

Western North Atlantic humpback whale fall and spring acoustic repertoire: Insight into onset and cessation of singing behavior

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Humpback whale songs have been described worldwide and studies exploring non-song vocal behavior continue to expand; however, studies on the transition periods when whales shift to and from the seasonal behavioral state of singing are lacking and may be potentially informative regarding the proximal factors controlling the onset and offset of humpback whale male singing. Acoustic recorders collected data off eastern Canada continuously from the Bay of Fundy in the fall of 2015 and near-continuously off northeast Nova Scotia in the spring of 2016. Humpback whale acoustic occurrence and behavior were identified by systematically reviewing a subset of acoustic recordings for presence before analyzing the highest quality recordings for behavior. The onset of singing in the fall was gradual over a period of about three weeks with an intermediate form, termed “song fragment,” occurring prior to full songs. In comparison, singing in the spring seemed to end abruptly with few song fragments. Song fragments could be produced by juveniles learning to sing for the first time or mature males preparing for breeding activities prior to migrating to southern breeding grounds. The authors propose an alternative hypothesis that the timing and manner of transitions could be driven by physiological processes similar to those documented in songbirds.

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I. INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a medium-sized mysticete found in all ocean basins.¹ It is known for its long migrations from high-latitude summer feeding grounds to low-latitude winter breeding grounds^{2–5} and its acoustic behavior. Sounds of the humpback whale have been studied globally with two overarching acoustic behavioral categories described: song and non-song calls.^{6–14}

Songs are a sexually selected male display that occur during the winter breeding season when humpback whales migrate from high latitude feeding grounds to lower latitudes.² The precise function of singing is still debated, with proposed functions including to attract mates,^{15,16} stimulate female receptivity,¹⁷ mediate male competitive interactions,¹⁸ form male coalitions,¹⁹ and/or establish dominance.²⁰ Humpback whale songs have a hierarchical structure in which discreet units (i.e., notes) are arranged in series to form stereotyped phrases, which repeat to produce themes that occur in sequence.^{6,21,22} Whales within the same population (region) sing a similar song that changes over time while whales in different populations sing different songs, although the rules governing song structure are similar in all ocean basins.²¹ In the South Pacific Ocean, Garland *et al.*¹¹ described the spread of humpback songs across an ocean basin, an example of repeated cultural transmission across populations at a large geographic scale.

Humpback whale songs have been studied much more extensively as compared to other types of humpback whale vocal behavior.^{12,13,23} Calls not associated with songs are produced by males, females, and calves throughout the year and have been linked to both social and feeding behaviors.^{7,23–26} Such calls that have been previously associated with humpback whale social behaviors include grunts produced by calves,²⁶ blows and cries produced by competing males,²⁷ snorts and wops produced within and between groups,²⁷ and grunts and barks that occur when groups meet.²⁷ Rekdahl *et al.*¹³ found that some of these call types are stable through multiple years while others are more variable and are often incorporated into songs. Cerchio and Dahlheim⁷ described cries in southeast Alaska that are associated with feeding behavior.

One aspect of humpback whale acoustic behavior yet to be described is the fall and spring transitional periods when seasonal singing behavior waxes and wanes, respectively. The complete repertoire of vocal behaviors during these transitional periods, or “shoulder seasons,” of the year remains largely undescribed. This knowledge gap reflects a lack of available data and, more so, the difficulty in describing an inherently dynamic behavioral transition when incorporating structured songs into the seemingly less structured non-song repertoire. Humpback whale songs have been well documented on high latitude feeding grounds, largely during early spring and late autumn, and on migratory routes.^{24,28–44} This indicates that the onset and cessation of singing occurs pre- and post-migration to low latitude breeding grounds. Kowarski *et al.*⁴⁴ suggested that vocal behavior neither belonging to the song or non-song category occurs during

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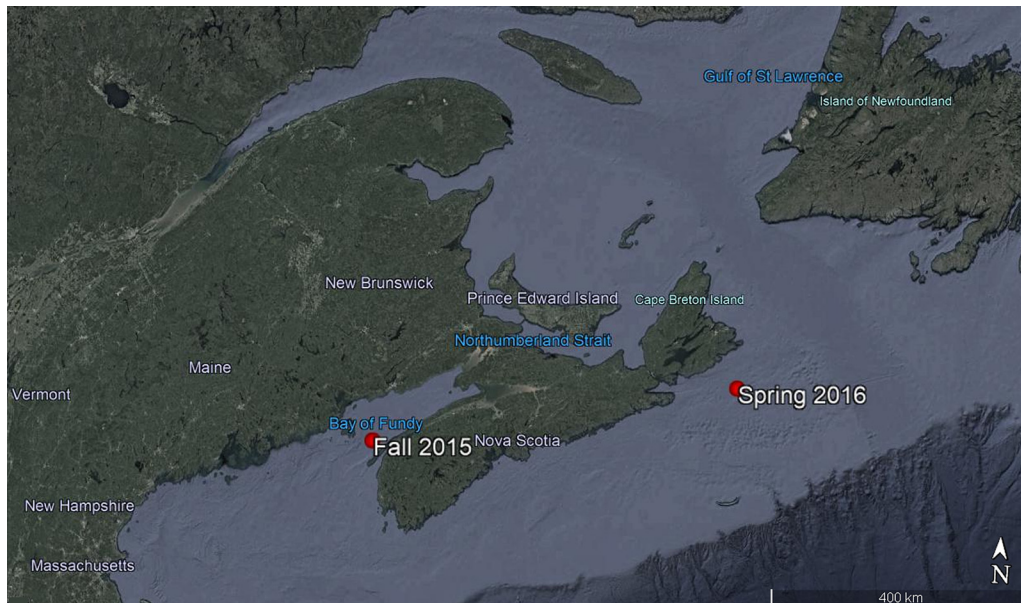


FIG. 1. (Color online) Fall 2015 and Spring 2016 stations off eastern Canada.

transition periods. Similarly, McSweeney *et al.*³⁰ and Mattila *et al.*²⁹ described singing behavior prior to migration that was not complete songs. In songbirds, transitional periods have been found to be hormonally driven, with low testosterone levels resulting in more variable vocalizations and high testosterone levels resulting in more structured songs.⁴⁵ Environmental factors also play a role in some oscine species with an increased photoperiod accelerating the effects of testosterone on singing behavior.⁴⁶

The present paper aims to explore the nature and timing of the Western North Atlantic humpback whale repertoire as it transitions through one fall and one spring. Western North Atlantic humpback whales overwinter from January to early April on breeding grounds in the Caribbean and Cape Verde Islands^{47–50} and summer on a number of known northern feeding grounds including those off eastern Canada.^{51,52} Songs have been detected in Canadian waters into winter months, indicating that transitions likely occur in the region.⁴⁴ We use data collected through static acoustic monitoring techniques to explore whether the transitions off eastern Canada are abrupt, fluid over time, or if they occur in stages that can be delineated into vocal categories. By shedding light on a new aspect of humpback whale acoustics, we give an additional perspective to attempts to understand the functions of the songs and sounds of the humpback whale.

II. METHODS

A. Data collection

Acoustic data collected off eastern Canada using static Autonomous Multichannel Acoustic Recorders (JASCO Applied Sciences Ltd.) were explored over two time periods: September to December (the “Fall 2015” data set) and during April to July (the “Spring 2016” data set). The Fall 2015 recordings were collected from the mouth of the Bay of Fundy while the Spring 2016 recordings were collected from off northeastern Nova Scotia (Fig. 1). The deployment

details and recording specifications for each data set are provided in Tables I and II.

B. Acoustic analysis

Acoustic analysis was completed in three phases. In phase 1, the occurrence (presence/absence) of humpback whale vocalizations was identified throughout the two data sets. In phase 2, the occurrence results were expanded to include the type of humpback whale vocal behavior that occurred in high quality recordings. In phase 3, songs and any vocalizations similar to songs were analyzed in more detail.

Phase 1 occurrence analysis was completed by experienced acousticians that manually reviewed a subsample of each data set using PAMlab (JASCO; hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s). For Fall 2015, this was done by reviewing 70-s samples extracted from the center of every other 10.5 min file sampled at 16 kHz from August 27, 2015 to January 15, 2016 (62 samples 23 min apart for each day). For Spring 2016, 1-min samples extracted from the center of every 11.3 min file sampled at 8 kHz (72 samples 20 min apart for each day) from April 1 to July 15, 2016. Humpback whale acoustic occurrence was indicated by annotating the entire duration and frequency range of the fundamental frequency contour of a single humpback whale vocalization per sample. Acoustic signals were deemed humpback whale vocalizations if they aligned with characteristics previously reported in the literature, e.g., Refs. 10 and 13. Effort was made to annotate the highest quality vocalization in a sample. In this manner, humpback whale acoustic presence/absence throughout the two data sets was assessed and then visualized using daily and hourly occurrence plots.

Results from the phase 1 acoustic occurrence analysis were used to guide the phase 2 analysis where vocal behaviors were analyzed and categorized. First, PAMlab calculated the signal-to-noise ratio (SNR) of each vocalization

TABLE I. Deployment and retrieval dates, location, water depth, and recorder position for the two recording stations.

Station	Deployed	Retrieved	Latitude (N)	Longitude (W)	Water Depth (m)	Recorder Position
Fall 2015	August 27, 2015	December 1, 2015	44° 33.5'	-66° 20.0'	151	On seafloor
	December 3, 2015	April 28, 2016	44° 33.8'	-66° 20.2'	148	
Spring 2016	November 3, 2015	July 21, 2016	45° 25.8'	-59° 46.3'	123	20 m above seafloor

annotated in phase 1 by extracting the annotation sound pressure level (SPL) and the ambient SPL, where the ambient SPL was measured immediately before the annotation (using the same duration and frequency range as the annotation). The inverse annotation SPL was divided by the inverse ambient SPL and the resulting value logged to obtain the SNR. Then, for every 6 h of data where humpback whale vocalizations occurred, we selected the acoustic file with the highest vocalization SNR. Each of the selected high-quality acoustic files (10.5 min duration in Fall 2015 and 11.3 min duration in Spring 2016) were analyzed and the presence/absence of one or more vocal categories was assigned. By limiting our analysis to a maximum of 1 file every 6 h, we reduced the chance of re-sampling the same whale(s) over consecutive 6-h periods. In this manner, we categorized vocalizations up to four times each day for days in which vocalizations occurred. To increase confidence of vocal category assignment, we analyzed humpback whale vocalizations in files immediately preceding and following the file of interest. In Fall 2015, where there was no gap (sleep mode) in the recorder's duty cycle, analysts could confirm humpback whale vocal behavior using many consecutive files, while in Spring 2016, there was an inevitable data gap between recordings as the duty cycle included 8 min of sleep mode (Table II). Phase 2 analysis was not carried out on data where the vocalization quality did not allow for confident classification of vocal categories.

When defining vocal categories, attention was placed on discerning vocalizations occurring in patterns or sequences from those lacking such structure. Vocal categories

TABLE II. Recording equipment specifications and recording schedule for the two stations.

	Fall 2015	Spring 2016
Hydrophone	M36-V35dB omnidirectional (GeoSpectrum Technologies Inc.)	HTI-99 omnidirectional (HTI, Inc.)
Hydrophone Sensitivity	-165 ± 3 dB re 1 V/μPa	-165 ± 3 dB re 1 V/μPa
Resolution	24 bit	24 bit
Gain	6 dB	6 dB
Duty Cycle (min)	11.5	20
High frequency sampling rate (kHz)	375	250
High frequency duration (min)	1	1
Low frequency sampling rate (kHz)	16	8
Low frequency duration (min)	10.5	11.3
Sleep duration (min)	NA	7.7

implemented here were largely based on those previously described in humpback whale acoustic literature, e.g., Refs. 7, 10, and 13. Six predominant vocal categories were identified and qualitatively assigned during vocal behavior analysis: cries, cry sequences, non-patterned calls, grunt sequences, song fragments, and songs (see Table III for definitions, Fig. 2 for exemplars). These can be further defined into the broader categories of non-song (cries, cry sequences, non-patterned calls, grunt sequences) and song vocalizations, though the placement of song fragments in this classic scheme is unclear. The temporal variation in humpback whale acoustic behavior was visualized using bar plots of the proportional occurrence of each vocal category over 5-day periods.

The time-frequency domain characteristics of each non-song vocalization category were summarized. For each day, we selected the file with the highest vocalization SNR and then annotated every humpback whale non-song vocalization in the file. The duration and centroid frequency of each annotation was extracted and is summarized in Table IV. Duration was the difference in time between the start and end of annotations and centroid frequency was the point at which 50% of the energy was above and below a given frequency of an annotated vocalization.

Songs and song fragments were differentiated based on structure and complexity. Songs included three or more themes repeated at least once while song fragments were variable in nature with complexity and structure occurring on a continuum ranging from a single phrase or subphrase to a series of two or more themes not repeated in its entirety. In phase 3, we further categorized song-fragments depending on the level of song structure observed. First, we analyzed the most well defined, high SNR songs for the occurrence of different themes and phrases. We reviewed eight songs from Fall 2015 and four from Spring 2016 to gain a representative library of themes and constituent phrases, for which a theme is defined as a sequence of stereotyped phrases of the same phrase type. This was challenging for the Spring 2016 data

TABLE III. Definition of each vocal category.

Vocal Category	Definition
Cries	Long, tonal, often down-sweeping; occur alone or simultaneously with other cries.
Cry sequences	Repeated cries (4-37); beginning and ending often frequency modulated.
Non-patterned	Any call (e.g., moans, grunts, wops, purrs) not in a recognizable series or pattern.
Grunt sequences	≥3 grunts in sequence.
Song fragments	1 subphrase to 2+ themes not repeated.
Songs	≥3 themes repeated at least once (Refs. 22 and 72).

Vocal Category

Example Spectrogram

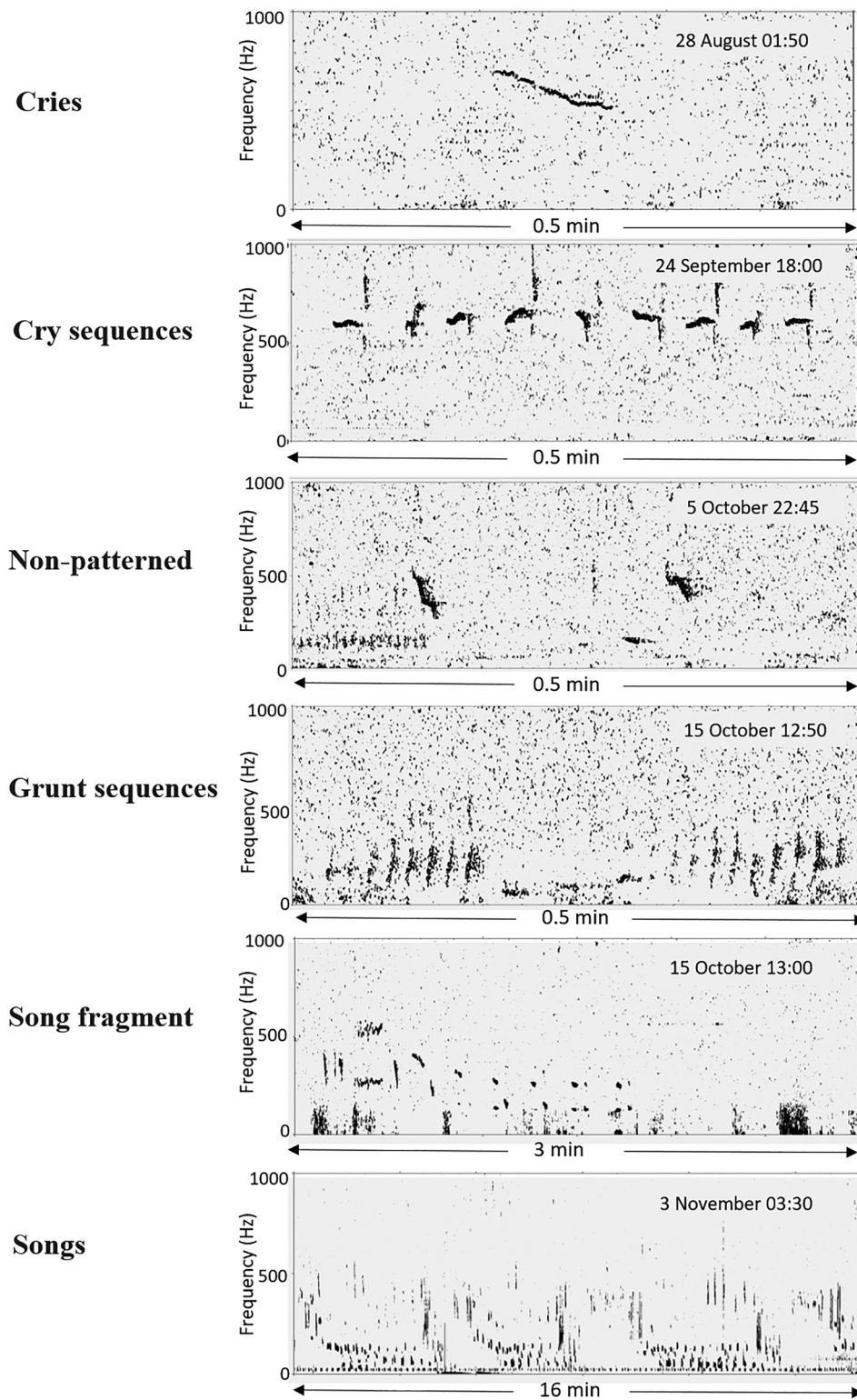


FIG. 2. Example spectrograms (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s) of each humpback whale vocal category.

set because the whales were consistently chorusing, making it difficult to separate one song from another; however, the high quality of the songs analyzed coupled with the review of files containing chorusing provided us with high confidence that our understanding of themes and phrases was sufficient for song fragment analysis. Second, we re-reviewed the data identified as song fragments in phase 2 and,

comparing it to established song themes and phrases, further categorized the vocalizations depending on the level of song structure observed into three increasing levels of complexity (Table V).

Our definition of song fragment did not require the fragment to eventually be incorporated into a song. Rather, a fragment composed of a stereotyped series of vocalizations

TABLE IV. Number of annotations (Ann.), mean and standard deviation (SD) of vocalization duration, and mean and SD of vocalization centroid frequency for each non-song vocal category.

Vocal Category	Ann.	Mean Duration \pm SD (s)	Mean Centroid Frequency \pm SD (Hz)
Cries	629	4.6 \pm 2.7	500.7 \pm 85.2
Cry sequences	289	1.6 \pm 0.4	578.7 \pm 67.3
Non-patterned	972	1.2 \pm 1.1	278.4 \pm 174.7
Grunt sequences	455	0.5 \pm 0.2	129.0 \pm 56.9

repeated once (two phrases) would be classified as a song fragment. The series must have some stereotyped variation (e.g., cannot be one vocalization type repeated such as a grunt or cry sequence). During analysis we noted which song fragments were observed in songs and which were not. All observed song fragments may eventually be incorporated into songs that were not recorded in the present data set (e.g., on the southern breeding grounds).

We performed a naive matching test to ensure our protocol for differentiating between song and song fragments was repeatable. An acoustic analyst was provided our protocol, our library of themes, and all files from Fall 2015 containing either a song or song-fragment and instructed to classify each sequence into a theme category. The analyst's results matched ours for 100% of files.

C. Diel analysis

An effort was made to explore possible diel patterns in vocal categories. The phase 2 vocal category analysis, with a maximum of four samples per day, resulted in an insufficient sample size for diel analysis on individual vocal categories. We instead used the results from the phase 1 occurrence analysis. We converted results from the phase 1 occurrence analysis into hourly presence/absence data and separated them into time frames per station. Every hour in a day where humpback vocalizations occurred was assigned to dawn (sun 12° below the horizon to sunrise), light (sunrise to sunset), dusk (sunset to sun 12° below horizon), or dark (sun is less than 12° below horizon) where light period times (sunset, sunrise, nautical dusk, and nautical dawn) were calculated using Reda and Andreas.⁵³ For every day, we subtracted the proportion of hours containing humpback vocalizations in a 24-h day from the proportion of hours with humpback vocalizations per light period in that day. Next, we calculated the average of these figures across the time frame of interest to determine the mean-adjusted hours with humpback vocalizations per light period. Through these calculations, we accounted for the change in light periods throughout the recording periods as well as the

TABLE V. Levels of song fragments.

Level	Definition
Song fragment 1	1 subphrase or phrase.
Song fragment 2	1 theme.
Song fragment 3	2+ themes not repeated.

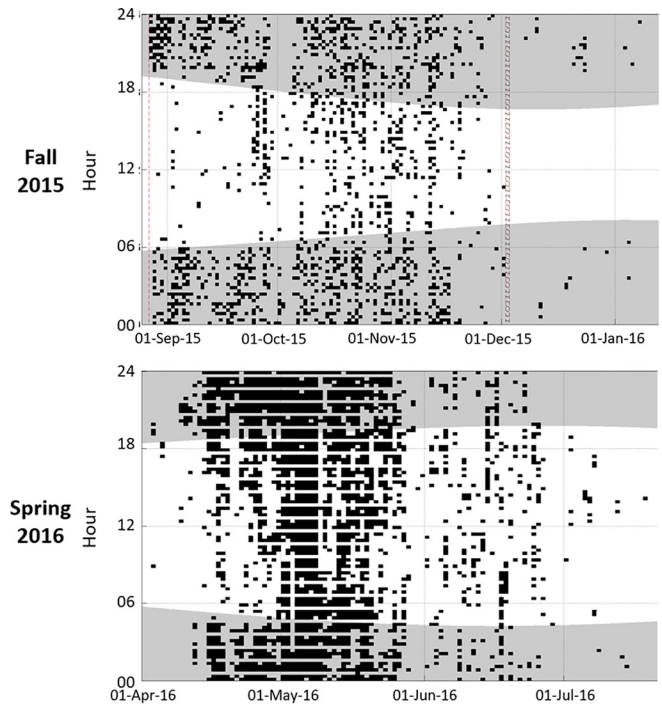


FIG. 3. (Color online) Daily and hourly occurrence of humpback whale vocalizations recorded in Fall 2015 (top) and Spring 2016 (bottom). Shaded areas indicate periods of darkness and dashed lines indicate the deployment and retrieval dates where such dates overlap with the timeframe presented.

variation in hours with humpback vocalizations each day. We applied Welch's analysis of variance to test the null hypothesis that the mean adjusted hours with humpback vocalizations were constant across diel light periods. Where Welch's was significant (P -value < 0.05), Tukey-Kramer multiple comparison tests were utilized to ascertain which light periods differed.⁵⁴

III. RESULTS

The phase 1 occurrence analysis revealed humpback whale acoustic presence from August 27, 2015 to January 8, 2016 in the Fall 2015 data set and from April 3, 2016 to July 20, 2016 in the Spring 2016 data set (Fig. 3). For the phase 2 vocal behavior analysis, 293 acoustic files from the Fall 2015 data set and 275 acoustic files from the Spring 2016 data set were selected for analysis based on having the highest SNR files within a 6-h period. However, only vocalizations of sufficient quality could be included in the vocal behavior analysis, and upon further examination of these files 238 were chosen to be included from the Fall 2015 data set and 175 were chosen to be included from the Spring 2016 data set. The fewer recordings analyzed from the Spring 2016 data set reflects a lower quality of vocalizations (e.g., lower SNR) compared to the Fall 2015 data set. The occurrence of vocal categories varied greatly between the two stations (Figs. 4 and 5).

A. Fall 2015 data set

During Fall 2015 in the Bay of Fundy, cries and non-patterned calls were present throughout the recording period

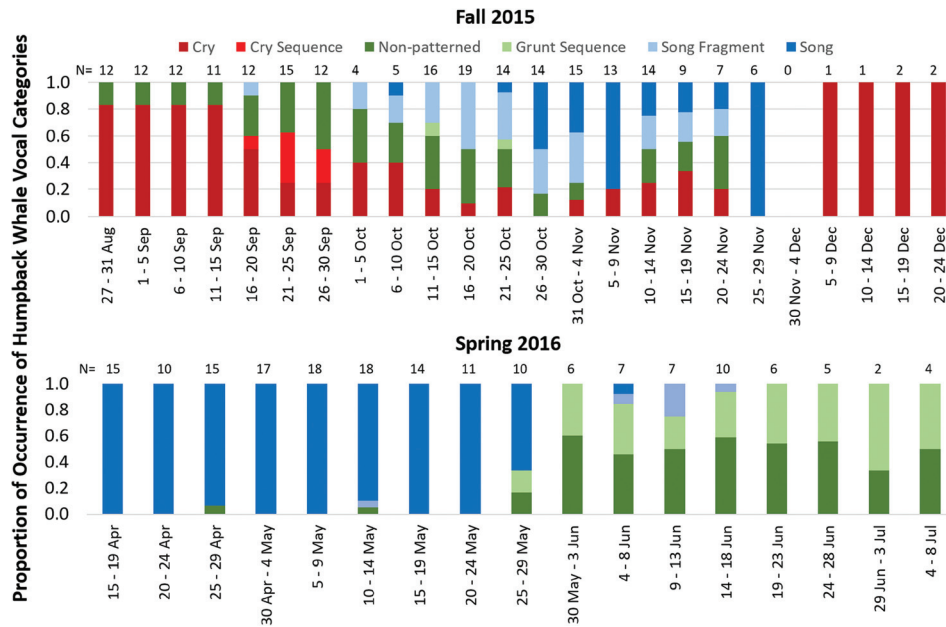


FIG. 4. Proportional occurrence of humpback whale vocal categories over 5-day periods in Fall 2015 (top) and Spring 2016 (bottom) that were cries, cry sequences, non-patterned, grunt sequences, song fragments, or songs. The number of acoustic files analyzed in each timeframe are included (*N*) where acoustic files were 10.5 min in duration in Fall 2015 and 11.3 min in duration in Spring 2016.

with broadly overlapping distributions, while cry and grunt sequences displayed isolated temporal peaks, and song fragments and songs were found predominantly in the latter half of the fall (Fig. 4). A clear progression throughout the season was noted: cries and non-patterned calls were the predominant vocalizations from August 26 to October 25, with cries accounting for a greater proportion of occurrences early on. Song fragments were first recorded on September 18 and then not recorded again until October 5, after which they became a consistently recorded vocalization through November. Complete songs were first recorded on October 7, then were absent until October 24, and occurred frequently between October 27 and November 29 (Fig. 4). Six files analyzed in December contained only cries (Fig. 4).

Complete song was preceded by song fragments: 19 days passed between the first occurrence of song fragments and the first occurrence of songs. Song fragments with two

or more unrepeated themes (level 3) were the most common song fragment type and the first observed in Fall 2015, occurring from September 18 to November 19 (Fig. 5). Single themes (song fragment level 2) were first observed on October 11 and continued to November 19. Phrases or sub-phrases on their own were observed only twice (Fig. 5). Out of the 38 acoustic files containing song fragments, 37 had phrases/themes like those observed in songs (e.g., Figs. 6 and 7), whereas 1 file had a level 1 song fragment composed of a phrase that occurred twice in the file.

B. Spring 2016 data set

In Spring 2016 off northeastern Nova Scotia, songs were the predominant vocal category from April 16 to May 27 (Fig. 4). The remaining periods analyzed were dominated by non-patterned calls and grunt sequences. Song fragments were observed in 6 acoustic files, 5 of which occurred from

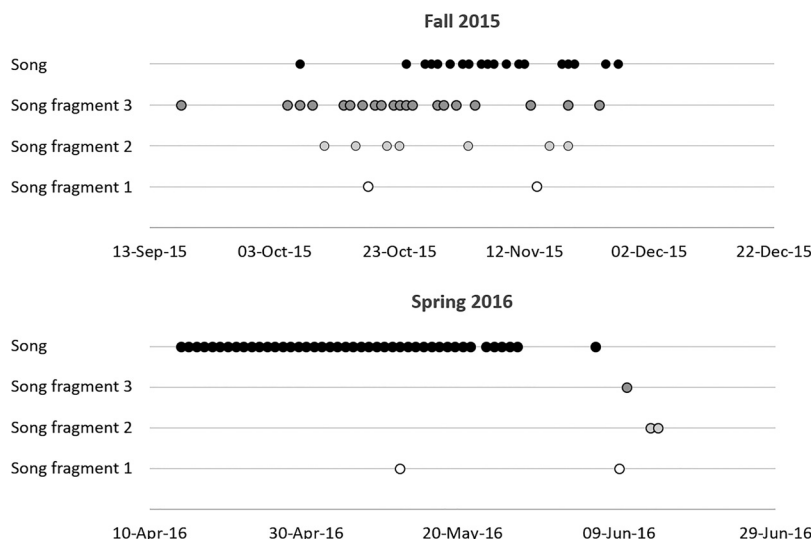


FIG. 5. The occurrence of different levels of song fragments (1–3) and full song at the two stations.

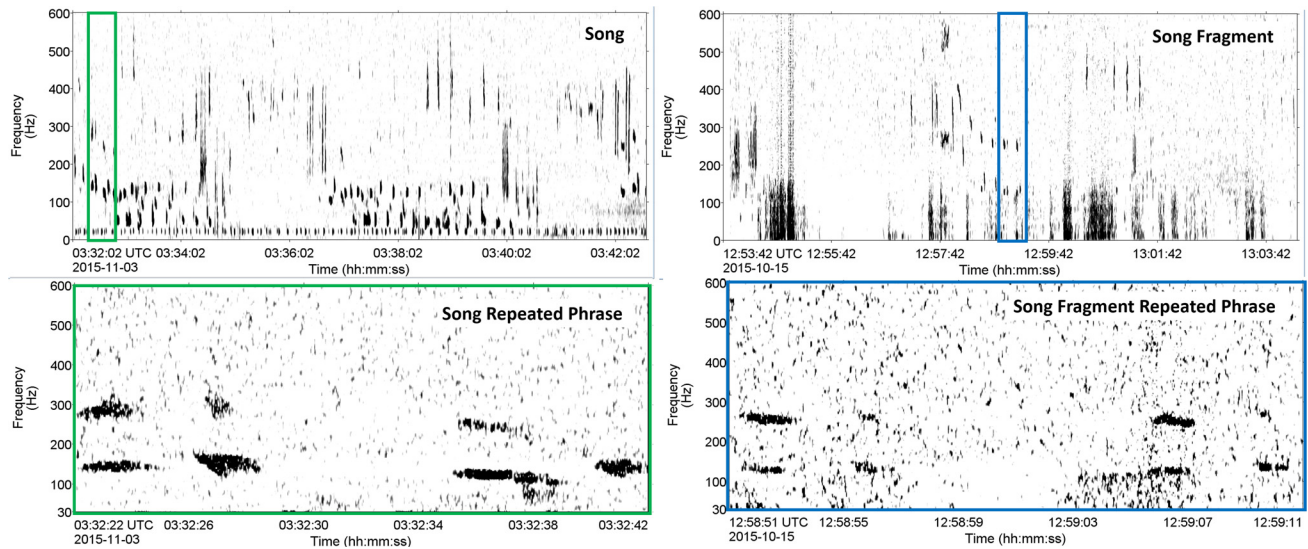


FIG. 6. (Color online) Spectrograms depicting examples of phrases observed in both a song (left; November 3, 2015) and a song fragment level 3 (right; October 15, 2015) in Fall 2015; lower panels represent details indicated within upper panels, illustrating the similarities between phrases found in songs and song fragment vocalizations (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s).

June 6–14 after complete songs had ceased and contained phrases/themes similar to those observed in the complete songs. There were two instances of single phrases or sub-phrases (song fragment level 1; May 12 and June 9), two instances of single themes (song fragment level 2; June 13 and 14), and one instance of two or more unrepeated themes (song fragment level 3; June 10; Fig. 5).

The acoustic occurrence results suggest an abrupt change in acoustic behavior in late May when humpback whale acoustic signal occurrence is drastically reduced (Fig. 2). When coupled with the vocal behavior results in which songs end on May 27 (apart from June 6) and song fragments are limited in their occurrence, it can be inferred that the cessation of humpback whale singing off northeastern Nova Scotia in Spring 2016 was relatively abrupt in nature as compared to the song onset in the Bay of Fundy in Fall 2015 where song fragments occurred regularly prior to and during the period of song. Furthermore, in the Fall 2015 data set, non-song calls overlap greatly with the period when song and song fragments occur. This is different from Spring 2016, where song and non-song temporal distributions seldom overlap, such that non-song calls are rarely detected until song essentially ceases, though it is difficult to separate this observation from the unavoidable masking effects chorusing humpback whales have on other acoustic signals, particularly singular or non-patterned calls.

C. Diel results

Data were separated into four timeframes (two in Fall 2015 and two in Spring 2016) chosen to correlate with periods when song and non-song vocalizations dominated (where we included song fragments in song). The results of the Tukey-Kramer multiple comparisons test revealed that when cries and cry sequences dominated, the mean adjusted hours with humpback vocalizations during light were significantly lower than dawn, dusk, and dark (Fig. 8). In Spring 2016 when songs dominated, the mean adjusted hours with

humpback vocalizations during dawn and light were significantly lower than dusk and dark (Fig. 8). When song and song fragments dominated in Fall 2015, the mean adjusted hours with humpback vocalizations during dawn was significantly lower than dark. No significant differences between light periods were apparent in any time frames when non-patterned calls and grunt sequences dominated (Fig. 8).

IV. DISCUSSION

Acoustic recordings from the Fall of 2015 in the Bay of Fundy and the Spring of 2016 off northeastern Nova Scotia captured the onset and cessation of humpback whale song production, respectively. Ideally, we would have sampled a fall and spring from the same location; however, apparent differences in residency or density of whales in these areas precluded doing so. While we had acoustic recordings both in Spring 2016 in the Bay of Fundy and Fall 2015 off northeastern Nova Scotia, humpback whale acoustic signals were either absent or minimal during these periods at these locations, suggesting low densities of whales, and thus did not allow for analysis of humpback whale vocalization during both periods at either location. Utilizing data from multiple sites allowed us to examine differences in the acoustic repertoire and vocal behavior of humpback whales off eastern Canada in fall and spring, which would not have been possible from either site alone.

Vocalizations captured in the Bay of Fundy were likely produced by whales that spent weeks or months foraging in this productive feeding ground.⁵¹ Indeed, Paquet *et al.*⁵⁵ suggested around 80 animals frequent the region in summer and fall. It is unclear how humpback whales utilize the waters off northeast Nova Scotia, though the vocalizations captured in the Spring of 2016 may have been produced by whales migrating to more northern feeding grounds off Newfoundland or in the Gulf of St. Lawrence.⁵¹ Acoustic files selected for analysis in the spring were therefore more

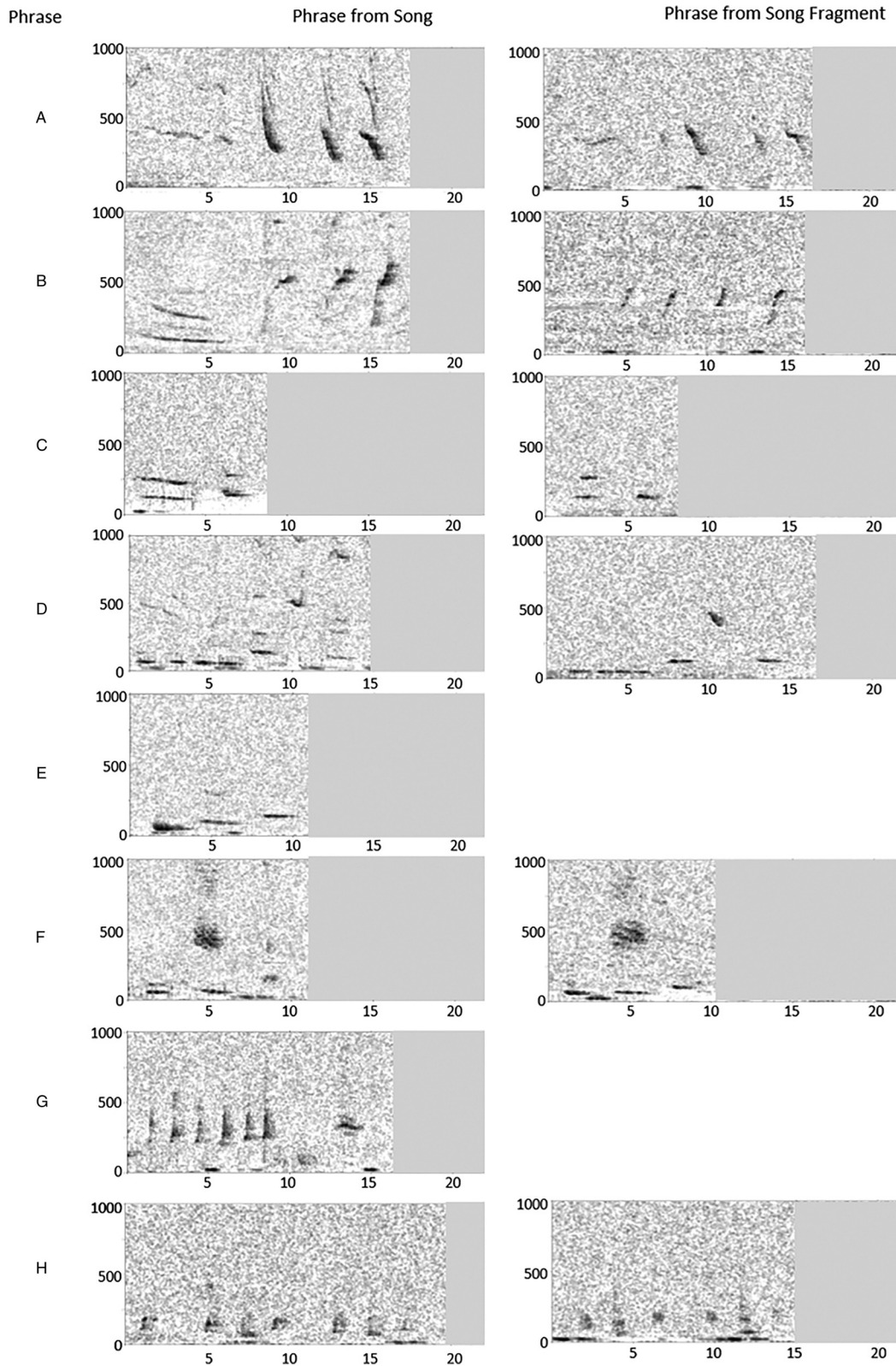


FIG. 7. Spectrograms depicting phrases observed in songs (left) and song fragments (right) in Fall 2015 (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s). The x axis is time in seconds and the y axis is frequency in Hertz. Not all phrases from songs occurred in the song fragments analyzed. Fin whale 20 Hz vocalizations occur in many of the spectrograms.

likely to be independent, sampling different individuals as they traversed the area, than in the Bay of Fundy where the same individuals are known to remain in the region for longer periods of time. These results do not indicate how any individual whale transitions its acoustic behavior through

time, but rather how the acoustic repertoire of the subset of a population transitions.

Some humpback whale vocalizations described here are indicative of certain specific behaviors or behavioral states. Non-patterned calls may be associated with social

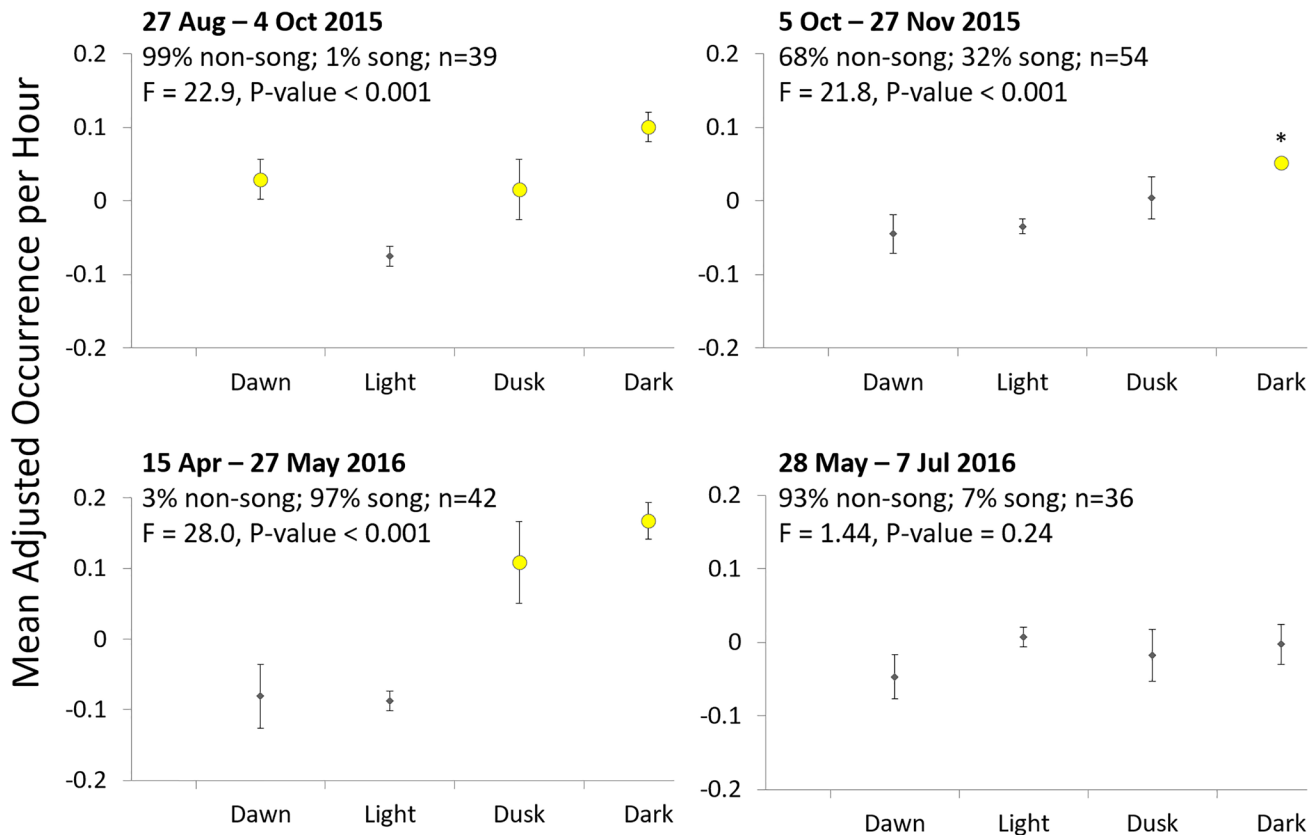


FIG. 8. (Color online) Mean adjusted humpback whale occurrence per hour for two periods in Fall 2015 (top) and two periods in Spring 2016 (bottom) with 95% confidence intervals in four light periods: dawn, light, dusk, and dark. Where non-song includes the vocal categories cry, cry sequences, non-patterned, and grunt sequences and song includes the vocal categories song and song fragment. Light period times were obtained from Ref. 53. Results of Welch's test are included for each period (F - and P -value) and Tukey-Kramer results are represented in colored means where different colors/sizes have significantly different values. *For October 5 to November 27, 2015, dark differed from dawn (P -value < 0.001) and light (P -value = 0.002), but not from dusk (P -value = 0.37).

interactions and could be produced by males, females, or calves.^{26,27} Grunt sequences appear similar to social grunt trains described by Dunlop *et al.*²⁷ that occur before groups merge. The lack of diel pattern during periods when both non-patterned and grunt sequence calls were predominant suggests that such social behavior occurs throughout the 24-h day. Indeed, the occurrence of these two vocal categories overlapped temporally both in the fall and spring data. The lack of non-patterned calls and grunt sequences in Spring 2016 when songs dominated may suggest that the majority of these animals may have been mature males, as they only moved onto social vocalizations after the cessation of song. Alternatively, other age and sex classes were present in Spring 2016, but their vocalizations were masked by singing or they were not acoustically active in April and May.

Until now, humpback whale acoustic behavior related to foraging has only been described in a southeast Alaskan population where feeding vocalizations have been associated with coordinated foraging events on schooling herring (*Clupea pallasii*).^{7,28,56,57} The cry sequences observed here in the Bay of Fundy match the feeding vocalizations of southeast Alaska and may similarly be linked to foraging. Grand Manan, an island located only 10 km from our recorder, has an active purse seine industry that targets aggregations of herring (*Clupea harengus*). Herring may aggregate seasonally in the region to spawn, as was historically reported,⁵⁸ or to feed. Grand Manan purse seine

fishing occurred on September 3, 21, 22, 23, 27–29, 2015 which closely aligns with our observations of cry sequences on September 15, 21, 23–29 and October 14, 2015 and further supports the Bay of Fundy as a feeding ground for humpback whales.⁷³ North Atlantic herring do not spawn in the spring, potentially explaining why cry sequences were absent from our spring acoustic data. Un-sequenced cries matching those described here have also been described in southeast Alaska⁷ and British Columbia (personal observation), but it remains unclear if they are related to herring feeding in the same manner as cry sequences. Some instances of un-sequenced cries throughout this sample may be more appropriately grouped functionally with social acoustic behaviors (non-patterned calls and grunt sequences) which would explain the broadly overlapping distributions of cries and non-patterned calls in October and November. Whereas there was no diel variation when non-song “social” calls (non-patterned calls and grunt sequences) were predominant, a significant diel variation was found when cries and cry sequences dominated in early Fall 2015. These vocal categories may be related to foraging as many humpback prey species including herring and krill are known to undertake diel vertical movements.^{59,60}

The characterization of song fragments described here have not been previously defined. This vocal behavior likely existed in other high latitude song data sets^{24,28–43} and some

authors have made observations reflecting such, e.g., Refs. 13, 44, and 61. Indeed, McSweeney *et al.*³⁰ allocated the term “partial songs” to three recordings from Alaska in the Fall of 1979 and “song fragments” have been observed off Maine in the spring of 1980,²⁹ but these authors did not categorize or describe the structural details of these vocalizations, or place their occurrence in the larger context of humpback vocal behavior.

A number of explanations for high latitude humpback whale singing have been proposed,^{36,40,61–63} three of which may lead one to expect behavior reflective of our song fragment category: males are practicing,³⁶ immature males are learning,⁶³ and it is a hormone induced behavior.⁶² Males may benefit from practicing singing in the form of song fragments before engaging in active mating behaviors, which is the ultimate goal. By only singing parts of songs, males may become proficient in their skill while continuing to allocate time and energy to foraging and socializing prior to undertaking an arduous migration. It seems these behaviors are not necessarily independent as Stimpert *et al.* (2016)⁶¹ recorded song in the presence of feeding lunges on a high latitude feeding ground. Although, if males were to produce song fragments for the sake of practice, we might expect to see the behavior throughout the year, an observation yet to be reported in the literature.

Alternatively, song fragments may be produced by immature males learning to sing for the first time, a behavior well described in juvenile songbirds.⁶⁴ This concept is supported by the greatly reduced occurrence of song fragments in the spring as the young males have had a full season to become proficient in singing. However, if we were observing juveniles learning a song from mature males, we would expect to see full songs prior to song fragments in the fall, so this hypothesis on its own seems unlikely, though such behavior may have occurred beyond the range of our recorders.

Perhaps the most compelling explanation for the existence and timing of song fragment vocal behavior is that there are physiological parameters that determine when animals produce complete songs. Such was found to be the case in several songbird species where brain nuclei have been identified that influence song production and nuclei size is associated with seasonal testosterone levels, e.g., Refs. 45, 65, and 66. Nottebohm *et al.*⁶⁵ found that when young male canaries first learn to sing, there is a period of subsong as the song develops which coincides with song nuclei growth. Once a full song is produced, the nuclei are adult sized and remain constant until the end of the breeding season when song nuclei diminish to the size expected of a bird only 3 to 4 months old. The following breeding season, the bird once again goes through a period of subsong as the song nuclei enlarge, though it has already sung a complete song the previous year.⁶⁵ We propose that the song fragments we designate in our study are analogous with the subsong observed in oscine birds; thus, humpback whales may similarly have a neurological song control system influenced by testosterone levels. Seasonal fluctuation would result in a period of song fragment behavior in the fall before the neurological control system attains a state

required for full song production. Cates *et al.*⁶⁷ concluded that male humpback whale testosterone levels peak in the winter, are lowest in the summer, and increase and decrease through the fall and spring, respectively, so it is reasonable to expect coincident fluctuations in singing behavior. One may expect a gradually increasing level of complexity in song fragments through the fall in support of this hypothesis, which was not observed here. Indeed, we did observe a spectrum of complexity, but it did not necessarily occur temporally. Such detail may only be observable at an individual level, rather than the population level that we are observing. Alternatively, whales may go through a period of variable song fragment complexity as their hormones increase.

We observed a brief period of subsong/song fragment behavior in the spring that, if our hypothesis is correct, is associated with reduction in testosterone below a certain threshold. Interestingly, the spring transition had a seemingly more abrupt cessation to singing with minimal song fragments when compared to the fall. Further spring data sets are required to confirm whether the spring transition is truly abrupt as singing males may have continued to produce songs or song fragments and transitioned gradually, but simply moved away from the area detectable by our recorder.

Both in the fall and spring, during weeks when song and song fragments occurred, humpback whale vocalizations occurred more at night than in the day. Such was similarly observed in singing humpback whales offshore Nova Scotia in the winter⁴⁴ and on breeding grounds in Hawaii,⁶⁸ Mexico,⁶⁹ Brazil,⁷⁰ and Angola⁷¹ suggesting that this diel pattern is a characteristic of the acoustic behavior and is not related to season or location. It has been suggested that the diel pattern reflects a switch in primary mating strategies where selection pressures have resulted in males utilizing physical competition in the day and acoustic sexual advertisement at night when visual displays would be less effective.⁶⁸

V. CONCLUSIONS

In describing humpback whale acoustic behavior in the fall and spring, we have provided insight into song initiation, that includes a period of song fragment production, and cessation, that seems more abrupt with minimal song fragments. Furthermore, we presented the first evidence of humpback whale feeding calls in a population outside of southeast Alaska and described how diel acoustic patterns vary over time. We discuss two potential proximate benefits and outcomes of high latitude song fragment behavior: for practice and for learning of immature males. We argue that these benefits alone cannot explain our observations, and thus hypothesize that the ultimate trigger of singing onset and cessation can be explained by physiological changes (e.g., hormone levels and neurological processes) that take place prior to migration outside of the breeding grounds. Sexual selective forces have shaped much of the mating behavior of humpback whales, and consequently the regulatory mechanisms that govern seasonal behavior. To further explore and develop our hypothesis, this research needs to be expanded

both spatially and temporally with an investigation into environmental factors that may correlate with song behavior and trigger physiological changes as is seen in songbirds.⁴⁶ Furthermore, acoustic tag studies of individual whales across sexes and age groups during the fall and spring season to capture individual whale acoustic transitions coupled with seasonal hormone analysis would be extremely illuminating.

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