THE EFFECT OF VESSEL NOISE ON THE VOCAL BEHAVIOR OF BELUGAS IN THE ST. LAWRENCE RIVER ESTUARY, CANADA

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Abstract

During June–July 1991, we monitored the vocal behavior of belugas before, during, and after exposure to noise from a small motorboat and a ferry to determine if there were any consistent patterns in their vocal behavior when exposed to these two familiar, but different sources of potential disturbance. Vocal responses were observed in all trials and were more persistent when whales were exposed to the ferry than to the small boat. These included (1) a progressive reduction in calling rate from 3.4—10.5 calls/whale/min to 0.0 or <1.0 calls/whale/min while vessels were approaching; (2) brief increases in the emission of falling tonal calls and the three pulsed-tone call types; (3) at distances <1 km, an increase in the repetition of specific calls, and (4) a shift in frequency bands used by vocalizing animals from a mean frequency of 3.6 kHz prior to exposure to noise to frequencies of 5.2–8.8 kHz when vessels were close to the whales.

Key words: *Delphinapterus leucas,* beluga, odontocete, whale, noise, disturbance, vocalization, behavior, St. Lawrence River.

The population of beluga whales (*Delphinapterus leucas*) inhabiting the St. Lawrence River estuary is currently estimated at 600–700 animals (Kingsley

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1996) and has been classified as endangered under CITES since 1983. The St. Lawrence River is also a major commercial waterway and an increasingly popular area for recreational boating and whale-watching. Although the whale-watching industry is not directed at the beluga, much of its activity is concentrated in an area that contains approximately 50% of the beluga population (Michaud 1993, Kingsley 1996). One of the immediate threats to belugas and other marine mammals in the St. Lawrence Estuary comes from persistent disturbance resulting from the high density of vessels operating in a very limited area rather than from harassment by individual vessels. It is not known whether the recent increase in boat traffic in the Estuary, and the concurrent increase in underwater ambient noise levels, affects belugas.

The effects of boat traffic on marine mammals in coastal areas are a topic of growing concern. Most of the studies addressing this problem have used behavioral attributes such as changes in site tenacity, dive patterns, swimming speed, orientation of travel, herd cohesiveness and dive synchrony to indicate possible disturbance or stress caused by vessel traffic (Richardson *et al.* 1995). Few studies have examined the effects of high underwater noise levels on the vocal behavior and hearing capability of marine mammals.

Given that marine mammals depend on the acoustic sensory channel for many of their activities, forcing an animal to modify its vocal behavior or reducing its hearing capability could reduce its ability to search for food, to navigate, or to contact conspecifics (Fletcher and Busnel 1978, Richardson *et al.* 1995). Modifications in vocal behavior have been reported in a few marine mammal species exposed to high underwater noise levels, but results are variable both within and between studies. Belugas exposed to a large ship and an icebreaker remained vocal and emitted a large proportion of falling tonal and noisy pulsive calls, thought to be alarm calls, while narwhals (*Monodon monoceros*) became silent when exposed to the same noise source (Finley *et al.* 1990). Gray whales (*Eschrichtius robustus*) along the Mexican coast reacted differently to outboard motor and drillship noise; their call rate increased in the first case and decreased in the latter (Dahlheim 1987). This variability in reactions could be due to a number of different physical and biological factors, including noise characteristics and levels at whale locations, the duration and predictability of the disturbance and, in the case of boats, the distance, number, type, speed, and angle of approach. Biological factors would include the hearing capability of the animals, their current activity, threshold of disturbance, degree of habituation, and need to remain in the area (Watkins 1986, Blane 1990, Acevedo 1991, Kruse 1991). In addition, adequate quantification of a marine mammal's vocal response to noise is hampered by technical limitations; it is rarely possible to determine the number of animals responsible for the calls recorded, and often only the loudest calls can be detected when high underwater noise levels prevail.

Here, we recorded continuously the vocal activity and observed the surface behavior of belugas before, during, and after controlled experiments in which whales were exposed to either of two types of vessels. One was an outboard motorboat moving rapidly and erratically on an unpredictable route. The other

was a ferry moving slowly and regularly through the study area on a predictable path. Our main objective was to determine if there were any consistent patterns in the vocal behavior of belugas exposed to these two familiar but different sources of potential disturbance. The relatively short distance of the observation tower and hydrophone from the whales, and the small sizes of the whale groups, reduced the effects of the technical limitations outlined above.

METHODS

This study was conducted from 13 June to 4 July 1991, from Île aux Lièvres in the St. Lawrence River estuary, Quebec, Canada (47°48′N, 69°46′W). It is the longest (13 km) of a chain of islands that divide the river into two main channels. The South Channel is 14 m deep, the North Channel 75 m deep, and waters in the immediate vicinity of the island are <10 m deep. Recordings and behavioral observations were made from a 7-m tower located at the southwest point of the island, providing a partial view of the North Channel and an expansive view of the South Channel, where whales were concentrated and recordings were made. Although boat traffic was frequent in the deeper waters of the North Channel (about 7 km from the island), larger vessels or recreational boaters were only occasionally observed in the South Channel at the time of the study. At this time of the year, only a ferry passes around the point, 6–10 times a day. This region is an important feeding area for belugas during the spring and summer (Michaud 1993, Lesage and Kingsley 1995).

Underwater sounds were received by a Vemco VCH-LF hydrophone (Vemco Ltd, Halifax, N.S., Canada) resting on the sea bottom in 3–6 m of water, depending on the tide. Recordings were made using a Sony TCM-5000EV recorder. This system had a flat (±3 dB) frequency response from 0.9 to 9 kHz. The maximum recording range of the hydrophone was estimated by striking on a partially submerged anchor at different distances from the hydrophone on a calm day and at slack water. Continuous spectrograms of whales' vocalizations were produced using a software program called Real-Time-Spectrogram© (version 1.20, Engineering Design). A low-pass filter was set at 16 kHz for analysis to prevent aliasing. Bandwidth was fixed at 49 Hz.

The sound signature of the Boston Whaler, a 7-m vessel powered by two 70-HP engines, was obtained from a recording made approximately 200 m from the outboard as it was moving at approximately 50 km/h in water 5.5 m deep. Hydrophone depth was 4.0 m. The ferry *Trans Saint-Laurent* is a 2,173-gross-ton vessel 80 m long with two 2,000-HP engines each fitted with a propeller 235 cm in diameter (no nozzle). Its sound signature was obtained from a recording made 700 m from the ship as it was moving in 8.5 m of water at approximately 28 km/h. Hydrophone depth was 4.5 m. The underwater noises produced by the ferry and the outboard engines were recorded in 1992 using a Sony Digital Audio tape recorder TCD-D10PROII. This system had a flat (±3 dB) frequency response between 0.3 and 20 kHz. Frequency spectra of the underwater noise generated by boats were produced using the software program Signal© (version 2.20, Engineering Design, Belmont, MA).

Each experimental trial consisted of a preexposure, exposure, and postexposure period during which the whales' vocal activity was recorded continuously. A preexposure recording session was initiated when a herd of belugas was within 2 km of the hydrophone and when no boat was seen <5 km from the tower. An exposure period for the outboard was initiated when the ferry was not expected to arrive within the next half hour and when no boat was seen <5 km from the tower 10 min after the beginning of the recording session. The Boston Whaler (anchored 3–4 km from the tower) was contacted by radio and was asked to either pass by, or stop, at a distance of 100 m from the herd. Exposure periods were variable in length. In the experiments involving the Boston Whaler, the exposure period began when the boat had started up its motors (and was usually faintly audible), whereas it began in the ferry trials when the engines were audible. The closest point of approach was defined as the time at which the distance between the vessel's course and the center of the beluga herd was minimal. The postexposure period started, in the case of the outboard trials, when the boat noise was no longer audible to us. In the experiments involving the ferry, the beginning of the postexposure period was arbitrarily fixed at 6 min after the closest point of approach of the ferry. By this time the ferry had move to at least 3 km away from whales and was only faintly audible on the tapes. Positions of boat and whales were determined from the tower by reference to nearby landmarks and were later mapped on a marine chart. Periods were identified *a posteriori* from the tapes.

To determine if surface behavior changed during an experiment, behavior was assigned to one of six categories: directional swimming, resting, social interaction (Sjare and Smith 1986*a*), milling, stationary diving, and porpoising. Whales were considered to be "milling" when they were swimming in a slow non-directional manner. "Stationary dives" were shallow dives typically made while facing a discernible current. "Porpoising" occurred when a whale pitched its head above water while swimming vigorously in a particular direction. Information on dive patterns was obtained by focal sampling of naturally marked individuals. Animals were identified by color as adults (white) or juveniles (grayish; Brodie 1989). Each herd of whales served as its own control, eliminating potential confounding effects of herd size, composition, behavior, or other extraneous factors.

To determine if belugas' vocal behavior changed during an experiment, vocalizations were classified using a scheme elaborated for arctic belugas (Sjare and Smith 1986*b*). For whistles, five acoustic variables were noted directly from spectrograms: minimum and maximum frequency of the fundamental, contour or shape of the fundamental (resolution = 62 Hz), duration of the signal (resolution = 16 msec), and harmonic structure. For pulsed calls, duration, pulse repetition rate, and frequency characteristics of the individual pulses were measured. Calls that did not correspond to any of the categories defined by Sjare and Smith (1986*b*) were classified as unknown, and their acoustic characteristics and aural impression were noted. Calls that were similar in frequency, type, and intensity, and were neither overlapping nor sepa-

rated by more than 2.0 sec, were considered a series (Caldwell and Caldwell 1968). Belugas' non-echolocation calls are centered on frequencies below 6.4 kHz, but may sometimes attain frequencies up to 14 kHz (Sjare and Smith 1986b; Faucher 1988). Hence, limitations of the recording system may have prevented the detection of non-echolocation calls with higher frequencies and did not allow detailed analysis of echolocation click series.

One determinant but uncontrollable factor for the quality of a recording was the position of animals relative to the hydrophone when noise pressure levels were high. To provide quantitative information on whale calling rates during noise exposure, high standards for the selection of trials were required to limit the potential bias of noise masking fainter calls. Experiments were rejected in the following situations: when marine mammals other than belugas were observed during a recording session, when whale counts were inconsistent during an experiment, when the preexposure period was less than 5 min, when the whales left the area before the end of the preexposure period, or when whale calls became faint relative to vessel noise at some point during a trial and some calls were suspected to be missed. A total of 77 experiments were conducted, but only six were found to satisfy the criteria for further analyses. Most trials were rejected because of the last condition; the whales' fainter calls often went undetected at some point during a trial due to masking. However, during a few trials ($n = 6$), belugas were so close to the hydrophone during vessels exposure that even faint calls were clearly detected on spectrograms and audible over the vessel noise. Although some calls may still have gone undetected during these trials, their number is likely to be small.

For detailed acoustic analyses, an experiment was split into consecutive 1-min sampling units. We examined between-period differences in call rate, call frequencies, the emission of calls in series, and the duration of constant tonal calls. The calling rate was determined by dividing the total number of calls detected during a 1-min sample by the number of whales in the group. Call frequencies in a 1-min sample were evaluated using the fundamental frequency of unmodulated calls and the central frequency (frequency range/2 + minimum frequency) of modulated calls. Clicks and unknown vocalizations were not included in this calculation.

When no significant differences ($P < 0.05$) were found among minutes within a preexposure period using the Kruskal-Wallis test for central tendencies and the Chi-square or G statistics (following Cochran's rule, Scherrer 1984) for proportions, a comparison between this period and minutes of exposure and postexposure periods was carried out using the same tests, to determine the effect of the vessel on the measured variable. Otherwise, a t-test, modified for a comparison between a sample (formed by the mean of the preexposure minutes) and a single value (*i.e.,* each minute of the exposure or postexposure periods) was used as a tendency indicator (Sokal and Rohlf 1981). This last test does not take into account the sample size for the computation of each mean. Multiple comparisons were performed using the Mann-Whitney U test and Chi-square or G statistics to determine which minute(s) differed when compared to the preexposure period. Calling rates were compared be-

tween periods using a t-test modified for comparisons between a sample and a single value. All statistical tests were two-tailed. Data are presented as mean ± 1 standard deviation.

RESULTS

From the seventy-seven recording sessions obtained in June–July 1991, six (outboard $n = 3$, ferry $n = 3$) satisfied the criteria outlined above. The outboard motorboat experiments documented here are two trials during which the outboard stopped at a distance of 100 m from a herd (OB100s1 and OB100s2) and one trial where it passed by a herd at a distance of 800 m (OB800p). Ferry trials were made at a distance of 30 m (F30p), 300 m (F300p), and 800 m (F800p) from the whales. Herd size during trials ranged from 5 to 15 animals. One herd was composed exclusively of adults, while the remaining five herds were composed of a majority of adults (Table 1).

Spectral analysis of the underwater noise generated by the two vessels showed that sound energy from the outboard motorboat was spread over a larger band of frequencies than that of the ferry (Fig. 1). Noise levels from the outboard remained high at frequencies up to at least 16 kHz, but peaked around 6 kHz, then declined slightly between 6 and 11.5 kHz, where a second peak was observed. In contrast, the underwater noise generated by the ferry was prominent below 6 kHz; its engines generated a tone at about 175 Hz.

The overall detection rate of beluga calls was influenced by the presence of both types of vessel (Table 2). Call detection rate, which averaged 3.4–10.5 calls/whale/min prior to exposure, increased to more than 10 calls/whale/min in three of the six trials during the first 1–2 min of exposure. Call detection rates then declined in five of the six trials as the vessels came within 1.5 km (outboard) to 2.6 km (ferry) of the herd. Whales became completely or almost silent in three of these five trials, as call detection rates declined to 0.0 or <1 call/whale/min. Call detection rates in the sixth trial (OB100s2) also declined to <1 call/whale/min, but this was not significantly different from preexposure rates ($\bar{x} \pm SD = 4.8 \pm 2.1$ calls/whale/min; $t_s = 5.6$, $df = 5$, $P = 0.15$). Reductions in call detection rate observed during the ferry trials persisted for 4–6 min, and therefore lasted 1–2 min longer than those observed during the outboard trials (Table 2).

Despite a reduction in call detection rate during boat exposure, the relative frequency of emission of the different call types remained generally constant (Lesage 1993). Exceptions were falling tonal calls and the three types of pulsed tones. Falling tonal calls usually composed 13% (SD = 7) of the St. Lawrence beluga vocal repertoire. This proportion increased to over 55% during the early phase of OB800p when the outboard had started up its engines and was preparing to move. Brief increases in the emission of falling tonal calls accounted for 33%–48% of calls recorded during 3 min of the F800p exposure period when the ferry was within approximately 2.2 km of the whales. Similarly, scream-, squawk-, and blare-type pulsed tones, which normally represented 8 (± 2)%, 7 (± 5)% and 5 (± 4)% of the repertoire, respectively, briefly

Table 1. Summary of modifications observed in 'at surface' and vocal behavior of St. Lawrence belugas during boat runs. SI = social interaction, DS = directional swimming, SD = stationary diving, M = milling.

Trial	Herd composition	Behavior prior to exposure	Reaction documented at the surface	Behavior after exposure	Modifications documented in vocal behavior	Timing between vocal and 'at surface' changes	Desertion of area
OB100s1	5 adults 4 juveniles	SI	DS, herd split into 2, and submerged	M	57% of calls were blare-type pulsed tones, long constant tonal calls and clicks (boat began moving) used higher frequencies then became silent	vocal 30s prior to 'at surface'	No
OB100s2	8 adults	DS	submerged + released bubbles changed direction	DS	16% of calls were squawk-type pulsed tones redundancy increased (motors started) calling rate declined	simultaneous	Yes[a]
OB800p	5 animals 'mostly adults'	DS	unknown	M	calling rate declined redundancy increased used higher frequencies	unknown	No
F30p	4 adults 2 juveniles	SD	possible increase in dive duration	SD	frequent scream-type and moan-type pulsed tones (approach) used higher frequencies calling rate declined	vocal prior to 'at surface'	No
F300p	4 adults 3 juveniles	M	DS porpoising change direction	DS	frequent squawk- and scream-type pulsed tones redundancy increased calling rate declined used higher frequencies	vocal 1 min prior to 'at surface'	Yes
F800p	11 adults 4 juveniles	SD	1 longer dive	SD	calling rate declined redundancy increased used higher frequencies	vocal prior to 'at surface'	No

[a] Departure may be unrelated to boat exposure; whales were swimming directionally prior to boat exposure and perhaps would have passed through the study area even without boat disturbance
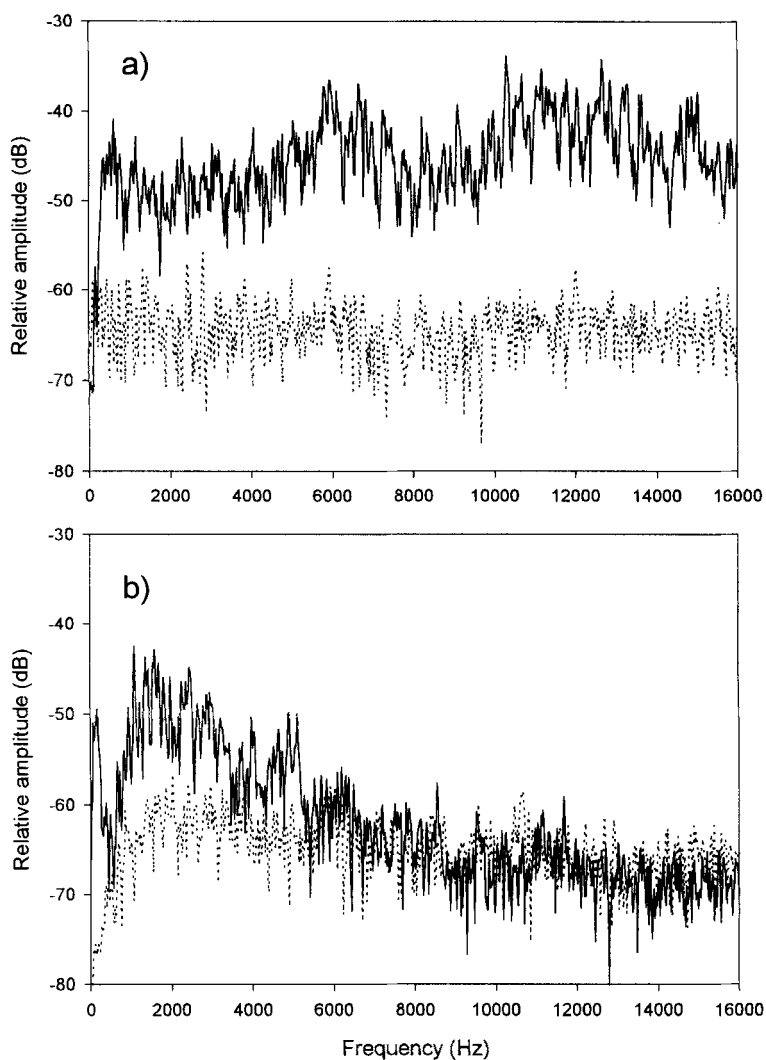
Figure 1.   Ambient   noise   spectra   (– – –)   in   absence   and   (———)   presence   of   (a) Boston Whaler and (b) Trans Saint-Laurent ferry.

increased during five of the six exposure periods to proportions of 17%–36% for scream-type (OB800p, OB100s2, F30p, F300p), 70%–76% for squawk-type (F300p), and 27%–29% for blare-type pulsed tones (OB100s1, F30p). The exception was trial F800p when the ferry was at the greatest distance from the whales; only three pulsed tones were heard during the entire exposure period. Blare-type pulsed tones, which are calls with low pulse repetition rates, were heard exclusively during the early phase of exposure periods: they were totally absent during the exposure period of OB800p, OB100s2 and F800p and were not heard when vessels were near the whales during the other three

Table 2. Call detection rate (calls/whale/min) before, during and after boat run. Each line shows rate for each min of exposure and postexposure periods. Each of these values compared to preexposure rate using *t*-test modified for comparisons between sample and single value. Changes, their direction and statistical significance, shown with arrows. ↑↓ = $P < 0.10$, NA = not applicable, "—" = not available. Approximate distance of vessels relative to whales can be calculated for each minute of exposure period by adding to, or removing from the distance of 'nearest point', 830 m for outboard (assuming mean speed of 50 km/h) or 460 m for ferry (mean speed of 28 km/h).

Outboard motor boat exposure

	Trial		
Phase	Pass at 800 m	Stop at 100 m (1)	Stop at 100 m (2)
preexposure $\bar{x} \pm$ SD (*n* of min)	5.5 ± 1.1 (7)	3.4 ± 1.4 (8)	4.8 ± 2.1 (6)
exposure			
starts motors (idling)	↑10.6	2.1	3.9
	7.2		
	6.2		
starts moving	→3.0	2.4	0.9
	NA	0.8	4.1
nearest point	4.6	→0.0	4.1
	6.6	NA	NA
postexposure			
stops motors	—	6.2	7.0
next 5 min	—	4.9	↑17.2
	—	←6.9	↑16.0
	—	10.0	—
	—	←7.9	—
	—	5.3	

Ferry Exposure

	Trial		
Phase	Pass at 800 m	Pass at 300 m	Pass at 30 m
preexposure $\bar{x} \pm$ SD (*n* of min)	4.7 ± 1.8 (7)	10.5 ± 0.8 (6)	6.5 ± 2.6 (6)
exposure			
arrival	↓0.9	↑14.0	10.2
		↓4.1	
	1.7	→5.1	12.0
	2.6	9.3	6.0
	1.2	4.4	1.2
	→0.7	→2.0	→0.7
	1.5	→2.6	→0.5
nearest point	→0.3	→4.4	1.3
	→0.5	→7.6	→0.3
	→0.1	→5.3	2.7
	→0.3	9.4	—
postexposure			
next 6 min	1.5	→8.6	—
	2.1	→3.7	—
	2.2	→2.1	—
	2.6	→6.9	—
	4.5	→6.0	—
	3.9	→6.7	—

Table 3. Proportion (%) of calls emitted in series observed before, during and after boat run. Each line represents proportion of calls that formed series in each min of exposure and postexposure periods. Figures in parentheses represent number of calls analyzed. Symbols as in Table 2, "A" = tested using *t*-test modified for comparison between sample and single value because of significant ($P < 0.05$) variation within preexposure period. Approximate distance of vessels relative to whales can be calculated for each minute of exposure period by adding to, or removing from distance of 'nearest point', 830 m for outboard (assuming mean speed of 50 km/h) or 460 m for ferry (mean speed of 28 km/h).

| | Outboard motor exposure | | |
| | Trial | | |
Phase	Pass at 800 m	Stop at 100 m (1)	Stop at 100 m (2)
preexposure $\bar{x} \pm$ SD (*n* of min)	33.0 ± 16.8 (7) A	32.0 ± 17.2 (8)	17.0 ± 11.0 (6)
exposure			
starts motors (idling)	15.1 (53) 47.2 (36) 48.4 (31)	31.6 (19)	↑ 45.2 (31)
starts moving	40.0 (15) —	27.3 (22) 28.6 (7)	0.0 (7) ↑ 42.4 (33)
nearest point	60.9 (23) 42.4 (33)	NA (0) NA	18.2 (33) NA
postexposure			
stops motors next 5 min	— — — — — —	32.1 (56) 50.0 (44) 37.1 (62) 25.6 (90) 35.2 (71) 29.2 (48)	12.5 (56) ↑ 33.3 (138) ↑ 29.7 (128) — — —

trials, *i.e.,* <1 km during outboard trial OB100s1, <1.2 km and <1.9 km during ferry trials F300p and F30p, respectively. In contrast, squawk- and scream-type pulsed tones, which have intermediate and high pulse repetition rates, were not restricted to any particular phase of boat exposure.

Falling tonal calls, squawk-type pulsed tones, constant tonal calls and clicks were responsible for an overall increase in repetition of calls during boat exposure. The proportion of calls emitted in series almost doubled in four of the six trials, during either the exposure or postexposure period as compared to the preexposure period (Table 3). This was most obvious at the beginning of the exposure period in the OB100s2 and F300p trials and when the outboard or the ferry was <1 km (outboard trials OB100s2 and OB800p) or <1.7 km

Table 3. Extended.

	Ferry exposure		
	Trial		
Phase	Pass at 800 m	Pass at 300 m	Pass at 30 m
preexposure $\bar{x} \pm$ SD (n of min)	26.3 ± 9.4 (7) A	35.1 ± 11.2 (6) A	40.8 ± 12.0 (6)
exposure arrival	35.7 (14)	↑ 74.5 (98) 20.7 (29)	50.8 (61)
nearest point	44.0 (25) ↑ 48.7 (39) 27.8 (18) ↑ 63.6 (11) 30.4 (23) 50.0 (4) 25.0 (8) 0.0 (1) 40.0 (5)	30.6 (36) ↑ 78.5 (65) ↑ 80.6 (31) 0.0 (14) 38.9 (18) ↑ 80.6 (31) 58.5 (53) 56.8 (37) 15.1 (66)	44.4 (72) 38.9 (36) 42.9 (7) 0.0 (4) 66.6 (3) 37.5 (8) 100.0 (2) 25.0 (16) —
postexposure next 6 min	36.4 (22) ↑ 46.9 (32) 36.4 (33) 30.8 (39) 23.9 (67) 44.1 (59)	33.3 (60) 7.7 (26) 13.3 (15) 31.2 (48) 21.4 (42) 21.3 (47)	— — — — — —

(ferry trial F800p and F300p) from the whales. In the last three cases, calls emitted in series accounted for more than 60% of all vocalizations. The higher proportions of these calls resulted from increases in the number of series rather than increases in the length of the series (Lesage 1993).

Physical characteristics of constant and falling tonal calls changed during boat exposure. Constant tonal calls were the most abundant calls throughout the experiments, representing 29%–31% of all calls emitted. They were also the most persistent calls when calling rate declined, being heard at least once in 39 of the 44 min of the exposure periods. However, we noted an alteration of duration and intensity of some of these whistles during boat exposure. Constant tonal calls, which normally lasted 478 msec (SD = 422), sometimes

Table 4. Frequency (kHz) used before, during and after boat run. Each line represents mean and standard deviation ($\bar{x} \pm$ SD) of frequency used in each min of exposure and postexposure periods. Figures in parentheses represent number of calls analyzed. Approximate distance of vessels relative to whales can be calculated for each minute of exposure period by adding to, or removing from distance of 'nearest point,' 830 m for outboard (assuming mean speed of 50 km/h) or 460 m for ferry (mean speed of 28 km/h). Symbols as in Table 2.

Phase	Outboard motor boat exposure		
	Trial		
	Pass at 800 m	Stop at 100 m (1)	Stop at 100 m (2)
preexposure $\bar{x} \pm$ SD (*n* of min)	2.7 ± 1.2 (188)	4.4 ± 3.2 (203) A	4.3 ± 3.8 (198)
exposure			
starts motors (idling)	3.1 ± 1.1 (50) 3.1 ± 1.2 (36) 3.2 ± 1.6 (30)	3.8 ± 2.2 (9)	4.3 ± 3.8 (26)
starts moving	4.9 ± 3.3 (14) —	3.6 ± 2.9 (18) ↑ 8.8 ± 1.2 (7)	2.1 ± 1.2 (3) 3.2 ± 1.9 (25)
nearest point	2.7 ± 1.1 (23)	NA (0)	2.7 ± 1.2 (26)
	↑ 3.8 ± 1.3 (30)	NA	NA
postexposure			
stops motors next 5 min	— — — — —	4.7 ± 2.9 (46) 3.3 ± 2.4 (33) 3.3 ± 2.6 (50) 3.4 ± 2.4 (78) 3.6 ± 2.3 (58) 3.7 ± 2.4 (39)	5.3 ± 4.0 (37) 3.8 ± 3.6 (103) 1.9 ± 2.1 (88) — — —

became very loud and very long (>3,500 msec) during this period. The mean frequency of these whistles was 3.0 ± 0.8 kHz (*n* = 82 calls). More than 93% of them (*n* = 77/82 calls) were heard during boat exposure, usually in series during this period. Similarly, unusual variants of falling tonal calls were heard during boat exposure in five of the six experimental trials. They were particularly harsh and loud, often covered a broad frequency band, and were always emitted in series (Lesage 1993).

The mean frequency used by whales was 3.6 kHz (range 2.6–4.4 kHz), but shifted upwards during the exposure period to 5.2–8.8 kHz when vessels were close to the whales (Table 4). The significant shifts in frequencies observed unlikely resulted from chance alone, given the consistency in the direction of the shifts and their close association with the short period of high noise levels

Table 4. Extended.

	Ferry exposure		
	Trial		
Phase	Pass at 800 m	Pass at 300 m	Pass at 30 m
preexposure $\bar{x} \pm$ SD (n of min)	3.8 ± 2.7 (388)	2.6 ± 1.9 (394) A	4.1 ± 2.9 (196) A
exposure arrival	2.4 ± 0.6 (13)	1.8 ± 1.5 (81) 3.7 ± 2.7 (27)	3.6 ± 2.3 (48)
nearest point	2.6 ± 0.6 (22)	4.7 ± 2.2 (30)	3.5 ± 3.1 (65)
	2.8 ± 1.7 (18)	2.5 ± 2.5 (60)	5.1 ± 2.9 (32)
	2.9 ± 1.3 (16)	2.3 ± 0.9 (27)	6.1 ± 2.3 (7)
	3.4 ± 2.5 (10)	↑ 5.2 ± 2.3 (11)	5.2 ± 2.7 (4)
	2.7 ± 1.4 (23)	2.7 ± 1.9 (17)	6.2 ± 3.8 (3)
	1.7 ± 0.1 (4)	1.7 ± 0.7 (31)	5.7 ± 2.6 (5)
	↑ 8.6 ± 1.5 (8)	2.8 ± 2.2 (49)	3.6 ± 0.1 (2)
	1.7 ± 0.0 (1)	3.8 ± 2.4 (34)	4.9 ± 2.6 (16)
	2.3 ± 1.1 (5)	3.2 ± 1.9 (63)	—
"postexposure" next 6 min			—
	2.7 ± 2.8 (21)	3.2 ± 2.6 (53)	—
	3.1 ± 2.0 (28)	3.8 ± 2.7 (17)	—
	4.0 ± 2.4 (31)	2.8 ± 2.1 (14)	—
	2.3 ± 1.3 (34)	3.5 ± 2.3 (40)	—
	4.1 ± 3.0 (60)	3.3 ± 2.3 (33)	—
	4.7 ± 3.3 (29)	4.1 ± 1.6 (40)	—

("nearest point"). This frequency shift was generally brief (1 min) and was notable in five of the six trials. When the outboard was <1.6 km from the whales and began approaching during the OB800p trial, 14 calls were heard. The first seven (five constant and two falling tonal calls) were all at frequencies above 7.2 kHz, and were heard in the first 10 sec. The following seven calls were heard more than 30 sec later and were very long and intense constant tonal calls with a frequency of about 2.2 kHz. During the OB100s1 trial, the last seven calls heard before the whales became completely silent for more than 1 min, all had frequencies greater than 7.1 kHz. This differed from the frequency range covered before boat exposure ($t_s = 3.0$; $df = 8$; $P < 0.02$). Similarly, when the ferry was within 1 km of the whales during the F30p trial, the few calls heard were emitted at frequencies slightly higher (5.2–6.1

kHz) than those used during the preexposure period ($\bar{x}$ = 4.1 kHz; t_s = 1.9; df = 5; P < 0.13). When the ferry was within 700 m of the whales during the F300p trial, 9 of 11 calls were emitted at frequencies higher than 5.1 kHz (t_s = 3.4; df = 5; P < 0.02). During the F800p trial, all eight calls emitted when the ferry was at a distance >1.3 km and moving away from the whales were above 7.3 kHz ($U_{379,8}$ = 344; P < 0.001). This increase in mean frequency used by whales did not result from the more frequent emission of particular types of calls.

Modifications in the whales' "at surface" behavior varied between trials from slightly longer dives or release of bubbles to directional swimming and departure from the study area (Table 1). In the five trials for which the surface behavior during boat exposure is well documented, changes in behavior were observed simultaneously with (OB100s2) or after the change in vocal behavior.

DISCUSSION

The number of experiments with a suitable recording quality was lower than expected. However, this study did provide new information on the effect of a small, rapid motorboat and a large, slow-moving ferry traveling in a more predictable manner on the vocal behavior of St. Lawrence belugas. Both vessels induced changes in calling rates, a tendency to emit calls repetitively, an increase in call duration, and an upward shift in the frequency range used to vocalize. However, the effects seemed to be longer lasting when the whales were exposed to the slow-moving ferry. Since we were dealing with animals exposed chronically to vessel traffic, habituation has unlikely developed or influenced the strength of the whales' responses during the study.

Two types of modifications in call detection rates were observed during boat exposures: call detection rates initially increased in three of the six trials and then eventually decreased in five of the six trials when boats moved closer to the whales. Both tendencies have been reported previously in marine mammals during stressful situations, but responses varied according to the type of disturbance and species involved. Belugas exposed to shipping and ice-breaking "remained vocal" while moving rapidly away from the ensonified area, but insufficient data on the numbers of whales being heard precluded any analyses of calling rates *per se* (Finley *et al.* 1990). An opposite reaction was observed from narwhals during the same experiment: they became silent and moved slowly or remained motionless. In a study on gray whales, call detection rates increased when whales were exposed to outboard motor noise, a familiar noise source in their area, but declined when whales were exposed to the unfamiliar noise from a drillship or to killer whale (*Orcinus orca*) vocalizations (Dahlheim 1987). Reductions in call detection rate have also been reported for sperm whales (*Physeter macrocephalus*) exposed to seismic pulses and sonar sounds (Watkins *et al.* 1985, 1993; Bowles *et al.* 1994) and for harp seals (*Phoca groenlandica*) exposed to shipping (Terhune *et al.* 1979), although it is uncertain whether this resulted from the departure of animals in the last two studies. These reductions in calling rates have been described as a survival strategy to

avoid detection by predators (Dahlheim 1987, Finley *et al.* 1990) or a listener strategy when facing unusual sounds (Watkins *et al.* 1985, Dahlheim 1987). The decline in calling rates observed in this study is probably not the result of such strategies, as there is no natural predator for belugas in the St. Lawrence Estuary and being exposed to a ferry or an outboard motorboat is certainly not an unusual event. The reduction of call detection rates may have resulted from the considerable overlap between the noise generated by the ferry and outboard engines and the normal frequency range used by belugas to communicate. This would explain the divergence in responses from belugas and gray whales when both faced a familiar noise source. For gray whales, the outboard noise did not overlap with their entire normal vocalization range and allowed the whales to maintain a high calling rate while concentrating their calls in a "free acoustic corridor."

Pulsed tones and falling tonal calls were heard both prior to and during boat exposures, but they were more common during boat exposures. Particularly harsh and loud variants of falling tonal calls also appeared during this period. Finley *et al.* (1990) hypothesized that pulsed tones and falling tonal calls were alarm calls, as they were heard from arctic belugas almost exclusively during ship and icebreaker exposure periods. In dolphins, falling tonal calls were also suggested to function as alarm calls, and pulsed tones were heard during close social interactions associated with alarm, fright, and distress situations (Dreher and Evans 1964, Caldwell and Caldwell 1967). Sjare and Smith (1986*b*) reported bursts of distinct stereotypical whistles, including falling tonal calls, during a number of different behavioral activities but found no evidence of higher rates of emission of either the pulsed tones or falling tonal calls during alarm situations. They suggested that some pulsed tones were indicative of whales in compact herds either socializing or resting, a conclusion supported by several other studies (*e.g.*, Caldwell and Caldwell 1967, Morgan 1979, Faucher 1988). We recorded high rates of pulsed tone emissions during trials where a cohesive and synchronized herd movement occurred (F300p, OB100s1, OB100s2), supporting the hypothesis of their association with close social interactions. However, the frequent occurrence of both falling tonal calls and pulsed tones, both prior to and during boat exposures, suggests that these calls do not function solely as alarm calls. In addition to being emitted at a higher rate during boat exposures, falling tonal calls and squawk-type pulsed tones were emitted repetitively and formed series, *i.e.*, were redundant. The tendency to repeat calls has been reported during periods of alarm in high-Arctic belugas (Sjare and Smith 1986*b*, Finley *et al.* 1990). However, the types of calls that were repeated differed between studies. In Finley *et al.* (1990) they were "long trains of rapid chirps" whereas in Sjare and Smith (1986*b*), they included many stereotypical whistles, as well as scream- and blare-type pulsed tones. Caldwell and Caldwell (1965) also observed that captive bottlenosed dolphins (*Tursiops truncatus*) in mildly stressful situations increased the emission rate of one basic whistle, thought to be the individual's "signature."

There are numerous possible reasons for redundancy of calls (Wilson 1975).

One reason invoked is that redundancy is a tactic to reduce signal degradation (see also Richards and Wiley 1980, Finley et al. 1990, Richardson et al. 1995). Redundancy appears to lower the hearing threshold and increases the probability of receiving a message in a noisy channel (Turnbull and Terhune 1993) or in habitats where a rapid degradation of the signals may occur (Morton 1975). Sharp intensity transients (as occur in pulsed sounds) degrade rapidly, but at short range they offer the advantage of easy locatability (Wiley and Richards 1978). Constant and falling tonal calls are simple in structure given their lack of amplitude modulation (and frequency modulation in the case of constant tonal calls) and are highly transmissible (Richards 1981). For relatively compact groups of belugas exposed to high noise levels, the use of these calls would help maintain communication among herd members and provide information on the spatial distribution of animals. Their repetition would further improve the probability of successful transmission of signals. A possible negative effect of call repetition, however, is that it may occur at the expense of the amount of information that can be transmitted, since it takes time or requires additional components that could otherwise be used to send other, or more refined, messages (Wiley 1983).

During the exposure period, there was an increase in intensity and duration of constant tonal calls. Finley et al. (1990) observed an increase in duration of some tonal calls when belugas were exposed to a ship and an icebreaker. These did not include constant tonal calls but chirp trains, falling tonal calls, and "morse" tonals. In gray whales differences in call duration were observed among regions, with longer pulses heard in the noisiest environments (Dahlheim 1987). Constant tonal calls are highly detectable and the most transmissible of all vocalizations emitted by belugas (Richards 1981). Among birds, tonal calls are thought to serve as the alerting syllable of a two-syllable message, aimed at warning conspecifics that the "message component" will follow (Richards 1981, Brenowitz 1982). Many pure-tone calls emitted by belugas represent ideal alerting components (Richards 1981), but the potential for such communication systems in marine mammals remains to be investigated.

The belugas used higher frequencies when exposed to the ferry and outboard motorboat. This shift in frequencies may have been an attempt to increase signal detectability by avoiding frequencies where masking was more severe. In the case of the ferry, this resulted in an avoidance of the frequency band where noise levels were the most intense. However, in the case of the outboard motorboat, shifts to higher frequencies did not result in the avoidance of the noisy frequency band, as the outboard noise remained strong at frequencies up to 16 kHz.

In their study on echolocation ability of belugas in environments with differing background noise levels, Au et al. (1985) observed that the whales shifted their click series toward frequencies with less ambient noise when in the noisiest environment. Although the use of high frequency click series was definitely related to the high ambient noise environment, it was also acknowledged that the high frequencies may be an inevitable by-product of producing a high intensity signal (Au et al. 1985, Au 1993). Avoidance of the noisiest

frequency band has also been reported in bottlenosed dolphins and gray whales facing high levels of biological noise (snapping shrimp) (Dahlheim *et al.* 1984). In contrast, Finley *et al.* (1990) did not observe any general upward shift in the frequencies used by belugas exposed to noise from two large ships. However, they did observe an alteration of the frequency emphasis of some calls during the exposure period, with undulating tonals (Ct6a and Ct6b) starting at lower frequencies and covering a wider frequency band. Frequency modulation of pure-tone calls would limit degradation of calls over long distances or in noisy environments (Richards and Wiley 1980), but we did not observe any significant changes in overall frequency-modulation width.

Not all modifications in vocal behavior described above were exhibited under conditions of high noise levels. Differences in movements and noise characteristics between the outboard and the ferry, in the noise level at the whales' location, in behavioral activity, and herd structure would account for some of this variability. Cohesive or synchronized herds may rely less on vocal displays than more dispersed herds, whose members cannot rely on visual or tactile communication. Also, in cohesive herds the exchange of information would be facilitated, because the distance over which information needs to travel is smaller, allowing fainter calls to be heard. An increase in cohesiveness of herds while fleeing was observed on many occasions during the course of this study, supporting earlier observations of alarmed beluga (Sjare and Smith 1986*b*, Blane 1990, Finley *et al.* 1990), humpback (*Megaptera novaeangliae*), and right whales (*Eubalaena glacialis*) (Herman and Würsig in Pryor 1986).

This study has shown how belugas modify their vocal behavior when exposed to temporary changes in background noise levels. The upward shift in frequencies, repetition of calls, and emission of strong and acoustically simple calls appear to be strategies to increase signal detectability. However, these changes, and the reduction in calling rate to almost silence, may reduce communication efficiency. Owing to the gregarious nature of belugas, this would not pose a serious problem for intraherd communication, given the relatively short distances between herd members; a source of noise would have to be very close to them to potentially limit any communication within a herd. However, communication is probably not limited to herd members, since interherd communication may be important during the breeding season, when locating food sources, when navigating in ice, or when reacting to large-scale disturbance. On these larger scales, high noise levels could impair communication.

The St. Lawrence belugas occupy a region used by commercial shipping and, seasonally, by recreational boating and whale-watching groups. Large-ship traffic is unlikely to have serious impacts on communication among belugas, because much of the noise emitted by these vessels is concentrated at frequencies <1 kHz, where beluga hearing sensitivity is quite poor. In contrast, an increase in the number of small vessels in areas frequented by belugas would be expected to interfere with communication among animals, because these vessels produce noise well above frequencies of 1 kHz.

This study not only confirmed in more controlled experimental settings the

findings from other studies but has also provided the grounds for a better understanding of the function of calls, and a basis for more predictive studies. As it still remains difficult to estimate the frequency of exposure of individual animals to boat traffic, and the noise levels they need to cope with, efforts in the future should be directed toward answering these questions. Recent advances in the miniaturization of hydrophones, dive recorders, and remote releasing devices offer great potential for the monitoring of vocal behavior, noise levels, and behavioral responses during dives.

ACKNOWLEDGMENTS

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