

Evidence for simultaneous sound production in the bowhead whale (*Balaena mysticetus*)

Outi M. Tervo^{a)} and Mads Fage Christoffersen

Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

Susan E. Parks

Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, Pennsylvania 16804-0030

Reinhardt Møbjerg Kristensen

Natural History Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen OE, Denmark

Peter Teglberg Madsen

Zoophysiology, Department of Biological Sciences, Building 113, I.C. F. Møllers Allé 3, 8000 Århus C, Denmark

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Simultaneous production of two harmonically independent sounds, the two-voice phenomenon, is a well-known feature in bird song. Some toothed whales can click and whistle simultaneously, and a few studies have also reported simultaneous sound production by baleen whales. The mechanism for sound production in toothed whales has been largely uncovered within the last three decades, whereas mechanism for sound production in baleen whales remains poorly understood. This study provides three lines of evidence from recordings made in 2008 and 2009 in Disko Bay, Western Greenland, strongly indicating that bowhead whales are capable of simultaneous dual frequency sound production. This capability may function to enable more complex singing in an acoustically mediated reproductive advertisement display, as has been suggested for songbirds, and/or have significance in individual recognition. © 2011 Acoustical Society of America.
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I. INTRODUCTION

Songbirds are able to produce two sounds independently using two separate sound generators located in the syrinx (Suthers, 1990; Fee *et al.*, 1998). This production of two independent signals results in the remarkable structural and temporal complexity of bird song that is used by females to select a mate, by males in territorial displays (Borror and Reese, 1956; Greenewalt, 1968; Searcy and Andersson, 1986), and for individual recognition in colonial breeding species (Aubin *et al.*, 2000). The song of baleen whales is, like bird song, considered to be a reproductive advertisement signal (Payne and McVay, 1971), likely playing a significant role in mate choice in a polygamous mating system (Tyack and Clark, 2000). Most species of baleen whales sing, including the bowhead whale *Balaena mysticetus* (Clark, 1990). The song of bowhead whales is composed of repeated series of highly stereotyped song notes, and the song notes change completely between years, resulting in distinctive songs in each year (Würsig and Clark, 1993; Tervo *et al.*, 2011). Multiple songs are produced within a season (Stafford *et al.*, 2008; Delarue *et al.*, 2009; Tervo *et al.*, 2011) with one dominant song of the season that is most common and

one or two other songs, which are heard less frequently (Stafford *et al.*, 2008; Tervo *et al.*, 2011).

Like songbirds, all toothed whales except for the sperm whales (*Physeteridae*) have a bilateral configuration for sound production (Cranford *et al.*, 1996). In non-physeterid toothed whales two sound generating structures, the paired phonic lips, are located in each of the nasal passages providing the toothed whales the possibility of simultaneous sound production (Cranford, 2000). So far, biphonation has been suggested for bottlenose dolphins *Tursiops truncatus* (Cranford, 2000) and killer whales *Orcinus orca* (Tyson *et al.*, 2007). Anatomical studies of baleen whales suggest that sounds are produced in the larynx (Reidenberg and Laitman, 2007). The arytenoid cartilages in the larynx support a U-shaped fold, which may function to regulate airflow through the larynx, much in the manner of true vocal folds (Reidenberg and Laitman, 2007). Despite there being only a single candidate organ for sound production in baleen whales, i.e., the larynx, the sounds produced by some species, including the minke whale *Balaenoptera acutorostrata* (Gedamke *et al.*, 2001) and North Atlantic right whale *Eubalaena glacialis* (Tyson *et al.*, 2007), suggest that biphonation occurs. These biphonate vocalizations include the production of two harmonically unrelated sounds by the minke whale (Gedamke *et al.*, 2001) and the presence of sidebands and unrelated nonparallel bands in the northern right whale

^{a)}Author to whom correspondence should be addressed. Electronic mail: ote@science.ku.dk

(Tyson *et al.*, 2007). Two simultaneously occurring song notes have also been reported for bowhead whales (Würsig and Clark, 1993), but it remains unclear whether these observations were due to a duet of two individuals or due to simultaneous sound production by a single individual.

To test the hypothesis that individual bowhead whales can produce two sounds simultaneously, we analyzed bowhead whale songs recorded with hydrophone arrays during the spring of 2008 and 2009 in Disko Bay, Greenland. Our results strongly indicate that singing bowhead whales include simultaneous dual frequency sound production as part of their singing behavior.

II. MATERIALS AND METHODS

A. Data collection

The data were collected in Disko Bay, Western Greenland, 69°N and 54°W, from March 12 to April 14, 2008, and from March 5–9, 2009. In 2008 recordings were made using two HTI-94-SSQ hydrophones (High Tech, Inc., Gulfport, MS) (−198 dBV/1 μ Pa) with a flat (± 2 dB) frequency response from 2 Hz to 30 kHz. The hydrophones were connected to a custom built amplifier (highpass filter at 30 Hz, 20 dB gain), and deployed through holes in fixed/stable sea ice 20 m apart at a depth of 10 m. The signals were recorded using a SONY DAT TCD-D8 tape recorder (SONY Corp., Toyko, Japan) with a sampling frequency of 44.1 kHz and with 16-bit resolution. The data were digitized into standard wave files in RAVEN PRO 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY).

In 2009 we used a non-linked array of three independent receivers that were synchronized with 50 μ s timing from GPS

satellite signals using a frequency shift keying device (FSK) (see Møhl *et al.*, 2001, for details). Each recording station consisted of a B&K 8101 hydrophone (Brüel & Kjær, Copenhagen, Denmark) (−184 dBV/1 μ Pa) connected to a low noise amplifier (40 dB gain) with 10 Hz highpass and a 25 kHz lowpass filters, a FSK device and a stereo M-Audio Microtrack II 24/96 digital recorder (Avid Technology, Inc., Burlington, MA). The FSK signal and acoustic signals were recorded on the two channels on the M-Audio Microtrack II 24/96 digital recorder sampling at 96 kHz with 16-bit resolution. The recordings from the three receivers were then time-aligned using the FSK signals. Hydrophones at each recording station were deployed at 25 m depth through holes in the fixed stationary coastal sea ice. The stations formed a linear array of 1 km where the spacing between stations was 700 m and 300 m [Fig. 1(a)].

B. Data analysis

Three analyses were conducted: (1) localization of the source with a three-hydrophone array, (2) comparison of time of arrival differences on a two-hydrophone array, and (3) spectral analysis of spectrograms of the recorded signals.

In 2009, the sources of the two simultaneously occurring sounds recorded with the three-hydrophone array were localized using the hyperbolic method in ISHMAEL 1.0 (D. Mellinger, Oregon State University, Newport, OR) with time of arrival difference (TOAD) of the song components time aligned via FSK recordings with an accuracy of 50 μ s (Møhl *et al.*, 2001). The localization of each song component was repeated 10 times in order to account for differences in the localization accuracy caused by the size of the measuring

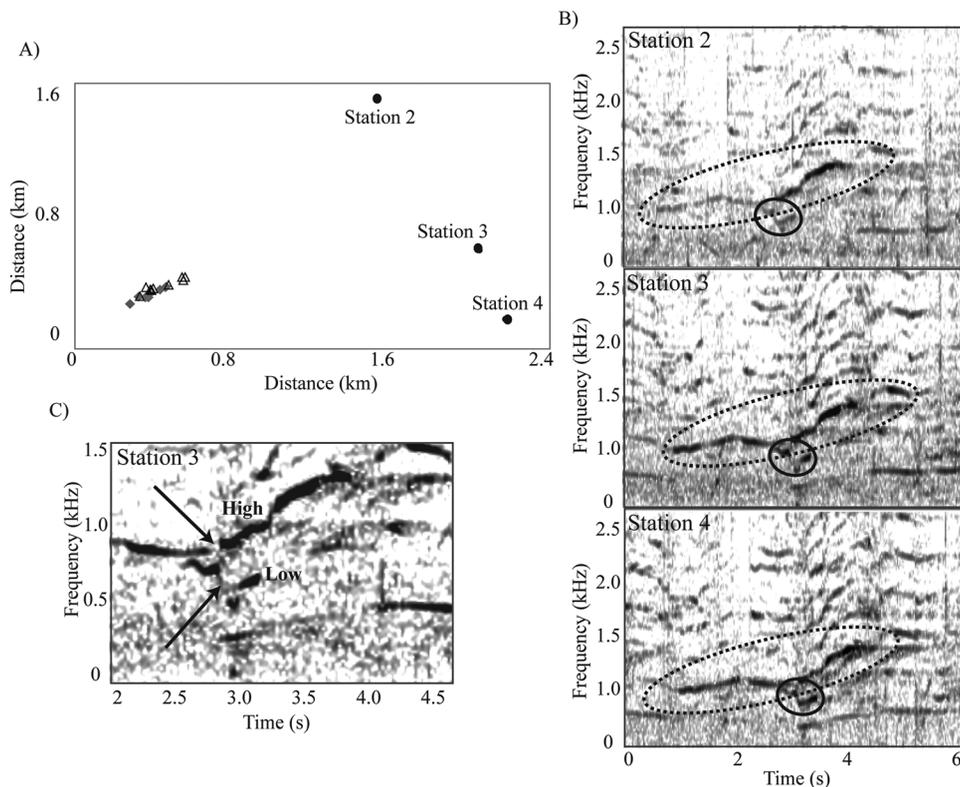


FIG. 1. (a) 10 repetitions of localization of the two simultaneously occurring song components with a three-hydrophone array in 2009. The high song notes are marked with black triangles and the low song notes with gray diamonds. The localizations form an elongated cluster perpendicular to the array. (b) Spectrograms of the simultaneous sound production event time aligned from the three recording stations. The high song component is marked with a dotted circle and the low component with a solid circle (Hamming window, FFT size 1024, 50% overlap, sampling rate 44 kHz). (c) A zoomed in section of the two song notes, high and low, from Station 3. The black arrows mark the areas of low intensity on the two song notes which coincide with areas of high intensity in the other song note.

window in ISHMAEL 1.0. The localization error for this type of array was estimated by assuming a $100 \mu\text{s}$ error in time measurements, 10 m/s variation in sound velocity and 1 m in receiver locations. For each location, 1000 iterations were computed and new locations were calculated accordingly. The low and high bounds of the new locations were used in estimating the localization error (*sensu* Wahlberg *et al.*, 2001).

In 2008, we measured the TOAD between the two hydrophone receivers for the two simultaneously occurring song components. If the two song components originated from two different, independently moving, sources the differences in the time of arrival between the two song components should change. If the different components are produced by a single source or by two sources with fixed distance to each other the time of arrival differences between the two song components should always be the same on both channels at any point of time. The onset time of signals was determined visually from the spectrogram with a time resolution of 11.6 ms and each measurement was repeated three times (Hamming window with 512-point FFT size, 50% overlap). The significance of the time of arrival differences between the two components was tested with a T-test in SPLUS 6.2 (TIBCO Software Inc, Palo Alto, CA).

For the spectral analysis of the data from 2008 and 2009 a Hamming window with a FFT size of 1024 was chosen yielding a frequency resolution of 43 Hz at 44.1 kHz sampling. The minimum amplitude of the first song note HI (a high note) was measured from three sequential 300 ms analysis windows. The measurement windows were labeled 1, 2, and 3 [Fig. 2(a)]. Window 1 started 600 ms before the onset of the second song note BS (a low note), window 2 started 300 ms before the onset of the second song note BS and the last window 3 started at the onset of the second song note BS. These measurements were made using the cursor tool in ADOBE AUDITION 3.0 (Adobe Systems Inc., San Jose, CA).

III. RESULTS

For the duration of the recording periods in 2008 and 2009 bowhead whales were the only baleen whale species heard and observed in Disko Bay. One other vocally active species, the bearded seal *Erignathus barbatus*, was recorded in 2009. As a result of the extensive ice coverage during the time of the recordings in both 2008 and 2009 it was not possible to obtain direct visual observations of the bowhead whales producing the recorded vocalizations.

In 2009, 4 h of data were analyzed and two simultaneously occurring song notes were recorded on March 6, 2009 as part of the second song type of that year [Fig. 1(b)]. The two song notes, high and low, were localized on average 59 m apart at a distance of about 1.6 km from the center of the array [Fig. 1(a)]. The 10 repeated localizations of the same high and low song notes resulted in an elongated location cluster with a width of 37 m and length of 317 m [Fig. 1(a)]. The minimum distance between a localized high and low song note was 6 m and the equivalent maximum distance was 317 m. Thus the expected localization error for this array based on the error analysis ranged between 20 m and 400 m.

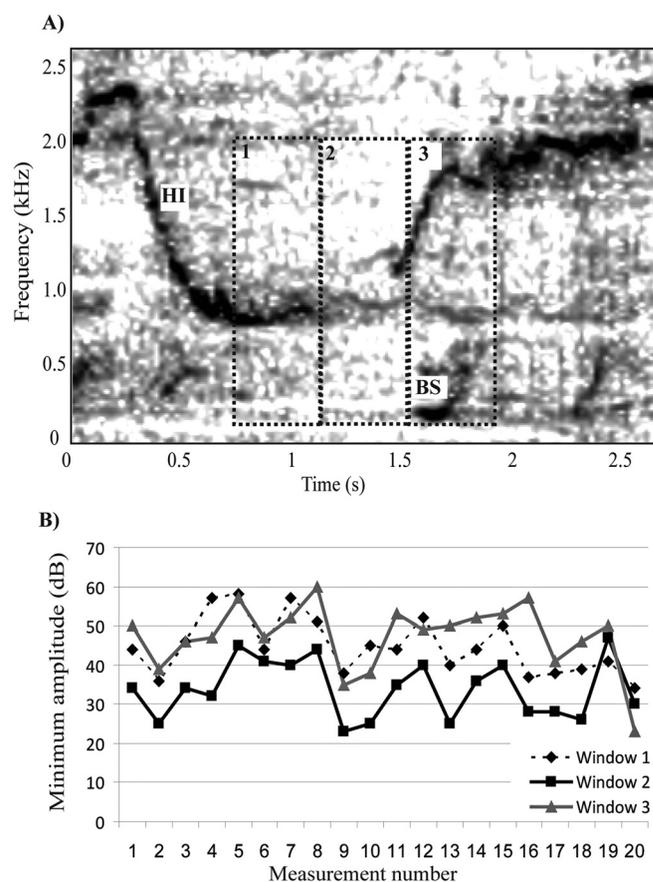


FIG. 2. (a) Spectrogram with song notes HI and BS (Hamming window, FFT size 1024, 50% overlap, sampling rate 44 kHz). The dotted squares illustrate the positioning of the three measurement windows 1, 2, and 3. Each window was 300 ms long. This particular spectrogram is from measurement number 3. Notice the decline in amplitude of song note HI in window 2. (b) Line chart of the minimum amplitude (dB) within the three windows 1, 2, and 3 for the different measurements from 2008 ($n = 19$) and 2009 ($n = 1$). On 96% of the measurements from 2008 (18/19) the lowest amplitude of HI was found in the center window number 2 illustrated with the solid black line. Notice the differing curve for the last measurement number 20 from 2009, which is presented in Fig. 1 in detail.

In 2008, 7.75 h of data were analyzed and 3 h contained a song type where two song notes, called HI and BS (Tervo *et al.*, 2011), occurred simultaneously (Fig. 3). Each song was composed of one HI song note together with three to 18 repetitions of song note BS. Song note HI was a continuous, highly frequency modulated signal with a mean duration of $15.2 (\pm 0.4)$ s ($n = 11$) and song note BS was a low frequency upsweep with a short mean duration of $0.2 (\pm 0.0)$ s ($n = 19$) [Fig. 3(a), Table I]. The harmonics of the fundamental frequencies of HI and BS extended to 3500 kHz and to 700 Hz, respectively (Fig. 3). The mean duration of a song was $15.2 (\pm 0.4)$ s ($n = 11$) and was the same duration as song note HI which completely overlapped the BS notes (Fig. 3). We extracted 11 songs from a 20 min song session recorded on March 19, 2008 for the analysis on the basis that no other songs were heard during this song session and all the songs had a signal-to-noise ratio of > 20 dB. The two song components HI ($n = 11$) and BS ($n = 19$) were significantly different in their minimum and maximum frequencies. The lowest frequency of HI was higher than the highest

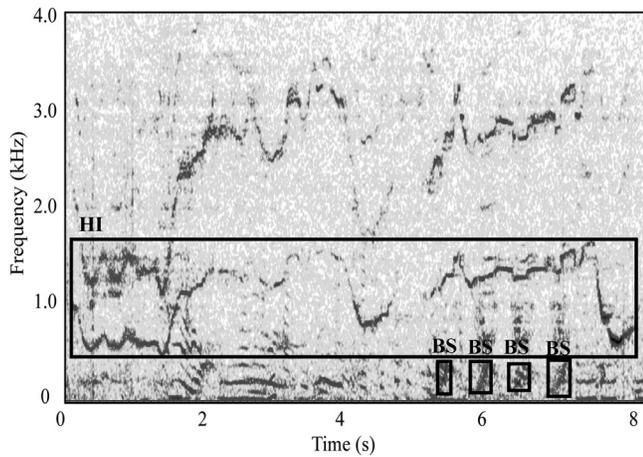


FIG. 3. Spectrogram showing a song with the two song components HI and BS marked with solid squares recorded in 2008. Notice the very different frequency contours of HI and BS, where the first is fluctuating with multiple inflection points and the latter is a frequency upsweep. There is a frequency modulated call of another bowhead whale in the background.

frequency of BS by more than an octave at any given time and the two components were not harmonically related (Table I). The measurements of the time of arrival differences between components HI and BS ($n = 11$) showed no significant difference (T-test: $t = 0.0029$, $p = 0.997$, $df = 36$). The time of arrival measurements from the 20 min song session were temporally spaced with an average time interval between consecutive measurements of $1.1 (\pm 2.4)$ min. This indicates that the source or sources producing the two song components HI and BS were always on the same hyperbola, even though the time of arrival difference between hydrophone 1 and hydrophone 2 (ranging from -20 ms to 40 ms) showed that the source or sources were moving.

The sound intensity measurements of the data from 2008 showed that the minimum amplitude of song note HI was lowest in measurement window 2 starting 300 ms before the onset of the song component BS ($n = 19$) [Fig. 2(b)]. The minimum amplitude of song note HI in the measurement window 2, right before the onset of BS was on average $10 (\pm 6)$ dB lower than the minimum intensity in the measurement window 1. Similarly, the minimum amplitude in the window number 3 after the onset of BS [Fig. 2(b)]. Only on one occasion [measurement number 19, Fig. 2(b)], the minimum sound amplitude of song note HI was not lowest in window 2. In this case, the minimum sound amplitude was lowest in window 1, 600 to 300 ms before the onset of song note BS.

The data from 2009 ($n = 1$) showed a different phenomenon. The window of lowest amplitude was in window 3, 300 ms after the onset of the low song component [measurement 20, Fig. 2(b)]. However, the ca. 60 ms long area of lowest amplitude in window 3 in the high song component coincides with an area of high amplitude in the low song component [Fig. 1(c)]. Furthermore, this is immediately followed by a 140 ms long area of high amplitude in the high song component which coincides with an area of low amplitude in the low song component indicating that the sources of these two sounds are connected [Fig. 1(c)].

IV. DISCUSSION

In this study we analyzed two different bowhead whale songs from 2008 and 2009 composed of simultaneously occurring song notes to test whether bowhead whales are capable of two-voice singing. In 2009, when localizing with a three-hydrophone array, we found that the two simultaneously produced sound sources were located to the same position well within the estimated localization error of the array. In 2008, when obtaining bearings with a two-hydrophone array, the two simultaneously occurring song notes in the song were always co-located on the same hyperbola during a 20 min long continuous song session. Finally, we found that the two simultaneously occurring sounds had an influence on the production of each other, indicating that they are produced by the same sound producing structures or that they are driven by the same pneumatic pressurization events.

For the 2009 data (three-hydrophone array), the potential error in absolute positions at the localized range was calculated based on random iterations to vary between 20 m and 400 m. Because the focus of this study is in the relative positions of the two song notes occurring at the same time, differences in the positions between the 10 repetitions of each song note caused by variation in the size of the measurement window and in the performance of the localization method when applied to different frequency contours in ISHMAEL 1.0 can be regarded as the relevant error of the system. In Fig. 1(a), the 10 repetitions of localizations of both song notes show a strong tendency to form an elongated cluster perpendicular to the array. This suggests that the differences in localization between repetitions are most likely due to bearing lines crossing at low angles resulting in minor error in the direction of the source but major error in the distance between the source and the array. We therefore argue that it is plausible that the two sounds were produced by a single source and that the relatively large maximum distance of

TABLE I. Measured parameters for the two simultaneously occurring song notes BS and HI from 2008. Notice the large difference between the maximum frequency of BS and the minimum frequency of HI.

Song component		Duration (s)	Minimum frequency (Hz)	Maximum frequency (Hz)
BS	mean	0.2	149.1	241.2
	SD	0.0	43.5	62.1
HI	mean	15.2	819.5	2465.8
	SD	0.4	86.8	145.7

317 m between localizations of low and high song notes is an artifact of the localization method.

The behavior of bowhead whales during winter at the time of the data collection is not well documented. The most commonly observed surface behaviors in March in Disko Bay include resting and traveling where animals are typically solitary spaced > 300 m from each other. Co-operative skim feeding at the surface and pairs of whales swimming next to each other is most commonly seen later in the season in April and May, lending weight to the contention that the co-located sound sources are from a single whale and not two close by conspecifics.

For the 2008 data (two-hydrophone array) the time resolution of the analysis was 11.6 ms, which corresponds to an error in distance of about 17 m. In this case as well, two bowhead whales could have been located right next to each other, each producing one song note in a duet, and our coarse resolution would have been unable to discriminate the two sources. Another explanation for the result that the two sounds from 2008 were co-located during a 20 min long song session is that two bowhead whales could have been located in different positions on the same hyperbola line with fixed distance to one another while performing a duet. In fact, the time interval between subsequent TOAD measurements ranged from 2 s to 10 minutes indicating that if the two sounds were produced by two animals, the two individuals must have maintained precise orientation and distance to one another with respect to the array throughout the entire song session. Duets have been described for many song bird species (Hall, 2009), a few terrestrial mammals (Janik and Slater, 1997) but never for marine mammals. Coordinated movements during the duet are rarer and described for some bird species (Hall, 2009), but again never for marine mammals. Instead of a duet with coordinated movements, it therefore seems more parsimonious that our results are due to simultaneous sound production by a single individual.

This interpretation is also supported by spectral and intensity analyses of the sounds. The spectral analysis of the 2008 data (two-hydrophone array) showed that the intensity of the first song note HI dropped before the onset of the second song note BS, on average 10 (\pm 6) dB. The spectral analysis of the 2009 data (three-hydrophone array) showed that the intensity of the first song note dropped after the onset of the second song note, but it also revealed areas of high and low amplitude shifting between the two sounds when high amplitude events in the one sound coincided in time with an area of low amplitude in the other, and vice versa. We propose that the intensity from one sound source within the animal is affected by the onset of activity in another source within the same animal, implying that the same whale simultaneously produced the two sounds. This phenomenon, where activity in the one sound producing organ has an impact on the performance of the other, has also been described for song birds that employ two-voice singing (Zollinger, 2007).

Simultaneous sound production enables individuals to produce complex acoustic signals in frequency and in time (e.g., Suthers, 1990; Gedamke *et al.*, 2001). Acoustic complexity of the song is an indication of high vocal motor con-

trol in songbirds (Nowicki *et al.*, 1986), which may be used as an honest signal of the singer's quality in a mate choice context (Vallet *et al.*, 1998; Ballentine *et al.*, 2004). In canaries, *Serinus canaria*, a certain phrase of the song, composed of two simultaneously produced syllables, is more difficult to produce than other phrases and females prefer the males that master the production of this section (Vallet *et al.*, 1998). Bowhead whales are known to have a high degree of seasonal and annual variation in their song repertoire (Würsig and Clark, 1993; Tervo *et al.*, 2009; Tervo *et al.*, 2011). The simultaneous production of two independent sounds enhances the potential for creating complex acoustic signals and this complexity could play a role in mate choice. Simultaneous sound production has also been documented to function for communicating identity (Aubin *et al.*, 2000; Miller *et al.*, 2007) and orientation of the signaler in relation to the receiver in some species (Miller *et al.*, 2007), which could be a function of dual sound production in bowhead whales as well.

In conclusion, the three lines of evidence presented in this study all point to simultaneous dual frequency sound production by bowhead whales. With the sound source localization results, we demonstrate the co-location of the sound sources, though it is not possible to definitely determine whether a single whale or two whales closely associated, produced the sounds. The analysis of the amplitude modification of one signal by the onset of the second signal provides additional evidence of a direct linkage between the sound production mechanisms for the two sounds. In combination, these observations strongly suggest that individual bowhead whales are capable of dual sound production. We propose that two-voice singing may have evolved through acoustically mediated sexual selection for individuals that demonstrate their ability to perform complex signals with a finely controlled vocal apparatus in a polygamous mating system. This result, together with the other reports on baleen whale simultaneous sound production emphasize the need for further investigations on the sound production of mysticetes which appears to be more complex than previously suggested.

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