

# Evidence of a Lombard response in migrating humpback whales (*Megaptera novaeangliae*)

Rebecca A. Dunlop<sup>a)</sup>

School of Veterinary Science, University of Queensland, Gatton, Queensland 4343, Australia

Douglas H. Cato<sup>b)</sup>

Defence Science and Technology Organisation, Australian Technology Park, Eveleigh, New South Wales 1430, Australia

Michael J. Noad

School of Veterinary Science, University of Queensland, Gatton, Queensland 4343, Australia

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The Lombard reflex is an increase in the subject's vocal levels in response to increased noise levels. This functions to maintain an adequate signal-to-noise ratio at the position of the receiver when noise levels vary. While it has been demonstrated in a small number of mammals and birds including some whales, it has not yet been shown to occur in one of the most vocal species of baleen whale, the humpback whale (*Megaptera novaeangliae*). Humpback whales were simultaneously visually and acoustically tracked (using an array of calibrated hydrophone buoys) as they migrated southward. Source levels of social vocalizations were estimated from measured received levels and a site-specific empirical sound propagation model developed. In total, 226 social vocalizations from 16 passing groups of whales were selected for final analysis. Noise levels were predominantly wind-dependent (from sea surface motion) and ranged from 81 to 108 dB re 1  $\mu$ Pa in the 36 Hz–2.8 kHz band. Vocalization source levels increased by 0.9 dB for every 1 dB increase in wind-dependent background noise levels, with source levels (at 1 m) being maintained  $\sim$ 60 dB above the noise level.

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## I. INTRODUCTION

Vocal communication involves the provision of acoustic information by a signaling animal that can be utilized by a receiving animal to make a decision. Measurable aspects of signaling behavior include the type of signal, as well as the signal level, frequency, and rates at which they are produced. These parameters can be related to the social context of the signaler, the environment in which the signal is produced, and/or the location and context of the intended receiver. Acoustic signal levels attenuate during transmission and, as the distance from source to receiver increases, the received signal level generally decreases. The signal-to-noise ratio (SNR) is a crucial factor in detecting acoustic signals (Klump, 1996); therefore, the signaler must produce the signal at an appropriate intensity for the receiver to detect and decode, and this intensity may vary with distance to the target or receiver (Wiley and Richards, 1982). In animals, certain signals have evolved and adapted to compensate for signal degradation. The end result is that adequate SNRs are maintained at the receiver even at considerable distances (Naguib, 1995; Brown and Hanford, 2000; Naguib and Wiley, 2001; Brumm and Slater, 2006; Miller, 2006; Naguib *et al.*, 2008). These are sometimes termed “long-range” signals.

Background noise is a competing factor in signal detection by the receiver and there are obvious benefits in producing signals of higher levels, at higher rates, or at different frequencies during periods of high background noise (Wiley and Richards, 1982). Human speech changes in response to noise are collectively called the Lombard effect, where signalers modify vocal characteristics such as level, pitch, and/or rate of signal production in a noisy environment to improve signal detection (Lombard, 1911). Most studies designed to test for the Lombard effect in animals look for an increase in signal level in response to increased broadband background noise levels. This response has been found to occur in birds (Potash, 1972; Cynx *et al.*, 1998; Brumm and Todt, 2002; Brumm, 2004), some species of cetacean (Holt *et al.*, 2009; Parks *et al.*, 2010), and primates (Brumm *et al.*, 2004). Further experiments in various species of bird showed that the noise had to be in the frequency band of the calls to be most effective at eliciting a Lombard response (Manabe *et al.*, 1998; Brumm and Todt, 2002). Signal duration, as well as signal level, has also been found to increase in response to playbacks of increased noise (Brumm *et al.*, 2004), suggesting that animals modify their signal in more than one way to solve the noise problem.

Marine mammals are very dependent on acoustic communication in an environment where visual and olfactory signals have very limited range. Humpback whales are one of the most vocal of the baleen whale species in that males “sing” and all cohorts produce a wide range of non-song vocal “social sounds.” The song is a male-only signal

<sup>a)</sup>Author to whom correspondence should be addressed. Electronic mail: [r.dunlop@uq.edu.au](mailto:r.dunlop@uq.edu.au)

<sup>b)</sup>Also at: University of Sydney Institute of Marine Science, Sydney, NSW 2006, Australia.

defined as being long, complex, repetitive, and highly stereotyped (Payne and McVay, 1971; Cato, 1991). Non-song social vocalizations in humpback whales are not clearly structured like song as they have little serial patterning and are heard as single sounds or in short bursts (Tyack, 1983; Tyack and Whitehead, 1983; Silber, 1986). Humpback whales utilize an extremely variable catalog of social vocalizations, from almost infra-sonic “grumbles” to high frequency “chirp”-like sounds (Dunlop *et al.*, 2007), and these sounds are apparently used by both sexes (Dunlop *et al.*, 2007; Dunlop *et al.*, 2008; Zoidis *et al.*, 2008), and for closer-range communication compared to song (Dunlop *et al.*, 2008; Dunlop *et al.*, 2013a). Social sounds also include sounds from behaviors such as “breaching” (leaping out of and slamming into the water), “pec slapping” (repeatedly slapping one or both pectoral flippers on the water surface), and “lobtailing” or “fluke slapping” (thrashing the flukes onto the water surface; Whitehead, 1985). Although the function of surface behaviors in humpback whales is not well understood, it has been suggested that breaching, especially, may have an important signaling role due to the loud splash made (Herman and Travolga, 1980; Norris and Møhl, 1983; Clark, 1990). Pectoral flipper and fluke slapping may also serve a communicatory function (Silber, 1986; Thompson *et al.*, 1986; Deakos, 2002; Wahlberg *et al.*, 2002; Dunlop *et al.*, 2008). Previous work has found that in periods of increased wind-generated noise, humpback whales switch from using primarily vocal sounds to primarily surface-generated sounds (Dunlop *et al.*, 2010). In other words, one way humpback whales solve the noise problem is to change their communication strategy.

Several studies have reported evidence of the Lombard effect (an increase in vocal source level) in a variety of species of cetacean including the North Atlantic right whale (*Eubalaena glacialis*; Parks *et al.*, 2010), beluga (*Delphinapterus leucas*, Scheifele *et al.*, 2005), and killer whale (*Orcinus orca*; Holt *et al.*, 2009, 2011). Source levels of humpback whale social vocalizations can be quite high (Thompson *et al.*, 1986), but can also vary by tens of dB (Dunlop *et al.*, 2013a). A previous study on a population of humpback whales migrating southward along the east Australian coastline found source levels of humpback whale social vocalizations ranging from 123 to 184 dB re 1  $\mu$ Pa at 1 m [root-mean-square (rms); Dunlop *et al.*, 2013a]. As general background noise levels in the same study ranged from 76 to 120 dB re 1  $\mu$ Pa (40 Hz–2 kHz), and up to 140 dB re 1  $\mu$ Pa when there were vessels in the area, many of the vocal sounds would exceed background noise for substantial distances. This suggests that humpback whales could be using some of their social vocalization sounds to communicate with groups in the area over ranges of several kilometers rather than just communicating within their own group (ranges of tens of meters). Therefore, some of the signals could be regarded as long-range and, following previous studies, it might be expected that humpback whales should increase the level of vocal sounds in noise to maintain an effective area of communication. Hence, the aim of this study is to determine if humpback whales increase the level of social vocalizations in response to increased levels of wind noise.

## II. METHODS

### A. Data collection

Recordings of humpback whale vocalizations were carried out during September and October in 2003, 2004, and 2008 at Peregian Beach (26°S, 153°E), Queensland, on the east coast of Australia during the whales’ annual southward migration from their breeding grounds inside the Great Barrier Reef to their feeding grounds in the Southern Ocean. About half of the migrating whales pass within 10 km of the shore at Peregian Beach and land-based behavioral observations were collected on these groups from an elevated survey point, Emu Mountain (73 m high), adjacent to the coast. Humpback whale groups were located using a theodolite [Leica TM 1100 in 2003 and 2004; TC407 in 2008 (Leica Geosystems)] connected to a notebook computer running *Cyclopes* software (E. Kniest, Univ. Newcastle, Australia). Each group position was annotated with observed behaviors and group compositions (e.g., adult and calf, two adults).

Acoustic recordings were made from five hydrophone buoy systems anchored in 18–28 m of water. Each hydrophone buoy consisted of a surface buoy [containing batteries, a custom-built amplifier (+20 dB), and VHF radio transmitter from an AN/SSQ 41B Naval sonobuoy] and a High Tech HTI-96-MIN hydrophone (High Tech Inc) with built-in +40 dB pre-amplifier and sensitivity of  $-164$  dB re 1 V/ $\mu$ Pa. The surface buoy was moored to a concrete block anchor. The hydrophone was moored separately suspended above the sea floor by a float and its cable attached along the buoy mooring rope from the anchor up to the buoy. This setup allowed the buoy to swing on its moorings without causing significant movement of the hydrophone. The five hydrophone buoys formed a T-shaped array where buoys 1–3 were in a line 1.5 km from the beach, parallel to the shoreline, and  $\sim 700$  m apart, and buoys 4 and 5 extended seaward from buoy 2 in a line perpendicular to the shore  $\sim 600$  m apart. Positions of the hydrophones were determined using two shore based theodolites at known positions taking cross bearings of a rod held above the hydrophone by a diver (see Noad *et al.*, 2004, for further details on the setup).

Radio transmissions from the buoys were received at a base station just behind the beach using a vertically oriented Yagi antenna matched to the radio transmission frequencies, and linked to a four-channel, low-noise, VHF receiver (type 8101) and a Winradio<sup>®</sup> receiver for the fifth channel. Signals were passed via custom made anti-aliasing filters ( $-30$  dB at 20 kHz) to two computers equipped with National Instruments E-series data acquisition cards (N6034E) and with *Ishmael* software (Mellinger, 2001). Recordings were made as wave files (.wav) with a sampling rate of 22.05 kHz and a depth of 16 bits. All measurements of received levels were made using the type 8101 receiver, while both receivers were used for localization of sources.

### B. Localization of whale sounds

Acoustic tracking was performed either in the field in real-time, simultaneously with the theodolite tracking, or during post-field analysis. Whale sounds were tracked by

time of arrival differences between hydrophone pairs using *Ishmael*. The T-shaped array allowed position ambiguities to be resolved. The accuracy of the acoustic tracking using the three hydrophones parallel to the beach has been determined previously by comparing acoustic positions of singers with their positions determined by theodolite when they surfaced (Noad and Cato, 2001; Noad *et al.*, 2004). Individual acoustic position accuracy varied from 5% of the range at 2 km to 10% at 10 km. The use of the five hydrophone array and taking the center of the positions of several consecutive sounds provided a more accurate estimate of the position of the vocalizing whale. Since vocalizing whales were in water depths <40 m, the depth of the source did not significantly affect the determination of its position.

Acoustic tracks of vocalizing whales were overlaid on the visual tracking map in *Cyclopes* (E. Kniest, Univ. Newcastle, Australia) and the combined acoustic/visual data were shared between the base and hilltop stations using a wireless network. This provided almost real-time superposition of acoustic and visual tracks out to the 10 km limit of the study area. Further details on this methodology are provided in Noad and Cato (2001), Noad *et al.* (2004), and Dunlop *et al.* (2013a). There were rarely more than six groups migrating through the 10 km-radius study area at any one time, and these were usually widely dispersed, unless a joining interaction between two groups was occurring. Given the accuracy of the system and the way in which groups could be simultaneously visually and acoustically tracked in real-time, there was no doubt as to which groups were vocalizing at any time. Within groups, however, it was not possible to determine which animal was vocalizing.

### C. Calculation of received levels and background noise

The hydrophones with built-in preamplifiers were calibrated at the Defense Science and Technology Organisation calibration facility in Woronora Dam, NSW. The rest of the recording chain was calibrated by inserting tones and white noise of known levels into the amplifier in the buoy in place of the hydrophone and recording these as per the whale sounds on the computer. Acoustic recordings were measured in the standard 1/3 octave bands using SpectraPLUS (Sound Technology Inc.). The results were imported into Microsoft Excel. The full system sensitivity varied by <1.5 dB in the 1/3 octave bands over the frequency range 40–10 000 Hz.

Received levels of social sounds ( $n = 302$ ) were measured in the standard 1/3 octave filter bands over the range 40 Hz–10 kHz from 16 migrating humpback whale groups. Two measures of received level were made: mean square pressure level,  $RL_{rms}$  (often referred to as rms level) between the start and end time ( $t_1$ – $t_2$ ) of the sound, and the peak-to-peak level of pressure of the wave form,  $RL_{pp}$ . An iterative process was used to determine  $t_1$  and  $t_2$  as described in Dunlop *et al.* (2013a)  $RL_{pp}$  was obtained by taking  $20 \log$  of the greatest change from positive to negative pressures in any one cycle in the wave form. Since the received levels included a contribution from the background noise, this was removed by subtracting the mean square voltage of the background noise

(measured just before or after the sound) from the mean square voltage of the vocalization over the period  $t_1$  to  $t_2$  for each 1/3 octave band. The resulting 1/3 octave band mean square voltages of the signal were summed and converted to decibels to give the broadband signal level.  $RL_{rms}$  and  $RL_{pp}$  were then determined from these results using the system calibration.

The mean square pressure source level of a social sound (dB re 1  $\mu$ Pa at 1 m) could then be calculated as

$$SL_{rms} = RL_{rms} + TL, \quad (1)$$

with a similar equation for the peak-to-peak source level  $SL_{pp}$ . The estimation of  $TL$  is described below.

Background noise mean square pressures were summed over the 40 Hz–2.5 kHz 1/3 octave bands (actual band 36 Hz–2.8 kHz) and converted to decibels to give the broadband noise level. This bandwidth was chosen because almost all the energy in the vocalizations lies within this band. Groups were only included in this analysis if there were no boats audible on the array (and there were no sighted boats traversing the study site), as well as no audible singing whales (so that singers would have been >10 km away and would not have contributed significantly to the background noise at the group) at the time the group was vocalizing. On a few occasions, there was very faint song audible but the singer noise contributed <1 dB to the broadband noise level. Since the background ambient noise was predominantly wind dependent (Dunlop *et al.*, 2010), and the wind speed was stable over the study site, the background noise measured at the array could be considered to be similar to that at the vocalizing whales.

The system electronic noise over the 36 Hz–2.8 kHz band had an equivalent input level of 76.7 dB re 1  $\mu$ Pa (using the type 8101 receiver). Ambient background noise levels below 81 dB re 1  $\mu$ Pa were excluded from the analysis as being too close to system noise to obtain a reliable measurement. For higher levels, the contribution of system noise was removed from the measurements by subtracting the mean square voltage of the system noise from the mean square voltage of the measured background noise and converted to decibels to give the true background noise level.

### D. Sound transmission empirical modeling

Transmission loss was measured (dB re 1  $\mu$ Pa re 1 m) at the site as described in Dunlop *et al.* (2013a), using a noisy boat as a source over distances from 100 m to 10 km from the hydrophones (determined from the Global Positioning System positions of the boat) and playback of octave band limited white noise, at three positions. These led to regression lines on the received levels as a function of distance from the sources of the form

$$TL = a + b \log(x), \quad (2)$$

where  $b$  is the slope of the regression line,  $x$  is distance (meters), and  $a$  is a constant (which may be frequency dependent). The horizontal distance was approximated as the slant range since water depths of the transmission paths were <40 m, and thus very small compared with the distances.

For most frequencies,  $b$  varied with distance, but could be well approximated by two values, one applying to distances less than, and the other greater than, a crossover value where the slope changed. Values of  $a$  and  $b$  and the crossover distances are given in Dunlop *et al.* (2013a). Both  $a$  and  $b$  varied with frequency so Eq. (1) was used in each 1/3 octave band to determine the source levels in these bands. Broadband source levels were determined by summing the mean square pressures in each band and converting to dB re 1  $\mu$ Pa.

## E. Analysis

There are two problems in testing the Lombard hypothesis using source levels of vocal sounds from measurements where the distance of the sources from an acoustic array vary significantly. The first problem is that the further the source is from the array, the more likely it is that lower source level sounds will be missed in the recording (as noted in Dunlop *et al.*, 2013a). The second problem is that increased background noise will increase the proportion of lower source level sounds missed, thus biasing the data to higher source levels in higher noise. The combination of these effects could potentially result in a false positive when testing for the Lombard effect, where lower level sounds are more likely to be missed in high noise. In higher noise (where sounds are likely to be missed), the variance of source levels measured would be expected to be unequal compared to variance of source levels recorded in low noise, where sounds should not have been missed (suggested by Holt *et al.*, 2011). If assuming a normal distribution of source levels, in high noise the data would be skewed to the right (where sounds of low source level would not have been captured in the sample).

To check for unequal variance and skew, the source level dataset was first categorized into sounds detected in low, mid, and high noise. Background (predominantly wind-dependent) noise levels ranged from 81–108 dB re 1  $\mu$ Pa in the 36 Hz–2.8 kHz band, and noise categories were selected to attempt to capture an even spread of noise data in each category. Low noise broadband values ranged from 81 to 90 dB re 1  $\mu$ Pa (with a modal value of 90 dB re 1  $\mu$ Pa). Wind speeds recorded half-hourly throughout the field season by an automatic weather station at the Sunshine Coast Airport ~10 km south of the study site and within 1 km of the sea, were generally below 10 kn. The mid-noise category broadband values ranged from 91 to 97 dB re 1  $\mu$ Pa (with a modal value of 95 dB re 1  $\mu$ Pa; wind speeds ranged from 10–15 kn). The high noise broadband values ranged from 98 to 108 dB re 1  $\mu$ Pa (with a modal value of 100 dB re 1  $\mu$ Pa; wind speeds of 16–22 kn). This categorization resulted in a 5 dB separations between the modal values of low, mid, and high noise categories. Non-constant variance of source levels among the three noise categories was tested using the Breusch–Pagan Test in “R” (R Foundation for Statistical Computing using the “car” package; Fox and Weisberg, 2011). Results are reported as a chi-squared value with associated degrees of freedom (d.f.) and  $p$ -value. Source level data within each noise category were also plotted as a histogram and a probability density function (describing the relative likelihood for each source

level to have a given value) fitted to look for evidence of skew (where, if low level sounds were being missed in high noise, then distribution of the data in the high noise category would be expected to be skewed toward a higher mean). A standard normal distribution curve was also fitted to the data within each noise category for comparison.

An obvious solution to ensure equal probability of detection of sounds within each noise category would be to limit the analysis to measuring only sounds very close to the array as a way of minimizing the chance of missing low level sounds. However, this would have reduced the sample size substantially. Another solution, used in this study, is to account for the detection limits of the system and create a situation where there is equal probability of detecting each sound regardless of noise and distance of the source from the array. To accomplish this, all sounds that potentially would be missed in high noise conditions were excluded from the analysis as follows. First, the received SNR ( $SNR_a$ ) at the array was calculated for all vocal sounds from

$$SNR_a = RL_{rms} - NL_a. \quad (3)$$

Sounds for which  $SNR_a \geq 5$  dB in the 1/3 octave band containing the spectral peak of the vocalization could be reliably detected and so were chosen for analysis, i.e., data for which  $SNR_a < 5$  dB were rejected (both  $RL_{rms}$  and  $NL_a$  were measured in this 1/3 octave band). A 5 dB  $SNR_a$  in the 1/3 octave band corresponded to  $-9$  dB for noise measured over the band 36 Hz–2.8 kHz (40 Hz–2.5 kHz 1/3 octaves), i.e., broadband noise. The modal broadband noise value of 90 dB re 1  $\mu$ Pa, 95 dB re 1  $\mu$ Pa, and 100 dB re 1  $\mu$ Pa were typical for the “low noise,” “mid noise,” and “high noise” conditions, respectively. Therefore the lowest received level of a vocal sound that could be reliably detected in low noise (using a  $SNR_a$  limit of  $-9$  dB in broadband noise) was 82 dB re 1  $\mu$ Pa, 87 dB re 1  $\mu$ Pa in mid-noise, and 92 dB re 1  $\mu$ Pa in high noise. However, most sounds had  $SNR_a$  values significantly greater than these values (the lowest  $SNR_a$  in the final sample was  $-6$  dB). From each of the three lowest detectable received levels, the equivalent  $SL_{rms}$  at various distances from the array was estimated using the transmission loss equation for the 125 Hz octave band (which was the most common transmission loss equation used to estimate the  $SL_{rms}$  of the vocal sounds).

A subset of the data was created that included only sounds that could have been detected in high noise conditions according to the detection limits of the system. This dataset was used in a mixed model analysis to determine the effect of noise level on  $SL_{rms}$  and  $SL_{pp}$  of vocalizations. Linear mixed effects models (in “R”) were fitted to each response variable (the two measure of source level) and included the random effect of “whale group” (and associated variance). Standard statistical models assume independence of errors, but when measurements are taken from the same group, they are correlated. Mixed-effects models account for interdependence in multiple observations within individuals as they assume the data within groups (in this case, each vocalizing group) are dependent among the observations and model the covariance structure introduced by grouping the data. The included random effect estimates the distribution

of the means as a standard deviation of the differences of the factor-level means around an overall mean, instead of estimating a mean for every single factor level. Linear mixed-effects models (using the lme4 package in “R,” Bates *et al.*, 2011) were used, which included the effect of noise category (categorical) and distance from the recording array (continuous) in the model. “Group ID” was included as a random factor. *P*-values were generated using the Markov Chain Monte Carlo (MCMC) method within the “language R” package. Effect sizes and the 95% highest posterior density intervals are also reported from the MCMC output. Residuals of each model were checked for homoscedasticity and errors were checked for normality. Within model *t*-values with associated *p*-values are reported for the effect size and significance of noise, while accounting for the effect of distance from the array.

### III. RESULTS

In total, 16 humpback whale vocalizing whale groups were selected for analysis and 302 social vocalizations were measured from these groups. The raw regression analysis (using all vocal sounds from all groups) suggests a positive correlation between  $SL_{rms}$  and broadband (36 Hz–2.8 kHz) background noise level, however, with a large amount of spread (Fig. 1). There was a large variation in the number of social vocalizations produced per recorded group (from 3 to 83) and each group had a different repertoire of sounds (ranging from 2 to 12 different vocal sound types).

The  $SL_{rms}$  of the vocal sounds were then plotted as a function of distance of each sound from the array (separated into the three noise categories), and a linear trend line added illustrating the relationship between estimated  $SL_{rms}$  of each sound and distance of the vocalizing whale from the array within each noise category (Fig. 2). The lower limit of detectability of sounds in low, mid, and high noise levels as a function of the distance from the acoustic array are also shown as the equivalent  $SL_{rms}$  of the lowest detectable vocal sound within each noise category (dotted lines).

After visual inspection of the graph, the dataset was curtailed to only use sounds recorded within 2.5 km ( $n = 279$ ) as detectability dropped off quite significantly beyond this

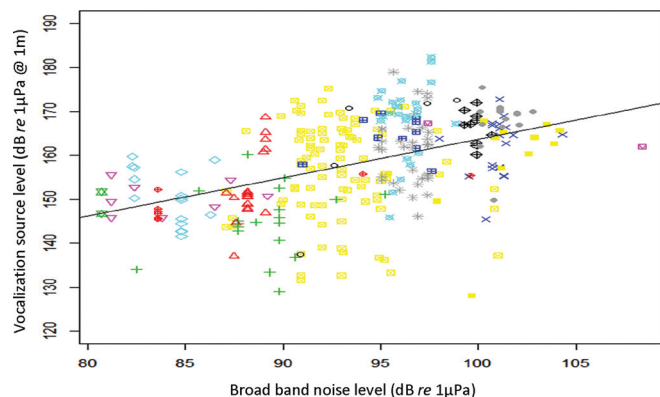


FIG. 1. The source level ( $SL_{rms}$ ) of humpback whale social vocalizations ( $n = 302$ ; dB re  $1 \mu\text{Pa}$  at 1 m) taken from 16 different humpback whale groups (each group is coded by color and symbol) as a function of broadband (36 Hz–2.8 kHz) background noise levels (dB re  $1 \mu\text{Pa}$ ).

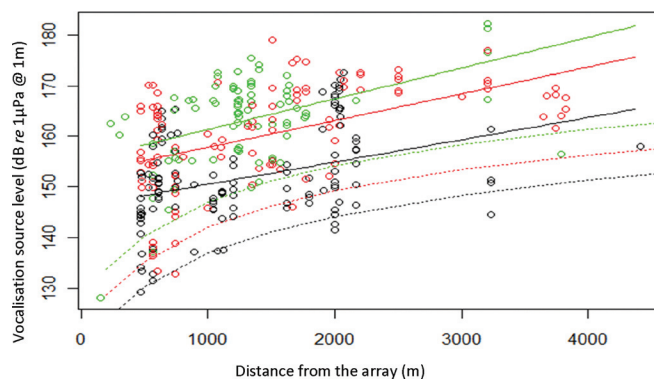


FIG. 2. The source level (rms) of humpback whale social vocalizations ( $n = 302$ ) taken from 16 different humpback whale groups categorized by low (black), mid (red), and high (green) noise levels at the array. A linear trend line for each noise category shows the relationship between estimated  $SL_{rms}$  of the sound and distance of the vocalizing whale from the array. The lower dotted lines illustrate the relationship between the lowest detectable  $SL_{rms}$  and distance within each noise category.

distance. Histograms of the remaining  $SL_{rms}$  data in the low, mid, and high noise categories were created using this dataset for visual inspection (Fig. 3).

Results of the non-constant variance score test (Chi-squared = 2.35, d.f. = 1,  $p = 0.12$ ) suggest that the assumption of non-constant variance has not been violated in this dataset, and the variance in measured source levels within each noise category is equal. However, the histogram for high noise shows that the data are slightly skewed, although not substantially, when comparing with a standard normal distribution curve. Therefore, there is the possibility that a

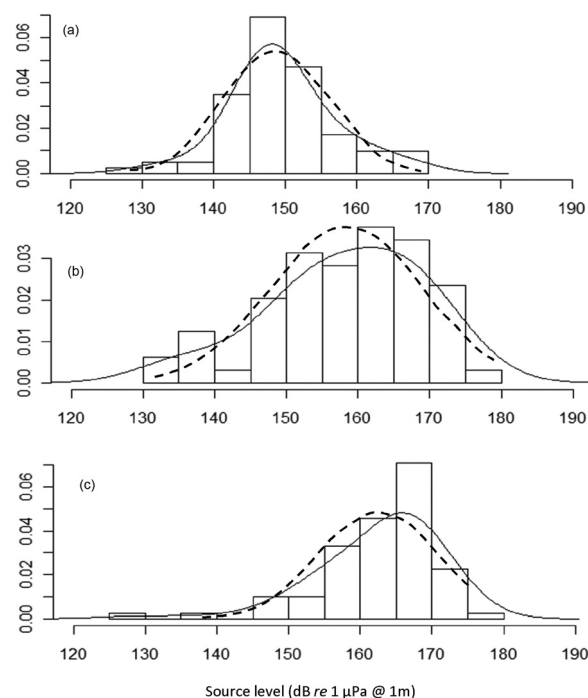


FIG. 3. Histograms showing the distribution of source level (rms) data of (a) humpback whale social vocalizations ( $n = 279$ ) within 2.5 km categorized into those recorded in low (81–90 dB re  $1 \mu\text{Pa}$ ), (b) mid (91–97 dB re  $1 \mu\text{Pa}$ ), and (c) high (98–108 dB re  $1 \mu\text{Pa}$ ) noise levels fitted with a probability density function (solid line) and a standard normal distribution curve (dashed line).

small sample of low level sounds were not recorded in high noise. Note, however, there is an increase in modal value of source levels within each noise category (145–150 dB re 1  $\mu$ Pa at 1 m in low noise, 160–165 dB re 1  $\mu$ Pa at 1 m in mid noise, and 165–170 dB re 1  $\mu$ Pa at 1 m in high noise). Even if sounds were being missed in high noise [and given the detectability of sounds in high noise (see Fig. 2, at 2.5 km), only sounds of received levels less than 154 dB re 1  $\mu$ Pa at 1 m would have not been detected], it is not likely that the modal value of source levels in high noise would change substantially.

The data subset that only included sounds that could be detected in high noise [based on the detection curves in Fig. 2 where only sounds above the high noise (dashed green line) were included] within 2.5 km from the array ( $n = 226$ ), was found to be normally distributed. The Breush–Pagan Test (chi square = 0.30, d.f. = 1,  $p = 0.58$ ) testing for unequal variance in this subset showed very low probability that the assumption of constant variance had been violated in the high noise category. Using this subset, the mixed model analysis (including noise category and distance from the array as fixed effects) found that both  $SL_{rms}$  and  $SL_{pp}$  values were significantly higher in the mid and high noise conditions compared to the low noise condition (Table I). From the model output, the estimated  $SL_{rms}$  (measured at the intercept of the relationship between distance and  $SL_{rms}$ ) was 144 dB re 1  $\mu$ Pa at 1 m in the low noise category. Vocal sounds in mid noise and high noise were found to be significantly (Table I) higher in level (9 dB and 11 dB, respectively) compared to vocal sounds in low noise (Fig. 4), but there was no significant difference found in measured levels between mid and high noise. The relationship between estimated  $SL_{rms}$  and distance from the array was not significantly different within each noise category. The  $SL_{pp}$  of social sounds also increased significantly (Table I) in mid noise conditions compared to low noise (by 9 dB according to the model intercept) and in high noise conditions (also by 9 dB according to the model intercept) compared to low noise (Fig. 4).

Source levels (rms) were then plotted as a function of measured noise to determine the relationship with each other (Fig. 5). In this plot, all data that could be detected under high noise conditions and within 2.5 km from the array was

TABLE I. Estimated difference of  $SL_{rms}$  and  $SL_{pp}$  of vocal sounds detected in mid and high noise compared with sounds detected in low noise (including the 95% highest posterior density lower and upper intervals,  $t$  value, and  $p$  value). The effect of distance from the array was also included in the analysis model (although the effect size is not reported in the table).

Source levels re low noise	Estimate	HPD 95	$t$ value	$p$ MCMC
$SL_{rms}$				
Low noise	144	(139–148)		
Mid noise	+9	(4–14)	3.4	0.0007
High noise	+11	(5–18)	3.1	0.0023
$SL_{pp}$				
Low noise	164	(159–168)		
Mid noise	+9	(4–13)	3.5	0.0007
High noise	+9	(2–16)	2.3	0.0190

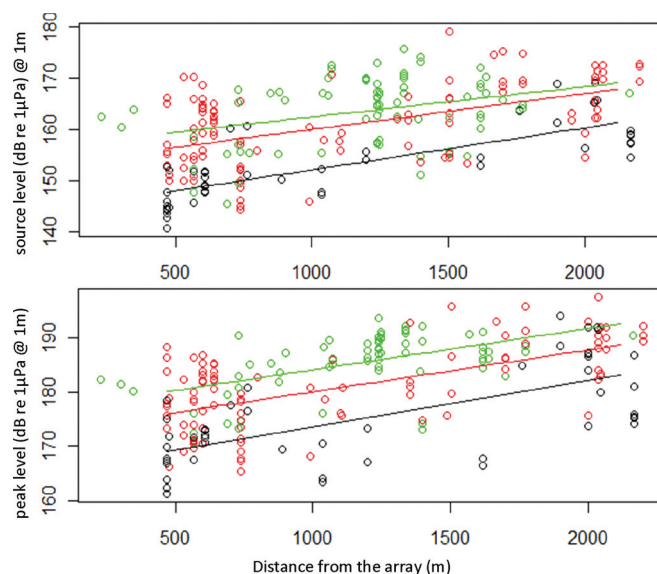


FIG. 4. The rms source level ( $SL_{rms}$ ) and peak-to-peak source level ( $SL_{pp}$ ) of humpback whale social vocalizations ( $n = 226$ ) taken from 16 different humpback whale groups categorized by low (black), mid (red), and high (green) noise levels. Only data for distances <2.5 km and above the threshold detectable in high noise conditions are included. A linear trend line for each noise category shows the relationship between the measured sound parameter and distance of the vocalizing whale from the array.

used. The Breush–Pagan Test for equal variance (Chi-squared = 0.61, d.f. = 1,  $p = 0.42$ ) was not significant suggesting there was a minimal effect of missing low level sounds in high noise. The linear regression line equation fitted to the data ( $y = 0.9x + 76$ ;  $R$ -squared = 0.214,  $p < 0.0001$ ) indicated a  $SL_{rms}$  increase of 0.9 dB per dB of noise, and source levels were maintained  $\sim 60$  dB above the noise level. There was unlikely to be substantial influence of the potentially “missed” data as, due to the results of the tests for unequal variance, only a few sounds below 154 dB re 1  $\mu$ Pa at 1 m could have been missed in high noise. Any sounds above that level would have been detected.

#### IV. DISCUSSION

The results of this study suggest that humpback whales increase the source level ( $SL_{rms}$  and  $SL_{pp}$ ) of social

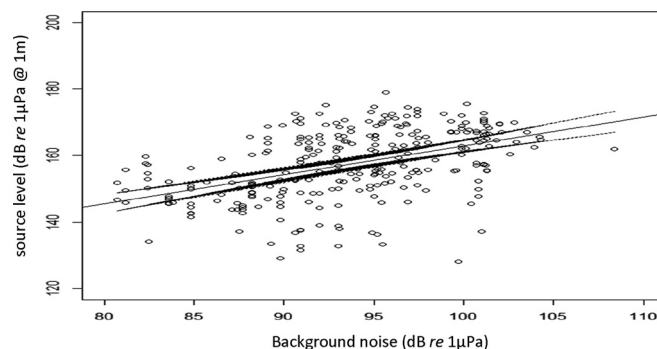


FIG. 5. The source level (dB re 1  $\mu$ Pa at 1 m) of humpback whale social vocalizations ( $n = 226$ ) taken from 16 different humpback whale groups as a function of broadband (36 Hz–2.8 kHz) background noise levels (dB re 1  $\mu$ Pa) including 95% confidence intervals. All source level measurements are included except those recorded at distances >2.5 km and those that would not have been detected in high noise conditions.

vocalizations in response to increasing wind-generated underwater noise. However, using data collected from a fixed array was problematic in that it was difficult to address the potential that sounds produced at lower source levels, and greater distances were missed in high noise conditions. One solution suggested by a previous study (Holt *et al.*, 2011) was to bootstrap the data to assess the probability of detecting high source level calls in low noise. They assumed that if the Lombard effect was real and not due to bias in the data, then the animals were unlikely to emit high level calls in low noise. From their results, they concluded that the Lombard relationship found for killer whales was unlikely to be due to missing low level sounds in high noise. The converse situation, the probability of detecting fewer low level sounds in high noise, was not tested in the Holt *et al.* (2011) study because it was not deemed possible. In this study, there was an obvious lack of high source level sounds in the low noise sample. The converse, the potential for missing low source level sounds in high noise, was also further explored. In the high noise category, the histogram of the  $SL_{rms}$  data showed evidence of being skewed. However, the data distribution did not deviate substantially from normal and there was no evidence of non-constant variance between noise categories, suggesting that only a limited number of sounds were missed when noise levels were high. To further account for the differences in sound detection with different noise levels, the data were also truncated to include only sounds with source levels that could have been detected in all noise conditions. In other words, low source level sounds that could be potentially missed were excluded so that all remaining sounds in the dataset were equally likely to be detected irrespective of noise level. This analysis is quite conservative given that, if the Lombard effect was operating, humpback whales would only have emitted these eliminated low level sounds in low noise. Therefore, curtailing the data in this way could potentially result in an artificial inflation of the mean source level of sounds emitted in low noise. Despite this potential inflation of the mean  $SL_{rms}$  in low noise, the Lombard effect hypothesis, in terms of finding an increase in source level with increasing noise, was still found to hold.

A previous study in North Atlantic right whales found the vocalizations levels to be  $\sim 5$ – $15$  dB above noise, although this study measured received levels recorded on digital recording tags attached to the vocalizing whale (Parks *et al.*, 2010). Right whale vocalizations range in source level from 137 to 192 dB re  $1 \mu\text{Pa}$  at 1 m rms (Parks and Tyack, 2005), similar to the range in source levels of social vocalizations of humpback whales (Dunlop *et al.*, 2013a). The trend line was not reported by Parks *et al.* (2010), however, the relationship between the increase in received level, and increase in noise, appeared to be approximately 1:1 in this study. Scheifele *et al.* (2005) found similar results in belugas with an increase of 0.9 dB per dB of noise and Holt *et al.* (2009) found an increase of 1 dB per dB increase of noise in killer whales. The vocal repertoire of killer whales includes “long-range” sounds (Miller, 2006), which perhaps explains the large signal excess (of 45 dB) in killer whales (Holt *et al.*, 2009). This study in humpback whales found source level to noise ratios of  $\sim 60$  dB (although with a large spread) and an increase of 0.9 dB per dB of noise, comparable to the results found in the other published studies in cetaceans.

Humpback whales have also been found to switch communication signal type, from primarily vocal signals to those generated at the surface in higher wind noise conditions (Dunlop *et al.*, 2010). This change in signaling behavior with noise has not yet been found in any other species of cetacean. Perhaps the Lombard response alone in humpback whales is not enough to maintain a constant SNR at other groups in the area (potential receivers) in periods of high noise. This study found that there was a substantial increase in source levels (9 dB) when comparing sounds recorded in low and mid noise, but little increase in source levels from mid to high noise (2 dB) suggesting the increase in signal level in high noise may not maintain a constant SNR as noise levels further increase (Dunlop *et al.*, 2013b).

The Lombard effect explains only part of the observed variation in source levels. It is likely that one of the sources of variation would have come from sound type, given that different sound types can have different source levels (Dunlop *et al.*, 2013a). However, all sound types were pooled in the analysis (up to 34 different sound types) as the sample size for each individual sound type was quite small. Another source of variance could be due to the social and/or behavioral context of the vocalizing group. A previous study found that humpback whale groups vocalize at different source levels depending on their social context. Lone animals and groups containing a singing whale, for example, tended to vocalize at higher levels compared to groups containing multiple animals (Dunlop *et al.*, 2013a). This analysis included many different group compositions: mother’s with a calf, lone adults, adult pairs, mother, calf being escorted by singing or non-singing whale, or by multiple escorts, but small sample sizes of each group meant it was not possible to account for this source of variance in the analysis. One potential bias, in that lone adults or groups containing a singing whale were more likely to be recorded in higher noise leading to a false positive result, was explored and discounted in the preliminary analysis. In this dataset, all group compositions were recorded in low, mid, and high noise levels meaning that the within-noise variance was probably due to differences in group social contexts, while the between-noise variance was not. Future work should therefore attempt to account for other sources of variance to determine if different sound types, which probably have different communication functions, change in source level with increased noise, as well as if groups in different social contexts respond to noise in the same way.

The noise levels used in this study were typical wind-dependent noise levels when there were no audible boats or singing whales. Stronger winds, increased vessel activity, and background shipping will obviously increase background noise levels and this could provide a better opportunity to test for a ceiling in the Lombard response. Noise in the ocean has increased, and will probably continue to increase, due to anthropogenic activity. It is essential, therefore, that effects like signal masking and reduced SNR at potential receivers in higher noise, as well as the function of communication sounds and the limits of how animals cope with noise through the Lombard effect and other

mechanisms, are continued to be investigated to ascertain potential life-history implications of this man-made effect.

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- Bates, D., Maechler, M., and Bolker, B. (2011). "lme4: Linear mixed-effects models using Eigen and Eigen++." R package version 0.999375-39, <http://CRAN.R-project.org/package=lme4> (Last viewed 12/11/2013).
- Brown, T. J., and Handford, P. (2000). "Sound design for vocalizations: Quality in the woods, consistency in the fields," *Condor* **102**(1), 81–92.
- Brumm, H. (2004). "The impact of environmental noise on song amplitude in a territorial bird," *J. Anim. Ecol.* **73**, 434–440.
- Brumm, H., and Slater, P. J. B. (2006). "Animals can vary signal amplitude with receiver distance: Evidence from zebra finch song," *Anim. Behav.* **72**, 699–705.
- Brumm, H., and Todt, D. (2002). "Noise-dependent song amplitude regulation in a territorial songbird," *Anim. Behav.* **63**, 891–897.
- Brumm, H., Voss, K., Kollmer, I., and Todt, D. (2004). "Acoustic communication in noise: Regulation of call characteristics in a New World monkey." *J. Exp. Bio.* **207**, 443–448.
- Cato, D. H. (1991). "Songs of humpback whales: An Australian perspective," *Mem. Queensland Mus.* **30**(2), 277–290.
- Clark, C. W. (1990). "Acoustic behaviour of mysticete whales," in *Sensory Abilities of Cetaceans*, edited by J. Thomas, and R. Kastelein (Plenum, New York), pp. 571–583.
- Cynx, J., Lewis, R., Tavel, B., and Tse, H. (1998). "Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*," *Anim. Behav.* **56**, 107–113.
- Deakos, M. H. (2002). "Humpback whale (*Megaptera novaeangliae*) communication: The context and potential functions of pec-slapping behavior on the Hawaiian wintering grounds," Master's thesis, University of Hawaii, Manoa.
- Dunlop, R. A., Cato, D. H., and Noad, M. J. (2010). "Your attention please: Increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*)," *Proc. R. Soc. B* **277**, 2521–2529.
- Dunlop, R. A., Noad, M. J., and Cato, D. H. (2008). "Non-song acoustic communication in migrating humpback whales." *Mar. Mamm. Sci.* **24**, 613–629.
- Dunlop, R. A., Noad, M. J., and Cato, D. H. (2013a). "Source levels of social sounds in migrating humpback whales (*Megaptera novaeangliae*)," *J. Acoust. Soc. Am.* **134**(1), 706–714.
- Dunlop, R. A., Noad, M. J., and Cato, D. H. (2013b). "Modification of humpback whale social sound repertoire and vocal source levels with increased noise," *J. Acoust. Soc. Am.* **133**(5), 3535.
- Dunlop, R. A., Noad, M. J., Cato, D. H., and D. Stokes. (2007). "The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*)," *J. Acoust. Soc. Am.* **22**(5), 2893–2905.
- Fox, J. and Weisberg, S. (2011). *An R Companion to Applied Regression*, 2nd ed. (Sage, Thousand Oaks, CA), <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion> (Last viewed 1/11/2013).
- Herman, L. M., and Tavolga, W. N. (1980). "The communication systems of cetaceans," in *Cetacean Behavior: Mechanisms and Functions*, edited by L. M. Herman (Wiley, New York), pp. 149–209.
- Holt, M. M., Noren, D. P., and Emmons, C. K. (2011). "Effects of noise levels and call types on the source levels of killer whale calls," *J. Acoust. Soc. Am.* **130**, 3100–3106.
- Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., and Veirs, S. (2009). "Speaking up: Killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise," *J. Acoust. Soc. Am.* **125**, EL27–EL32.
- Klump, G. M. (1996). "Bird communication in the noisy world," in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 321–338.
- Lombard, E. (1911). "Le signe de l'elevation de la voix" ("The sign of the elevation of the voice"), *Ann. Mal. Oreil. Larynx* **37**, 101–199.
- Manabe, K., Sadir, E. I., and Dooling, R. J. (1998). "Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect," *J. Acoust. Soc. Am.* **103**(2), 1190–1198.
- Mellinger, D. K. (2001). "Ishmael 1.0 User's Guide," NOAA, Technical Memorandum OAR PMEL-120, 2001.
- Miller, P. J. O. (2006). "Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations," *J. Comp. Physiol. A* **192**, 449–459.
- Naguib, M. (1995). "Auditory distance assessment of singing conspecifics in Carolina wrens—The role of reverberation and frequency-dependent attenuation." *Anim. Behav.* **50**, 1297–1307.
- Naguib, M., Schmidt, R., Sprau, P., Roth, T., Florcke, C., and Amrhein, V. (2008). "The ecology of vocal signaling: Male spacing and communication distance of different song traits in nightingales," *Behav. Ecol.* **19**(5), 1034–1040.
- Naguib, M., and Wiley, R. H. (2001). "Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication," *Anim. Behav.* **62**, 825–837.
- Noad, M. J., and Cato, D. H. (2001). "A combined acoustic and visual survey of humpback whales off southeast Queensland," *Mem. Queensland Mus.* **47**(2), 507–523 (special issue on humpback whales).
- Noad, M. J., Cato, D. H., and Stokes, M. D. (2004). "Acoustic tracking of humpback whales: Measuring interactions with the acoustic environment," in *Proc. Acoustics 2004, Annual Conference of the Australian Acoustical Society*, 3–5 November 2004, Gold Coast, pp. 353–358.
- Norris, K. S., and Møhl, B. (1983). "Can odontocetes debilitate prey with sound?," *Am. Nat.* **122**, 85–104.
- Parks, S. E., Johnson, M., Nowacek, D., and Tyack, P. L. (2010). "Individual right whales call louder in increased environmental noise," *Bio. Lett.* **7**, 33–35.
- Parks, S. E., and Tyack, P. L. (2005). "Sound production by North Atlantic right whales (*Eubalaena glacialis*) in surface active groups," *J. Acoust. Soc. Am.* **117**(5), 3297–3306.
- Payne, R. S., and McVay, S. (1971). "Songs of humpback whales," *Science* **173**, 585–597.
- Potash, L. M. (1972). "A signal detection problem and possible solution in Japanese quail (*Coturnix coturnix japonica*)," *Anim. Behav.* **20**, 192–195.
- Scheifele, P. M., Andrew, S., Cooper, R. A., Darre, M., Musiek, F. E., and Max, L. (2005). "Indication of a Lombard vocal response in the St. Lawrence River beluga," *J. Acoust. Soc. Am.* **117**, 1486–1492.
- Silber, G. K. (1986). "The relationship of social vocalizations to surface behaviour and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*)," *Can. J. Zool.* **64**, 2075–2080.
- Thompson, P. O., W. C. Cummings, and Ha, S. J. (1986). "Sounds, source levels, and associated behaviour of humpback whales, southeast Alaska," *J. Acoust. Soc. Am.* **80**(3), 735–740.
- Tyack, P. L. (1983). "Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds," *Behav. Ecol. Sociobiol.* **13**, 49–55.
- Tyack, P. L., and Whitehead, H. (1983). "Male competition in large groups of wintering humpback whales," *Behavior* **83**, 132–154.
- Wahlberg, M., Lunneryd, S.-G., and Westerberg, H. (2002). "The source level of harbour seal flipper slaps," *Aquat. Mamm.* **28**(1), 90–92.
- Whitehead, H. P. (1985). "Humpback whale breaching," *Investigations on Cetacea* **17**, 117–155.
- Wiley, R. H., and Richards, D. G. (1982). "Adaptations for acoustic communication in birds: Sound transmission and signal detection," in *Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller (Academic, New York), pp. 131–181.
- Zoidis, A. M., Smultea, M. A., Frankel, A. S., Hopkins, J. L., Day, A., McFarland, A. S., Whitt, A. D., and Fertl, D. (2008). "Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii," *J. Acoust. Soc. Am.* **123**, 1737–1746.