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To cite this article: Katie Kowarski, Salvatore Cerchio, Hal Whitehead, Danielle Cholewiak & Hilary Moors-Murphy (2022): Seasonal song ontogeny in western North Atlantic humpback whales: drawing parallels with songbirds, *Bioacoustics*, DOI: [10.1080/09524622.2022.2122561](https://doi.org/10.1080/09524622.2022.2122561)

To link to this article: <https://doi.org/10.1080/09524622.2022.2122561>



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Published online: 19 Sep 2022.



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Seasonal song ontogeny in western North Atlantic humpback whales: drawing parallels with songbirds

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ABSTRACT

The use of song as a reproductive display is common in the animal kingdom; however, for many taxa, little is known of song ontogeny. Male humpback whales produce elaborate songs on low latitude breeding grounds in winter and begin to sing on high latitude feeding grounds in late summer, yet songs from the two locations are rarely compared. Seasonal song ontogeny in western North Atlantic humpback whales was explored by comparing songs recorded in high latitude feeding grounds (Canada in spring 2016 and fall 2016 to winter 2017) with songs recorded in a low latitude breeding ground (Dominican Republic in winter and spring 2017). High-quality song samples were selected, and every phrase annotated. Song theme order, song duration, and number of phrase repetitions were compared across samples. The most variability in theme order was found between November and December in the Canadian recordings, a phase in song ontogeny that may be important for learning. Song duration gradually increased, via an increase in phrase repetitions, through the breeding season, before peaking in the Dominican Republic between January and March. A comparison to oscine bird seasonal song ontogeny revealed many similarities, highlighting potentially similar physiological processes between humpback whales and songbirds.

ARTICLE HISTORY

Received 18 May 2022
Accepted 31 August 2022

KEYWORDS

Humpback whale; song; ontogeny; breeding display; oscine birds

Introduction

Vocalisations classified as songs have been described for decades in the animal kingdom in insects (e.g. Čokl et al. 1999; Simmons et al. 2001; Kindl et al. 2011; Ölveczky 2013), frogs (e.g. Leininger and Kelley 2015), bats (e.g. Behr et al. 2006), mice (e.g. Campbell et al. 2010), apes (e.g. Clarke et al. 2006), whales (e.g. Payne and McVay 1971; Cummings and Thompson 1977; Watkins et al. 1987), and birds (e.g. Kroodsma and Byers 1991; Catchpole and Slater 2003). However, for many of these taxa, little is known about the early ontogeny of singing behaviour. Indeed, only for the oscine birds has song development been described in any detail with much of the development literature restricted to when birds learn to sing for the first time (e.g. Nelson and Marler 1994).

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In some species, the production of song not only develops when young birds first begin singing, but seasonally at the onset of the breeding season (e.g. Nottebohm et al. 1986), hence the distinction between developmental ontogeny and seasonal ontogeny. Without understanding seasonal song ontogeny, it is difficult to fully comprehend the drivers of these acoustic signals and their significance for reproductive success. Here, we explore seasonal song ontogeny in a species with one of the most elaborate mammalian songs, the humpback whale (*Megaptera novaeangliae*).

First described in the 1970s, humpback whale songs are produced by males during the winter breeding season (Payne and McVay 1971; Winn and Winn 1978) when individuals from most populations migrate from their high-latitude feeding grounds to their low-latitude breeding grounds (Kellogg 1929; Dawbin 1966). Song is a sexually selected display limited to males, and one of several tactics employed by males to gain reproductive success, although the exact function(s) within the mating system remain under debate (e.g. mate attraction vs male–male interactions; Winn and Winn 1978; Tyack 1981; Darling and Bérubé 2001; Darling et al. 2006; Smith et al. 2008; Dunlop and Noad 2016; Cholewiak et al. 2018; Cholewiak and Cerchio 2022). Songs are hierarchically structured in a classification nomenclature initially proposed by Payne and McVay (1971) that continues to be used in the literature. Discrete units (analogous to notes) make up stereotyped phrases; phrases are repeated, and an uninterrupted series of like phrases is labelled a theme; and several themes are sung in sometimes invariable order to make up what is referred to as a ‘song’ (Payne and McVay 1971; Payne et al. 1983; Cholewiak et al. 2013; Schneider and Mercado 2019). Songs are repeated in bouts that can last for many hours referred to as song sessions (Payne and McVay 1971; Wwl et al. 2006; Parsons et al. 2008). Several authors have noted the similarity between the classification level of ‘phrase’ and a typical ‘song’ in the birdsong nomenclature and the analogy of the repeated sequences of phrases with ‘eventual variety’ singing behaviour in some songbirds (Cerchio et al. 2001; Cholewiak et al. 2013). All males in the same region generally conform to the same song, which changes through time via social learning and progressive cultural evolution, with songs and song sessions gradually and progressively changing in duration through the breeding season (Tyack 1981; Payne et al. 1983; Cerchio et al. 2001; Garland et al. 2011). At the onset of a breeding season, the whales seem to pick up the same song that they left off singing in the previous season, implying a certain level of memorisation (Payne et al. 1983). While singing is predominant on breeding grounds, this behaviour also occurs during migration, and in high latitudes before and after migration, indicating that annual song development initiates before males reach the breeding grounds (Mattila et al. 1987; McSweeney et al. 1989; Magnúsdóttir et al. 2014; Kowarski et al. 2018, 2019).

In the western North Atlantic, the primary low-latitude winter breeding grounds are found in the West Indies (Winn et al. 1975), with the highest concentrations of animals in the Greater Antilles off Silver and Navidad Banks (Whitehead and Moore 1982; Kennedy and Clapham 2018; Stevick et al. 2018). Humpback whales occur in these waters off the Dominican Republic from December to June (Heenehan et al. 2019). Northern feeding grounds include the waters of eastern Canada (Whitehead and Moore 1982; Martin et al. 1984; Katona and Beard 1990; Palsbøll et al. 1997; Smith et al. 1999; Jann et al. 2003). Humpback whales occur in these higher latitude waters in all months of the year, but in many Canadian areas their occurrence decreases in winter with the species least common

through February and March (Kowarski et al. 2022; Delarue et al. 2022). Individual photographic identification and satellite tags have been used to document movements of individuals between these high latitude feeding areas and low latitude breeding areas in the West Indies, including off the Dominican Republic (Clapham and Mattila 1988; Mattila and Clapham 1989; Smith et al. 1999; Kennedy et al. 2013; Stevick et al. 2018). Individual humpback whales migrate at different times (Craig et al. 2003), with some on breeding grounds as early as December, while others remain on feeding grounds through January. Some individuals may undertake shorter migrations south or not migrate at all (Brown et al. 1995; Stevick et al. 2003; Kowarski et al. 2022).

Humpback whale song has been recorded in eastern Canadian waters in the fall and winter from Labrador to the Bay of Fundy, as well as in the spring off Nova Scotia (Kowarski et al. 2018, 2019, 2022). Two categories of singing behaviour have been described in this region during song onset in the fall: song fragments, produced early to mid-fall, and full songs, produced mid-fall through to the winter (Kowarski et al. 2019, 2022). Song fragments were defined as vocalisations arranged into various levels of incomplete songs ranging from a single phrase or subphrase occurring in no sequence to three themes in succession that are not repeated. Full songs were defined as three or more themes repeated at least once (Frumhoff 1983; Cholewiak et al. 2013; Kowarski et al. 2019). Kowarski et al. (2019, 2022) documented a gradual fall transition of singing behaviour, from the production of only non-song calls, to song fragments, to full songs. The transition occurred over many weeks with about a month separating when songs first appeared and when singing became regular (five consecutive days with singing).

The fall transition from song fragments to full songs is likely only a small part of the picture of how songs develop seasonally. There are currently limited studies on how the full songs that occur on feeding grounds compare to those produced on the breeding grounds. In the North Pacific, McSweeney et al. (1989) recorded songs in Alaska that were similar to those sung in Mexico and Hawaii, but more abbreviated. In the South Pacific, Garland et al. (2013) recorded themes on an Antarctic feeding ground that matched those from breeding grounds in eastern Australia and New Caledonia. In both McSweeney et al. (1989) and Garland et al. (2013), high latitude songs were only recorded over two to three days and therefore provide only a glance into song ontogeny. The present paper uses passive acoustic monitoring (PAM) data to observe how the theme order, song duration, and number of phrase repetitions of western North Atlantic humpback whale songs change through seasons both off eastern Canada and the Dominican Republic. In doing so, we provide a piece to the humpback whale song puzzle, specifically how the song changes through time in a process of seasonal ontogeny.

Methods

Data collection

PAM data were collected from four stations in the Atlantic Ocean, three in Canada (Strait of Belle Isle, St Ann's Bank, and Cape Breton South) and one in the Dominican Republic (Figure 1; Table 1). Canadian recordings were collected using Autonomous Multichannel Acoustic Recorders (AMARs; 24 bit; 6 db gain) with HTI-99 omnidirectional hydrophones (sensitivity of -165 ± 3 dB re 1 V/ μ Pa). Strait of Belle Isle and Cape Breton South

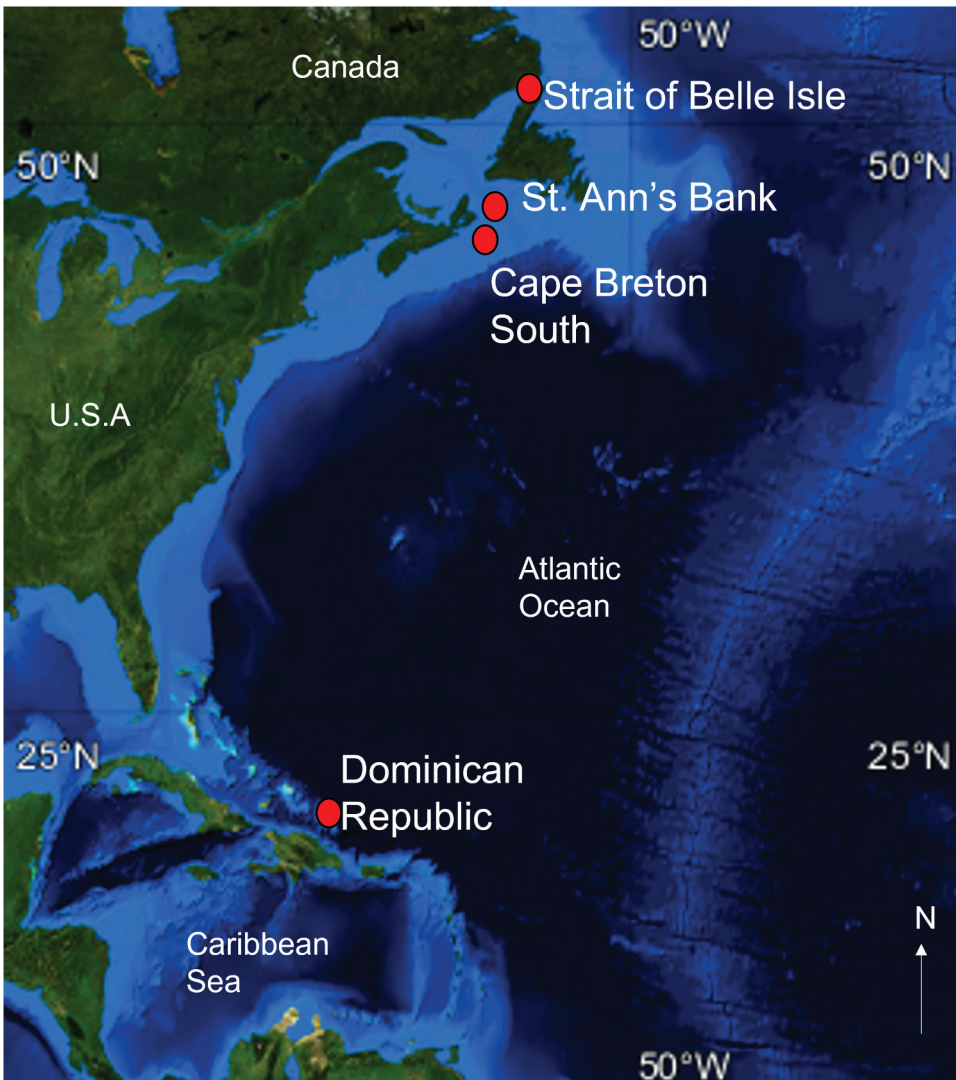


Figure 1. Location of four recording stations in the Atlantic Ocean.

data were part of JASCO Applied Science's Environmental Science Research Fund (ESRF) acoustic monitoring programme (Delarue et al. 2018; Kowarski et al. 2019). Data from St. Ann's Bank were part of the Department of Fisheries and Oceans (DFO) Canada Maritimes Region ongoing PAM programme. Canadian recordings had a recording schedule of 1 min sampling at 250 kHz, followed by 11.3 min sampling at 8 kHz, then 7.7 min of sleep (Table 1). The Dominican Republic data were collected using a Marine Autonomous Recording Unit (MARU; 16 bit; 6 db gain) with a HTI-94-SSQ omnidirectional hydrophone (sensitivity of -198 dB re 1 V/ μ Pa) as part of the collaborative Caribbean Humpback Acoustic Monitoring Program (CHAMP) project, lead by NOAA Fisheries' (NOAA) Northeast Fisheries Science Center (NEFSC) (Heenehan et al. 2019). Dominican Republic data sampled at 2 kHz and recorded continuously (Table 1).

Table 1. Deployment and retrieval dates, location, recorder depth, recording schedule, and acoustic recorder used to collect data from four stations.

Station	Deployed - Retrieved	Latitude Longitude	Water Depth (m)	Recorder distance from seafloor	Recording Schedule (sampling rate, duration)	Recorder
Strait of Belle Isle	10 Jul 2016– 11 Jul 2017	51° 16.6'N –57° 32.1'W	110	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
St Ann's Bank	23 Sep 2016– 29 Oct 2017	46° 0.1'N –59° 8.5'W	100	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
Cape Breton South	3 Nov 2015–9 Jul 2017 ^a	45° 25.8'N –59° 46.3'W	123	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
Dominican Republic	7 Dec 2016 – 3 Jun 2017	20° 36.5'N 69° 49.2'W	179	1–2 m	2 kHz, continuous ^b	MARU

^aRedeployed 21 Jul 2016; ^b15 min acoustic files.

Song analysis

The three Canadian data sets were previously analysed for humpback whale song acoustic occurrence (Kowarski et al. 2019, 2022). Cape Breton South recorded full songs in spring 2016 (Kowarski et al. 2019) and all three stations captured full songs in the proceeding fall to winter of 2016–2017 (Kowarski et al. 2022). While acoustic signals used in the previous studies were of sufficient quality to identify whether a whale was singing or not, not all occurrence results reported in these previous studies used vocalisations with a high enough signal-to-noise ratio (SNR) for song analysis. With the aim of identifying acoustic data of sufficiently high quality for song analysis, these previous occurrence results were used as a guide to identify data appropriate for the present research question. Acoustic data were considered 'sufficiently high quality' when 1) the humpback whale acoustic signals had high SNR (at least 10 dB), 2) a song could be confidently differentiated from other songs being sung simultaneously (only one singer was present or signals from one singer were consistently louder than others), and 3) at least two song cycles from (presumably) one individual of sufficient quality were present. Every 11.3-min acoustic file previously found to contain at least one song unit with an SNR of 10 dB or greater in the Canadian data (see SNR calculation method in Kowarski et al. 2019) was reviewed for song sessions that met this criteria. Each selected 11.3 min file and the four files immediately before and after it were manually reviewed to identify high-quality samples for analysis, where a sample was considered a continuous series of songs (i.e. the song session) assumed to be produced by the same individual if the apparent timing and amplitude were consistent over a one- to two-hour period. When the recorders entered sleep mode (which occurred for a period of <8 min, Table 1), resulting in a gap in the data, songs before and after sleep mode were assumed to be from the same individual or sample. This assumption may be a source of error, but it is unavoidable due to the limitations of duty-cycled data and sample size requirements. Samples were selected on different days to limit the chances of resampling the same whale. Therefore, any given sample can be identified by date. After restricting the Canadian data to the highest quality songs, 12 samples were analysed: three from April to May 2016 (Cape Breton South) and nine from November 2016 to January 2017 (two from Cape Breton South, four from St. Ann's Bank and three from Strait of Belle Isle).

While the Dominican Republic data set includes recordings from December 2016 to June 2017 (Table 1), analysis was restricted to the months of January and March for the present study because humpback whale song was found to occur continuously throughout this period (Heenehan et al. 2019). For each month, four samples were selected for analysis spaced as far apart as possible to reduce the chance of resampling the same whale. All acoustic files from the 1st, 10th, 20th, and 30th of each month were reviewed and the highest quality sample within each day (based on the same parameters applied to the Canadian data) was selected and analysed using the same protocol as the Canadian data, but without the extra considerations for sleep mode as the Dominican Republic data were continuous (Table 1). Eight Dominican Republic samples from 2017 were analysed, four in January and four in March. The Dominican Republic data set had a lower sampling rate (2 kHz) than the Canadian data (8 kHz), limiting the ability to observe some of the higher frequency sounds, which were assumed to match those observed in Canada based on the sequence of units. Any error in song structure analysis resulting from this was likely minimal as most humpback whale vocalisations are captured below 1 kHz. Sixteen samples of humpback whale songs recorded in the Heenehan et al. (2019) Dominican Republic data set were independently analysed by a separate research team (NOAA NEFSC), resulting in the identification of all of the same phrases identified here (in both the Dominican Republic and Canada), thus validating the phrase classification that we present (unpublished data, Cholewiak, NEFSC). The only variation was which unit was used as the first unit in some phrases, which is unsurprising given that phrase delineation is subjective. For example, phrase 3 (Figure 2) initially was delineated as starting with repetitions of the same unit type and finishing with the non-repeating unit. After comparing phrases between research groups, consistency in phrase delineation was increased to ensure inter-project consistency. During phrase delineation, repetitions of the same, or similar, unit type were always grouped into the same phrase (Figures 2 and 3) (Cholewiak et al. 2013).

Samples were manually analysed in PAMlab (JASCO; 2 Hz frequency resolution (df), 0.125 s time resolution (dt) of FFT with an overlap of 75%, Hamming window, normalised across time) with each song phrase annotated (numerically), such that each song was transcribed at the phrase level (where theme 1 contained repetitions of phrase 1). When transcribing song, the decision of which theme to assign first is arbitrary, but the convention is to use the theme during which the singer breathes. One of the quietest periods of the song, where units were often faint, unclear, or inconsistent, was suspected to be the time within the song cycle when the whales surface to breathe (due to the attenuation associated with refraction in the surface layer) and was chosen as the start of the song (containing theme 1) (Tyack 1981). Transition phrases (phrases that occur between two different phrase types; often comprised of units from both the previous and preceding phrase) were also annotated but were not included in subsequent analysis or phrase count results. When sleep mode caused a gap in the sample, the theme at the beginning of a file following sleep was not assumed to be the theme that followed the one at the end of the previous file. Similarly, where singing ceased (or became too faint) for at least 60 sec, the singing following the break was not assumed to be the theme that followed the one immediately before the break. In a continuous singing bout, a new song occurred when a theme already observed in the song, occurred again, such that no song contained two of the same theme (Garland et al. 2012). For example, if the following

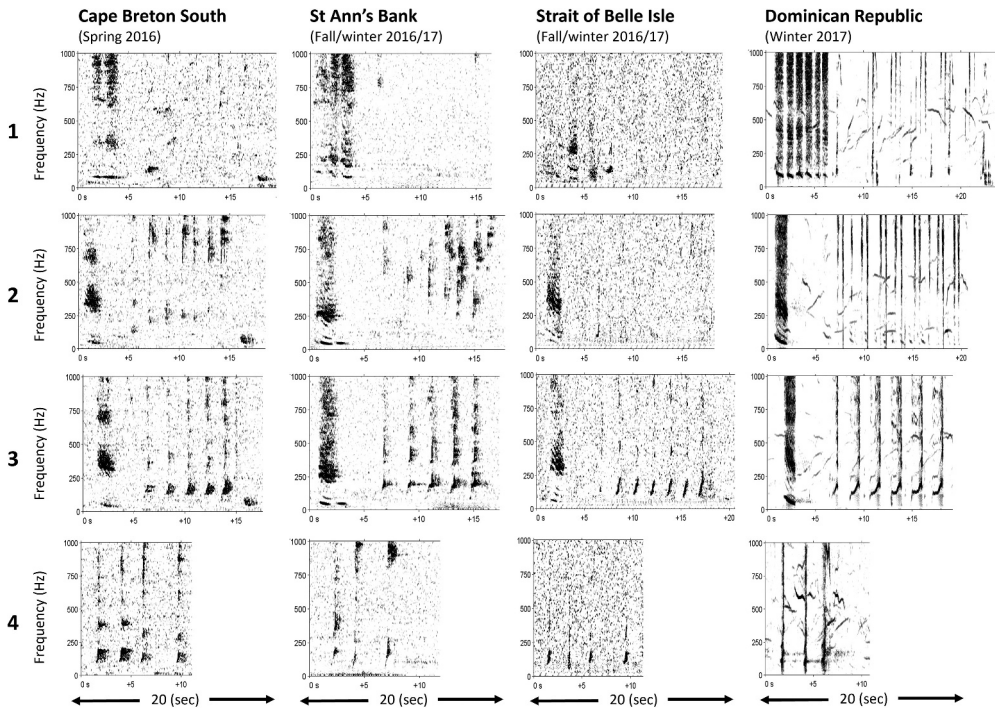


Figure 2. Spectrograms of exemplar humpback whale song phrases 1–4 that occurred at the four recording stations where each spectrogram has a frequency range of 0–1000 Hz and was viewed with the following parameters: 2 Hz frequency resolution (df), 0.125 s time resolution (dt) of FFT with an overlap of 75%, Hamming window, normalised across time.

theme order was observed in a continuous singing bout, ‘1,2,3,4,1,2,3,1,2,3,4’, that would be considered three songs: ‘1,2,3,4’, ‘1,2,3’ and ‘1,2,3,4’.

Songs were described in two ways. First, all samples analysed were compared temporally across the four stations in terms of theme order. Theme order was described using a numerical representation for each theme type. Every unique theme order present in a sample was recorded to describe the variation in theme order within and between samples. For the Canadian data, at times the sleep mode prevented the observation of all the themes in a song. In this instance, where the theme order matched that of a full song observed elsewhere in the sample, a consistent theme order was assumed. For example, if the following was observed ‘1,2,3,4,1,2,3,4, sleep, 3,4,1,2,3,4’, the song ‘1,2,3,4’ was assumed to have continued through sleep.

Subsequent song description was restricted to the most commonly observed song theme order (1,2,3,4,5,6,7,8), henceforth referred to as the primary song, to maintain consistency, as recommended by Cholewiak et al. (2013). For the primary song, song duration (start of first theme to end of last theme where the same theme never occurs twice in a song), and number of phrase repetitions within themes were measured. The average primary song duration per sample was plotted over time for samples that captured primary songs from start to finish continuously. To investigate phrase

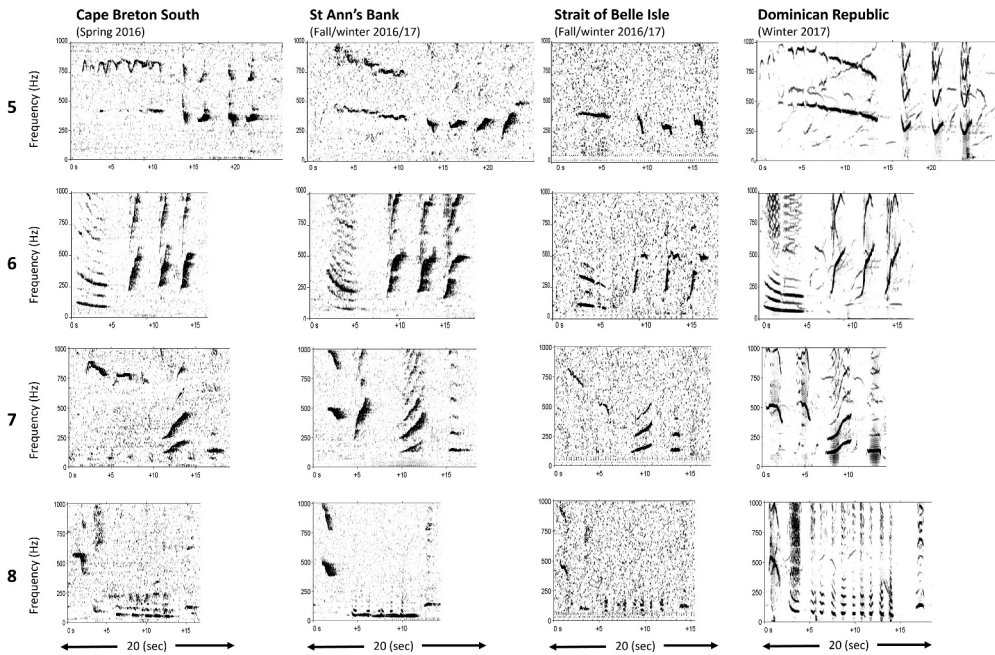


Figure 3. Spectrograms of exemplar humpback whale song phrases 5–8 that occurred at the four recording stations where each spectrogram has a frequency range of 0–1000 Hz and was viewed with the following parameters: 2 Hz frequency resolution (df), 0.125 s time resolution (dt) of FFT with an overlap of 75%, Hamming window, normalised across time.

repetitions, the average number of phrase repetitions per theme was calculated for each primary song sample and was plotted over time. Themes were not included in the primary song phrase repetition analysis when they occurred at the beginning or end of a sample, bordered on sleep mode or bordered on a break in singing.

Results

Themes 1–8 were identified at all stations (Figures 2 and 3) with each phrase annotated, resulting in 3864 phrase annotations (themes identified through each sample included in Appendix). Variants of phrases (e.g. different number of unit repetitions) existed within and between samples but followed the same general unit patterns (Figures 2 and 3), allowing for confident delineation of phrases (Darling et al. 2019). Theme 1 was qualitatively the most variable, especially in the Canadian data where it could be particularly faint and was initially suspected as a transition, though it was a clear theme in the Dominican Republic data where unit repetition was greater (Figures 2 and 3). This apparent change in theme 1 through time may be indicative of the theme evolving through the season.

The three samples in spring 2016 (April to May 2016) only had one song theme order which was the primary song (theme order 1, 2, 3, 4, 5, 6, 7, 8) (Table 2). In contrast, in the

four samples in fall 2016 (21 November to 5 December 2016) 10 different theme orders were observed, in addition to the primary song. Of note, in the sample on 21 November 2016, there were four unique theme orders, none of which were the primary song. Then, on 5 December 2016, five unique theme orders (including the primary song) were observed in a single sample. Variations in song theme order skipped themes from the primary song, though which themes were left out varied (Table 2; see details in Appendix). In late fall 2016 to early spring 2017 (6 December 2016 to 30 March 2017) nine of the 13 samples contained only the primary song. In the remaining four samples, five unique theme orders, in addition to the primary song, were observed. In the 16 January 2017 sample, the primary song was not observed (Table 2). Details on theme order analysis results for each sample are provided in the Appendix.

Primary song duration (theme order 1, 2, 3, 4, 5, 6, 7, 8) and repetition of phrases varied through time (Figures 4 and 5). Primary song was shortest in November and

Table 2. Every unique humpback whale song theme order observed for each sample (each unique day represents a sample) at the four stations. The number of songs analysed in each sample (N) was estimated for the Canadian stations because at times only parts of songs were observed due to the sleep mode of the recording schedule. Songs are represented as starting at the lowest theme number for ease of comparability, but bouts are cyclical, and the first theme observed could be anywhere in the cycle. The primary song (1, 2, 3, 4, 5, 6, 7, 8) is highlighted in **bold**.

Year	Month	Day	N	Cape Breton South	St Ann's Bank	Strait of Belle Isle	Dominican Republic
2016	April	17	2	1, 2, 3, 4, 5, 6, 7, 8			
		19	3	1, 2, 3, 4, 5, 6, 7, 8			
	May	20	3.5	1, 2, 3, 4, 5, 6, 7, 8			
		November	21	4		1, 4, 5, 7, 8 1, 3, 4, 5, 7, 8 2, 4, 5, 6, 7, 8 1, 2, 3, 4, 5, 6, 7	
	25		3.5	1, 2, 3, 4, 5, 6, 7, 8 2, 4, 5, 6			
	27		4		1, 2, 3, 4, 5, 6, 7, 8 3, 4, 5, 6, 7, 8 2, 3, 4, 5, 6, 7, 8		
	December	5	6			1, 2, 3, 4, 5, 6, 7, 8 1, 2, 3, 4, 5, 6, 8 1, 2, 3, 8 1, 2, 8 2, 3, 4, 5, 6, 7, 8	
			6	3			1, 2, 3, 4, 5, 6, 7, 8 2, 3
		23	3.5			1, 2, 3, 4, 5, 6, 7, 8	
		29	6		1, 2, 3, 4, 5, 6, 7, 8		
2017	January	1	6				1, 2, 3, 4, 5, 6, 7, 8 1, 2, 4, 5, 6, 7, 8
		9	2.5		1, 2, 3, 4, 5, 6, 7, 8		
		10	6				1, 2, 3, 4, 5, 6, 7, 8
		16	3	1, 2, 3, 4, 5, 7, 8			
	March	20	5				1, 2, 3, 4, 5, 6, 7, 8
		30	6				1, 2, 3, 4, 5, 6, 7, 8
		1	5.5				1, 2, 3, 4, 5, 6, 7, 8
		10	5				1, 2, 3, 4, 5, 6, 7, 8
		20	6				1, 2, 3, 4, 5, 6, 7, 8
		30	5.5				1, 2, 3, 4, 5, 6, 7, 8 1, 2, 3, 5, 6, 7, 8 1, 2, 3, 7, 8

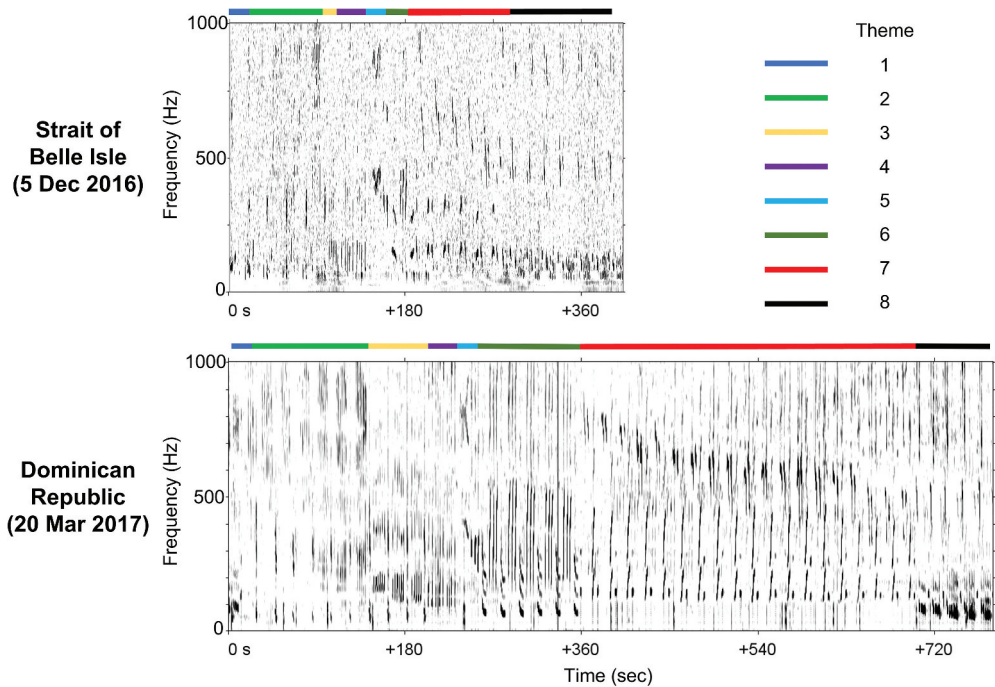


Figure 4. Spectrogram of an exemplar humpback whale primary song recorded in December 2016 in Canada (top) and a song recorded in March 2017 in the Dominican Republic (bottom) with the themes (1–8) colour coded for each song (2 Hz frequency resolution (df), 0.125 s time resolution (dt) of FFT with an overlap of 75%, Hamming window, normalised across time).

December 2016 in Canada, early in the singing season, lasting only 5 to 6 min. It was longest in March 2017 in the Dominican Republic, lasting up to 25 min, and the few samples in spring 2016 in Canada were an intermediate duration (6 to 10 min) (Figures 4 and 5). The increase in primary song duration through the fall and winter appeared gradual from this sample, potentially peaking at some point in February or March, though more samples are required to confirm this. The changing primary song duration through time was caused by an increase in phrase repetitions observed in almost all themes, with theme 7 having the most phrase repetitions both in Canada and the Caribbean (Figures 4 and 5). Comparing early spring (April 2016) to late winter (late January and early March 2017), the maximum average phrase repetitions per sample increased for all themes except theme 1, ranging from an increase of only 1.2 phrases for theme 5 to an increase of 30.2 phrases for theme 7 (Figure 5). For many themes (2, 3, 4, 6, 7, and 8), the number of phrase repetitions appeared to peak in late January to early March and decreased again in late March 2017 (Figure 5). This trend was particularly clear for themes 2 and 4 (Figure 5).

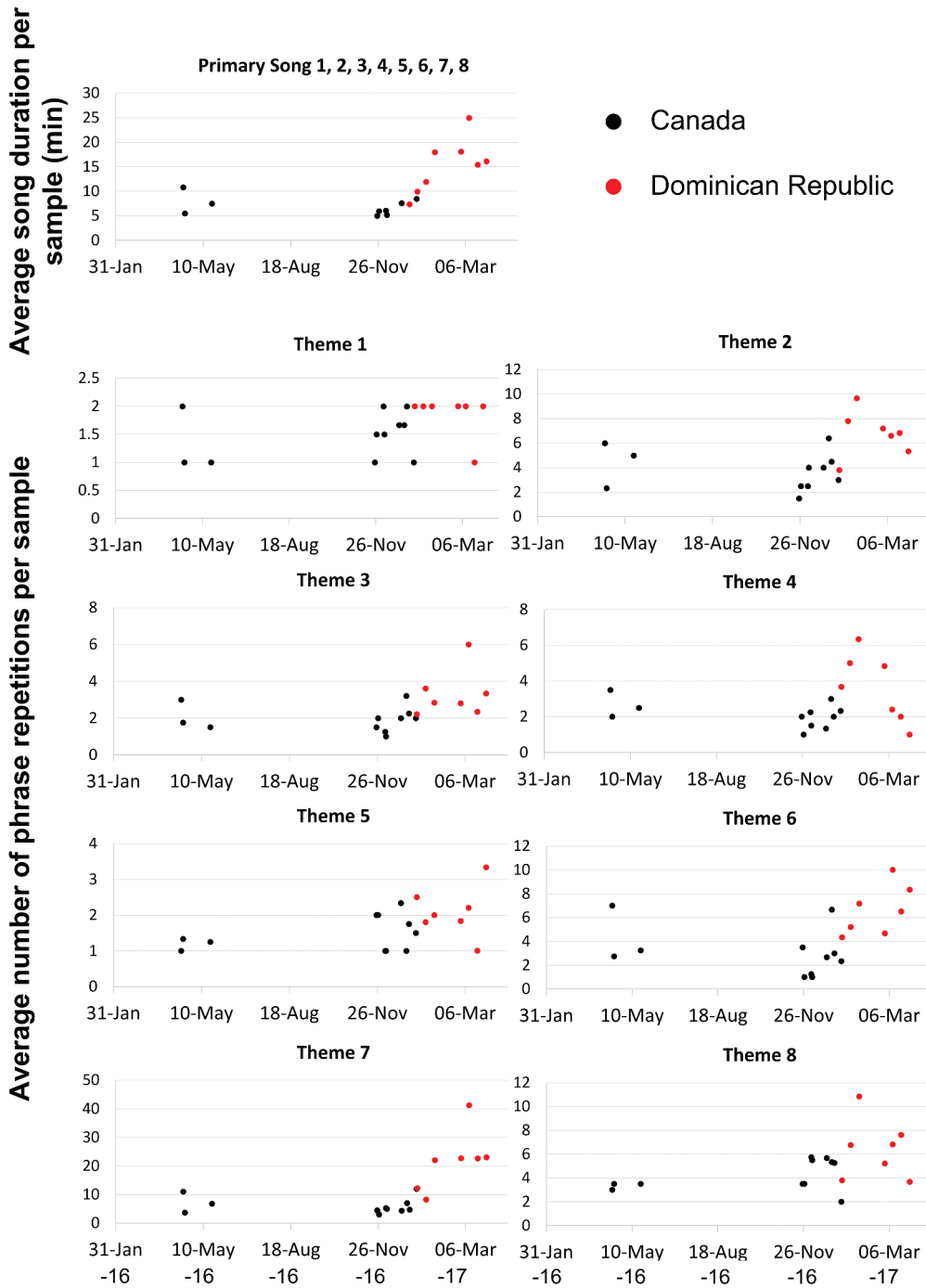


Figure 5. The average humpback whale primary song (song 1,2,3,4,5,6,7,8) duration per sample (top) and the average number of phrase repetitions per sample for each theme in the primary song (bottom) recorded at three stations off eastern Canada (black) and one station in the Dominican Republic (red).

Discussion

Acoustic recordings captured songs of western North Atlantic humpback whales at the end of the 2015–2016 winter breeding season (in Canada during the spring), at the start of the subsequent 2016–2017 breeding season (in Canada through the fall and early winter), and into the peak of the 2016–2017 winter breeding season (in the Dominican Republic in winter to early spring). Songs changed from the fall to early winter and through the breeding season, becoming more consistent in theme order and longer in duration. We have observed seasonal song ontogeny at the population level for western North Atlantic humpback whales and interpret our observations as reflecting the seasonal song ontogeny of individuals. The sample size included in this analysis was small (20), especially for the Canadian stations (3–5 per station) where it proved challenging to find singing bouts of sufficient quality for reliable song analysis. Ideally, numerous samples spread evenly over the recording period (such as was done in the Dominican Republic by examining songs from every 10 days) would have been analysed, but, while songs occurred throughout these Canadian data sets (Kowarski et al. 2019, 2022), few were of sufficiently high SNR with enough song repetitions to be suitable for analysis. The low availability of quality song samples in Canada could reflect 1) there being fewer individuals in the recorder area 2) the males in the recorder area are generally less motivated to sing, therefore fewer singing males relative to peak breeding season, reducing the chances of one singing near a recorder, 3) those males that do sing are also less motivated to produce full song (e.g., the song fragments described in Kowarski et al. 2019) or 4) singing males are less motivated to produce loud songs. The number of songs per sample was lower in Canada compared to the Dominican Republic, which can be explained, in part, by the whales singing shorter song sessions (Tyack 1981; Vu et al. 2012). Regardless, even with the small sample size over a single breeding season, obvious temporal trends in humpback whale song were observed.

Humpback whale singing behaviour has been examined in the context of avian singing behaviour and song systems for years (Tyack 1981; Cerchio et al. 2001; Cholewiak et al. 2013, 2018; Allen et al. 2018; Garland and McGregor 2020), due to the many parallels between humpback whale and songbird singing behaviour, particularly when considering the functional unit of the bird song as equivalent to a humpback whale song phrase. Furthermore, bird songs have been studied in great depth, both in lab and field settings, in a manner that is unachievable for the large, free-ranging humpback whales. Changes in bird song can be studied at the individual level, while changes in humpback whale song through time and space are typically described at the population level, with song changes largely considered to be through social learning and cultural transmission (e.g. Tyack 1981; Payne et al. 1983; Cerchio et al. 2001; Garland et al. 2011), although innate drivers of change have also been proposed (e.g. Cerchio et al. 2001; Mercado 2022). Here, we consider how analogous are the song processes employed by these evolutionarily disparate groups. Could convergent evolution have produced the same mechanisms in both birds and marine mammals? Fee and Goldberg (2011) believe so, drawing parallels between mammalian and songbird basal ganglia circuitry for vocal and motor learning. If comparable physiological processes were at play across these different groups, we would expect to see similar behavioural and physiological trends through the song season.

Bird song development after hatching has been described in three consecutive phases: subsong (quiet babbling), plastic song (variable, non-stereotyped), and crystallized song (stereotyped or stable) (Thorpe and Pilcher 1958; Clark et al. 1987). These song phases are driven by an increase in testosterone levels in the young male birds that effect song control brain nuclei (Lofts and Murton 1968; Nottebohm et al. 1986; Meitzen et al. 2007). Some bird species maintain their crystallised song through their life (closed-ended or age-limited learners), while other bird species continue to learn new songs through adulthood (open-ended learners) and seasonally produce non-stereotyped song early in the breeding season (Marler et al. 1988; Van Hout et al. 2009), a pattern similarly described for humpback whales. In adult birds, similar song development phases and associated plastic physiological processes that occur in the first year of a bird's life also take place seasonally during the breeding period on an annual cycle (Nottebohm et al. 1986; Marler et al. 1988; Van Hout et al. 2009; Allende et al. 2017).

The initial subsong period of bird song development is reminiscent of the song fragments described early in the singing season in humpback whales (Kowarski et al. 2019, 2022). Indeed, while the earliest song analysed here was in November, singing behaviour began as early as September (Kowarski et al. 2019, 2022), but was not defined as 'full song'. These song fragments were analysed in more detail in the feeding area of the Bay of Fundy in fall 2015 (Kowarski et al. 2019) and were almost always composed of phrases that later occurred in full songs. Most of these song fragments were composed of one or two themes that were not repeated. Future work to look closely at early season song fragments on a broader scale and gain an understanding of which themes are heard first would be revealing.

The second phase of bird song development, termed plastic song, is a period of novel combinations of song patterns or 'combinatorial improvisation' (Marler and Peters 1982; Nelson 1997). The description of plastic song appears similar to what we observed in November to December, when the order of themes in humpback song was inconsistent within and between samples, as different themes were skipped. Nottebohm et al. (1986) found that male adult canaries acquired most new syllables during the plastic phase of song instability. Plastic song may similarly be important for social learning and song evolution in humpback whales. Here, we observed songs eventually returning to the same pattern (theme sequence) observed the previous spring, indicating a level of memorisation. Canaries can similarly retain vocal motor memory for an extended period, such that songs can be recovered once they are developed (Vellema et al. 2019).

The final phase in bird song development is when song becomes crystallised. We observed a similar increase in stereotyped singing in January and March when most samples contained only one order of themes which was consistent across samples (Table 2). However, humpback whale songs have been described changing within and between breeding seasons (Payne et al. 1983; Noad et al. 2000; Cerchio et al. 2001; Garland et al. 2011) so the 'crystallisation' analogy is flexible for this open-ended learner. Some of the described changes involved dropping, or extinction of themes, and also variation in theme order (Cholewiak et al. 2013). Moreover, humpback whale song evolves progressively through a breeding season in a manner comparable to the village indigo bird (*Vidua chalybeata*) and yellow-rumped cacique (*Cacicus cela*) (Thompson et al. 1981; Cerchio et al. 2001). Having observed only one year and likely one population, it is not unsurprising that song evolution at the theme order level was not apparent here.

A closer look at the unit level would almost certainly reveal more subtle changes through time (for example, theme 1 seemed to have evolved by the end of March 2017) as has been described over short time periods (within a single season) in a number of studies including Payne et al. (1983), Cerchio et al. (2001), and Arraut and Vielliard (2004).

To summarise, many aspects of the humpback whale song ontogeny align with that of songbirds, with the canary, an open-ended learner that undergoes seasonal song development, being a notable example. At the onset of the breeding season, both species produce song fragments, or subsongs, for a period before transitioning into static songs and finally producing crystalized songs during the peak breeding season (Nottebohm et al. 1986).

One consideration is the relationship between the changes in song that we documented (from a feeding area to a breeding area) and the changes that have been described from other studies focused on a breeding area. The present study did not delve into the meticulous song analysis of some of the seminal work on this topic (notably, Payne et al. 1983). In part, this was because of less-than-ideal data quality in northern recordings as previously discussed. Nonetheless, some value can be gleaned from investigating even a few measures, including song duration which had a notable trend despite the small sample size. Song duration increased during the study period (changing from 5 to 25 min long) with some evidence of a peak between January and March that was achieved at least in part via the increased repetition of phrases for all themes. Ryan et al. (2019) similarly reported an increase in song duration through the breeding season for the high-latitude northeast Pacific humpback whales, where songs increased in duration from an average of 5 min in October to a peak of 10 min in January before reducing to 8 min in February. Other studies explored changes in humpback whale song duration through time solely on breeding grounds, and the trends were less consistent and dramatic than observations at high latitudes (e.g. present study and Ryan et al. 2019). Cerchio et al. (2001) reported a less dramatic but significant increase in song duration through the breeding season of humpback whales in Hawaii and Mexico, with songs in January/February being 2 min shorter than those in April. Cerchio et al. (2001) reported that the increase in song duration in Hawaii and Mexico was attributed to both an increase in phrase repetitions and the animals singing longer phrases (a characteristic not explored here). In Hawaiian humpback whales, Payne et al. (1983) found in one year song duration increased through the early season (December to February), while in the following year it decreased (November to February), with the trends reflected in the number of phrases per theme. It may be that two separate processes are involved: early season songs on high latitudes follow more annually consistent trends (e.g. increasing in duration) in an ontogenetic process analogous to birdsong development, as subsong (with short themes) develops into crystalized song, whereas changes in song duration on low latitudes where songs are well developed reflect the processes of progressive cultural evolution and can either increase or decrease.

Changes in song duration have also been documented in response to social interactions, as well as non-biological stimuli. On a migratory route off eastern Australia, Smith (2009) documented lone singers producing songs that were 23% to 26% longer than the songs of males escorting a female and calf. The increased song length of lone whales reflected an increase in phrase repetitions of some themes. Similarly, Cholewiak et al.

(2018) found that males changed their phrase repetition rates, and therefore the overall 'length' of song, in the presence of other singing males.

The longest songs in the present study were observed in the Dominican Republic. Miller et al. (2000) found that humpback whales in Hawai'i increased song length (by producing longer themes as described here) in response to sonar, potentially to compensate for the sonar's auditory interference. The many simultaneous singers on the Dominican Republic breeding ground may cause interference in the audibility of each individual song and, much like with sonar, to compensate, the whales sing longer songs. Overall, with no information on behavioural context, it is challenging to postulate on the underlying drivers behind variability in song length on the breeding ground. Differences in song length across social groups may be reflected in our findings that different song samples from the same month vary in the number of phrase repetitions for each theme (Figure 5).

It is important to emphasise the trends observed here regarding song duration are based on a small sample size, one season and this is only one of a myriad of song characteristics that can change through time. Therefore, while the above explanation regarding auditory interference can inform future research questions, it is likely only part of many contributing factors that influence singing behaviour.

A possible proximate mechanism driving the seasonal trends in song length observed here may be the physiological processes of the male humpback whale. Male testes size increases with the onset of the breeding season (Chittleborough 1955). Furthermore, male testosterone levels have been found to increase through the breeding season, peaking in January and February (Cates et al. 2019), a process that may reflect on song development observed here with song length peaking between January and March and potentially signifying crystallisation. Indeed, as testosterone levels begin to rise in the fall, whales produce song, but they may not yet be able (or motivated) to consistently sing the same pattern until testosterone levels reach some threshold. This trend in testosterone levels and its relationship with song is well described in many oscine bird studies where hormone levels impacting the development of song control brain nuclei which develop through the breeding season before once again reducing in size (Lofts and Murton 1968; Nottebohm et al. 1986; Meitzen et al. 2007; Dawson 2013). Such a link between testosterone, inherently connected to reproductive readiness, and song has implications for the sexual selection of singing behaviour. Indeed, females could use song as a cue for mature males. Mingramm et al. (2020) found principal male escorts of females to have higher testosterone levels than that of secondary escorts. Future work at the individual singer level for song development in relation to testosterone levels and other physiological processes would be revealing.

This similarity between bird and humpback whale song systems has implications for the selective forces acting on humpback whale song, as findings in avian literature could be extremely informative and should be taken into consideration in future research. For example, Robinson et al. (2019) reviewed the song systems of closed- and open-ended learning songbirds and proposed that female selection for large repertoire size and elaborate songs resulted in the evolution of open-ended learners and plastic song in adults. Plastic song in oscine birds was further correlated with polygynous mating systems, which have been described in humpback whales (Cerchio et al. 2005; Robinson et al. 2019). The change in humpback whale song production through the

breeding season is possibly connected not only to physiological changes (e.g. producing fragments when testosterone levels are low and stereotyped full song when levels are high) but also to the whales singing for different reasons in different contexts (Cholewiak and Cerchio 2022). Early season singing behaviour outside of known breeding grounds has been recorded globally, but it is unclear if this indicates that these areas are also important for mating (Mattila et al. 1987; McSweeney et al. 1989; Magnúsdóttir et al. 2014; Kowarski et al. 2018). During the present and previous studies (Kowarski et al. 2019, 2022), it has become apparent that early-season western North Atlantic humpback whale songs look quite different than what is observed later in the season (in high or low latitudes). Ryan et al. (2019) and Magnúsdóttir and Lim (2019) similarly saw a progression through the breeding season in high latitudes. Ritters et al. (2019) concluded that in songbirds, songs produced outside of the context of territory defence and mate attraction are an important form of play that is stimulated by intrinsic reward mechanisms and is key for song learning and maintenance. The idea that migratory routes and feeding grounds are important places for song learning has similarly been proposed by Payne et al. (1983); Garland et al. (2013); Owen et al. (2019), Mcloughlin et al. (2018), and Magnúsdóttir and Lim (2019). Early season plastic songs in canaries are when most new song syllables are acquired (Nottebohm et al. 1986). This period of song instability may also be important for humpback whales, allowing for social learning and song evolution.

Conclusions

This study has provided a glimpse into seasonal song development of humpback whales at the population level and placed the findings within the context of songbird ontogeny. As previously described by Payne et al. (1983), male humpback whales sang the same song in the fall as they did the previous spring in Canada. However, they did not simply 'remember' and continue singing in the same manner as they left off. Rather, they went through a period of plastic song, where the order of the themes was varied as different themes were omitted, that is potentially related to intermediate testosterone levels and could be an important time for song evolution and social learning. After a few months of plastic song, humpback whales returned to consistently singing the same song that was produced the previous spring. Even then, song behaviour did not go unchanged, but rather increased in phrase repetitions gradually through time. These trends are based on a small sample size and should be confirmed with additional data across time for multiple breeding seasons. This work highlights the importance of including high latitude songs in the observation of humpback whale song change through time, without which, such telling trends may not be apparent.

Acknowledgements

Thank you, Andrew Horn, and David Barclay of Dalhousie University for your feedback on the manuscript. Edda Magnúsdóttir of the University of Iceland, thank you for your time and thoughts when the analysis was being planned. The Dominican Republic acoustic data were kindly shared by Sofie Van Parijs, and Genevieve Davis. We also thank Heather Heenahan, Joy Stanistreet, Leah

Crowe, and the Dominican Republic's National Authority for Maritime Affairs. The Dominican Republic data were collected under authorisation from the Ministro de Medio Ambiente y Recursos Naturales.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Mitacs Accelerate programme through Grant number 15622 as part of Katie Kowarski's PhD research. Funding for the DFO AMAR in St. Ann's Bank was provided by DFO's National Conservation Plan funding. Funding for the data collected at Strait of Belle Isle and Cape Breton South was provided by ESRF. Funding for the collection of the Dominican Republic data was provided by NOAA and the NEFSC. In-kind support was provided by the Dominican Republic's National Authority for Maritime Affairs

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Data availability statement

For access to the Canadian acoustic data used in this study, please contact the corresponding author at katiekowarski@gmail.com; for access to the Dominican Republic data, please contact Danielle.cholewiak@noaa.gov.

Ethical statement

The present study followed the ethical guidelines for scientific research of Dalhousie University.

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Appendix

Table A1. Description of song for each sample (represented by date) where song is described as one number (1–8) for each theme. ‘Sleep’ indicates the recording entered sleep mode. When samples included less than 6 songs, an indication of why song description stopped is included (e.g. singing ends or gets faint). Where there was a ‘break in singing’ (50–120 s) it was unclear whether the whale stopped singing temporarily or if the song temporarily got faint.

Station	Sample	Song
Cape Breton South	17 Apr 2016	7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6 singing ends
Cape Breton South	19 Apr 2016	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, break in singing, 5, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, overlap started
Cape Breton South	20 May 2016	2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, singing gets faint
Strait of Belle Isle	5 Dec 2016	6, 8, 1, 2, 3, 4, 5, 6, 8, 1, 2, break in singing, 5, 6, 7, 8, sleep, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 8, 1, 2, 8, sleep, 2, 3, 4, 5, 6, 7, 8, 2, 3, 4, 5, 6, 7, 8, sleep, 8, 1, 2, 8, 1, 2, 8, singing ends
Strait of Belle Isle	6 Dec 2016	8, 1, 2, 3, 4, 5, 6, 7, 8, 2, 3, 2, 3, 4, 5, 6, 7, sleep, 7, 8, 1, 2, break in singing, 5, 6, 7, 8, 1, 2, 3, 4, sleep, 7, 8, singing ends
Strait of Belle Isle	23 Dec 2016	2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, break in singing, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, singing ends
Cape Breton South	25 Nov 2016	6, 7, 8, 1, 2, 3, 4, break in singing, 6, 7, 8, 1, 2, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 5, 6, 7, 8, break in singing, 5, 6, 2, 4, 5, 6, 2, 4, 5, 6, 7, sleep
Cape Breton South	16 Jan 2017	3, 4, 5, 7, 8, sleep, 7, 8 break in singing, 3, 4, 5, 7, 8, sleep, 7, 8, 1, 2, 3, 4, 5, 7, 8, singing gets faint
St. Ann’s Bank	21 Nov 2016	2, 3, 1, 4, 5, 7, 1, 3, 4, 5, 7, 8, 2, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 1, sleep, 4, 5, 7, singing ends
St. Ann’s Bank	27 Nov 2016	1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 7, 8, 1, sleep, 5, 3, 4, 5, 6, 7, 8, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, singing gets faint
St. Ann’s Bank	29 Dec 2016	6, 7, 8, 1, 2, 3, 4, 5, 6, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 6, 7, 8, 1, 2, 3, 4, sleep, 3, 4, 5, 6, 7, 8, 1, 2, sleep, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, sleep.
St. Ann’s Bank	9 Jan 2017	5, 6, 7, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, sleep, 3, 4, 5, 6, 7, singing gets faint
Dominican Republic	1 Jan 2017	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8,
Dominican Republic	10 Jan 2017	7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	20 Jan 2017	8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	30 Jan 2017	7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	1 Mar 2017	3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8,
Dominican Republic	10 Mar 2017	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	20 Mar 2017	8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	30 Mar 2017	1, 2, 3, 5, 6, 7, 8, 1, 2, 3, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 7, 8, 1, 2,