant seals serve as rigid and powerful signals that convey individual identity within noisy breeding colonies rather than as honest indicators of size, status, or motivation. © 2019 Acoustical Society of America. <https://doi.org/10.1121/1.5139422>

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## I. INTRODUCTION

Vocal communication is central to the social behavior of northern elephant seals (*Mirounga angustirostris*), supporting life-history events related to parental care and reproduction (Bartholomew and Collias, 1962; Sandegren, 1976). While most true seals mate aquatically (Reidman, 1990), northern elephant seals return to natal colonies to give birth, nurse their pups, and breed (Le Boeuf and Laws, 1994). Reproduction is annually synchronous, with sexually mature individuals returning from foraging migrations to aggregate on islands and mainland rookeries during winter months along the Californian and Mexican coasts. Vocalizations produced by all age and sex classes during this time are often loud and repetitive, including threat calls, mother calls to their pups, pup calls to their mothers, and male competitive vocal displays (Bartholomew and Collias, 1962; Schusterman, 2008). Density is typically high within these rookeries, as seals cluster into shoreline aggregations (referred to as “harems”) that may contain as many as 100 mature females, their dependent pups, and the adult and sub-adult males that surround these social groups to compete for reproductive opportunities.

Males spend more than 2 months ashore during the annual breeding season and establish structured dominance

hierarchies that determine access to estrous females (Le Boeuf, 1972). The breeding system is one of extreme polygyny, with adult males weighing upwards of 2000 kg—3 to 4 times the size of females—and possessing exaggerated secondary sexual characteristics including a robust chest shield and dramatically enlarged proboscis (Le Boeuf and Laws, 1994). To reduce the energetic costs of chasing and fighting while fasting, males produce extremely loud, broadband, and stereotyped vocal displays during male–male interactions (Bartholomew and Collias, 1962; Le Boeuf, 1974; Sandegren, 1976). Each male’s display call contains a unique pattern of pulses (Shipley *et al.*, 1981), which functions as a vocal signature that rivals learn and subsequently respond to throughout the breeding season (Casey *et al.*, 2015; Mathevon *et al.*, 2017; Shipley *et al.*, 1981). Surprisingly, adult male elephant seals do not attend to body-size linked acoustic features during rival assessment (Casey *et al.*, 2015). Among adults, the spectral, temporal, and amplitude characteristics of each male’s call are stable within and between seasons, and do not fluctuate as a function of motivational state (e.g., willingness to fight) or behavioral context (Casey *et al.*, 2015).

Calling males elicit approach or avoidance responses from rivals near the harem or in adjacent harems (Bartholomew and Collias, 1962; Sandegren, 1976; Southall *et al.*, 2003), even in circumstances where visual cues are

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limited (Shipley and Strecker, 1986). Thus, more dominant males control the movement of less dominant individuals through the exchange of these ritualized vocalizations (Le Boeuf, 1972; Casey *et al.*, 2015). Additionally, the calls produced by males contain directional cues, and listeners are sensitive to the spatial orientation of callers relative to their own position within the breeding rookery (Holt *et al.*, 2010). In general, crowded and noisy conditions on the breeding colony appear to favor the production of loud, directional, repetitive, recognizable calls to increase probability of signal detection by others (Schusterman, 2008).

The influence of background noise on the detection of calls by conspecifics can be evaluated by measuring the amplitude of a given vocalization and the corresponding noise conditions in which the signal is produced. Prior research integrated these data with laboratory studies of hearing and field measures of acoustic propagation to provide estimates of potential communication space for northern elephant seals (Southall *et al.*, 2003). These results demonstrated that predicted detection ranges can vary tenfold, from ~50 to 510 m, depending on specific signal and noise combinations. Due to their high intensity and apparent importance to intrasexual competition, the amplitude of male vocal displays has been previously reported (Sanvito and Galimberti, 2003; Southall *et al.*, 2003). These assessments considered source levels in terms of root-mean-square (rms) sound pressure level SPL determined using temporal integration times of 125 ms (i.e., standard “fast” weighting) and C-weighted filters rather than unweighted (linear, or “Z” weighted) metrics. Results indicate high call amplitudes exceeding 104 dB re: 20  $\mu$ Pa based on traditional rms metrics (Sanvito and Galimberti, 2003). Given the impulsive nature of many (but not all) of these vocalizations (Casey *et al.*, 2015), this rms metric may be insufficient to fully characterize the source level of male elephant seal vocalizations, and other metrics may be needed to capture the true amplitude of these signals (e.g., peak SPL) (Madsen, 2005).

This study provides a long-term assessment of vocalization source levels for adult male northern elephant seals paired with corresponding ambient noise conditions. Sampling occurred over four disparate breeding seasons spanning 17 years. Multiple source level measurements were obtained from known individuals in terms of fast time-weighted rms, impulse time-weighted rms, and peak SPLs to enable a more complete characterization of source levels for calls with both impulsive and non-impulsive features. Most source levels were measured directly at close range (1 m) and on axis with callers to eliminate the need to estimate source levels from signal propagation estimates. Source levels determined for a subset of calls were evaluated in the context of associated ambient noise on the rookery, and these noise measurements were considered relative to varying biotic (e.g., seals) and environmental (e.g., surf activity) sources. Percentile statistics were applied to describe amplitude and spectral variability in these local ambient conditions to characterize different contributions to background noise. These measurements clarify the relationship between the amplitude of elephant seal calls and their function, enable predictions of the conditions under which partial or

complete masking (caused by both biotic and abiotic sources) is likely to occur, and provide insight as to whether males adjust the amplitude of their vocalization as environmental noise levels increase (i.e., the Lombard effect).

## II. MATERIALS AND METHODS

### A. Study site and animals

The study was conducted on the mainland beaches of Año Nuevo State Park (37.1086N, -122.338W) in San Mateo County, California. Male northern elephant seals at this site exhibit a high tolerance for disturbance during the annual reproductive season, which allows acoustic measurements and behavioral observations to be obtained at close range to individuals engaged in typical social interactions. As a consequence, breeding rookeries at this location have been the site of extensive, long-term studies of behavior and communication of northern elephant seals.

### B. Source level measurements

Data were collected during four breeding seasons between the months of December and March: 1999–2000, 2004–2005, 2010–2011, and 2015–2016. Recordings were obtained from adult males with 5 years of separation between each sampling period to prevent pseudo-replication of individuals based on available life history and survival data. Because adult males produce calls that are individually reliable and exhibit low within-individual variation (Le Boeuf and Petrinovich, 1974; Casey *et al.*, 2015; Shipley *et al.*, 1981), only sexually mature males aged 7+ years were sampled. Each male’s adult status was confirmed by independent experienced observers based on scarring of the chest shield, development of the proboscis, and body length (Le Boeuf, 1972; Deutsch *et al.*, 1994). To enable individual identification and sampling of individuals over multiple days within seasons, males were dye-marked with an alphanumeric code near their rear flippers and photographed (as in Casey *et al.*, 2015).

Calls of male northern elephant seals were recorded opportunistically during natural behavior rather than being elicited by researchers, as has been done in studies of southern elephant seals (Sanvito and Galimberti, 2003). Source level measurements were obtained for display calls while males were in typical head-reared calling posture (Bartholomew and Collias, 1962; Sandegren, 1976; Shipley *et al.*, 1981). In the 1999–2000 season, calls were measured using a hand-held Brüel & Kjær 2230 precision sound level meter (Brüel & Kjær A/S, Nærum, Denmark) with fast-response setting and C-weighting (as in Southall *et al.*, 2003). In the 2004–2005 season, the same 2230 sound level meter was used, but with linear (Z) frequency weighting (Insley and Southall, 2005). For the 2011–2012 and 2015–2016 seasons, calls were recorded and simultaneously measured with a hand-held Brüel & Kjær 2250 sound analyzer (24-bit/48 kHz sampling rate) with a calibrated 4189 free-field microphone (Brüel & Kjær A/S, Nærum, Denmark, 0.006 to 20 kHz, 50 mV/Pa) and a UA-1650 windscreen, with linear (Z) weighting and several level metrics. All calls included in the analyses were

obtained at an estimated range of 1 m from vocalizing animals, in the horizontal plane of the mouth (at a height of approximately 2 m, depending on the size of the seal). Researchers extended the sound level meter toward vocalizing seals and positioned the receiving microphone at a visually estimated range of 1 m ( $\pm 0.2$  m). Sampling at this close range could result in greater variability in measured levels due to distance error than sampling at a farther range. However, a 1 m sampling distance was selected for reasons related to the trade-offs associated with the dynamic nature of the environments sampled that would ultimately result in greater source level error. These trade-offs include variable propagation conditions ranging from 12 to 20 (median 17) log R due to fine-scale differences in substrate type and atmospheric condition spanning multiple seasons. Additionally, sampling occurred within crowded rookeries where the presence of other vocalizing animals may have interfered with measurements from focal individuals if sampled at greater ranges.

Individuals were recorded on axis with reference to the dorsal midline ( $\pm 10^\circ$ ), which was most easily estimated and controlled at a 1-m range relative to greater sampling distances. Receiving sensitivity of the sound level meter was adjusted to prevent clipping of high amplitude calls recorded at close range. This configuration resulted in signal-to-noise ratio (SNR) values commonly exceeding 40 dB, meaning ambient noise did not contribute to measured vocalization source levels.

Source level measurements obtained at 1 m were close to the acoustic near field of the calls in some cases. Our aim was to obtain direct measurements at a consistent range without requiring assumptions about transmission loss. As the peak frequency of male vocalizations is 460 Hz (Casey *et al.*, 2015), the estimated acoustic near field is less than 0.75 m. This is within the 1 m range at which calls were sampled, although for lower frequencies this range could extend to or slightly exceed 1 m.

While measurements for a few individuals (<10%) were obtained within a single recording period, the calls produced by the majority of individuals were recorded over multiple days and in different behavioral contexts (e.g., directed toward other males or in isolation). A minimum of four calls (maximum 15) were measured per individual. To ensure a matched sample size, the data were later randomly subsampled to include only four calls per individual.

Vocalizations were measured using a metric of rms fast weighting (125 ms). Therefore, mean source level and standard deviation measures based on this metric were compared to evaluate potential inter-seasonal variation and to determine an overall mean source level based on the largest possible sample of individuals. Additionally, this metric allowed for comparison to published studies of elephant seals calls (e.g., Sanvito and Galimberti, 2003) and calls of other mammals. However, while the features of elephant seal threat display calls are stable within individual males, they exhibit a high degree of structural variation between individuals (Casey *et al.*, 2015). The calls of different males may contain brief single impulses (<0.1 s), bursts of pulses (>0.2 s), and/or more continuous sounds (>1 s), as described by Casey *et al.* (2018). Therefore, to fully characterize vocalizations

with variable temporal structure, source levels during the 2010–2011 and 2015–2016 seasons were determined with two additional metrics: rms with impulse-weighting (35 ms) and peak (instantaneous) pressure. This enabled source levels to be compared both between individuals and between metrics.

### C. Ambient noise measurements and analysis

Noise conditions on an elephant seal breeding rookery are influenced by both biotic sources (e.g., seals, birds), environmental (e.g., surf activity, wind), which vary in intensity depending on factors including tidal conditions, wave height, animal density, and activity. To characterize ambient noise, representative recordings were obtained at close proximity to elephant seal harems. Ambient noise measurements were taken with the Brüel & Kjær 2250 sound analyzer using linear (Z) weighting. Thirty individual 1-min noise measurements were obtained in three different ambient conditions: 10 samples each in low, moderate, and high intensity contexts of both environmental (wave) and biotic (seals) sources. Categorical intensity conditions for each noise context were subjectively defined in the field by experienced field personnel. For environmental noise: *low*, *moderate*, and *high* intensity categories were based on wave height and tidal state relative to the sampling location. For biotic noise: *low*, *moderate*, and *high* intensity categories were based on the relative activity levels and animal density of breeding rookeries relative to the sampling location. Environmental noise was measured at locations away from the main breeding rookeries (i.e., in *low* biotic noise conditions). Biotic noise was characterized adjacent to breeding rookeries well away from surf break areas and/or in mild wave conditions (i.e., in *low* abiotic noise conditions). The subjective noise category, sampling location, sea state, and proximity to elephant seals in the vicinity of the recorder were noted for all ambient noise measurements.

Ambient noise was measured from 0.045 to 22.4 kHz using the Brüel & Kjær 5503 Utility Software Spectrum Analyzer. For each recording, unweighted rms equivalent levels (LZeq) exceeded for 90%, 50%, and 10% of the 1-min recording interval were calculated. These corresponded to 90th, 50th, and 10th percentile ambient noise levels (i.e., noise levels that are exceeded 90%, 50%, and 10% of the time, respectively) within 1/3-octave bands with center frequencies ranging from 0.05 to 20 kHz. Broadband LZeq and median 1/3-octave LZeq values were then determined for the ten recordings in each noise condition. Ambient noise spectral density levels (dB re: 20  $\mu\text{Pa}^2/\text{Hz}$ ) within each band were calculated for each noise condition and percentile level as the median 1/3-octave band LZeq value minus 10 log (bandwidth). The inclusion of 10th to 90th percentile noise statistics enabled an objective measure of temporal variance in ambient noise.

### D. Assessment of Lombard effect

To determine whether individuals modulate source levels in response to changing ambient noise conditions (Lombard effect), we recorded a subset of identified adult

males during two successive breeding seasons in 2015–2016 and 2016–2017. Call amplitude was measured with the Brüel & Kjær 2250 sound level meter as described above, either at 1 m or at ranges up to 5 m. For calls recorded at distances greater than 1 m, source levels were estimated from an empirically measured sound propagation-loss relationship ( $17 \log R$ ) for elephant seal vocalizations within this environment. Immediately after recording each vocal display, a 1-min ambient noise measurement was obtained using the methods described above. Source level measurements were thus paired with ambient noise levels obtained within a few minutes of calls in the same area.

Broadband vocalization source levels were evaluated relative to corresponding ambient noise levels in three relatively low-frequency 1/3-octave bands (0.315, 0.4, and 0.5 kHz), which correspond to the predominant spectral energy in elephant seal vocalizations (Casey *et al.*, 2015; Southall *et al.*, 2003). A potential Lombard effect was first evaluated for four individuals with more than eight measurements over multiple days and a reasonable ( $>10$  dB) range of ambient noise conditions within the analysis frequency bands. Data were then pooled for all males with paired ambient noise measurements, which included these four males and an additional eight individuals for which at least four source levels were measured in different ambient noise conditions. These data both within and across individuals were evaluated by linear regression of source level rms-fast, rms-impulse, and peak pressure source level metrics relative to noise in specified bands using Rstudio (version 1.1.456).

### III. RESULTS

#### A. Vocalization source levels

Over 1000 source level measurements were obtained for more than 60 adult male northern elephant seals during four independent sampling periods from 1999 to 2016. Of these,

256 calls produced by 36 individuals were obtained at 1 m, on axis, and at least 5 m from other vocalizing individuals. Source levels for 144 subsampled calls (four calls per individual) were used in the final analysis (fast-weighted rms for all years; rms impulse weighted and peak pressure level for 2010–2011 and 2015–2016; see the supplementary material<sup>1</sup>).

To consider source levels of adult males across all seasons using a common metric, and for comparison with previous measurements in elephant seals, rms fast-weighted measurements were compared for individuals within each season (Fig. 1). Across seasons, source levels ranged from 98 to 114 dB re: 20  $\mu$ Pa (rms-fast) for individual males, with a combined mean source level value of 107 dB re: 20  $\mu$ Pa (rms-fast). Differences in mean call levels across seasons were consistently low ( $<5$  dB), with standard deviations of  $<2.3$  dB across metrics, indicating similar levels for all sample periods despite difference in individual males and, in some cases, different equipment.

To evaluate source levels within and between males with respect to call amplitude, calls for which all three metrics were available (2010–2011 and 2015–2016 breeding seasons) were compared ( $n = 18$  individuals). Source level metrics determined for each male based on a random subsample of four calls are given in Figs. 2(A)–2(C). Figure 2(D) represents the average values for each metric across all individuals for these two breeding seasons. The average maximum rms fast-weighted (125 ms time integration) source level was 107 dB re: 20  $\mu$ Pa (avg. std. dev. 2.7), while the impulse-weighted (35 ms integration) value was 111 dB re: 20  $\mu$ Pa (average std. dev. 2.5) for the same set of calls. The difference between the values of the two metrics was significant (unpaired  $t$ -test;  $t: 5.085$ ;  $df: 68$ ;  $p < 0.0001$ ). The mean call source level derived from the peak pressure metric was 126 dB re: 20  $\mu$ Pa (average std. dev. 2.6).

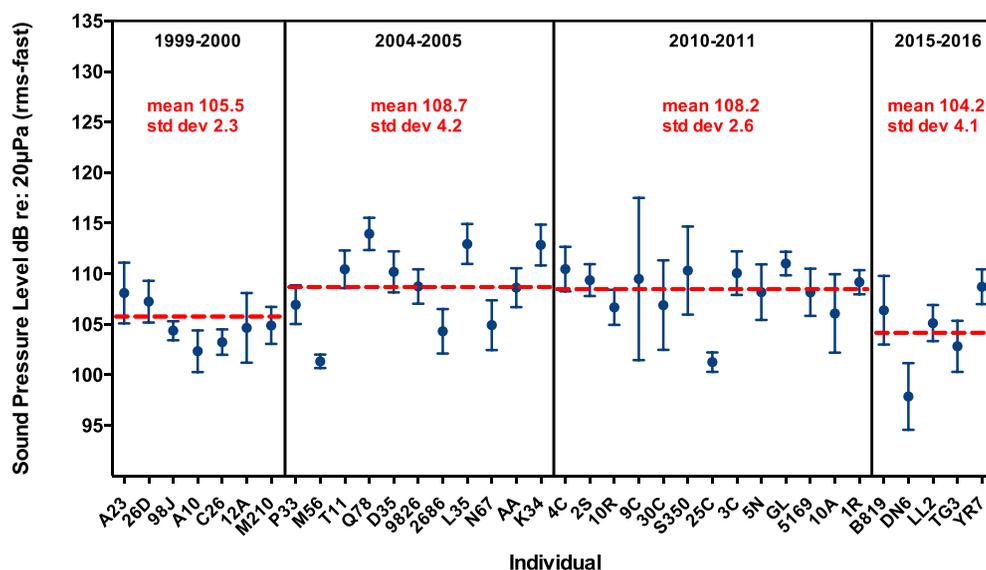


FIG. 1. (Color online) Source level measurements of display vocalizations emitted by 36 adult male elephant seals. Measurements were obtained during four independent breeding seasons over a 17-year period. Source levels are reported in dB re: 20  $\mu$ Pa at 1 m using the rms fast-weighted (125 ms) metric to enable between-season comparisons. Mean values (data points) and std. dev. (error bars) are shown for a subsample of 4 calls per individual (see the supplemental material<sup>1</sup>). Highlighted text and dashed lines show mean and std. dev. source level values for all males within each season.

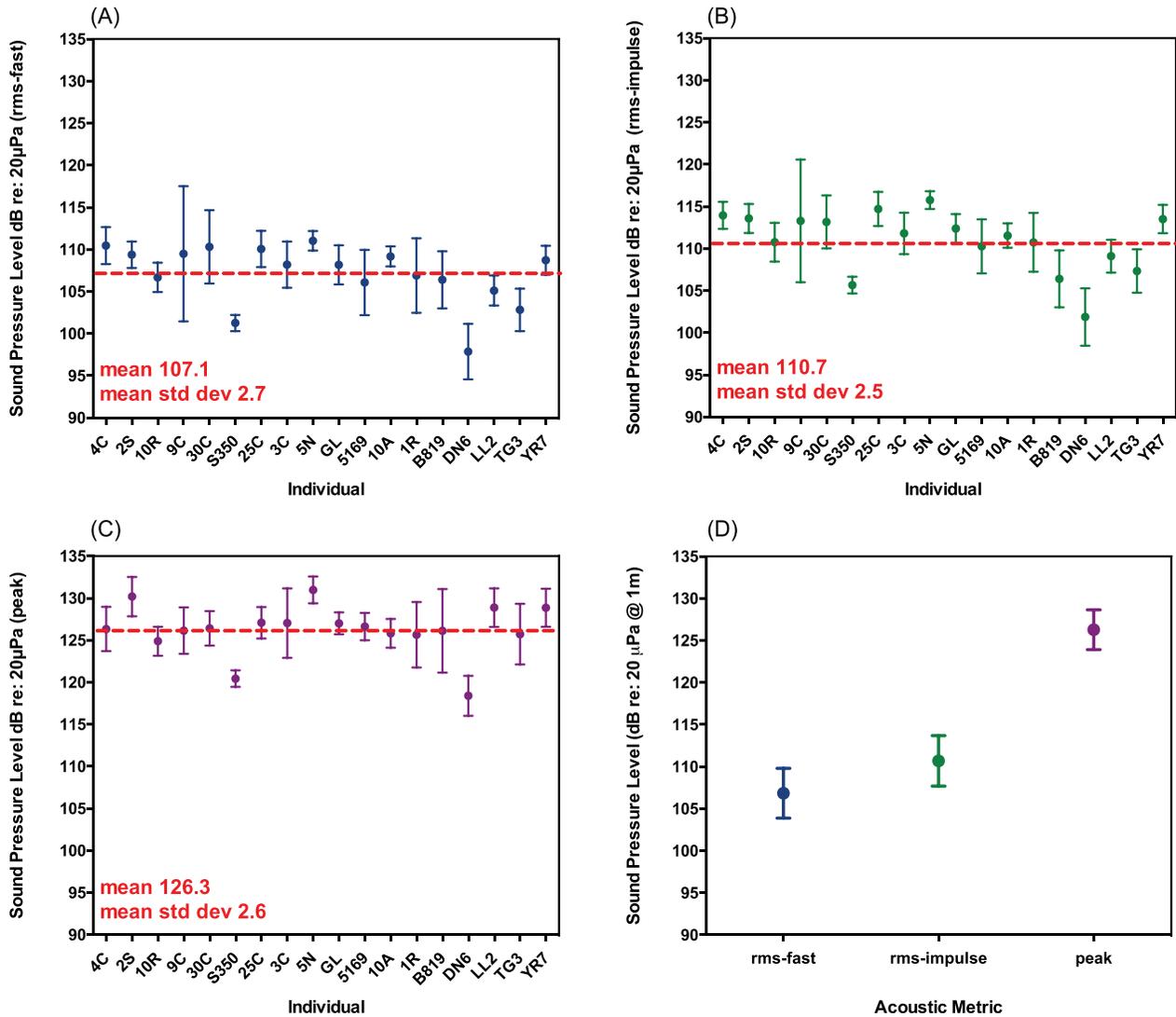


FIG. 2. (Color online) Source level measurements of display calls emitted by 18 adult male northern elephant seals during the 2010–2011 and 2015–2016 breeding seasons. Values are presented as (A) fast-weighted rms (125 ms), (B) impulse-weighted rms (35 ms), and (C) peak pressure levels referenced to 1 m for a subsample of the same 4 calls per individual [see the supplemental material (footnote 1)]. In (A)–(C), mean values (data points) and std. dev. (error bars) are shown. Highlighted text and dashed lines indicate mean source levels and mean std. dev. across males for each acoustic metric. (D) provides a comparison of the overall mean and std. dev. across males for each acoustic metric.

## B. Ambient noise measurements

Ambient noise measurements revealed differences in acoustic conditions dominated by escalating biotic (colony noise) and environmental sources (surf noise). Median noise spectrum levels are provided in Table I, for *low*, *moderate*, and *high* levels of activity in each context. In order to reflect variability within and between conditions, each calculated percentile level is presented for all conditions for both biotic (Fig. 3) and abiotic (Fig. 4) noise sources in panels (A)–(C). Figures 3 and 4 also include a comparison of the median (50th percentile) noise levels for the *low*, *moderate*, and *high* noise conditions in panel (D). The median (50th percentile) levels best represent typical conditions during periods where noise is dominated by biological activity and are the most appropriate comparison for average ambient noise during other periods, while the relative contributions of loud but brief (in the context of a 1-min sample) seal vocalizations are most obvious when evaluating the upper metric of noise

variance (i.e., 10th percentile levels). Nonetheless, deviations from the more typical noise levels exceeded 90% or 50% of the time (90th and 50th percentile levels) were greatest during *moderate*- and *high*-activity level conditions, showing noise energy predominantly below 1 kHz where the majority of energy in most elephant seal vocalizations occurs.

Differences among *low*, *moderate*, and *high* abiotic noise (surf) conditions were less pronounced between percentile levels for biotic noise. The ambient soundscape in many areas of the breeding rookery (in the absence of seal vocalizations) is primarily dominated by noise from nearby waves. This abiotic noise has a frequency spectrum that is relatively uniform in terms of spectral energy, and which decreases in spectrum level with increasing frequency. As wave noise is more continuous than the discrete vocalizations of seals, there is generally less variation across conditions. It is notable that ambient noise spectral levels were greatest below 0.9 kHz in the *high* surf condition, but were greatest at frequencies above 0.9 kHz in *moderate* surf conditions.

TABLE I. Ambient noise spectrum levels [in dB re:  $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$ ] for each 1/3-octave frequency band from 0.05–20 kHz. Median levels are given for biotic (colony) dominated noise and environmental (surf) dominated noise in each of three (low, moderate, and high) background noise conditions. The median levels shown in each column are derived from ten recordings.

Frequency (Hz)	Colony Noise			Surf Noise		
	Low	Moderate	High	Low	Moderate	High
50	44.8	46.8	50.1	44.7	51.0	58.6
63	44.6	46.3	49.9	44.9	50.7	57.4
80	44.2	45.9	49.2	44.5	50.2	56.3
100	45.1	46.1	50.5	43.6	49.7	56.1
125	45.3	48.7	51.9	43.4	49.4	56.4
160	44.0	47.7	51.4	43.0	48.5	53.8
200	42.8	43.9	48.2	41.2	46.6	51.3
250	41.3	42.5	47.4	38.3	44.2	48.8
315	41.0	42.5	48.7	35.5	44.7	47.6
400	43.6	44.9	51.8	35.8	44.1	47.4
500	37.7	42.7	48.6	35.0	41.9	48.5
630	34.6	36.9	43.8	31.7	39.8	43.3
800	34.0	36.8	40.7	29.4	37.4	43.2
1000	33.6	41.0	42.1	28.4	35.1	47.7
1250	29.2	37.4	38.4	25.2	32.6	35.5
1600	26.4	32.0	35.4	23.5	30.3	32.1
2000	22.9	29.2	32.2	21.4	27.7	28.3
2500	21.2	25.2	29.9	19.7	25.5	27.6
3150	20.1	23.4	26.8	17.1	22.9	24.3
4000	17.4	19.3	24.1	13.7	20.0	19.9
5000	12.9	15.0	21.5	10.2	17.2	16.4
6300	9.3	8.5	17.9	7.2	14.5	13.4
8000	7.0	4.6	15.8	3.2	11.5	10.0
10 000	3.6	1.7	13.2	-1.8	8.6	5.6
12 500	-1.2	-2.4	8.3	-7.8	5.1	1.7
16 000	-5.9	-7.8	4.7	-15.3	1.1	-3.0
20 000	-11.0	-15.9	0.1	-23.6	-4.6	-9.7
Broadband (unweighted)	71.6	77.8	84.0	69.3	75.6	92.5

### C. Lombard effect analyses

There was no evidence of a positive relationship between call level and ambient noise level for the four individuals with the most samples (Fig. 5). An analysis of the same relationship for all 12 males with available data also failed to show a potential Lombard effect; vocalization source levels pooled for these males are shown in Fig. 6 [panel (A): rms-fast; panel (B): rms-impulse; panel (C): peak pressure] relative to noise levels within three frequency bands corresponding to spectral regions containing the most signal energy in male elephant seal calls. A perfect Lombard effect would be predicted by an equivalent positive slope (i.e., a 1 dB increase in call level per 1 dB increase in noise spectrum level). However, call amplitude did not increase with increasing background noise ( $R^2 < 0.03$  and  $p > 0.05$  for each metric in each noise band). Figure 5(D) illustrates the relative SNR for calls as a function of noise level in the 0.4 kHz frequency band. In this case, a Lombard effect would be predicted by a constant SNR (no slope). That is, animals exhibiting a Lombard effect would increase source level with increasing noise to maintain a constant relationship in SNR. In contrast, the observed data demonstrate a

significant negative relationship between calculated SNR and median ambient noise within this band for all metrics ( $R^2 > 0.52$ ,  $P < 0.0001$ ).

## IV. DISCUSSION

Vocal displays produced by male northern elephant seals while ashore reliably reach broadband rms SPLs up to 114 dB. Thus, the competitive signals of northern elephant seals are among the loudest calls measured among terrestrial mammals, exceeding those of African elephants *Loxodonta africana* (Payne *et al.*, 1986) and howler monkeys *Alouatta spp.* (de Cunha *et al.*, 2015), and comparable in level to those of lions *Panthera leo* (McComb *et al.*, 1994), North American bison *Bison bison* (Wyman *et al.*, 2008), and southern elephant seals *Mirounga leonina* (Sanvito and Galimberti, 2003). When considering the most instantaneous elements of northern elephant seal airborne calls, peak pressure reaches 131 dB, an intensity rivaled only by the echolocation signals of some trawling bats, *Noctilio spp.*, at much higher frequencies (Surlykke and Kalko, 2008). The calls of male northern elephant seals often contain non-impulsive and impulsive elements (Casey *et al.*, 2018), which pose challenges to the accurate measurement of call amplitude. Fast-weighted (125 ms) rms SPL measurements provide a traditional metric of call amplitude that enables comparison to other mammals. However, impulse-based (35 ms) rms and peak sound pressure measurements enable a more comprehensive characterization of amplitude for these temporally complex signals. For a given individual, differences in these source level metrics arise from the presence and timing of non-impulsive and impulsive elements. Here, the conventional rms-fast setting underestimated the amplitude of most vocalizations. Measurement of call level was improved through the use of the impulse-based rms metric, with a shorter integration window. However, calls with transient elements (<0.1 s in duration) required instantaneous (peak pressure) metrics to fully characterize source level.

The breeding environment of the northern elephant seal has likely shaped the transmission, structure, and detectability of the male vocal display. While one may assume that these intense, broadband signals are intended to transmit over large distances, as is the case with other species (McComb *et al.*, 2003; Mitani and Stuht, 1998; Zuberbühler *et al.*, 1997), our observations indicate that competing males typically signal one another at much closer ranges (<100 m) during the breeding season. Indeed, given the close proximity between individuals in a tightly-clustered colony, a longer range detection of calls may not be necessary between rival males (Southall *et al.*, 2003). Previous work evaluating hearing sensitivity in this species has revealed that elephant seals possess poor sensitivity to airborne sounds relative to other pinnipeds that have been tested (Kastak and Schusterman, 1999). Thus, high-amplitude vocal signals appear to support effective short-range communication given poor aerial hearing in high (and often variable) ambient noise environments.

While ambient noise is elevated at lower frequencies by both biotic and abiotic sources on the colony, variation in ambient noise is particularly evident with respect to noise

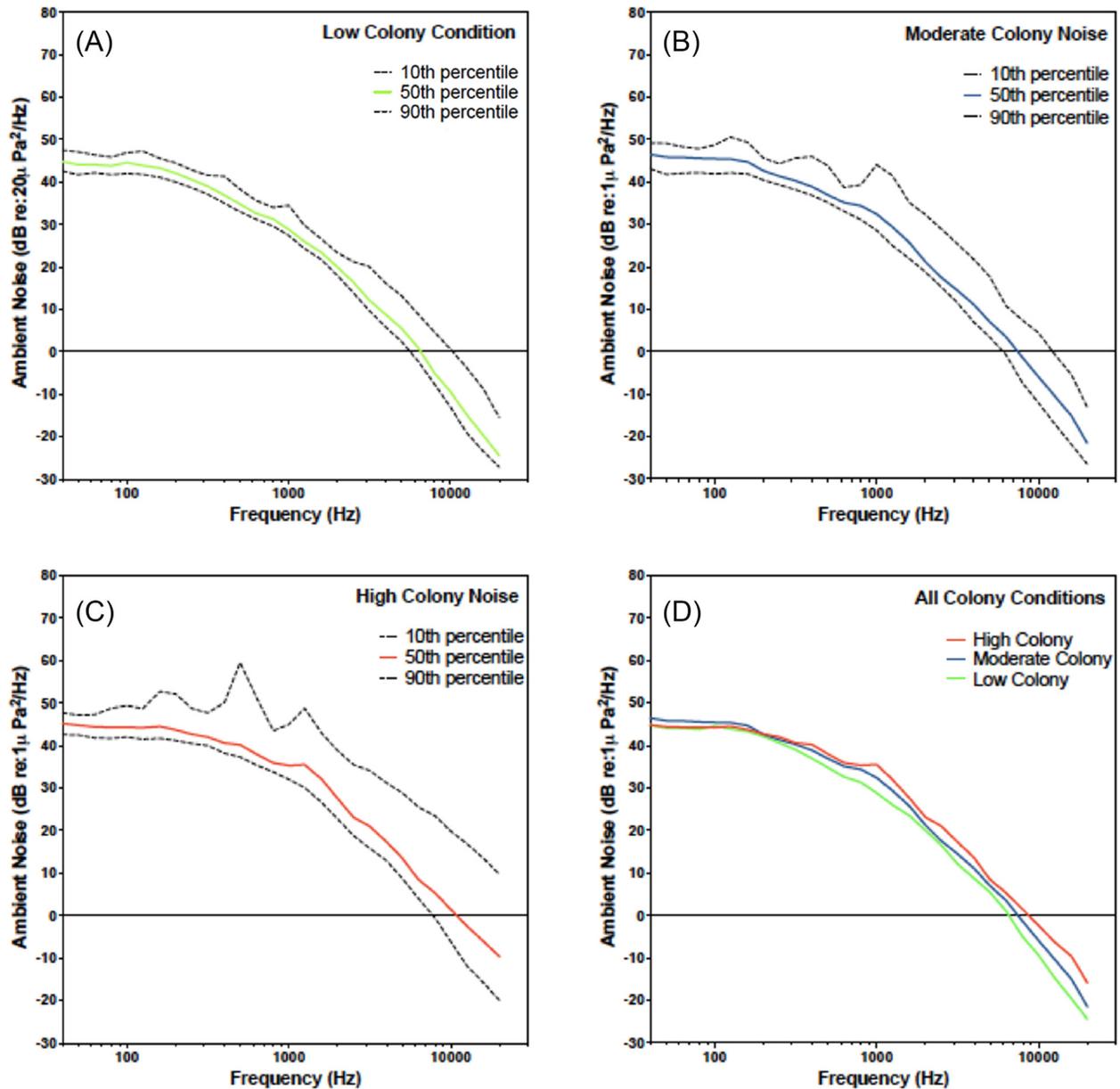


FIG. 3. (Color online) Biotic (seal-dominated) noise at the Año Nuevo breeding rookery measured during (A) low-activity, (B) moderate-activity, and (C) high-activity conditions (see Table 1). Ambient noise profiles comprise power spectral density levels [in dB re:  $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$ ] calculated from median 1/3-octave bands. Solid lines show median (50th percentile) levels for 1/3-octave center frequencies from 0.05–20 kHz; dashed lines show the corresponding 10th percentile noise levels (above) and 90th percentile noise levels (below). (D) compares the median levels for all intensity conditions (low, moderate, and high) associated with biotic noise.

associated with seal vocalizations. When comparing the median of the 10th percentile levels among three intensity conditions associated with biotic noise, we report a difference of up to 10 dB re:  $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$  between *low* and *high* background noise conditions at frequencies below 1 kHz. Variation in biotic noise is influenced by many factors, including animal abundance and density, the spatial distribution of different sex and age classes, the motivation of individuals within the colony, and the presence of vocalizing males during the measurement interval. Although our characterization of ambient noise levels at this colony does not reflect all possible conditions, it likely provides a fair representation of the typical acoustic conditions within which these signals have evolved.

Many animals face challenging conditions when attempting to communicate in noisy environments. A common compensatory strategy is to increase call levels as a function of increasing ambient noise (i.e., the Lombard effect). The Lombard effect has been demonstrated in birds (Brumm and Todt, 2002; Cynx *et al.*, 1998; Manabe *et al.*, 1998), bats (Hage *et al.*, 2013), macaques (Sinnott *et al.*, 1975), cetaceans (Holt *et al.*, 2009; Melcón *et al.*, 2012; Scheifele *et al.*, 2005), and humans (reviewed in Lane and Tranel, 1971). However, some studies of amphibians have demonstrated either weak effects (Halfwerk *et al.*, 2016) or an absence of this phenomenon (Love and Bee, 2010). Preliminary observations suggested that male northern elephant seals might increase the levels of their calls as a

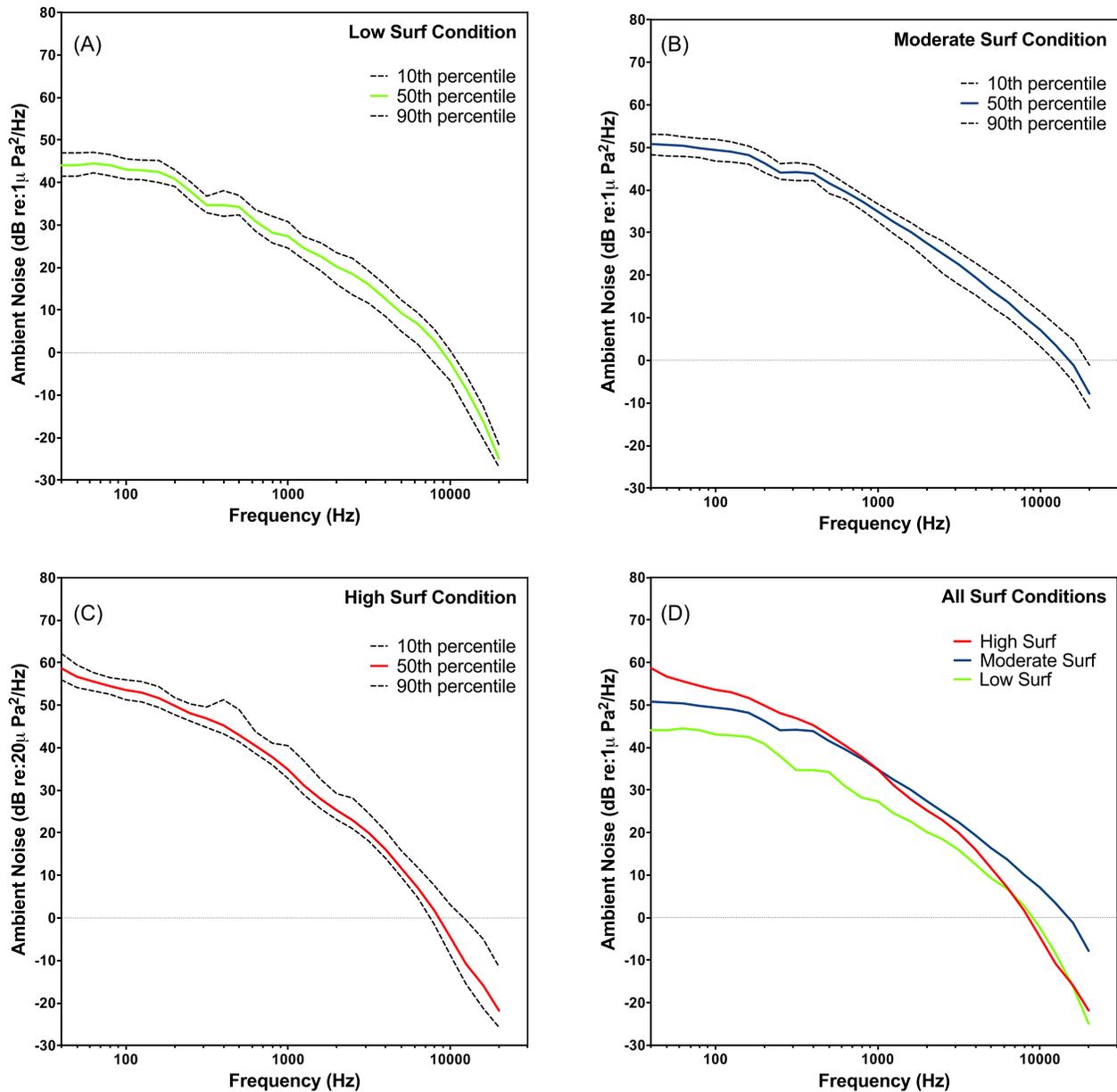


FIG. 4. (Color online) Environmental (surf-dominated) noise at the Año Nuevo breeding rookery measured during (A) low, (B) moderate, and (C) high conditions (see Table I). Ambient noise profiles comprise power spectral density levels [in dB re:  $(1 \mu\text{Pa})^2 \text{Hz}^{-1}$ ] calculated from median 1/3-octave bands. Solid lines show median (50th percentile) levels for 1/3-octave center frequencies from 0.05–20 kHz; dashed lines show the corresponding 10th percentile noise levels (above) and 90th percentile noise levels (below). (D) compares the median levels for all intensity conditions (low, moderate, and high) associated with environmental noise.

function of background noise (Insley and Southall, 2005). However, the more comprehensive data from the present study show that—for broadband levels across many males, metrics, and recording periods—there is little individual variation in call characteristics, both in general and in relationship to increasing background noise.

Noisy conditions within breeding colonies paired with poor aerial hearing ability have apparently selected for male northern elephant seals that produce high-amplitude vocal displays. Their consistent source levels indicate that these seals may be operating close to their physiological limit with regards to vocal production. Thus, males may not be able to compensate for increasing levels of ambient noise by emitting even higher amplitude signals, which would explain the lack of evidence for a Lombard effect in this species. The

mechanisms supporting call production in male northern elephant seals are not fully resolved, although they are assumed to involve flow-induced self-sustained vibrations of the vocal folds as in other mammals (Fitch, 2006; Harrison, 1995; Titze, 1998). An improved description of vocal tract anatomy is needed to determine the anatomical constraints placed on sound production among male seals. If males always operate at the upper limit of their vocal capacity, either because of auditory constraints or within the context of sexual selection (as has been observed in male displays in frogs; Love and Bee, 2010), this could explain why males in this study did not increase the amplitude of their vocalization in response to increasing background noise levels.

We note several alternative explanations for the lack of an observed Lombard effect in northern elephant seals.

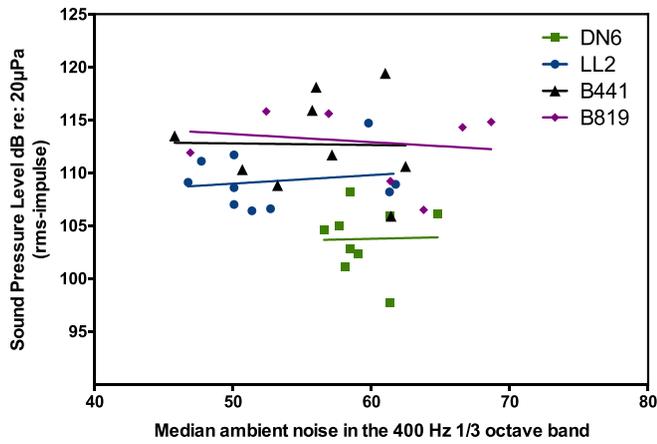


FIG. 5. (Color online) Assessment of potential Lombard effect using source level data for four individual males with at least eight recorded vocalizations and concurrent ambient noise measurements. Impulse-weighted (35 ms) rms source levels are plotted against associated median ambient noise level in the 0.4 kHz 1/3-octave bands. A Lombard effect would be indicated by a positive slope in source level with increasing noise.

Humans and some other vertebrates (e.g., echolocating bats) exhibit an enhanced Lombard effect at relatively low SNRs (see [Luo et al., 2018](#)). In contrast, northern elephant seals emit high-amplitude vocalizations that consistently exceed background noise within the same frequency bands by 30–40 dB. At such high SNRs, a strong Lombard effect might not be expected. Therefore, it is not possible to conclude that male seals never increase the level of their calls, particularly in lower SNR contexts. However, sampling occurred over a wide range of representative environmental and biological noise conditions, other than extreme weather or rookery noise events. Thus, the very static nature of their high call source levels suggest that a Lombard effect is practically absent in typical ambient contexts.

Further, the absence of a Lombard effect could be related to the signal's function. In other species, the amplitude of an animal's vocalization may predict the outcome of sexual competition. Signal amplitude has been correlated to a male's fighting ability, age, or size (as in [Castellano et al., 2000](#); [Fischer et al., 2004](#); [Wyman et al., 2008](#); [Kitchen et al., 2013](#)), and can

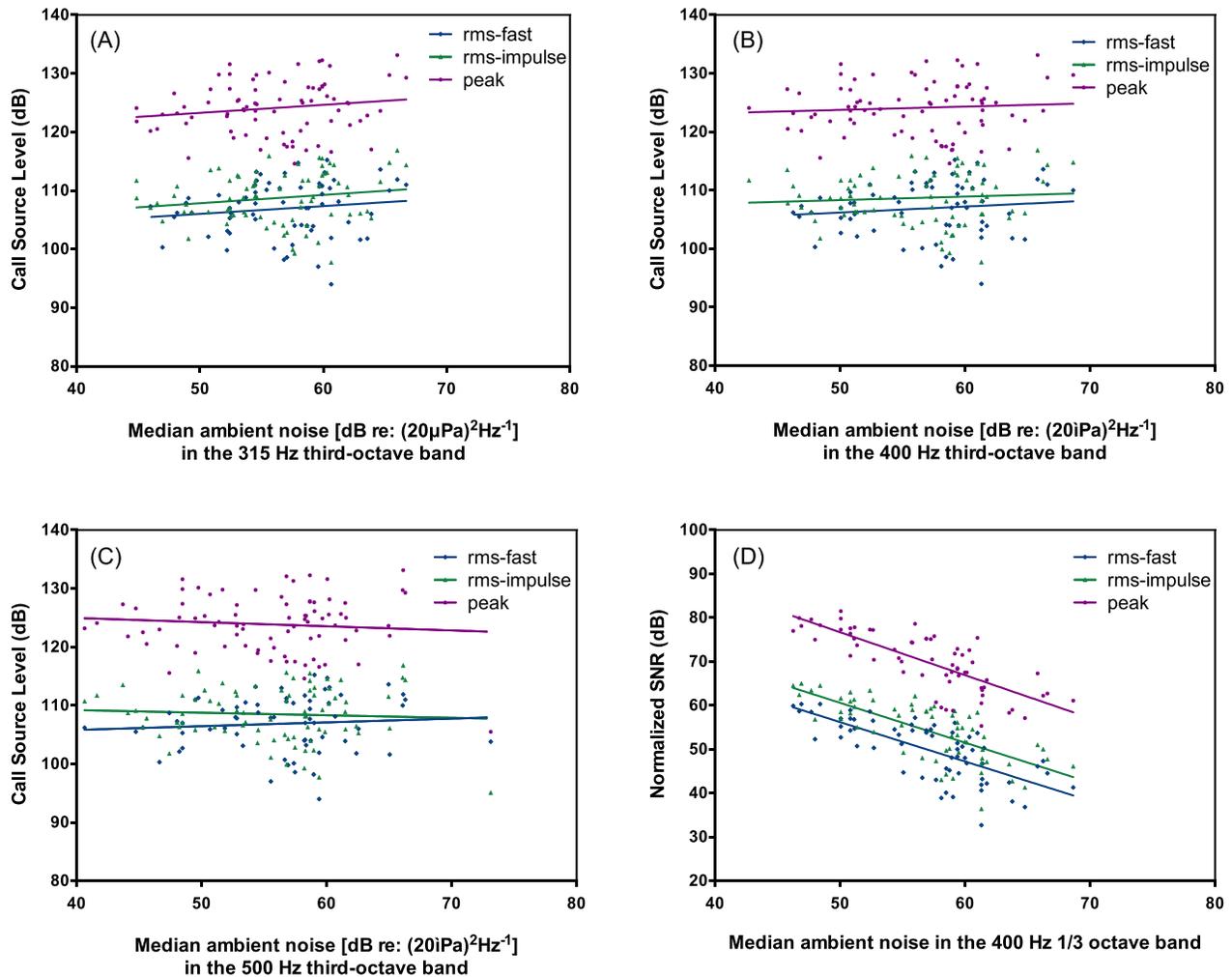


FIG. 6. (Color online) Assessment of potential Lombard effect using pooled source level data for 12 males and concurrent ambient noise measurements. Fast-weighted (125 ms) rms, impulse-weighted (35 ms) rms, and peak pressure levels of the same calls are plotted against associated median ambient noise level in the (A) 0.315 kHz, (B) 0.4 kHz, and (C) 0.5 kHz 1/3-octave bands. A Lombard effect would be indicated by a positive slope in these metrics with increasing noise. (D) shows the SNR for each measurement plotted against median ambient noise in the 0.4 kHz band, which contains the frequency of maximum energy for male northern elephant seal vocalizations. A Lombard effect would predict that males should maintain a constant SNR with increasing noise levels; in contrast, the data show that males maintain a constant source level of acoustic displays with increasing ambient noise and thus exhibit a negative slope in the effective SNR.

serve as an honest signal of resource holding potential to listeners (Bradbury and Vehrencamp, 1998). Notably, prior research on northern elephant seals indicates that the source level of an adult male's vocal display does not correlate with body size or dominance status (Casey *et al.*, 2015). Additionally, call amplitude does not reflect motivational state or social context among adult male competitors (Casey *et al.*, 2015), as would be predicted by common motivation-structural relationships in animal vocalizations (Bradbury and Vehrencamp, 1998). Instead, the stereotyped calls of each male, including the very stable source levels exhibited by individuals in this study, appear to aid in conveying identity and the process of associative learning (Casey *et al.*, 2015).

These findings build on several decades of research concerning the production and function of male northern elephant seal vocalizations. Taken together with available hearing data, ambient noise conditions of the environment, and various aspects of vocal behavior, the source level measurements presented here advance a holistic understanding of the constraints on acoustic communication in this species.

## ACKNOWLEDGMENTS

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<sup>1</sup>See supplementary material at <https://doi.org/10.1121/1.5139422> for source level metadata and raw data for all individuals.

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