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Song sharing and diversity in the Bering-Chukchi-Beaufort population of bowhead whales (*Balaena mysticetus*), spring 2011

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Abstract

Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort population migrate in nearshore leads through the Chukchi Sea each spring to summering grounds in the Beaufort Sea. As part of a population abundance study, hydrophones were deployed in the Chukchi Sea off Point Barrow, (12 April to 27 May 2011) and in the Beaufort Sea (12 April to 30 June 2011). Data from these sites were analyzed for the presence of bowhead whale song. We identified 12 unique song types sung by at least 32 individuals during ~95 h of recordings off Point Barrow. Six of these songs were detected at the Beaufort MARU site as well as six additional song types that were not analyzed. These results suggest a shared song repertoire among some individuals. This report represents the greatest number of songs to date during the spring migration for this population. We attribute this greater variety to population growth over the 30 yr since acoustic monitoring began in the early 1980s. Singing during early to mid-spring is consistent with the hypothesis that song is a reproductive display, but further research is necessary to understand the exact function of this complex vocal behavior.

Key words: bowhead whale, *Balaena mysticetus*, Barrow Alaska, song, acoustic monitoring.

Cetaceans rely on sound for social communication and sensing their environment, an expected adaptation given that sound propagates more efficiently and therefore much further in water than light or chemical cues (Tyack and Clark 2000). Baleen whales (order Mysticeti) use sound to navigate, communicate among conspecifics, and as a reproductive display. In general, all baleen whales produce simple "calls" (typically frequency modulated signals a few seconds in duration) that are used to maintain and coordinate long-distance contact and communication (*e.g.*, Clark and Clark 1980, Clark and Johnson 1984, Parks *et al.* 2007, Munger *et al.* 2008).

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In contrast to calls, several mysticete species also produce long, patterned sequences of sounds, referred to as "songs," during certain periods of the year (humpback, *Megaptera novaeangliae*, Payne and McVay 1971; bowhead, *Balaena mysticetus*, Ljungblad *et al.* 1982; fin, *Balaenoptera physalus*, Watkins *et al.* 1987; blue, *B. musculus*, Mellinger and Clark 2003; minke, *B. acutorostrata*, Clark and Gagnon 2004). Studies of blue, fin, and humpback whale song have revealed that singers are exclusively male (*e.g.*, Winn and Winn 1978, Croll *et al.* 2002, Oleson *et al.* 2007) and, at least in the comparatively well-studied humpback whale, song primarily plays a role in reproductive behavior (*e.g.*, Darling *et al.* 2006) even though it has been observed in nonbreeding times and locations (*e.g.,* Clark and Clapham 2004).

There are differences in the complexity and organization of songs among species. Humpback whales, arguably the best known cetacean singers, produce long, complex songs made up of multiple phrases (each consisting of distinctly different notes with clear spacing between them, that may be frequency- or amplitude-modulated), grouped in themes and repeated in a specific order that is common to all males in a geographic area during a breeding season (Payne and McVay 1971). Each year, a different song is produced by animals in the same population (Winn and Winn 1978). Fin whales, in contrast, simply repeat the same simple downswept "20-Hz pulse" over and over (Watkins *et al.* 1987), although differences in note spacing characterize different areas (Delarue *et al.* 2009*b*; Castellote *et al.* 2011). Blue whales are similar, but use 1–4 longer notes (Stafford *et al.* 2011). Both fin and blue whales use the same song structure every year (Watkins *et al.* 1987, McDonald *et al.* 2006). This repeated signaling has also been called "song" because it is produced primarily during the presumed breeding season and, to date, exclusively by males (Watkins *et al.* 1987, Croll *et al.* 2002). There is, therefore, a broad range in the definition of "song" within the baleen whales. Nevertheless, there is sufficient consistency in the song structure and note features within a species such that one can recognize a species, and often even a population, by its song (Payne and Guinee 1984, Stafford *et al.* 2001, Castellote *et al.* 2011).

Early bowhead acoustic studies of the Bering-Chukchi-Beaufort (BCB) population of bowhead whales documented that songs were different from one year to the next and all whales in the same year sang the same general song (Würsig and Clark 1993). Würsig and Clark (1993) described bowhead whale song structure as being composed of repeated phrases (made up of 1–5 notes) that make up one to multiple themes. These "songs" are repeated as bouts. The bowhead whale's ability to simultaneously produce multiple, harmonically unrelated sounds contributes to the complexity of the song (Würsig and Clark 1993, Tervo *et al.* 2011). Songs typically last about one minute, but can be repeated in sequences that extend over many hours (Würsig and Clark 1993).

More recently, however, longer-term recordings have shown that bowhead whale populations produce multiple songs each year and these have been divided into "simple" and "complex" songs based on the type and structure of notes and phrases produced. For instance, Delarue *et al.* (2009*a*) observed six unique songs in a year from the BCB population, four of which were recorded during the fall or early winter. Stafford *et al.* (2008) identified three unique song types in the Eastern Canada-West Greenland (EC-WG) population in just a 9 d recording effort. Sixty-six unique song types were documented in a yearlong study of the much smaller Spitsbergen bowhead population (Stafford *et al.* 2012). It appears, then, that bowhead whale singing behavior differs from that of other mysticetes in that multiple songs are sung each year. The question then becomes, do different whales or groups/

cohorts in a population sing different songs or does the population as a whole change song type rapidly during a year with the same animals singing multiple songs?

The springtime migration off Point Barrow offers the best location to attempt to answer this question as acoustic studies have been periodically conducted in this area using similar methods for nearly 30 yr and an observation program to track whales on their northward migration has been in place at the same time (George *et al.* 2004, 2012). The whales passing Point Barrow are of the Bering-Chukchi-Beaufort (BCB) population, which is defined by its seasonal residence in and migrations between wintering grounds in the Bering Sea and summering grounds in the Beaufort Sea *via* the Chukchi Sea. The BCB is the largest stock of bowheads in the Arctic Ocean (Rugh *et al.* 2003). Increases in the number of songs in this region are more likely to reflect biological changes than artifacts of sampling. If multiple songs are indeed present and repeated, the location of Point Barrow along a migratory corridor, where whales pass by and do not return until months later, allows inferences to be made regarding the extent of song repertoire size and song type sharing between different singers.

Methods

Study Site and Data Acquisition

Acoustic data were recorded during the 2011 bowhead whale survey conducted by the North Slope Borough Department of Wildlife Management (NSB-DWM; George *et al.* 2004, 2012). The visual census took place off Point Barrow, Alaska from 13 April to 1 June 2011. Visual survey data (counts of animals seen during hours with daylight) were obtained from George *et al.* (2012). The Cornell Bioacoustics Research Program oversaw the deployment of an acoustic array consisting of five synchronized marine autonomous recording units (MARUs) placed along a transect parallel to the edge of the land fast ice on 10 April 2011 prior to the start of the visual survey (see Clark *et al.* 2009). We only analyzed data from the MARU located nearest to the primary census observation perch. This recorder (Pt. Barrow MARU) was located at 71.364°N, 156.717°W less than 1 km from the edge of the land fast ice, which extended approximately 4 km from shore (Fig. 1). Water depth was approximately 37 m. The Pt. Barrow MARU recorded continuously at a 2 kHz sample rate with a flat frequency response (±3 dB) in the 10–800 Hz frequency band. Analysis was conducted on >1,200 h of recordings made from the initial deployment date on 10 April through 14 May 2011 when singing effectively ceased.

Supplementary acoustic data were taken from a MARU deployed in the Beaufort Sea (henceforth Beaufort MARU) to compare the chronological sequence and consistency of song types between the two different recording sites as well as to determine whether some higher frequency song notes were missed by the lower sampling rate of the Pt. Barrow MARU. The Beaufort MARU recorded on a 30% duty cycle at a sampling rate of 8.2 kHz with a frequency response (±3 dB) in the 10–4,096 Hz band. Data from 1 April through 30 June 2011 were analyzed for this recorder. It was located at 71.55°N, 155.56°W or about 45 km northeast of the Pt. Barrow MARU in approximately 72 m of water (Fig. 1).

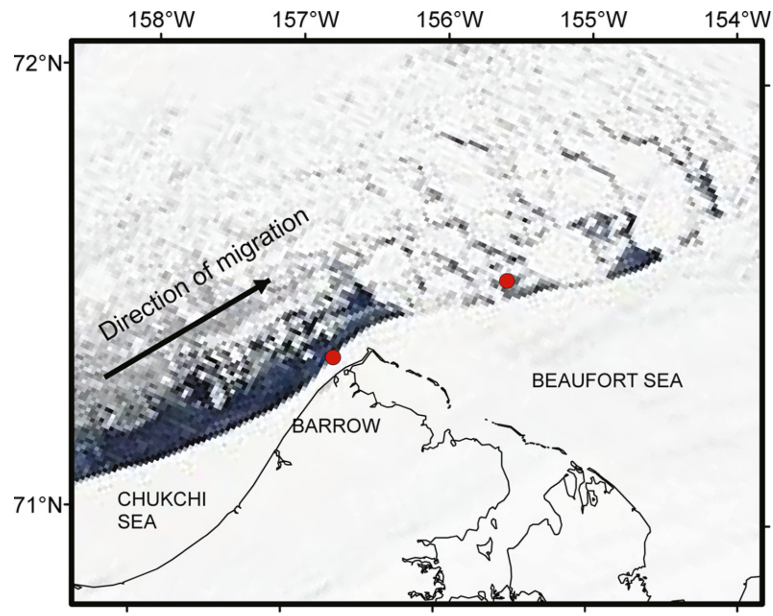

Figure 1. Location of two hydrophones (red dots) 45 km apart near Point Barrow, Alaska used to record bowhead whale songs during the 2011 spring migration. The lead in which bowhead whales migrate can be seen offshore of the fast ice. Sea ice data are from 1 May 2011 from MODIS (http://lance-modis.eosdis.nasa.gov).

Data Processing

The approximately 1,200 h of recordings from the Pt. Barrow MARU were separated into five minute sections and displayed as spectrograms (1,024 point FFT, 90% overlap, Hann window for a frequency resolution of 1.9 Hz and time resolution of 45 ms) using Raven Pro 1.4 software (Bioacoustics Research Program 2011) to identify the presence of bowhead songs. Spectrograms of the data were visually reviewed, supplemented with listening to short segments, to ensure that all songs were detected. A song was characterized by the repetition of 1–3 different notes (Würsig and Clark 1993, Stafford *et al.* 2008). Only songs that were repeated three or more times consecutively and that the analyst could confidently distinguish from background noise, calls, or songs from other singers were selected for further analysis.

Songs identified for analysis were measured for descriptive song characteristics. These included song duration (measured from the start of the first note to the end of the last note in the song); minimum frequency; maximum frequency recorded by the MARU (although the low Pt. Barrow MARU sampling rate may not have permitted the recording of the maximum frequency of the measured notes); duration of each note in the song; and the number of song notes. These characteristics, in combination with the arrangement of song notes, were used to categorize each song. A song bout was defined as multiple sequences of the same song type separated from earlier and later bouts by time intervals greater than 1 h.

An alphanumeric system of nomenclature was devised to simplify comparison between song types, bouts, and notes. Each song type was assigned a number based on the order of occurrence in the acoustic record. Song-1 refers to all observations of the first song type detected on the Pt. Barrow MARU. Specific bouts were referenced with an additional number such that bout-1.1 refers to the first observed bout of song type 1. Each note type in a song type was assigned a letter identifier. Thus note 1A refers to all type A notes in song type 1.

Songs from two different singers were considered the same song type if they shared the same arrangements of repeating notes as stated in Stafford *et al.* (2012). If two bouts of the same song type were separated by a time gap of more than approximately 24 h without singing we assumed that the two songs were sung by different singers. This is based on behavioral observations of migrating whales and likely instrument detection limits (*e.g.*, Clark *et al.* 1986, Koski *et al.* 2010). Multiple bouts of song types 1, 2, 4, 5, 8, and 12 that were of sufficient quality and separated by more than 24 h were used to estimate a minimum number of singers. A Spearman's rank correlation analysis was used to see if there was a relationship between the total number of hours of singing per day and total number of whales seen per day by visual observers.

Songs from the Beaufort MARU were identified and measured by the same methods and compared with song types 1–12 from the Pt. Barrow MARU but measurements were not made of the time-frequency characteristics of these songs.

Results

Song Detection and Diversity

Bowhead songs were recorded on the Pt. Barrow MARU on 25 out of 32 d spanning the first observation of song on 12 April until 14 May 2011 (Fig. 2). During

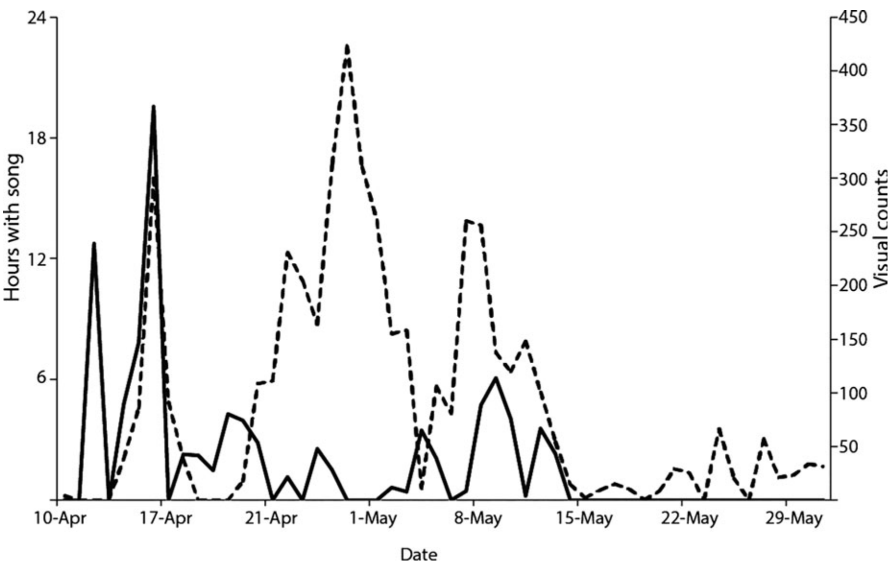

Figure 2. Daily number of hours with song (solid line) and the corrected visual count of bowhead whales (dashed line) during the migration near Point Barrow, Alaska in spring 2011.

Barrow (primary)

Song	April 2	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	May 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1				1.1		1.2	1.3	1.4 1.5																													
2				2																																	
3						3.1	3.2																														
4							4.1				4.2	4.3		4.4	4.5		4.6			4.7																	
5							5.1												5.2																		
6								6																													
7								7																													
8										8.1			8.2		8.3 8.4				8.5					8.6	8.7		8.8		8.9								
9											9																										
10																										10.1				10.2	10.3	10.4					
11																																	11				
12																																		12.1 12.2	12.3		

Beaufort (supplementary)

Song	April 2	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	May 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1		1	1	1				1	1		1				1																					
2						2																															
4	4																			4																	
5																5	5		5			5		5		5				5	5	5	5				
8					8				8	8											8				8					8							
12																																					12

Figure 3. The days on which specific song types were recorded during 32 d in the spring of 2011 when bowhead whales were migrating past Point Barrow, AK and in the Beaufort Sea. Song bouts are given a sub number (*i.e.*, 8.1 was the first observed bout of song type 8).

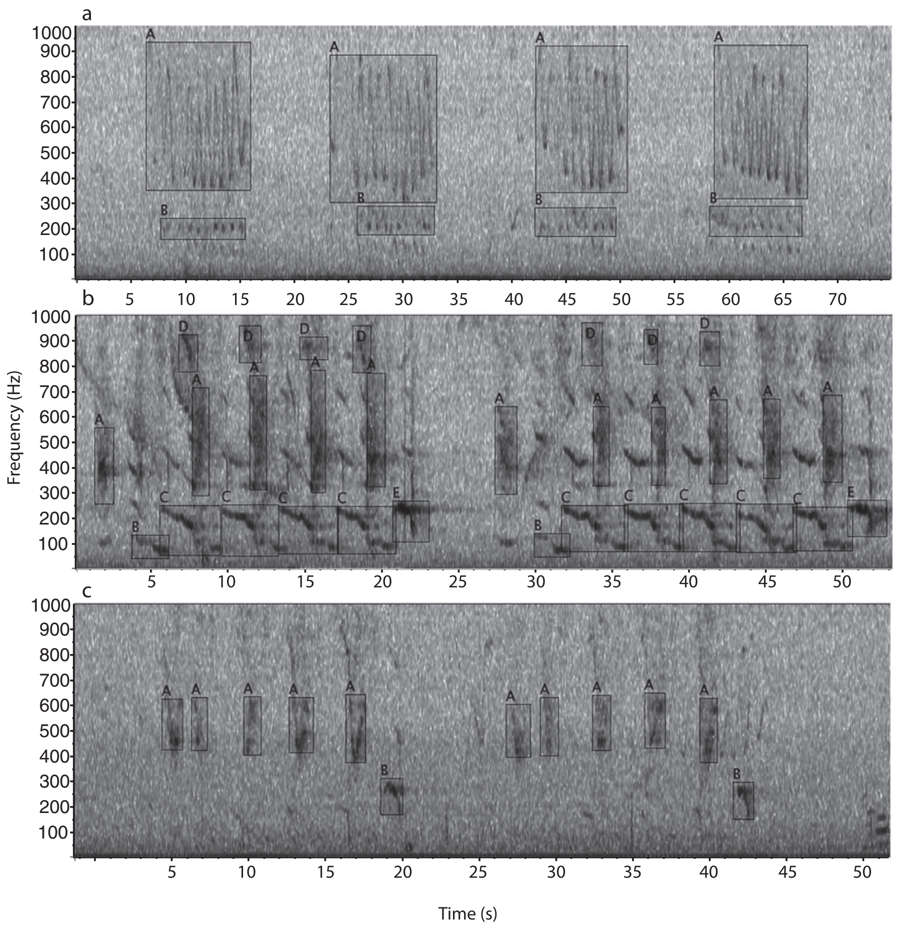

Figure 4. Examples of three bowhead whale song types during the spring 2011 migration: (a) Song-1 (four songs), (b) Song-2 (two songs), and (c) Song-3 (two songs), and their labeled notes (1,024 pt. FFT, 90% overlap, Hann window).

that period, 12 distinct song types were identified. The total number of different song types observed was greatest early in the season. Song types 1, 4, and 8 occurred most frequently, with types 4 and 8 present throughout the majority of the 32 d sampling period. There was an average of 1.4 song types observed on days with song and a maximum of 4 song types occurred on 15 April. No song type, with the exception of type 5, was repeated after being absent from recordings for more than 5 d (Fig. 3).

Daily number of hours with song was defined as the sum of hours of singing, regardless of song type or singer, throughout a calendar day's recording period. The daily number of hours with song ranged from 0 to nearly 20 h. Song types 1, 2, 4, 8, and 10 made up 86% of the total song hours. Corrected visual counts, defined as total number of confirmed new and conditional whale sightings corrected for survey effort, ranged from 0 to 423 per day (George *et al.* 2012). There was no significant

Table 1. Mean frequency and duration parameters (with standard deviation) of 12 bowhead whale songs recorded near Point Barrow, Alaska from 12 April to 14 May 2011.

Song	Duration (s)		Low frequency (Hz)		High frequency (Hz)		*n*
1.1	86.1	(44.8)					30
Note 1A	9.0	(1.3)	381	(45)	906	(75)	242
Note 1B	8.3	(1.7)	186	(31)	331	(39)	226
1.3	63.4	(32.7)					33
Note 1A	5.9	(1.0)	369	(25)	849	(62)	67
Note 1B	5.8	(0.9)	172	(13)	265	(20)	67
1.4	107.0	(22.6)					16
Note 1A	6.3	(1.3)	354	(20)	804	(83)	60
Note 1B	5.0	(1.2)	185	(19)	282	(17)	53
2	16.9	(4.1)					76
Note 2A	1.6	(0.4)	314	(25)	668	(72)	73
Note 2B	2.3	(0.5)	46	(5)	136	(11)	19
Note 2C	3.9	(0.3)	65	(8)	253	(7)	59
Note 2D	1.0	(0.2)	798	(33)	951	(24)	53
Note 2E	2.0	(0.3)	118	(14)	283	(11)	50
3	19.5	(4.4)					51
Note 3A	1.3	(0.2)	402	(33)	651	(41)	61
Note 3B	1.3	(0.2)	142	(16)	291	(13)	46
4.1	56.0	(30.7)					13
Note 4A	0.8	(0.1)	514	(89)	842	(70)	85
Note 4B	0.6	(0.1)	129	(48)	346	(45)	81
Note 4C	1.1	(0.2)	237	(40)	658	(126)	17
4.2	72.0	(23.9)					8
Note 4A	0.7	(0.2)	398	(73)	944	(83)	83
Note 4C	1.0	(0.1)	216	(53)	942	(92)	27
4.4	48.8	(12.6)					13
Note 4A	1.0	(0.3)	393	(70)	977	(31)	90
Note 4C	1.2	(0.4)	279	(53)	986	(28)	20
5.1	46.0	(12.4)					18
Note 5A	1.1	(0.2)	372	(75)	963	(48)	84
Note 5B	0.6	(0.2)	103	(31)	373	(45)	80
5.2	68.1	(22.9)					14
Note 5A	1.4	(0.2)	343	(35)	988	(22)	65
Note 5B	1.0	(0.3)	96	(42)	316	(39)	59
6	41.2	(10.7)					11
Note 6A	9.9	(2.6)	233	(28)	447	(65)	11
Note 6B	17.8	(8.0)	238	(33)	562	(81)	14
Note 6C	3.0	(0.8)	215	(35)	369	(50)	11
7	66.9	(18.1)					6
Note 7A	1.7	(0.5)	98	(15)	319	(55)	66
8.1	75.8	(18.2)					17
Note 8A	1.0	(0.2)	679	(97)	988	(12)	17
Note 8B	1.1	(0.1)	580	(76)	861	(94)	17
Note 8C	0.9	(0.2)	511	(69)	689	(88)	12
Note 8D	1.6	(0.3)	291	(28)	556	(48)	22
Note 8E	0.9	(0.2)	107	(34)	313	(44)	51

(Continued)

Table 1. (Continued)

Song	Duration (s)		Low frequency (Hz)		High frequency (Hz)		*n*
Note 8F	1.7	(0.3)	104	(28)	991	(44)	63
8.6	44.8	(13.9)					11
Note 8A	0.8	(0.2)	574	(38)	803	(86)	25
Note 8B	0.9	(0.1)	541	(45)	721	(65)	26
Note 8C	0.8	(0.1)	470	(37)	593	(52)	25
Note 8D	1.1	(0.2)	318	(26)	465	(29)	26
Note 8E	0.8	(0.2)	94	(8)	265	(34)	73
Note 8F	1.3	(0.2)	89	(18)	992	(5)	19
9	111.2	(42.2)					10
Note 9A	1.7	(0.4)	577	(61)	969	(48)	60
Note 9B	1.2	(0.2)	159	(58)	472	(22)	55
10.1	84.2	(27.4)					41
Note 10A	1.2	(0.2)	392	(30)	966	(65)	95
Note 10B	1.1	(0.3)	316	(33)	985	(40)	31
10.2	85.7	(20.9)					9
Note 10A	1.2	(0.3)	379	(60)	930	(114)	100
Note 10B	1.1	(0.4)	254	(36)	968	(57)	23
11	50.0	(4.6)					8
Note 11A1	1.6	(0.4)	347	(52)	537	(68)	8
Note 11A2	1.9	(0.5)	293	(42)	568	(58)	7
Note 11A3	2.2	(0.5)	277	(33)	545	(45)	8
Note 11A4	1.9	(0.3)	255	(29)	488	(50)	8
Note 11A5	2.6	(0.4)	237	(22)	464	(25)	7
Note 11B	3.2	(0.3)	154	(9)	383	(20)	40
12	65.9	(13.9)					34
Note 12A	1.0	(0.2)	846	(24)	976	(23)	57
Note 12B	1.6	(0.4)	543	(26)	629	(29)	51
Note 12C	1.7	(0.3)	270	(66)	481	(29)	59
Note 12D	3.2	(0.5)	252	(9)	349	(14)	34

correlation between daily sum of hours with songs and number of whales counted per day (Fig. 2, Spearman's rank correlation $r = 0.20$ $P > 0.05$).

Descriptions of 12 Song Types from the Pt. Barrow MARU

Song-1—A simple song observed on four of the first five days of recording (Fig. 3). It was composed of 5–7 repetitions of a phrase of two FM notes that occurred simultaneously. A typical rendition of song-1 lasted between 30 and 120 s (Fig. 4a, Table 1). Variability in each song parameter was similar among bouts. Based on bout duration and timing, an estimated minimum of 4–5 different animals sang this song (Fig. 5).

Song-2—A complex song that was only observed in one long bout of 12 h on 12 and 13 April (Fig. 5). It was composed of five different notes that occurred in the same repeating pattern that lasted 17 s on average (Fig. 4b). Note 2A was a pulsive shriek that initiated the song and repeated 2–5 times. Note 2B was a very low frequency burst that only occurred once every song. Both notes 2C and 2D were

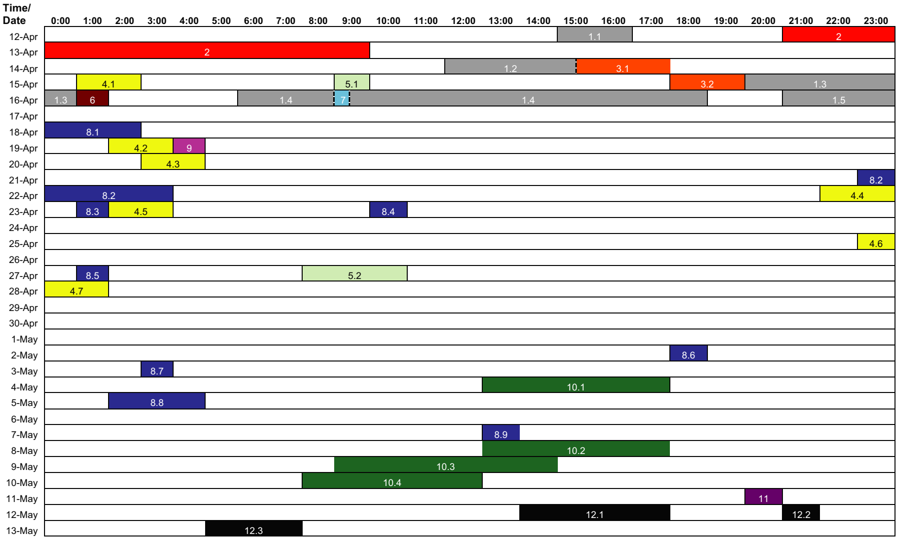

Figure 5. Daily patterns of singing bouts for 12 different bowhead whale songs recorded near Point Barrow, Alaska from 12 April to 13 May 2011.

downsweeps; note 2C was more inflected, lower in frequency and longer in duration. Notes 2A, 2C and 2D occurred together and were repeated 2–5 times. Note 2E, a relatively louder downsweep, signaled the end of the song (Table 1). Based on bout duration and timing, an estimated minimum of 1 animal sang this song (Fig. 5).

Song-3—A simple song that only occurred in two bouts, one each on 14 and 15 April (Fig. 3). The two bouts were separated by over 24 h (Fig. 5). Song-3 consisted of 2–5 repetitions of note 3A, a FM swoop, followed by a loud, single statement of note 3B (Fig. 4c). Note 3B was a relatively louder downsweep that signaled the end of each song. The durations of both notes were consistent, but the frequency range of note 3A was much more variable than that of note 3B (Table 1). Based on bout duration and timing, an estimated minimum of 2 different animals sang this song (Fig. 5).

Song-4—A complex song first recorded on 15 April and subsequently on six different occasions throughout the rest of the season (Fig. 3). All bouts were separated by more than 24 h (Fig. 5). All bouts were composed of 3–6 repetitions of note 4A and 4B followed a single note 4C. Note 4A was a single FM swoop that occurred simultaneously with, or closely followed by, note 4B, a low, pulsive tone (Fig. 6a). Note 4B was only observed in bout-4.1. Both note 4A and 4B were short, lasting about 1 s, on average (Table 1). Note 4C was a loud downsweep that signaled the end of each song. Based on bout duration and timing, an estimated minimum of 6–7 different animals sang this song (Fig. 5).

Song-5—A complex song documented on 15 and 27 April (Fig. 3). It was composed of 3–6 repetitions of simultaneous notes 5A and 5B (Fig. 6b). Note 5A was an inflected, downswept FM note while note 5B was a lower frequency, pulsive tone (Table 1, Fig. 6b). Based on bout timing, at least 2 different animals sang this song (Fig. 5).

Song-6—A complex song that lasted 41 s and only occurred in one bout on 16 April (Fig. 3). It was comprised of three notes that each occurred once per song

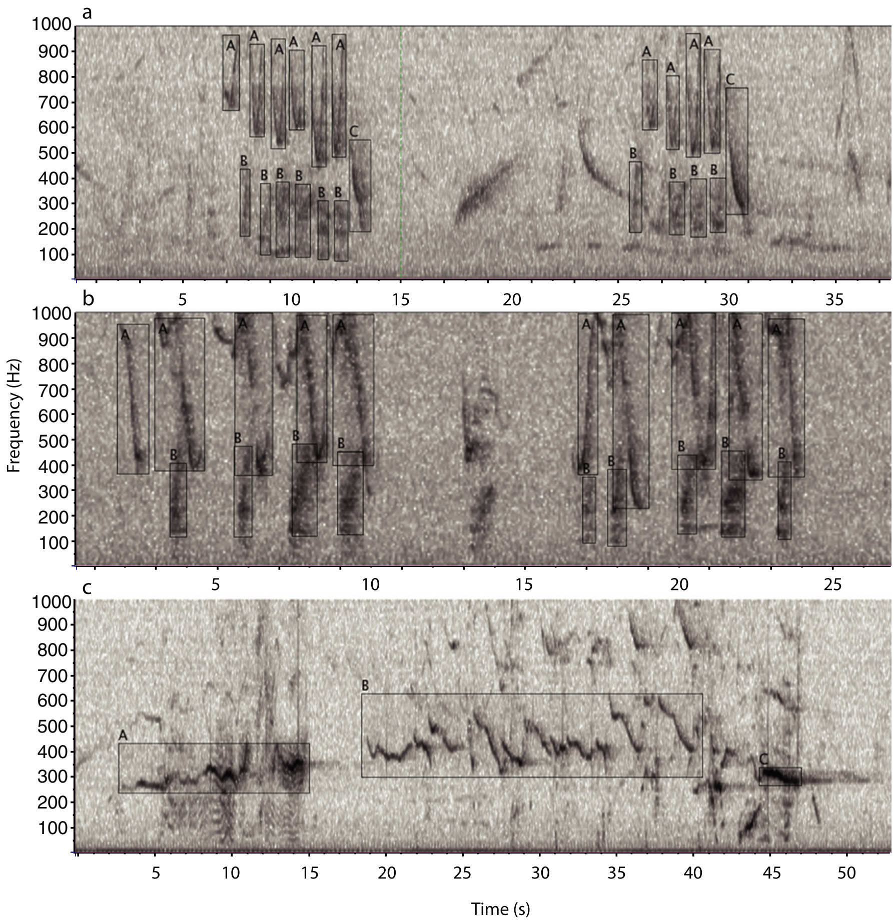

Figure 6. Examples of three bowhead whale song types during the spring 2011 migration: (a) Song-4 (two songs shown), (b) Song-5 (two songs shown), and (c) Song-6 (one song shown), and their labeled notes (1,024 pt. FFT, 90% overlap, Hann window).

(Fig. 6c). Note 6A was a loud, prolonged FM note with numerous inflections. Note 6B consisted of another, irregularly fluctuating FM note that lasted from 10 s to almost 30 s. Note 6C was a relatively loud downswept FM note that indicated the end of each song (Table 1). Based on bout duration, likely only 1 animal sang this song (Fig. 5).

Song-7—A simple song only observed on 16 April in a single bout (Fig. 3, 5). It consisted of three similar notes that were repeated in groups of three (Fig. 7a). The frequency structures and durations of these notes were similar, and each song lasted 67 s on average (Table 1). Based on bout duration, likely only 1 animal sang this song (Fig. 5).

Song-8—The most common song recorded and lasted from 45 to 76 s (Table 1). It was a complex song first recorded on 18 April and was subsequently observed on seven more occasions (Fig. 3, 5). Most instances of song-8 included five different note

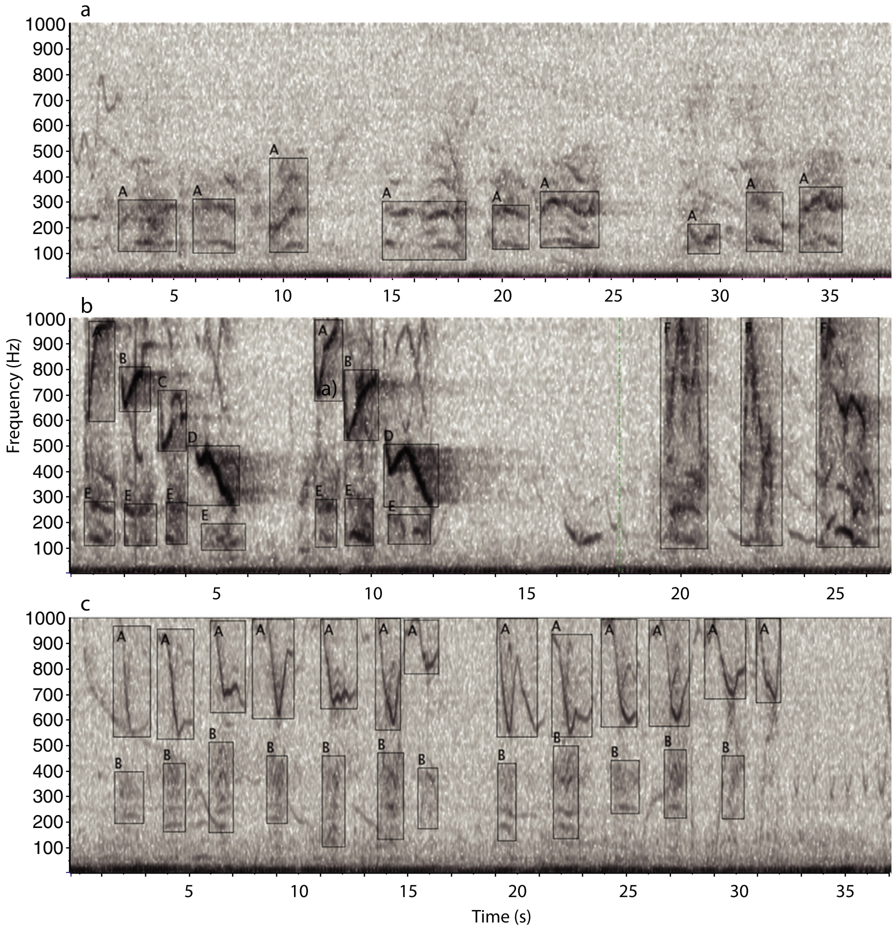

Figure 7. Examples of (a) Song-7 (three songs), (b) Song-8 (one song), and (c) Song-9 (two songs), and their labeled notes (1,024 pt. FFT, 90% overlap, Hann window).

types, but the two bouts with the highest relative intensity included a sixth (Note F, Fig. 7b). Notes 8A, 8B, and 8C were all FM inflected upsweeps lasting about 1 s (Table 1). Note 8D was a loud, inflected downsweep. Note 8E was a low-frequency, pulsive tone that co-occurred all other notes. Note 8F was an unstructured, broadband sound that occurred in groups of three and ended the song. Based on bout duration and timing, an estimated minimum of 8–9 different animals sang this song (Fig. 5).

Song-9—A complex song only recorded on 19 April (Fig. 3) and lasted less than 1 h (Fig. 5). It consisted of two simultaneous notes (Fig. 7c). Note 9A was a single FM inflection that often began above the recording system's cutoff frequency. Note 9B was a low, pulsive tone that was occasionally omitted. This song was the longest recorded, with a maximum duration of ~111 s, although song length was highly variable (Table 1). Based on bout duration, likely only 1 animal sang this song (Fig. 5).

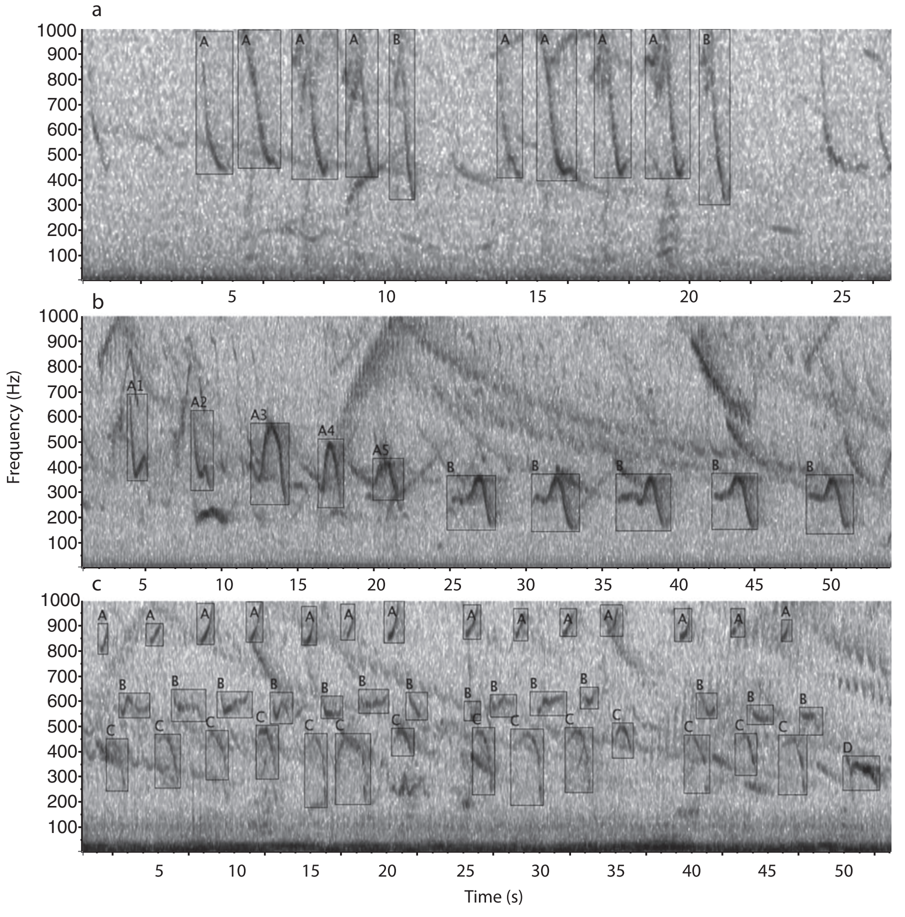

Figure 8. Examples of three bowhead whale song types during the spring 2011 migration: (a) Song-10 (two songs), (b) Song-11 (one song), and (c) Song-12 (one song), and their labeled notes (1,024 pt. FFT, 90% overlap, Hann window).

Song-10—A simple song that occurred on three different days near the end of the recording period (Fig. 3). It consisted of two different FM notes (Fig. 8a). Note 10A, which was typically repeated four times per song, ended with an upsweep while note 10B was simple a FM downsweep that ended at a lower frequency than note 10A (Table 1). Based on bout duration and timing, an estimated minimum of 4 different animals sang this song (Fig. 5).

Song-11—A simple song only observed on 11 May in a single bout (Fig. 3). It was comprised of two different types of notes that were similar but occurred at different frequency ranges (Fig. 8b). Both note 11A and note 11B were single FM notes with various inflections. Note 11A was divided into subnotes 11A1 through 11A5 to account for the gradual trend in decreasing note frequency during a song. Note 11B was a lower frequency note repeated 3–5 times after the same number of repetitions of note 11A. The entire song lasted approximately 50 s (Table 1). Based on bout duration, likely only 1 animal sang this song (Fig. 5).

Song-12—A complex song and the last recorded song type in the recording season (Fig. 3). It was made up of four different notes (Fig. 8c). Note 12A was a short, high frequency upsweep that occurred at regular intervals throughout each song. Note 12B was a relatively short, narrowband FM note with several inflections. Note 12C was a FM downsweep. Notes 12A and 12C often occurred simultaneously (Fig. 8c). Note 12D was a relatively louder and lower frequency downswept note ended each song (Table 1). Based on bout duration and timing, an estimated minimum of 1–3 different animals sang this song (Fig. 5).

Song Structure

Seven of the 12 songs described were complex in that they had two notes of different frequencies and structure produced at the same time. The overall average song duration was 60.0 s, although average individual song durations ranged from 16.9 s to 111.2 s (Table 1). Some songs were repeated in bouts that lasted up to 12 h, as was the case for bout-1.4 (Fig. 5). The termination of all songs except 1, 7, and 9 was announced with a relatively higher intensity FM downsweep. The types of notes observed included FM downsweeps, upsweeps, and inflections; complex mixtures with both AM and FM and chaotic components, *i.e.*, pulsive sounding tonals. Song overlap, when two whales were singing at the same time, was only observed twice during the season. Bout-1.2 and bout-3.1 overlapped on 14 April, and bout-1.4 and bout-7.1 overlapped on 16 April (Fig. 5).

Beaufort MARU Comparison

Bouts of song types 1, 2, 4, 5, 8, and 12 were detected during analysis of the Beaufort MARU, which was only 45 km NE of the Pt. Barrow MARU. Singing was first documented on 2 April and continued sporadically until the last bout was observed on 15 May. Song types 1, 5, and 8 were observed on 8, 10, and 6 separate occasions, respectively (Fig. 3). The remaining song types (2, 4, and 12) only occurred once with sufficient signal-to-noise ratio (SNR) and replication to confidently identify them. Song types 2 and 12 occurred on approximately the same dates at both MARUs, while song types 1 and 8 were first observed at the Beaufort MARU, and song types 4 and 5 were first documented at the Pt. Barrow MARU. At least six additional song types were recorded on the Beaufort MARU that were not on the Pt. Barrow MARU (Fig. 9). Conservatively, then, BCB bowhead whales produced 18 different song types during the 2011 spring migration.

The higher sampling rate of the Beaufort MARU allowed us to detect additional notes in song-8 that occurred above 1 kHz, and were thus undetectable on the Pt. Barrow MARU (Fig. 10). Notes above 1 kHz were rare in songs recorded on the Beaufort MARU; song-8 was the only one of all songs detected on the Beaufort MARU to include such high frequency notes.

Discussion

The acoustic repertoire of western Arctic bowhead whales is the best-studied of any population of bowhead whales, with the first reports published over 30 yr ago (Ljungblad *et al.* 1979, 1982; Clark and Johnson 1984; Cummings and Holliday 1987). We measured and categorized 12 song types, 7 of which were repeated on

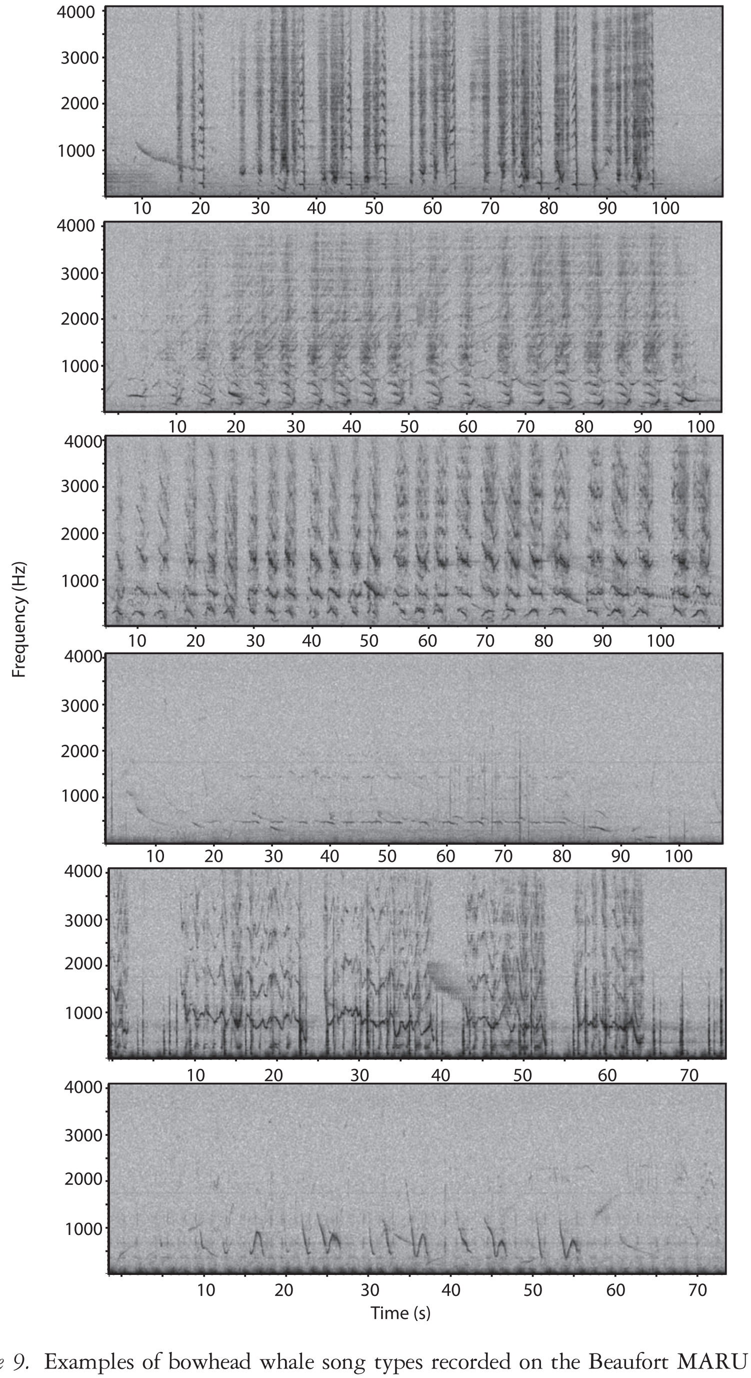

Figure 9. Examples of bowhead whale song types recorded on the Beaufort MARU in the spring of 2011 that were not observed in the recordings made off of Point Barrow in the same year (1,024 pt. FFT, 90% overlap, Hann window).

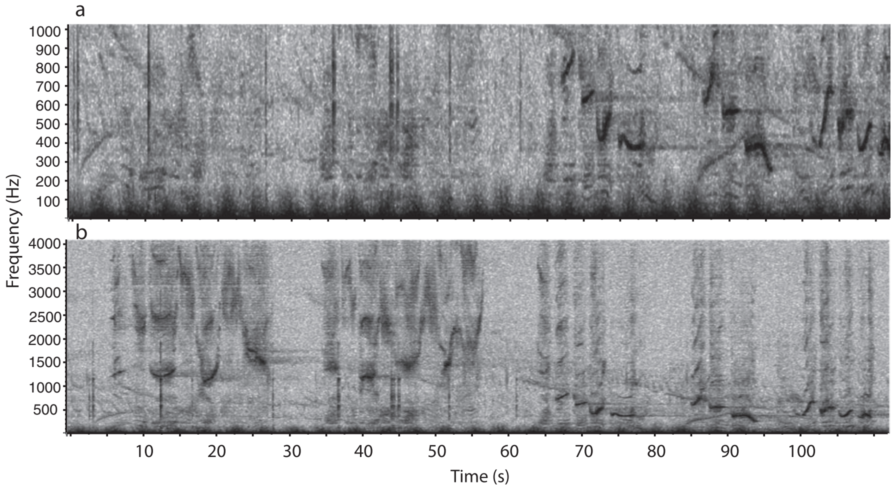

Figure 10. Examples of bowhead whale song-8 types recorded on the Beaufort MARU using (a) a 1 kHz upper frequency, or (b) a 4 kHz upper frequency. (1,024 pt. FFT, 90% overlap, Hann window).

more than one occasion, along the migratory route near Point Barrow from 12 April to 14 May 2011 (Fig. 3, 5). Six additional song types that were documented at the Beaufort MARU site, outside of the main study area of interest, were not analyzed (Fig. 9). Our results represent the highest number of song types documented during the spring migration season for this population. This is a conservative estimate of song diversity because a much greater sampling effort is necessary to accurately describe the complete annual BCB song repertoire. Our results also provide relevant information regarding song sharing, song structure and song variation over a month during the spring migration, while offering the opportunity to compare bowhead songs seasonally and geographically.

Song types appeared and subsequently disappeared throughout the spring migration-recording season, suggesting that there is a distinct seasonal progression of song types. Even the most commonly recorded songs did not occur throughout the entire recording period. With the exception of song-5, we did not detect any other song type again after it was absent from Pt. Barrow MARU recordings for more than four days (Fig. 3). In the Beaufort MARU data set, only song-8 occurred again after an absence of more than four days (Fig. 3). Delarue *et al.* (2009*a*) also noted clustering of specific song types and attributed them to either the production of new song types, as observed in some humpback whale populations (Noad *et al.* 2000), or song sharing in a "pulse" of migrating whales. The "cultural transmission" of new song types from one population to another is not occurring here in the same way as has been described in humpback whales (Noad *et al.* 2000, Garland *et al.* 2011); rather, our data reveal a rapid transition from one song type to another on the order of hours or days, likely due to the passage of different individuals or groups of whales.

Bowhead whales of the BCB population migrate persistently north and eastwards at about 3–4 km/h during the spring after leaving the Bering Sea on their way to the eastern Beaufort Sea (Braham *et al.* 1980, Zeh *et al.* 1993). The detection limit of the recording devices used is about 20 km under quiet acoustic conditions (Clark *et al.* 1986, George *et al.* 2004). If vocal, migrating whales are first detected 20 km to the south, along the migratory corridor up to 20 km north of the instrument, then they should be detectable on the recordings for fewer than 24 h, even swimming at only 3 km/h. Migrating whales seldom remain in the vicinity of the observation perch longer than an hour or two in early spring, but by June lingering for several days becomes more common (Koski *et al.* 2010). Assuming that individuals were passing through, and not remaining in or reentering the acoustic detection area, we can conservatively conclude that different whales produced the songs that were separated by more than one day, particularly early in the season. Bouts separated by 5–8 h, as in song types 1, 8, and 12, cannot be confidently ascribed to different individuals even though it is unlikely for a whale to remain in the area long enough to sing two full bouts separated by such a long resting period (Fig. 5).

Assuming a single whale did not switch songs while within recording range, we estimate that at least 32–38 different individuals were recorded singing on the Pt. Barrow MARU during the 32 d period when singing was observed. Other reports have mentioned that the same songs were produced by more than one whale (Stafford *et al.* 2008, Delarue *et al.* 2009*a*), but to date none has explicitly quantified this phenomenon or attempted to estimate the minimum number of animals singing a particular song.

The songs we describe are different from those previously identified in the BCB population (Würsig and Clark 1993, Delarue *et al.* 2009*a*), the Eastern Canada-West Greenland population (Stafford *et al.* 2008), and the Spitsbergen population (Stafford *et al.* 2012). Each song from the spring migration in the Chukchi during 1980, 1985, 1986, and 1988 had a similar note lexicon but different structures than those that we observed (Würsig and Clark 1993). While changes in technology through time have expedited the sound analysis process, they have not improved detection rates in any way that would explain this change in number of songs in the spring. Rather, it is possible that the increase in song diversity is simply linked to the increase in population size as has been shown in some bird species (Laiolo *et al.* 2008, Valderrama *et al.* 2013). The size of the BCB population has increased by nearly a factor of four since the early 1980s: from ~4,200 in 1983 to ~8,200 in 1993, to ~17,000 in 2011 (Krogman *et al.* 1989, Raftery and Zeh 1998, Givens *et al.* 2013). Interestingly, within year song diversity has not increased in humpback whales, which have shown similar population increases (Barlow *et al.* 2011), or blue whales, which may also be increasing, although the decrease in frequency of some blue whale songs has been attributed to increasing population size (McDonald *et al.* 2009). A large population, however, is not necessarily a prerequisite for a large song repertoire (*e.g.,* Stafford *et al.* 2012).

The results of the comparison between Pt. Barrow and Beaufort MARUs suggest that the 2011 BCB repertoire contained even more song types than we analyzed in detail. Furthermore, the Beaufort MARU detected some song types a full 10 d before the Pt. Barrow MARU was deployed. George *et al.* (2004) report that whales typically begin moving passed Point Barrow in mid-April, but there is significant variation in monitoring effort and environmental conditions each year. This invites the possibility that we did not document the songs for a portion of the population that may have already migrated past Point Barrow before either of the MARUs were deployed, or further offshore from them, but confirms that at least some of the song types recorded off Barrow were recorded beyond the detection limits and/or prior to the deployment of the Pt. Barrow MARU.

Because we only recorded one song type with notes above 1 kHz, the use of a higher sampling rate instrument with this population only appears necessary for highly detailed song analysis and not for a qualitative study, as long as the lower frequency notes are repeated in such a way that they are distinguishable as song versus calls (*e.g.,* Würsig and Clark 1993). It is worth noting that other populations may sing more consistently at higher frequencies (*e.g.,* Stafford *et al.* 2012) and that two of the six song types reported by Delarue *et al.* (2009*a*) for the BCB population in late 2007 contained notes above 1 kHz. The lack of higher frequency energy in the late spring may be due to songs recorded in the late spring being degraded versions of songs produced earlier in the season (Würsig and Clark 1993). The songs we analyzed had relatively simple structure compared to those described for the fall (Delarue *et al.* 2009*a*). By the time migrating bowhead whales pass Pt. Barrow in the spring, the breeding season is essentially over. The lower complexity of recorded songs and eventually their disappearance by mid-May is likely the result of a shift in behavioral motivation towards foraging.

None of the current BCB acoustic studies have documented the level of song diversity reported in the much smaller Spitsbergen population by Stafford *et al.* (2012). The BCB population might have a smaller repertoire than the Spitsbergen population, but it is more likely that the BCB repertoire was underestimated as a result of where and when the acoustic monitoring took place. The areas monitored by Delarue *et al.* (2009*a*) and in our study do not encompass the Bering Sea winter range for BCB whales and only sampled the "shoulder season" for singers in the Chukchi Sea. Indeed, the lack of a correlation between the number of whales seen during the 2011 census and the number of hours with song (Fig. 2) underlines that song is not the dominant type of acoustic activity during the spring migration. Other sounds (individual calls and call sequences) were abundant in late April and early May 2011 and corresponded well with the number of whales seen (Clark *et al.* 2013, Givens *et al.* 2013). A more detailed study of acoustic data from wintering regions, for instance near St. Lawrence Island (Citta *et al.* 2012), may show that the song repertoire of the BCB population is even more diverse than reported here.

It is to our benefit that bowheads sing, and sing prolifically, because this allows us to study them more effectively in the Arctic. Their endangered cousins in temperate waters, the right whales, call sparsely and unremarkably, yet passive acoustic monitoring remains the most effective tool for their research and management (Clark *et al*. 2010). Bowheads call in a similar way, but their song, so rich with variation, could convey considerably more information. In time we may find that song diversity is an important index for population viability, as it is in songbirds (Laiolo *et al*. 2008), and measuring it could prove an effective and relatively inexpensive management practice. Songbird song diversity is also influenced by anthropogenic noise (Slabbekoorn and Ripmeester 2008), and in bowheads song diversity and complexity may serve as a barometer of the impact of encroaching development in the Arctic.

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