Indication of a Lombard vocal response in the St. Lawrence River beluga

P. M. Scheifele, S. Andrew, R. A. Cooper, and M. Darre
Animal Science Department, University of Connecticut, Storrs, Connecticut 06269

F. E. Musiek and L. Max
Communications Science Department, University of Connecticut, Storrs, Connecticut 06269

(Received 2 August 2004; revised 27 October 2004; accepted 1 November 2004)

Noise pollution is recognized as a potential danger to marine mammals in general, and to the St. Lawrence beluga in particular. One method of determining the impacts of noise on an animal's communication is to observe a natural and repeatable response of the vocal system to variations in noise level. This is accomplished by observing intensity changes in animal vocalizations in response to environmental noise. One such response observed in humans, songbirds, and some primates is the Lombard vocal response. This response represents a vocal system reaction manifested by changes in vocalization level in direct response to changes in the noise field. In this research, a population of belugas in the St. Lawrence River Estuary was tested to determine whether a Lombard response existed by using hidden Markhov-classified vocalizations as targets for acoustical analyses. Correlation and regression analyses of signals and noise indicated that the phenomenon does exist. Further, results of human subjects experiments [Egan, J. J. (1966), Ph.D. dissertation; Scheifele, P. M. (2003), Ph.D. dissertation], along with previously reported data from other animal species, are similar to those exhibited by the belugas. Overall, findings suggest that typical noise levels in the St. Lawrence River Estuary have a detectable effect on the communication of the beluga. [DOI: 10.1121/1.1835508]

PACS numbers: 43.80.Nd, 43.80.Ka, 43.80.Lb [WWA] Pages: 1486–1492

I. INTRODUCTION

The St. Lawrence River Estuary is habitat to a sub-Arctic population of beluga whales on a year-round basis. This region is also a mainstream route for commercial shipping and, in the last 10 years, has become the primary region of eco-tourism activities primarily consisting of whale watching. A great debate continues regarding whether or not these activities have any effect on the hearing and communication abilities of these animals. One mechanism that can be used to determine whether noise is having an effect on an animal's ability to communicate is to observe some natural and repeatable response of the vocal system in response to changes in noise level. The fact that an animal has to alter its vocalization level in the presence of anthropogenic noise is indicative that its vocalizations are being influenced by that noise, possibly with long-term adverse energetic consequences. Vocal changes in response to noise may also impede normal auditory feedback or "sidetone" levels (Lane and Tranel, 1971; Lombard, 1911).

One natural reaction such as this has been observed in humans and is known as the Lombard vocal response (Lombard, 1911). The Lombard vocal response (also known as the Lombard effect or reflex) represents a reaction of the vocalization system directly manifested by changes in vocalization level (Egan, 1966) and refers to a noise-induced phenomenon and the unconscious tendency of a person or animal to raise their voice when confronted with a noisy environment. The underlying principle is the maintenance of the normally expected loudness of the vocalizer's sidetone. Measuring the Lombard response allows the study of the communication system in an integrated manner. It may also be used as an indicator of noise effects on animal communication. While exhibiting a Lombard response provides a mechanism for animals to cope with varying levels of noise, the response is also indicative of the animal attempting to cope with noise levels that are potentially rising toward a point where masking will occur. This level is the ceiling of the Lombard response. During the process of responding to elevated levels of noise, the animal is also expending more energy than normal to achieve total communication.

Acoustic communication relies on the integrated and interdependent functioning of the auditory and vocal systems (Levelt, 1989; Bradbury and Vehrencamp, 1998). The auditory subsystem plays a pivotal role as an external feedback loop in the overall ability of the animal to communicate. With no external feedback loop, the ability to properly construct, deliver, and process sounds is severely reduced (Guenther, 2001).

The Lombard vocal response is a phenomenon not limited to humans; it is known to occur in monkeys, bats, cats, quail, nightingales, and budgerigars (Potash, 1972; Sinott *et al*., 1975; Manabe *et al*., 1998; Egnor *et al*., 2003; Cynx *et al*., 1998); however, studies have not been made to determine whether it occurs in marine mammals. Observation of this response is a critical step in the analysis of vocalization-in-noise studies and the study of the general dynamic relationship between auditory feedback and acoustic communication, especially under conditions of altered auditory feedback (Lane and Tranel, 1971). Table I shows gross comparative results of Lombard tests on various animals and humans. Although the Lombard response has not been tested in

TABLE I. Human/animal Lombard response comparisons showing the level of the vocalization during a Lombard response per dB increase in noise level.

Animal	Increase in Lombard response as function of increase noise level (dB)	Reference
Human	1.3	Egan, 1966; Lane and Tranel, 1971
Human	1.09	Scheifele, 2003
Tamarin	2.8	Egnor *et al.*, 2003
Macaque	2.0	Sinott *et al.*, 1975
Zebra finch	3.3	Cynx *et al.*, 1998
Quail	0.60	Potash, 1972
Budgerigar	0.35	Manabe *et al.*, 1998
Cat	1.8	Nonaka *et al.*, 1997
Beluga	1.0	Scheifele, 2003

many animals, Table I illustrates a range of response levels in mammals and songbirds. The current study was conducted with a group of sub-Arctic beluga whales in the St. Lawrence River Estuary to investigate whether a vocalization-as-a-function-of-noise response exists in the St. Lawrence beluga whale.

II. METHODS

A. General methodology

Vocalizations of subgroups of the population of 700 St. Lawrence River belugas were collected at different sites of the upper estuary where these whales congregate during the summer. A selection of these sites, all near the confluence of the Saguenay River and the St. Lawrence Estuary, was made in view of the

(1) Different vessel traffic and use causing individual background noise intensities;
(2) Regular use by different social groups of belugas during the same portion of the summer range (in an effort to reduce confounding factors due to differences among whales of different social groupings and/or of different areas);
(3) Intrinsic quality of the site's acoustical environments (topography, depth); and
(4) Proximity to one another and, hence, ability to sample them numerous times during a single day.

Site 1. Saguenay site (latitude: 48°07.34′, longitude: 69°41.40′) is located approximately 1 km outside of the harbor of Tadoussac at the mouth of the Saguenay fjord.

Site 2. The Channel Head site (latitude: 48°67.83′, longitude: 69°33.38′) is located approximately 8 km east of the Saguenay site on the north side of the St. Lawrence estuary.

Site 3. The Alouette site (latitude: 48°02.56′, longitude: 69°40.71′) is located 8 km west of the Saguenay site on the south side of the St. Lawrence River.

Site 4. Baie St. Marguerite site (latitude: N48° 15.00, longitude: W69° 55.30) is a cul-de-sac located north of Tadoussac and up the Saguenay tributary. Recordings of whales vocalizing in background noise were taken in July and August at each site during the hours of 0700, 1000, and 1400. In addition, some recordings were taken by following the pod from site to site during peak mid-day hours.

Lombard testing in humans is well known. Typically, the test involves having a person repeat a set of sentences or words while the tester varies the noise level presented to the subject. A Lombard effect would be indicated by the subject's voice level rising and/or falling in coincidence with the increase and decrease in the presented noise. In this study noise was generated by the presence or nonpresence of ships. The "sentences" were replaced by known beluga vocalizations that were chosen by a hidden Markhov classification system devised by Clemins and Johnson (2003) at Marquette University. Four classified vocalizations that the belugas routinely made at all of the sample sites were chosen. All four vocalizations were whistles.

Recordings were taken on groups of whales at selected sites when no vessels were present, followed by the purposeful presence of a vessel passing through that site and again, afterward (when the vessel was gone). The selected vocalizations were inspected during the before-vessel (no-noise) and during the vessel present (in-noise) situations to determine more specifically whether the noise had a direct effect on the vocalization level of that group of animals by sampling during these specifically created treatments. In all cases the group (subpod) of animals was first identified (group and identification number) and the standoff range from the boat to the pod was at most 400 m but not less than 100 m. The animals in the pod were kept in sight at all times during the test as best as could be done from the observation/recording boat. In two instances digital video recordings of the pod were made during the test. The recording hydrophone was deployed from the recording boat to a depth of 8 m and at no time were whales seen close to or approaching the hydrophone.

B. Data acquisition and analyses

Recordings were made from the R/V BLEUVET of the Center d' Interpretation des Mammifers Marins (CIMM) near the shoreline of the Saguenay River tributary and St. Lawrence Seaway. The BLEUVET is a 26 ft. Cabin cruiser with a Volvo 6 cylinder 3, 21 Turbo diesel 200-hp engine and Volvo Penta Dp stern drive with dual counter-rotating propellers. A total of 230 h of recording was used for this research.

All recordings were made with an International Transducer Corporation model ITC-1042 omnidirectional hydrophone with preamplifier (frequency response flat ± 3 dB from 20 Hz to 40 kHz). Recordings were made on a Sony TCD-D8 digital audio (DAT) tape recorder with 48-kHz sampling frequency and 16-bit linear quantization using the LINE input. The TCD-D8 recorder had a flat frequency response from 20 Hz to 20 kHz. Recording instrumentation was calibrated relative to a 1000-Hz calibration tone. Edited portions of the recordings were analyzed with a PC using PRAAT 4.1 speech analysis program (Boersma and Weenink, 2003) for spectrographic wideband analysis with a sampling rate of 20–48 kHz and ATSPEC PRO spectrum analysis soft-

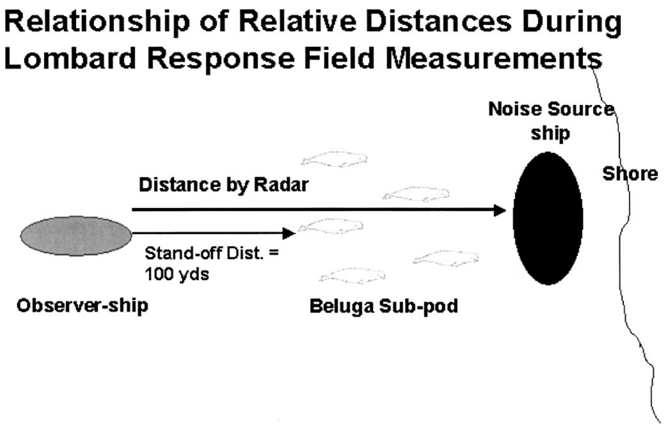

FIG. 1. Showing logistics and the negligibility of changes in vocalization level of any animal based on logistical standoff distance from the recording vessel.

ware (Taquis Corp.) for power spectra (sampling rate of 50–80 kHz was used, vocalization dependent, and an FFT size of 2048 points).

During recordings the recording vessel was shut down. Recordings of merchant- and whale-watching ship noise were made with the omnidirectional recording hydrophone placed at 8-m depth and situated such that the whale subpod was at a standoff distance of 100 m from the recording ship (required by law) and with the whale-watching vessel (noise source) on the far side of the pod. The position of the recording vessel and recording hydrophone in relation to the pod was with the pod directly forward of the recording hydrophone. A census of whales was taken at the beginning of each recording and again upon completion. In most cases the whales remained at or near the surface and the pods generally remained together. That is, the pod remained grouped within a roughly 50-m circle. The distance from the recording vessel to the whale-watching vessel was taken by radar and never exceeded 500 m. The logistics are shown in Fig. 1.

PRAAT 4.1 was used to segment individual whale vocalization "sound cuts" from the recordings. Using the software, each vocalization that was visible above the noise was extracted in its entirety (signal and noise). To get specific vocalizations for use in Lombard response analysis presorting of all beluga calls followed by vocal classification methods was used: batch spectral moments and hidden Markhov (HMM) classification. Spectral moments were run on each signal to make an initial similarity grouping. The batch spectral moments program of Milenkovic (1999) provided an assessment of four moments of each vocalization signal in 20-ms windows with 10-ms overlap to facilitate looking for changes in spectral content within a single call (similar to changes in sound within a single syllable). The moments are

(1) Moment no. 1: amplitude-weighted average frequency of the spectrum;

(2) Moment no. 2: standard deviation of the frequency spectrum;

(3) Moment no. 3: skewness of the frequency spectrum; and

(4) Moment no. 4: kurtosis of the frequency spectrum.

The spectral moments were then averaged across all windows to define a frame of each whole vocal production. A MATLAB 6.1 artificial neural net toolbox software (Mathworks, 2003) script was used to group all simple tonal calls together based on the weighting of the moments. The script used unsupervised network architecture. Average frequency and skewness were weighted preferentially above the standard deviation and kurtosis moments for specific tonal vocalization grouping as well as to differentiate the vocalizations from water sounds. Average frequency and skewness showed greater variability between vocalization types, giving further reason for their use in weighting by the network. A matrix of spectral moments versus frames of data comprised the input for each vocalization, and training was accomplished through a set of iterations. This constituted the initial sorting of the whistles.

Given the great variety of vocalizations made by belugas, it was important to compare like vocalizations in both the noise and no-noise conditions. Therefore, a hidden Markhov classification system (Clemins and Johnson, 2003) was used to further classify and to find specific groups of vocalizations that the St. Lawrence belugas routinely made at all sites and that could be reliably identified into four specific calls. Four vocalizations were chosen to be representative of "typical" acoustic communication by these animals. These four vocalizations served as the sample word list for the Lombard assessment. The HMM network used for the beluga vocalization classification was a set of n nodes. The "n" was either 5 or 10, which corresponded to the number of natural clusters desired. The nodes represented a type of vocalization, and each node was initialized to represent the "average" vocalization plus a small perturbation so that each node was slightly different. Each node was a 5-state HMM. In the end, each node represented the middle vocalization in each cluster of a "natural" clustering of the vocalizations. The HMM model did not use phoneme information, although each model had state transitions. The data used were mel-frequency cepstral coefficients and an energy measure across each 300-ms frame as input into the classifier. Although these were not technically geometric patterns, they represented a heavily smoothed version of the spectrum.

Training was done through a set of iterations. The vocalizations were first converted to framed data. Those data were input into the nodes, each of which used an HMM to evaluate its similarity to the vocalization the node represented. The entire data set was run to determine which cluster each vocalization belonged in (i.e., determine which node each vocalization was "closest" to). Then, using those labels, each node was adjusted based on the vocalizations that were assigned to it. A reestimation was then performed on each HMM (node) using the vocalizations that were assigned to it. The process was repeated until the HMMs were stable (meaning when the HMMs did not significantly vary after each iteration/reestimation). The HMM itself was not self-organizing in a technical sense. It did do automatic alignment, which, in a sense, is unsupervised. The self-organizing part was the set of HMMs that was used to construct a competitive network.

The vocalizations that were selected for analysis were those whose spectral characteristics were such that they oc-

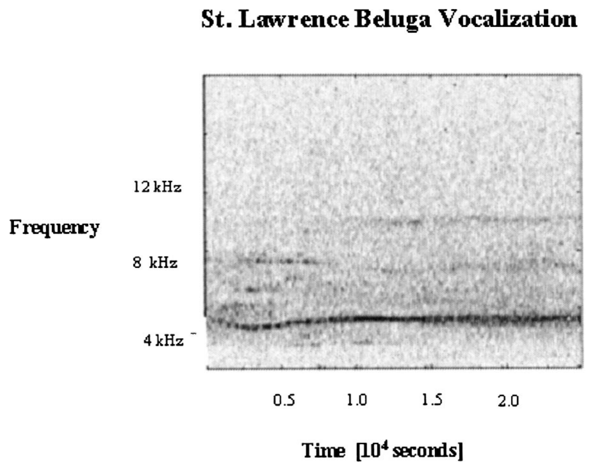

FIG. 2. Shown is a sample sonogram of one of the selected beluga vocalizations used in the Lombard vocal response testing in the St. Lawrence River Estuary.

curred in a frequency band that was above the noise band. The specific vocalizations chosen were all in the 5- to 10-kHz band. This yielded 978 individual vocalization cuts, each containing at least one of the four classified vocalizations and the noise that was occurring with that vocalization at the instant that it was made. These were the samples used in the statistical vocalization versus noise analysis. Most of the vocalizations in these recordings were of sufficient intensity to be heard.

The digital recordings of the classified beluga vocalization signals and accompanying noise from each site were fed into automated code routines that were programed using MATLAB 6.1 software (Mathworks, 2003). Low-pass and bandpass digital filtering were used to separate the vocalization signal (VL) from the noise (NL). This method assumed that the noise was in a different frequency band than the signal, so the filter cutoff frequency of 5 kHz was chosen by observing the noise frequency spectrum at each site when no vessels or animals were present and during the presence of ship noise. The frequency at which the noise level dropped by 20 dB *re*: 1 μPa was chosen as the cutoff frequency to use in filtering with a steep roll-off. This occurred at 5 kHz, and all signals chosen for analysis and use for detecting the phenomenon were between 5 and 10 kHz. Frequencies in the band of 5–10 kHz were considered the vocalization signal (VL) based upon the classified selected vocalizations. The frequency range of the signals was specifically chosen by the HMM classification system grouping to assure that the vocalization frequencies did not include ship noise. The particular filter method chosen in MATLAB was an elliptical forward–reverse process. The sound cut was filtered in the forward direction; the filtered sequence was then reversed and run back through the filter with the output of the second filtering operation time reversed. This ensured that the result had zero phase distortion and a magnitude modified by the square of the filter's magnitude response. The low/bandpass elliptical digital filters were designed with a roll-off of 80 dB per octave. The rms intensity averages were computed for the VL and NL and archived. A sample vocalization sonogram is shown in Fig. 2. Analyses for the groups of in the no-vessel and vessel present tests were conducted using the same techniques as described above.

C. Statistical methods

1. Signal versus noise observational analysis

The rms values of the VL and NL were statistically compared in correlation and regression analyses using SAS/STAT software Proc Mixed Model. A regression analysis using SAS Proc Mixed Model was performed on the paired noise level (NL)–vocalization level (VL) data using the values obtained by the filtering process previously described ($N=978$). Regression and correlation analyses were also performed to see whether vocalization levels changed as a function of noise and whether or not they differed from those that occurred at ambient levels at each site. The linear regression is shown in Fig. 3.

2. Noise versus no-noise treatment analysis

Confidence intervals were calculated due to the small amount of data ($N=43$) that was collected using two treatments: ship present and no-ship present. These tests were also chosen because the experimental unit could not be adequately defined as corresponding to individual subjects. These subpods were chosen at random across time of day and site. Thus, the pre- and postvessel (vessel off site) recordings were designated as the "no-noise" treatment, and the recordings taken while the vessel was on site were designated as the "with-noise" treatment. The statistical analysis consisted of calculating confidence intervals for the noise and no-noise vocalizations as further indication of the "vocalization as a function of noise level" phenomenon. In addition, regression analyses of vocalization level and noise level were completed for the vessel and no-vessel conditions separately.

III. RESULTS

Results were obtained on the following data:

(1) Beluga vocalization signal versus noise level observation relationship.
(2) Beluga vocalization signal versus noise level during vessel present–no-vessel present treatments.

A. Signal versus noise observational results

Results of the vocalization versus noise analysis indicated that a direct correlation exists. The coefficient of correlation had a value of 0.795. The coefficient of determination was calculated as $r^2=0.6301$. This indicates that 63% of the variability in the beluga vocalization intensity is accounted for by the background noise. These results suggest that beluga vocalization levels vary as a function of noise in the environment.

A regression analysis was conducted to further clarify the nature of the relationship between VL and the NL. The equation of the regression line was $y=0.88x+9.57$. The linear regression is shown in Fig. 3. The dashed lines indicate

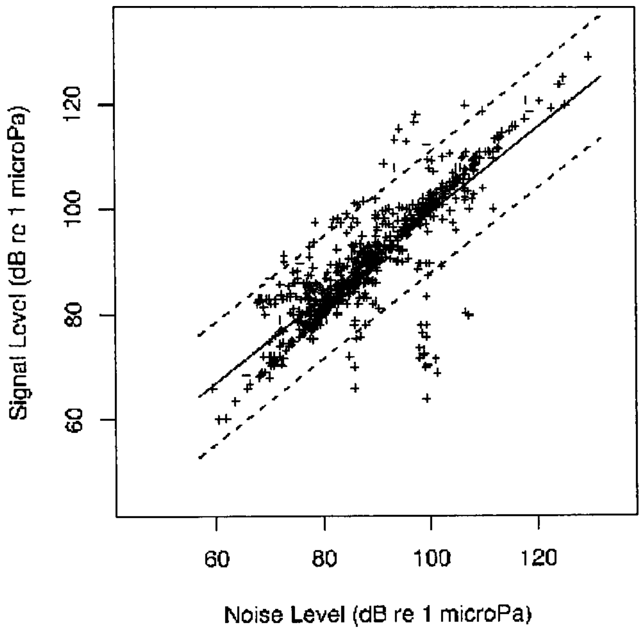

FIG. 3. Regression of beluga vocalization level (VL) versus changing noise levels from extracted beluga vocalizations at all sites in the presence of noise ($N=978$).

the 95% confidence interval for the estimation of the linear regression line. The regression shows outlying data points that are indicative of random effects.

B. Noise versus no-noise treatment results

Two tests were run on the ($N=43$) noise–no-noise treatment data: a 95% confidence interval was computed and a regression run. The confidence limits for vocalizations in the no-noise condition were 86.76 to 80.46 dB, while those for vocalizations made in noise were 99.10 to 91.74 dB. The lack of overlap in these confidence intervals confirms vocal intensities differed between the noise and no-noise conditions. The mean noise level before and during the presence of the vessel were clearly above the hearing threshold of the beluga (as reported in Au, 1993) at all sampled frequencies, and the vocalization levels of the whales in both cases ranged above the noise during all treatments as shown in Fig. 4. In these treatments the whales were recorded before, during, and after the presence of a vessel of opportunity to artificially cause the vocalization-as-a-function-of-noise phenomenon to occur.

IV. DISCUSSION

Based on the variability of ambient noise levels previously sampled at each site over 6 sample years (1996, 1998, 1999, 2001, 2002, and 2003), it is clear that the beluga whales of the St. Lawrence River Estuary are subject to relatively high noise levels, the sources of which were largely anthropogenic in these samples and a highly variable ambient acoustic environment. Results of the analysis of ambient noise at each site that the belugas visit during the summer months indicate that the noise levels vary from site to site as well as within each site. These variations are based on conditions of weather, bathymetry, tides, current regimes, and topography. The addition of anthropogenic noise exacerbates these noise fluctuations. In large baleen whales, body size allows the animals to produce low-frequency signals at high intensities that serve to increase the range over which they can be heard by conspecifics. By combining these acoustical characteristics with the selection of suitable depths and bottom types, they can match signal form with ambient medium characteristics for long-distance communication. That is not

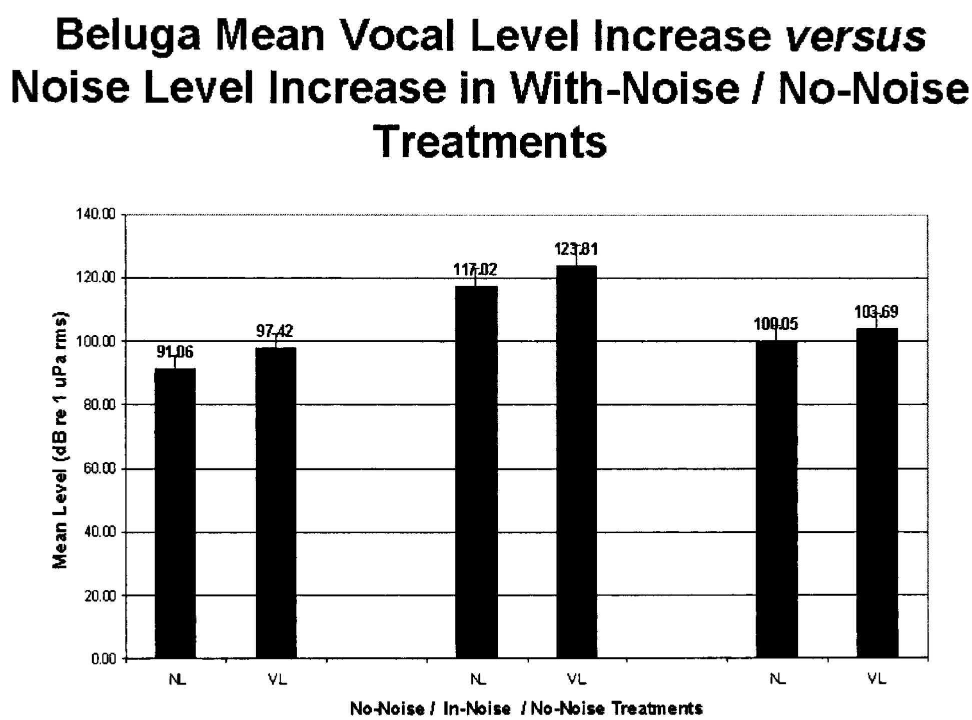

FIG. 4. Shows the response of the beluga vocalizations (VL) in no-noise (ship not present), noise (ship present), and no-noise (after the ship had left the site) conditions.

the case with the belugas of the St. Lawrence River Estuary, who constrain themselves to a considerably smaller body of water where currents and tides have a greater effect on signaling. Thus, physical environment and animal physiology (modality) both impose constraints on signal design and optimization for the beluga.

Belugas may employ a number of strategies for vocalizing that would allow them to optimize their acoustic signals to communicate with their conspecifics. These are limited to changing the frequency of their vocalizations, changing the type of call emitted, such as switching to pulsed calls instead of tonal calls, leaving the site for quieter waters, or changing vocalization intensity. Each of the former approaches has been observed in the past; however, their use of the latter tactic has not been well documented.

The belugas must select design features for their communication vocalizations that will optimize their vocalizations in noise. A design feature is a signal characteristic that is determined by environmental or other selective forces and affects the optimality of the signal (Bradbury and Vehrencamp, 1998). The optimum design scheme would use the smallest number of signal features common to most modalities that reflect both information content and transmission properties common to most signals employed by the animal. For auditory signals the maximum range, ability of the signal to be localized by sender and receiver (directionality), duty cycle, and modulation strength are all factors that have to be considered with regard to altering signal intensity. These factors are all accounted for by the Lombard response.

To increase confidence that the Lombard response exists, controlled testing on captive belugas should be evaluated. It should be noted, however, that although results from such a test may help to confirm the Lombard response, it might not accurately serve to quantify it with respect to Lombard thresholds due to the nature of the captive (pool) environment, which is reverberation limited. That is, the thresholds at which the response begins to be exhibited and at which complete masking occurs are not known. In a reverberation-limited versus noise-limited environment, these thresholds may not be able to be determined accurately.

Although this response cannot be attributed to the wild beluga with certainty, the phenomenon of "beluga vocalization-as-a-function-of-noise" unquestionably appears to exist based on the consistency of the phenomena throughout the recordings. In most cases the vocalization level either rose or fell in coincidence with the noise level at the moment that vocalization was made. This is highly indicative of a Lombard vocal response, as seen in humans and other animals that have been tested for the Lombard response. Less than 4% of selected vocalizations were not above the noise level. The data taken throughout the recordings support the hypothesis that the St. Lawrence belugas exhibit a vocalization-as-a-function-of-noise phenomenon based on the strong positive correlation between elevated noise and subsequent elevation of the belugas' vocalizations. The robust sample size seems to indicate that the phenomenon is not coincidental nor is it likely to be caused by physical factors. The regression data indicate a linear relationship between the beluga vocalization signal and noise at the time the signal was made, which is typical of the Lombard response.

Evidence that this phenomenon exists is further supported by the noise versus no-noise treatments, although the sample size was small. Once again, the regression relationship was linear. The data regarding the acoustical response agree well with data gathered on other animals with respect to the Lombard vocal response. That is, the vocalization level per decibel increase in noise lies between 1.0 dB VL/1 dB NL increases for humans and 3.3 dB VL/1 dB NL increase for finches.

In comparing the beluga data of vocal increase as a function of noise increase and vocal increase as a function of noise decrease with that of human subjects tested by Scheifele (2003), the values of the rate of increase and decrease per decibel compared favorably. The data from each of the tests conducted during this study strongly imply a Lombard vocal response. In addition, tests with other animals that have been shown to exhibit the response yield similar response results in their data. Overall, our findings indicate that a Lombard vocal response does exist in belugas. Thus, the data presented here suggest that environmental noise has an observable effect on the communication process of these animals. Given that elevated noise levels occur so routinely at all sites in the St. Lawrence River Estuary during summer, it is likely that observing such a response taking place so often represents a significant impact on the ability of these animals to communicate effectively with potential impact on their energetics. Since the state and stability of this threatened population of belugas is so tenuous, and since these sites represent such popular sites for the ecotourism industry, routine demonstration of a Lombard response should be viewed as a warning of potential adverse impacts of noise on these animals given that the Lombard vocal response is a first-order reaction to noise. Once the Lombard ceiling for a species or individual has been reached, the next level of noise would be masking. As such, a monitoring program should be initiated using the Lombard response as an indicator and measure for the low-level effects of noise on the St. Lawrence beluga. Further studies of the Lombard response in the beluga whale should focus on determining the floor (level at which the Lombard response begins to be exhibited) and the ceiling (level at which the Lombard response reaches its peak and where the animal's communication system cannot accommodate the noise further). This has not been determined for any species to date. Knowing these limits would provide a metric for gauging the effects of noise on populations of wild animals such as the St. Lawrence beluga whale in the future.

Au, W. W. L. (**1993**). *The Sonar of Dolphins* (Springer, New York), p. 34.

Boersma, P., and Weenink, D. (**2003**). "PRAAT: Doing phonetics by computer," University of Amsterdam, Netherlands. http://www.fon.hum.uva.nl/praat/. Viewed 12 November 2003.

Bradbury, J. W., and Vehrencamp, S. L. (**1998**). *Principles of Animal Communication* (Sinauer Associates, Inc., Sunderland, Massachusetts), pp. 1–16.

Clemins, P. J., and Johnsosn, M. T. (**2003**). "Application of speech recognition to African elephant (*Loxodonta Africana*) vocalizations," Proceedings ICASSP-03.

Cynx, J., Lewis, R., Tavel, B., and Tse, H. (**1998**). "Amplitude regulation of vocalizations in noise by 2 songbird (Taeniopygia guttata)," Animal Behavior **56**, 107–113.

Egan, J. J. (**1966**). "Psychoacoustics of the Lombard Voice reflex," Ph.D. dissertation, Case Western Reserve University.
Egnor, S. E., Dingle, K., Guvench, A., Hicks, C., and Hauser, M. D. (**2003**). The Lombard Effect on the Cotton-top Tamarin (Saguinus oedipus). Presentation given at the First International Conference on Acoustic Communication by Animals, July 27–30, at the University of Maryland, College Park, Maryland.
Guenther, F. H. (**2001**). "Neural modeling of speech production," Proceedings of the 4th International Nijmegen Speech Motor Conference, Nijmegen, The Netherlands, 13–16 June, 2001.
Lane, H., and Tranel, B. (**1971**). "The Lombard Sign and the role of hearing in speech," J. Speech Hear. Res. **14**, 677–709.
Levelt, W. J. M. (**1989**). *Speaking: From Intention to Articulation* (MIT Press, Cambridge, MA).
Lombard, E. (**1911**). "L'indication de l'elevation de la voix," Annales Des Malades de l''creille, Vol. 37, No. 2.
Manabe, K., Sadr, 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**, 1190–1198.
MathWorks. (**2003**). "MATLAB: The language of technical computing," Natick, MA. http://www.mathworks.com/
Milenkovic, P. H. (**1999**). "Moments: Batch Spectral Moments Analysis," University of Wisconsin-Madison. (http://www.wisc.edu/cgi-n/wisc.ph/ph.cgi?source = brief.xml&name = Paul + H+Milenkovic&email =&division=&phone=). Created 1999 and accessed 2003.
Potash, L. M. (**1972**). "A signal detection problem and a possible solution in Japanese quail," Anim. Behav. **20**, 192–195.
Scheifele, P. M. (**2003**). "Investigation of the response of the auditory and acoustic communications systems in the beluga whale of the St. Lawrence River Estuary to noise using vocal classification," Ph.D. dissertation, University of Connecticut.
Sinott, J. M., Stebbins, W. C., and Moody, D. B. (**1975**). "Regulation of voice amplitude by the monkey," J. Acoust. Soc. Am. **58**, 412–414.