Chapter 12
Singing Behavior in the Bowhead Whale

Kathleen M. Stafford

> *Captain Kelley was the first to discover this singing … In 1882, several ships lay at anchor under Indian Point (Cape Chaplino,* Chukotka*, Russia.). As usual the masters got together, and in the midst of their conversation, Captain Kelley broke in "There's a bowhead!" Everybody laughed about "Kelley's band," but he insisted that there were whales nearby, and he was going to give chase. One master suggested that it was the copper on the ship, another that it was seals, another that it was the ice, and so on. But when Captain Kelley took up anchor and set sail, every ship followed him. One whale was caught. Soon more singing was heard. The result was the capture of several whales. After having attention thus forcibly called to the singing, it was not long before the masters were on their guard for it. As singing is almost never heard in the Arctic, it is inferred that it is a sort of a call, or signal for whales when making a passage through Behring Sea, to notify each other that they are bound north, and perhaps that the Straits are clear of ice.*—Aldrich (1889, pp. 32–33)

Abstract Bowhead whales are the only baleen whale endemic to the Arctic. There are four recognized populations globally, all of which were driven to commercial extinction before the twentieth century. As an ice-adapted species which spends much of its life under the ice in polar night, acoustic communication is critical to bowhead whale life history, but only recently have we been able to listen to them year-round. The acoustic behavior of bowhead whales consists of calls which are produced year-round and are low-frequency, short duration signals, and song, which is a seasonal, likely reproductive, behavior that occurs primarily in winter. Bowhead whales sing complex, varying songs that change completely from week to week and year to year. Individual songs are short (45 s–2 min) and are repeated over many hours in long bouts. Some individual whales share the same song within a winter, but others do not. Why song varies so much within and between years, and within and between individuals remains a puzzle to be solved.

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A pair of bowhead whales (*Balaena mysticetus*) surfacing in a spring lead, surrounded by *sikuliaq* (the Inupiat word for young ice) northwest of Utqiaġvik Alaska, April 29, 2015. The whales are navigating through a lead system with some heavy sea ice. Once the whales pass Point Barrow, about 16 kilometers to the northeast, they will enter the Beaufort Sea, which is mostly 100% ice-covered. They will continue to migrate eastward through the ice and spend the summer foraging in the Canadian Beaufort Sea. *Photo Credit* Kathleen Stafford

12.1 Introduction

The bowhead whale (*Balaena mysticetus*) is a whale of superlatives. It is the only baleen whale to live year-round in the Arctic, and as such, is capable of breaking up through ice half a meter thick to breathe (George et al. 1989). In the high Arctic, three populations of bowheads are recognized, and each is named largely by its known distribution: the Bering-Chukchi-Beaufort (BCB) or western Arctic population, the East Canada-West Greenland (ECWG) population, and the East Greenland-Svalbard-Barents (also referred to as the Spitsbergen, SP) population. The Okhotsk Sea population (SO) occurs south of the Arctic circle in the geographically isolated Sea of Okhotsk (Baird and Bickham 2020). Each population was heavily depleted by commercial whaling beginning as early as the 1500s, such that by the advent of the twentieth century, all four populations were commercially extinct (George and Thewissen 2020). Whalers targeted bowheads for two of their exceptional attributes: bowheads have the thickest blubber and the longest baleen of any baleen whale

species (Bockstoce 1986). Perhaps most remarkable, bowheads can live to be over 200 years old (George et al. 1999; George and Bockstoce 2008). Lastly, and most importantly for this chapter, bowhead whales are prolific singers with populations frequently changing songs within a season and between years (Stafford et al. 2018). "Kelley's band" may be the first direct attribution of song to any species of whale (Aldrich 1889), and the confusion of the sounds heard through the wooden hull of a whaleship perfectly encapsulate the variability of the songs of the bowhead which can screech and cry like ice, warble like a seal, and moan like the timbers of a wooden sailing ship.

Of all species of baleen whale, only the humpback (*Megaptera novaeangliae*) and the bowhead sing complex, varying songs that change rapidly over time: from song to song in the bowhead (Stafford et al. 2008, 2012, 2018) and from population to population across ocean basins in the humpback (Noad et al. 2000; Garland et al. 2011; Chap. 11). In both species, songs differ dramatically from the sounds they typically produce during summer and fall (Ljungblad et al. 1982; Blackwell et al. 2007; Dunlop; Chap. 9). This is not the case for other species of baleen whale to whom singing behaviors have been attributed. Any seasonally produced repeated patterned signals are often termed "song." Blue (*Balaenoptera musculus*), fin (*B. physalus*), and minke (*B. acutorostrata* and *B. bonaerensis*) whales, the rorquals that sing, all share aspects of their singing behavior, including conservation of most song structures over time. Although only a few populations have been sampled, it seems likely that, like humpback whales, rorqual singers are male (Croll et al. 2002; Oleson et al. 2007). Blue and fin whales produce very low-frequency songs that overlap each other in frequency range (Chaps. 2 and 9). Fin whales produce what appear at the outset to be relatively simple songs composed of one to three short duration sounds (often referred to as pulses, units, or notes) repeated in a series, with the "20-Hz" sound type being the most common. Globally, this 20-Hz sound is characteristic of the species, while song features such as unit center frequencies, presence of other units, and intervals between units (i.e., inter-note intervals) vary geographically (Watkins et al. 1987; Thompson et al. 1992; Hatch 2004; Archer et al. 2020). Blue whales produce songs composed of repeated phrases of 1–6 much longer units that may be amplitude- and/or frequency-modulated (Chap. 9). Blue whale songs are considered geographically distinct, stereotyped and remain relatively stable over long-time (decades). Minke whale song appears to vary geographically in frequency band and song structure, but within a region frequency features and song structure are conserved (Gedamke et al. 2001; Rankin and Barlow 2005; Risch et al. 2014; Chap. 14). The uniting characteristic of *Balaenoptera* songs as presently described is that they exhibit little variability among individuals or over time. A recent report of North Pacific right whale (*Eubalaena japonica*) "song" found multiple different patterns in the production of gunshot sounds, with evidence that the same patterns were repeated within and between years (Crance et al. 2019; Chap. 13). For all these species, some of the units that may be part of songs are also produced throughout the year, either as single calls or as part of calling bouts. For instance, northeast Pacific blue whales produce singular "A" and/or "B" sounds during different behavioral contexts than when these same sounds are produced in

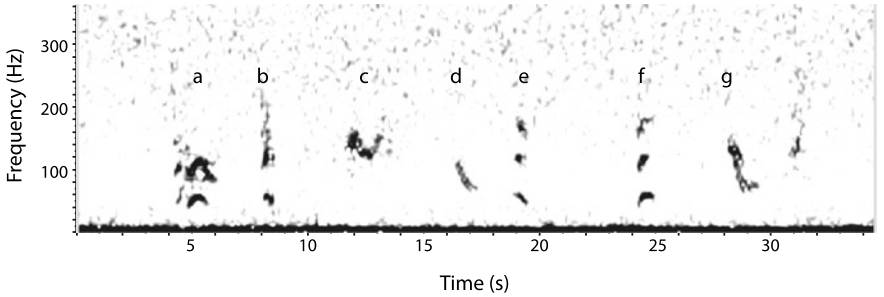

Fig. 12.1 Examples of eight different bowhead whale calls recorded in the Beaufort Sea on October 1, 2009. From left to right: **a** complex growl, **b** upsweep, **c** inflected, **d** downsweep, **e** complex, **f** complex, **g** downsweep (2048 sample FFT, 50% overlap, Hanning window)

songs (Oleson et al. 2007; Chap. 9). In contrast, bowhead and humpback whales change their songs within and between years, and song units are often distinct from calls, particularly in their bandwidth and frequency composition (but see Rekdahl et al. 2013 for a discussion of humpback "song-unit calls").

Bowhead whale calls are produced year-round, although in mid-winter they are often drowned out by low-frequency song units (reviewed in Stafford and Clark 2020). Calls are generally low-frequency (50–500 Hz), short duration signals that may be frequency- or amplitude-modulated (Clark and Johnson 1984). Most calls are simple frequency-modulated signals, and there appears to be a relatively limited repertoire of call types: frequency-modulated downsweeps and upsweeps, tonals, inflected calls as well as calls that are more complex and are less readily characterized (Fig. 12.1). Calls are produced relatively infrequently. Indeed, a recent study of the BCB population during the fall migration found that the population-wide mean call rate was only 1.3 calls/whale/hour (range 0.5–5.4, Blackwell et al. 2021).

In contrast to calls, songs are sung seasonally (generally November through April and into May depending on location), and the continuum of units that compose the different song types is extensive and has not been fully defined. In the two populations for which inter-annual comparisons have been studied (ECWG and SP), the units that make up each season's songs appear to change annually with no between-year repetitions (Tervo et al. 2011b; Stafford et al. 2018). This is one distinction between bowhead song and humpback song; humpbacks within a population produce songs with similar units and phrases between years (Darling et al. 2019; Allen et al. 2019; Chap. 11). Further, adjacent humpback populations in the Southern Hemisphere acquire songs from each other through cultural transmission on shared migratory routes (Garland et al. 2011; Owen et al. 2019; Chap. 8). Until very recently, all four bowhead whale populations were geographically isolated from each other by areas of heavy ice, or by distance in the case of SO bowheads, precluding the possibility that one population has learned songs from another. Other distinctions include humpback whale songs being of much longer duration than bowhead whale songs, composed of numerous phrases and themes, and all males in a population are assumed to sing

the same song within a singing season (Payne and McVay 1971; Payne and Payne 1985).

Bowhead songs, in contrast to those of humpbacks, are composed of a single theme of 1–3 phrases repeated over and over (Fig. 12.2; Clark and Johnson 1984; Würsig and Clark 1993). Further, bowhead whales within a population sing dozens of

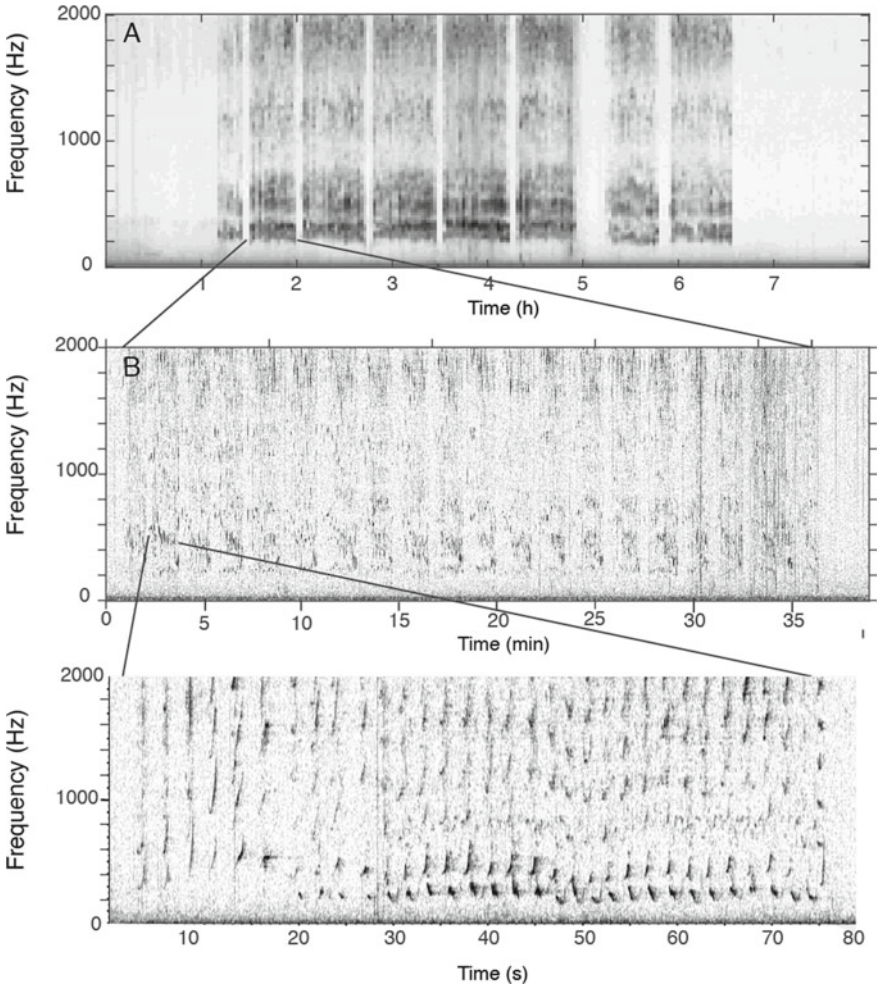

Fig. 12.2 Singing behavior of a bowhead whale recorded north of Point Barrow, Alaska, May 15, 2016. **a** An 8 h spectrogram showing a song session from a single bowhead whale. Each dark band represents many (8–20) songs sung repeatedly with long gaps ("rests") from 4 to 18 min between song bouts (120 s average, 256 sample FFT); **b** one song bout from A showing 20 complex songs separated by ~15 s (256 sample FFT, 0% overlap, Hanning window); **c** single song from song bout shown in **b**. Two-voiced singing can be seen in the lowest frequency downsweeps that occur simultaneously with the harmonic upsweeps from 25 to 75 s (512 sample FFT, 0% overlap, Hanning window)

song types composed of different phrases which consist of individual units that vary by song type during a season, and these song types are not repeated from one season to the next (Stafford et al. 2012, 2018; Johnson et al. 2014). This within-year and between-year variability is a relatively new discovery, with only recent observations of this feature due to the difficulty of studying this Arctic species year-round.

Most baseline information on bowhead whale singing behavior was the result of joint visual–acoustic censuses of BCB bowhead whales as they migrated north past Point Barrow, Alaska, in the Chukchi Sea in spring, in addition to earlier studies (Cummings and Holliday 1987; Zeh et al. 1993). These early efforts documented that, like humpback whales, the song of the bowhead whale changed annually (Würsig and Clark 1993). These data, which were recorded from early–mid-April into mid-late May suggested that all singing whales sang the same overall song type during the migration, although there was variation between and within individuals (Würsig and Clark 1993). Further, a unique characteristic of bowhead whale song was described whereby bowheads are capable of producing two very different sounds simultaneously (Würsig and Clark 1993). This suggests that bowhead whales use two separate sound sources while singing (Würsig and Clark 1993; Tervo et al. 2011a), an observation that implies that there must be some unique features in the bowhead whale laryngeal sound production mechanism (Schoenfuss et al. 2014; Chap. 3).

Before 2008, despite extensive recording effort during the spring migration off Barrow (now Utqiaġvik), Alaska, detections of bowhead whale singing were infrequent and when heard, only one singer was recorded at a time, and the perception was that all whales in the same year sang the same general song (Clark 1990). From two studies elsewhere (northwest of Spitsbergen, Norway and Disko Bay, Greenland), there was some indication that bowhead whales might sing more than a single song in a season (Clark et al. 1990; Stafford et al. 2008). The initiation of year-round monitoring of bowhead whales in Fram Strait beginning in 2008 showed that Spitsbergen bowhead whales sang nearly continuously from late October through early April and that dozens of distinct songs were produced by animals in this population (Stafford et al. 2012, 2018). In Fram Strait, distinct song types appeared and then disappeared somewhat sequentially over a season, where "season" refers to the presumed annual breeding season (Tarpley et al. 2020), in this case from about November to the following April or May (Stafford et al. 2012, 2018). As an example, a song type first heard in November might also be heard the next month in December, but it is unlikely to be recorded after this time. A song type heard for the first time in March will not have been noted in prior months. Furthermore, based on four years of duty-cycled recordings (12-min every hour), no song type was ever recorded in more than one season (Stafford et al. 2018). While similar long-term, year-round data from other populations of bowhead whales either do not exist or have not been analyzed, the data that do exist from two of these (BCB and ECWG) indicate that each population sings more than one distinct song each season. Data recorded in the northeastern Chukchi Sea (BCB population) from 2007 to 2008 detected song nearly continuously from October 30 to January 1, during which time six distinct song types were recorded (Delarue et al. 2009). In contrast, from April 10 to May 15, 2011, one dozen different songs were recorded in just six weeks during the spring migration off

Utqiaġvik, Alaska (Johnson et al. 2014). Recordings from late winter and early spring months from Disko Bay, Greenland (ECWG population) included several distinct songs from February to April in the same year, and entirely different repertoires of units that compose songs during those months in different years (Stafford et al. 2008; Tervo et al. 2011b).

For the three populations of bowhead whales for which song has been described (only the SO is lacking), all songs shared similar characteristics: They were composed of 1–2 repeated phrases, some of which were "two voiced," and included highly variable combinations of frequency-modulated and amplitude-modulated units (Clark and Johnson 1984; Würsig and Clark 1993; Stafford et al. 2008, 2012; Delarue et al. 2009; Tervo et al. 2011a; Johnson et al. 2014). What is unknown, or has not yet been explored, is whether there are population-level differences in singing behavior. For instance, are there differences in seasonal patterns in singing behavior, does each population sing many different song types within and between seasons, and are song structures similar among the different populations?

Our understanding of singing behavior in the bowhead whale is decades behind our understanding of humpback whale singing behavior (although even for that species new discoveries are being made, e.g., Garland et al. 2011; Cholewiak et al. 2018; Allen et al. 2019; Darling et al. 2019; Owen et al. 2019; Chap. 11). Unlike humpback whales, which mostly spend winter periods in tropical climes with clear water and warm temperatures, and are therefore easier to observe, bowhead whales winter in heavy pack ice and in polynyas in the Arctic and sing during frigid atmospheric temperatures of the polar night. For the BCB and ECWG populations, satellite tracking data have provided some indication of wintering and presumed breeding areas (Heide-Jørgensen et al. 2006; Citta et al. 2011), while passive acoustic data have done so for SP bowheads (Stafford et al. 2012, 2018). For the SP population, northern Fram Strait appears to be a wintering ground, and several years of passive acoustic data exist for this region. For the BCB population, Anadyr Strait and Saint Lawrence Island, Alaska, are wintering grounds (Noongwook et al. 2007; Citta et al. 2011); some long-term passive acoustic data exist from the northern Bering and southern Chukchi Seas but have been largely unanalyzed to date. The ECWG population appears to winter in Hudson Strait, Canada (Heide-Jørgensen et al. 2006), where passive acoustic monitoring data show the presence of acoustically active bowheads from December through April (Simard, unpublished data). All of the information on ECWG bowhead whale song has come from Disko Bay, Greenland, where the sex ratio is highly skewed toward females (~85%, Heide-Jørgensen et al. 2007). There are still no publications on acoustic data from the SO population.

12.2 Song Variability

For species such as blue and fin whales, song structure can be diagnostic of the distribution of males, and by association, females, such that song structure characteristics

can be used to identify where the animals reside (e.g., Stafford et al. 2001; Castellote et al. 2011). In the Southern Hemisphere, humpback whale song can be traced from one population to another over a span of a few years (Garland et al. 2011). For bowheads, at least based on data from Fram Strait and Disko Bay, Greenland, the within-population monthly and inter-season variability in song unit types and song composition is so great that distinguishing between populations by using some form of acoustic identification could be a remarkably difficult undertaking. We know that songs recorded from all bowhead whale populations share similar characteristics. That is, a song lasts from 45 to 180 s and is composed of a song type with repetitions of 1–3 phrases, each containing relatively few (less than 10 on average) sounds. Individual song types are generally broadband (50 Hz–5 kHz) and repeated over and over again with short gaps between them, and singing can last for many hours at a time (Fig. 12.2).

Songs have been classified as "simple" or "complex" (Stafford et al. 2008; Delarue et al. 2009). "Simple songs" (Fig. 12.3) are composed of fewer than four relatively low-frequency units (<2 kHz) that are frequency-modulated, do not have harmonics, and no simultaneous production of two different sounds (Stafford et al. 2008; Delarue

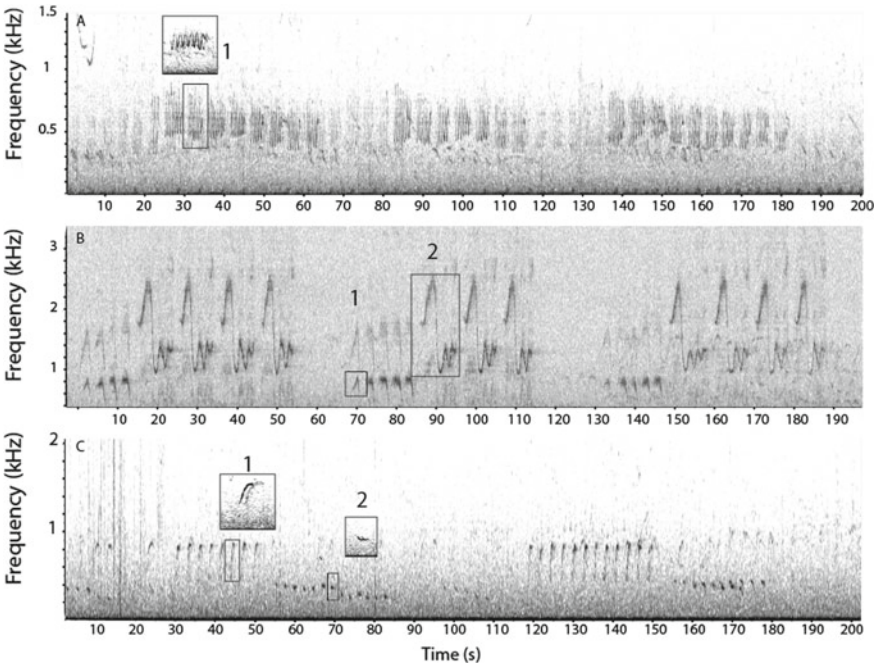

Fig. 12.3 Three examples of simple songs recorded in Fram Strait. **a** Three iterations of a single phrase song composed of repetitions of one sound unit, recorded December 20, 2010; **b** three iterations of a phrase incorporating 2 units, recorded January 3, 2013; **c** two iterations of a single phrase song composed of two units, recorded December 18, 2013 (2048 pt. FFT, 50% overlap, Hann window). Expanded units for song types in **a** and **c** are shown as insets in those spectrograms

et al. 2009). In some instances, a simple song may consist of a single unit type repeated over and over again (Fig. 12.3a).

The distinction between these simple songs and repeated calls (Ljungblad et al. 1982; Würsig and Clark 1993) is that simple songs repeat for long periods of time (e.g., hours), whereas a repeated call event is not repeated over and over. "Complex song" (Fig. 12.4) has broader bandwidth (with some units having fundamental frequencies over 2 kHz), most often includes two-voiced singing, and is composed of a greater number of units, many of which are considered complex, and may be frequency- and/or amplitude-modulated (Würsig and Clark 1993; Stafford et al. 2008, 2018; Delarue et al. 2009). Presently, the distinction between simple and complex songs is subjective as it is based only on human perception, and it is unknown if these different song forms serve different roles in bowhead whale behavioral ethology.

Based on three years of year-round data from Fram Strait, the numbers of simple versus complex songs recorded in each month from October to April were similar among years and showed similar seasonal patterns, with the greatest number of all song types in December, January, and February (Fig. 12.5). Further, there were no clear differences among the number of units per song in complex songs over a season, with complex songs averaging 5 units each (range 3–9). What is unknown is whether there were differences in song length or in the acoustic features of units that might indicate seasonal changes in songs over time. The only study to examine this in bowhead whales (Tervo et al. 2009) documented changes in the vocal behavior of whales in Disko Bay, Greenland. In that study, the bowhead whale songs recorded in February and March included more, and more complex, song units in each song type than were heard in song types recorded in April and May, suggesting that overall song complexity decreased from February to May.

A detailed analysis of mid-winter singing for the BCB population has not yet been undertaken to examine seasonal differences in song complexity, but a relatively short-term study during the spring migration off Point Barrow in April and May 2011 documented 12 different song types, many of which were complex (Johnson et al. 2014). Unlike later season song recorded in Disko Bay, Greenland, there was no decrease in the number of units or duration of songs as spring progresses (Tervo et al. 2009; Johnson et al. 2014). What was clear in the Alaska data, similar to Fram Strait and Disko Bay, was an overall decrease in singing behavior from winter through spring, whether measured in units/hour (Tervo et al. 2009) or in hourly and daily occurrences of song (Tervo et al. 2009; Johnson et al. 2014) from winter through spring (Stafford et al. 2018). This seasonality, where singing increases in fall, peaks in winter, and decreases in spring, is presumably reflective of breeding season. This is similar to what is known for other singing whales and aligns with what is known of the testosterone cycle, and related changes in testes size, in bowheads and other whale species (Chittleborough 1955; Vu et al. 2014; Hunt et al. 2018).

With the establishment of long-term, year-round recordings in wintering regions of the BCB, ECWG, and SP populations, there are now ample opportunities to study in detail the singing behavior of bowhead whales throughout the Arctic. Current information gaps include studying within-song variation within song bouts of individual singers, intra-individual and inter-individual differences in songs for whales that

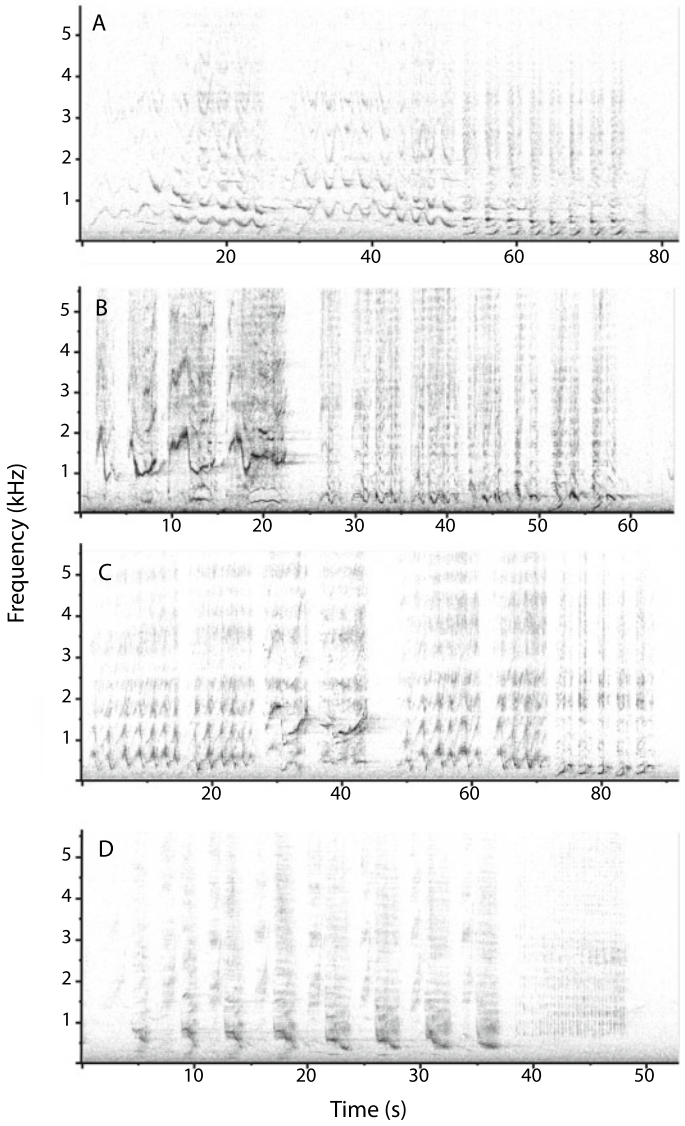

Fig. 12.4 Examples of single iterations of four different complex songs recorded in Fram Strait. **a** 5-unit song recorded January 19, 2013; **b** 8^{+}-unit song recorded October 23, 2012; **c** 4-unit song December 15, 2012; **d** 3-unit song recorded November 19, 2012 (2048 pt. FFT, 50% overlap, Hann window)

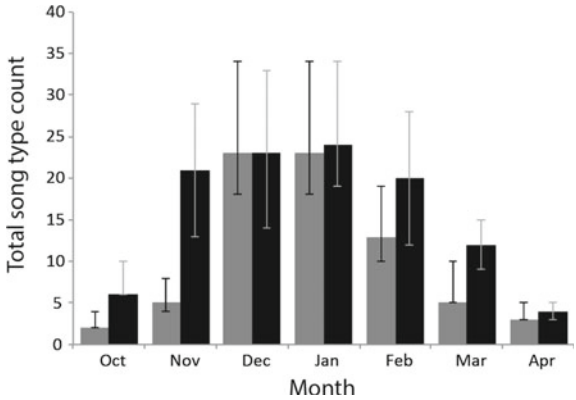

Fig. 12.5 Total number of simple (gray) and complex (black) song types for 2010–11, 2012–13, and 2013–14 from Fram Strait. Whiskers show the minimum and maximum number of song types recorded by month over the three years

share song types, and the extent of song sharing within populations; for example, how often do different singers share units or phrases (Fig. 12.6); how do songs "evolve" throughout the singing season from late October through the following April or May; do simple versus complex songs serve different biological functions (or is this division simply a human construct?); how do song characteristics (e.g., song duration, number of units, the use of two-voiced singing) differ between different populations? As sea ice continues to decline in the Arctic, essentially opening borders between

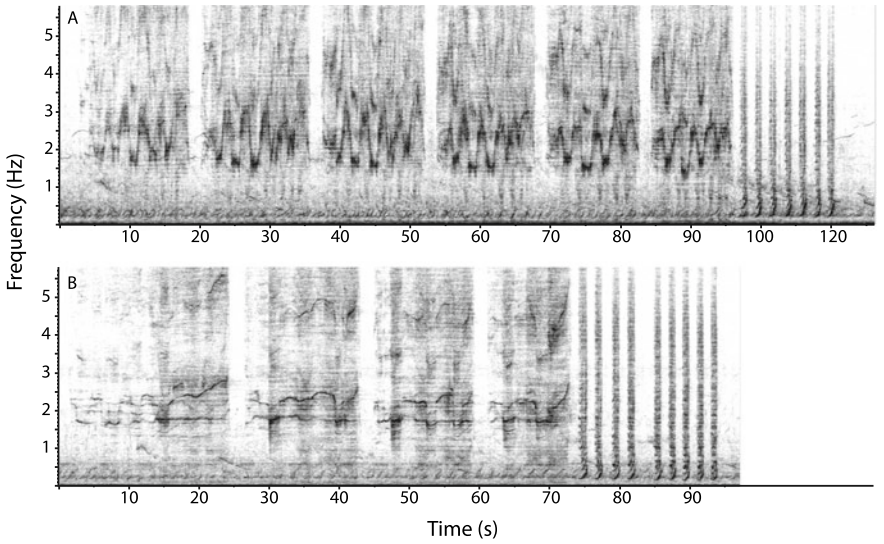

Fig. 12.6 Example of two songs recorded 10 h apart in the northern Bering Sea. Each song begins with distinctly different high frequency-modulated and amplitude-modulated long units but ends with multiple repetitions of the same unit. **a** Song recorded on March 6, 2018; **b** song recorded on March 7, 2018 (4096 pt. FFT, 50% overlap, Hann window)

populations, will we hear (and could we discern) cultural transmission of song types between western and eastern Arctic populations?

12.3 Reproductive Tactics in the Right Whales: Why Do Bowheads Sing?

The only other genus of Balaenidae is the right whale (*Eubalaena* spp.). Bowheads and right whales have similar feeding ecologies, morphologies, acoustic call types, and, in the males, extremely large testes (Clark and Johnson 1984; Brownell and Ralls 1986; Chap. 13). Unlike bowhead whales, right whales are not known to sing, although a recent study of a remnant population composed of >70% males in the Bering Sea has attributed song characteristics to right whale gunshot sequences (Crance et al. 2019). Female right whales in surface active groups (SAGs), produce sequences of sounds called "screams" or "high calls" which attract one or more males to the female (Clark 1982; Parks 2003; Parks and Tyack 2005). These SAGs are hypothesized to play a role in reproduction, as copulation is frequently observed, sometimes including more than one male copulating with a single female at a time (Cummings et al. 1974; Mate et al. 2005; Chap. 13). As right whale SAGs occur in many months of the year and can involve combinations of whales of different ages and sex, including juvenile animals, this behavior likely serves multiple purposes (Payne 1986; Best et al. 2003; Parks et al. 2007). It is worth noting that North Atlantic (*E. glacialis*) and South Atlantic (*E. australis*) right whales have been acoustically monitored for decades with no reports of singing behavior. While it is possible, it seems unlikely that such behavior would have been missed by researchers studying the sounds of right whales. Similar to right whales, bowheads aggregate in groups that often are social and/or sexual in nature (Würsig and Clark 1993). Like right whales, in bowheads sperm competition has been proposed as a reproductive tactic (Brownell and Ralls 1986). Unlike right whales, however, bowhead whales sing profusely from late fall into spring.

Song throughout the animal kingdom is often considered to be a male reproductive tactic, produced to mediate male–male interactions and provide information to females about the physical quality or social status (fitness) of the singer (e.g., Clutton-Brock and Albon 1979; Catchpole and Leisler 1996; Davidson and Wilkinson 2004; Byers and Kroodsma 2009; Chabout et al. 2015; Cholewiak et al. 2018; Clark et al. 2019). Although available data are limited, bowheads (and other baleen whales) show clear annual seasonal peaks in levels of testosterone in their baleen (Hunt et al. 2018). It seems reasonable to hypothesize that the seasonality of these peaks should match the seasonality of singing behavior and that changes in testosterone drive the seasonal changes in song as observed in birds (Galeotti et al. 1997; Smith et al. 1997; Brenowitz 2004). Since bowhead whales both sing and have large testes, this suggests that bowheads employ inter- and intra-sexual reproductive tactics and have multiple mating strategies. But why?

One clue may lie in the Arctic habitat of the bowhead whale. This species spends most of its life associated with sea ice, particularly during the time of year that singing occurs (October–April) and when bowheads occur in >90% sea ice cover (Stafford et al. 2012). Sea ice is dynamic, and open water cracks and leads are constantly shifting. This habitat is clearly not conducive to the formation or maintenance of SAGs, nor to escalation of male-male competition as has been documented in humpback whales (Tyack and Whitehead 1982). Therefore, song may be the most efficient, or only, reproductive tactic under heavy ice conditions. Not only might song convey the location of potential mates and their overall fitness, perhaps this dynamic environment has also led to song serving to advertise a different resource to females (e.g., Croll et al. 2002), which in this case would be open water, i.e., oxygen to breathe. It has long been assumed that some of the longer time gaps in cetacean songs (sometimes called "rests," Fig. 12.2a) occur when animals surface to breathe (e.g., fin whales: Watkins et al. 1987; Clark et al. 2019; Clark pers. comm.). Perhaps a singer's pattern of singing, and not singing, relays information about the ice environment overhead. As leads open in bowhead whale habitat and whales begin to migrate in the late winter and early spring when sea ice cover becomes looser, sperm competition in sexually active groups may become a more straightforward reproductive strategy than singing. This speculation about the drivers of multiple mating strategies in bowhead whales is untested, and perhaps untestable, but highlights one of the many areas where advances in our understanding of bowhead whale ethology can be made.

12.4 Why Such Intra-annual Diversity in Song?

One of the most interesting puzzles with regard to bowhead whale singing behavior as we currently understand it, is why does song vary so much within and between years and within and between individual bowheads? Song diversity could be linked to population size, if the number of different songs in a season is related to the number of male whales in a population. During the bowhead whale census efforts off Utqiaġvik, Alaska in the 1980s–2000s only single song types were identified during the spring migration (Würsig and Clark 1993). More recent data from this region clearly show multiple songs recorded during spring migration and in the fall (Delarue et al. 2009; Johnson et al. 2014). This increase in song types may in some way be related to a consistent increase in the size of this population of bowhead whales (George et al. 2004; Givens et al. 2016), although the extremely high song diversity from the Spitsbergen population, which may number in the low hundreds, seems to contradict this explanation (Vacquié-Garcia et al. 2017; Stafford et al. 2018). The increase in song diversity could also be a result of immigration of whales from one population to another, if songs are population specific. The three high-Arctic populations, BCB, ECWG, SP were geographically isolated from each other for millennia due to extensive, impenetrable sea ice cover in the High Arctic, but recent extreme reduction in sea ice extent and thickness has permitted at least a few animals

from two of these populations to migrate between regions with the possibility of introducing novel acoustic behaviors (Heide-Jørgensen et al. 2012). However, this does not adequately explain the high diversity in song types sung each season nor the lack of recurrence of songs from one year to the next.

While some bowhead whales in a population appear to share the same song within a year (Clark 1990; Johnson et al. 2014), others do not, as evidenced by the overlapping singing of different songs from Greenland, Spitsbergen, and Alaska (Stafford et al. 2008, 2018; Tervo et al. 2009; Johnson et al. 2014). Whether individuals switch songs within a season, between years, or perhaps choose which song they sing from a repertoire of songs, is currently unknown (Würsig and Clark 1993; Stafford et al. 2008, 2012, 2018; Johnson et al. 2014). Perhaps long-term cultural innovation in songs, or song novelty, might somehow confer a reproductive advantage to the singer as an indicator of male quality (e.g., Noad et al. 2000; Laiolo et al. 2008; Byers and Kroodsma 2009; Chabout et al. 2015). It has been hypothesized that song characteristics such as song duration, types of phrases used, or amplitude of the song might serve as indicators of a humpback singer's physical condition (e.g., Chu and Harcourt 1986; Frankel et al. 1995). Likewise, in fin whales the combination of swimming speed and amount of singing has been proposed as an indicator of a singer's physical stamina (Clark et al. 2019). For bowheads, perhaps a singer's quality can be assessed by other bowheads via song complexity under the ice.

Innovation in song could also be driven by the acoustic habitat in which bowheads sing. Singing peaks in the middle of winter under heavy ice cover and the polar night and overlaps with times when other Arctic marine mammal species are vocalizing (Stafford et al. 2012, 2018). Perhaps novelty in bowhead song is in response to the dynamic abiotic sounds of ice and less variable sounds of other marine mammals, including walrus, belugas, and bearded seals (Clark et al. 2015). Although some bowhead whale sounds are quite distinct from these other Arctic endemic species, at times, bowhead whales seem to be imitating said species (beluga whales in particular). Likewise, units of some songs sound so much like some sounds produced by ice that only the clear pattern and repetition of those units convinces the listener that they are, in fact, produced by a singing bowhead. What purpose this might serve is a mystery, but the bowhead whale's vocal plasticity strongly suggests that this species has a remarkable ability to learn and reproduce novel sounds in their acoustic environment. Bowhead whales are constantly innovating new songs and new song units, they imitate conspecific calls and even appear to mimic other Arctic species and ice noise (Clark 1990; Rendell and Whitehead 2001).

The singing behavior of bowhead whales, a species that lives in tight association with sea ice, certainly suggests that there has been strong evolutionary pressure, possibly via sexual selection, driving extreme complexity in song. The very environment in which they live, and the polar night during which they sing, has in the past limited so much of our understanding and interpretation of bowhead whale acoustic behavior to those few locations and times of year when they can be studied. The technology for studying polar environments is rapidly evolving, and, as bowhead populations recover from whaling, there is tremendous potential for new discoveries about the acoustic ecology, especially the singing behavior, of the bowhead. What is

presently known about singing behavior is only "the tip of the iceberg" for this polar whale.

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