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Seasonal and geographical patterns of fin whale song in the western North Atlantic Ocean

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Male fin whales, *Balaenoptera physalus,* produce a song consisting of 20 Hz notes at regularly spaced time intervals. Previous studies identified regional differences in fin whale internote intervals (INI), but seasonal changes within populations have not been closely examined. To understand the patterns of fin whale song in the western North Atlantic, the seasonal abundance and acoustic features of fin whale song are measured from two years of archival passive acoustic recordings at two representative locations: Massachusetts Bay and New York Bight. Fin whale 20 Hz notes are detected on 99% of recorded days. In both regions, INI varies significantly throughout the year as two distinct periods: a "short-INI" season in September–January (9.6 s) and a "long-INI" season in March–May (15.1 s). February and June–August are transitional-INI months, with higher variability. Note abundance decreases with increasing INI, where note abundance is significantly lower in April–August than in September–January. Short-INI and high note abundance correspond to the fin whale reproductive season. The temporal variability of INI may be a mechanism by which fin whale individuals encode and communicate a variety of behaviorally relevant information.
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I. INTRODUCTION

Male fin whales, *Balaenoptera physalus,* produce bouts of stereotyped song consisting of repeated sets of 1–3 note types (Watkins *et al.*, 1987; Clark and Gagnon, 2002; Clark *et al.*, 2002; Croll *et al.*, 2002). Songs typically last between 1–20 min, and song bouts last hours to days, with short interruptions between songs for respiration (Watkins *et al.*, 1987). Of the three note types from which songs are composed, the most common is a frequency-modulated downsweep with a dominant frequency between 25–17 Hz, often centered around 20 Hz, and an average duration of 1 s. This note type has been referred to as a "20-Hz pulse" (Watkins *et al.*, 1987), but, following Castellote *et al.* (2012), herein, it will be referred to as a 20 Hz note. Because of the high amplitude (Širovic *et al.*, 2007) and long propagation distance of fin whale song (Payne and Webb, 1971; Širovic *et al.*, 2007), combined with the widespread global distribution of fin whales (Gambell, 1985), 20 Hz notes are a common feature of the world's ocean acoustic ecology (e.g., Schevill *et al.*, 1964). In the western North Atlantic, fin whales sing from approximately September through June (Clark and Gagnon, 2002; Simon *et al.*, 2010), and song is most abundant during the reproductive season, likely for mate attraction, from November through March (Watkins *et al.*, 1987; Watkins *et al.*, 2000). Additionally, Croll *et al.* (2002) suggested that fin song communicates the location of prey to females.

In fin whale song, the interval between two adjacent 20 Hz notes is referred to as the internote interval (INI), and also referred to as the inter-pulse interval (Watkins *et al.*, 1987) or pulse interval (Delarue *et al.*, 2009). INIs are typically consistent within the song of an individual, but have been observed to vary between geographic areas (Watkins *et al.*, 1987; Edds, 1988; Clark *et al.*, 2002; Hatch, 2004; Rebull *et al.*, 2006; Delarue *et al.*, 2009). Researchers are exploring how these geographic differences can be used to distinguish different populations and be applied to develop specific approaches to conservation management (Hatch, 2004). While population dynamics of fin whales in the western Atlantic remain poorly understood, Delarue *et al.* (2009) suggest that the fin whale feeding aggregations in the Gulf of St. Lawrence and the Gulf of Maine could be distinguished from each other as distinct management stocks based on differences in INI.

Studies have documented changes in INI within a region during the reproductive season (Watkins *et al.*, 1987, around Bermuda; Delarue *et al.*, 2009, in the Gulf of Maine), but due to limited sampling, these did not investigate intra- or inter-annual variability.

In the western North Atlantic, fin whales regularly occur within Massachusetts Bay and New York Bight (Hain *et al.*, 1992). The migration patterns of fin whales between these areas are unknown, but both regions are contained within the western North Atlantic fin whale stock, as defined by the International Whaling Commission (Donovan, 1991). To document the regional and seasonal variability in fin whale songs, we examined the acoustic features, including INI, of 20 Hz notes in songs recorded over 2 yr, and we assessed the relative abundance of 20 Hz notes as an indication of cumulative vocal activity in Massachusetts Bay and New York Bight.

II. METHODS

A. Recording equipment and study sites

Underwater acoustic data were recorded in the Massachusetts Bay and New York Bight regions using arrays of marine autonomous recording units (MARUs) (Calupca *et al.*, 2000;

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Clark and Clapham, 2004) at depths of 23–278 m (Fig. 1). Each MARU was anchored 1.5–2.5 m above the seafloor and programmed to record continuously at a 2 kHz sampling rate. Each MARU had a HTI-94-SSQ hydrophone (High Tech, Inc., Gulfport, MS) (frequency response of 2 Hz–30 kHz; sensitivity of -168 dB re 1 V/μPa), an amplifier with a gain of 23.5 dB, and an A/D converter with a sensitivity of 10^3 bit/V (Parks *et al.*, 2009). The overall system had a flat frequency response ($\pm$1.0 dB) between 10 and 585 Hz. Each MARU recorded for approximately three months, at which point it was recovered, refurbished, and re-deployed within a week in the same location to provide near-continuous, year-round recordings, when possible. In Massachusetts Bay, continuous, 24 h sound data were collected at 19 locations on 817 days (of 878 possible days) from 23 October 2007–18 March 2010 (Table I). In the New York Bight, continuous, 24 h sound data were collected at ten locations for a total of 266 days (of 376 days) from 27 February 2008–8 March 2009 (Table I).

Data from all locations in each regional array, within a three month recording period, were synchronized and concatenated into a set of multi-channel, chronological sound files for analysis. Multi-channel spectrograms [fast Fourier Transform (FFT) at 2048 points, 85% overlap, Hann window, 2048 window length, 0.977 Hz resolution, and brightness and contrast at 50%] of the sound data were reviewed in the 0–100 Hz frequency range using the Raven Pro 1.4 software package (Bioacoustics Research Program, 2011).

TABLE I. Time periods and total number of days (total days, daily presence) that MARUs recorded continuously in Massachusetts Bay and New York Bight and were analyzed for the daily presence of fin whale 20 Hz song notes. "Total days, 20 Hz note analysis" is the total number of days (randomly selected for 1 January 2008 through 31 December 2009) on which fin whale 20 Hz note features (peak frequency, center frequency, low frequency, high frequency, bandwidth, and INI) and relative abundance of 20 Hz notes were measured.

Dates of recording in each region	Total days, daily presence	Total days, 20 Hz note analysis
Massachusetts Bay		
23 October 2007–7 January 2008	76	2
16 January–10 April 2008	83	22
15 April–7 July 2008	82	21
10 July–7 October 2008	86	28
11 October 2008–20 January 2009	101	32
27 January–3 May 2009	97	32
11 May–21 August 2009	100	28
28 August–10 December 2009	100	24
15 December 2009–18 March 2010	92	5
Total days	817	188
New York Bight		
27 February–16 May 2008	77	12
27 August–8 December 2008	97	19
3 December 2008–8 March 2009	92	19
Total days	266	50
Total days in both regions	1083	238

B. Acoustic analysis

We reviewed the spectrograms of all multi-channel days of recorded sound (817 days in Massachusetts Bay and 266 days in New York Bight) to identify the presence of fin whale 20 Hz notes on each day (Table I).

For detailed analysis of 20 Hz note acoustic features, we randomly selected 188 days in Massachusetts Bay and 50 days in New York Bight that were recorded from 1 January 2008 through 31 December 2009 (Table I). For detailed analysis of each of these 238 total days, we identified two to three 20 Hz fin whale songs that were not masked by background noise. Following Watkins *et al.* (1987), we defined a fin whale song as a series of at least five 20 Hz notes that had a low-frequency limit no greater than 20 Hz, a high-frequency limit no less than 20 Hz, but no greater than 30 Hz, and that began

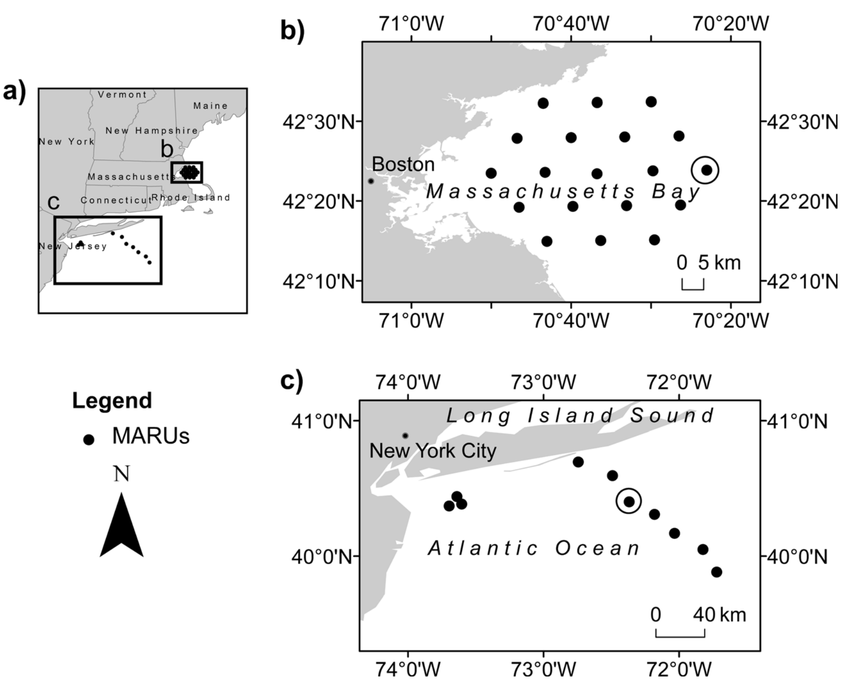

FIG. 1. (a) Map of locations for MARUs in two study regions off the east coast of the United States. (b) The Massachusetts Bay array consisted of 19 MARUs, spaced approximately 7 km apart. (c) The New York Bight array consisted of 10 MARU, spaced approximately 20 km apart. Acoustic data from all MARUs were used for fin whale 20 Hz note analysis; data from the two, circled MARUs were used for fin whale 20 Hz note abundance analysis.

and ended within a time gap from subsequent notes that was at least three times the duration of the measured INI of the song.

The same fin whale songs were often recorded on multiple recorders in the array; therefore, we analyzed songs that did not overlap in time on separate MARUs to avoid pseudoreplication. We cannot determine if fin whale songs recorded at different times of the day on different MARUs are from the same individual, therefore, we treated each song as an independent event.

We measured the start time, peak frequency, center frequency, low frequency, high frequency, and bandwidth of every 20 Hz note in a total of 610 fin whale songs using a combination of robust and selection-based measurements in Raven (Charif *et al.*, 2010; Fig. 2). Peak frequency is the value at which the maximum energy in the signal occurs. Center frequency is the frequency value at which half of the energy is above and half the energy is below this value. Peak frequency and center frequency are robust measurements, where the measurements are based on the energy within the selection, not the time and frequency boundaries of the selection. Selection-based measurements are based on the boundaries of the user-created selection, and include low frequency, measured as the lower frequency bound of the note; high frequency, measured as the upper bound of the note; bandwidth, the difference between the high and low frequencies. The INI, also selection-based, is measured as the time difference between the start time of one 20 Hz note and the start time of the subsequent note (*sensu* Watkins *et al.*, 1987) (Fig. 2). Acoustic feature measurements of 20 Hz notes were averaged for each song. Significant differences within feature measurements, over the acoustic recording period, were tested for using the JMP 9.0 statistical package (SAS Institute, Cary, NC) with a 2-way analysis of variance (ANOVA) without interaction as a function of geographic region and year. The change in INI over time was modeled with a generalized additive model implemented in the mgcv library (Wood, 2011) with the R statistical package (R Development Core Team, 2001).

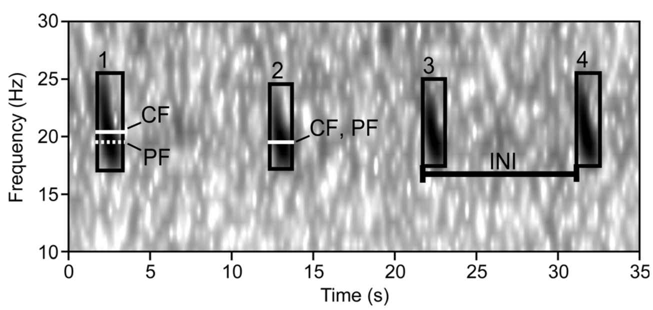

FIG. 2. Spectrogram (FFT at 2048 points with an 85% overlap, Hann window) of four fin whale 20 Hz notes illustrating measurement analysis. Selection boxes were drawn around each song note using Raven software. Notes 1 and 2 illustrate robust measurements of center frequency (CF; solid, white, horizontal line) and peak frequency (PF; dashed, white, horizontal line), which can have equal values, as seen in note 2. The high and low frequencies are determined by the high and low frequency bounds of the selection boxes. Internote interval (INI; solid, black, horizontal line) is measured as the time value from the start of one 20 Hz note to the start of the next note, as illustrated for notes 3 and 4.

C. Relative 20 Hz note abundance analysis

To estimate the relative abundance of fin whale 20 Hz notes over a recording period, we used the band-limited energy detector in Raven (Charif *et al.*, 2010) with the same spectrogram settings used for the fin whale song analysis. We optimized the detector by varying the detector parameters and running detector performance trials on a dataset that contained 5281 confirmed fin whale 20 Hz notes in varying, representative noise conditions. The detector performance trials measured the percentages of true positives, false positives, and false negatives. The percent of true positives is defined as the number of detected events that were 20 Hz notes divided by the total number of known 20 Hz notes in the test dataset. The percent of false positives is the number of detections that were not 20 Hz notes (i.e., noise) divided by the total number of detections. The percent of false negatives refer to the number of 20 Hz notes missed by the detector divided by the total number of known 20 Hz notes in the test dataset. Based on the results of 41 detector performance trials, we selected the band-limited energy detector parameters that resulted in a high true positive percentage (79%), a low false positive percentage (20%), and a low false negative percentage (21%) (Table II).

To avoid pseudoreplication due to detection of the same song on multiple MARUs, we applied the detector to a single MARU location in each region (Fig. 1). To maximize the probability of detecting songs in the regions, we applied the detector to 238 days of acoustic data for the MARU location that had a qualitatively observed high signal-to-noise ratio for fin whale songs and that had yielded the highest number of analyzed fin whale songs (Table I). Random inspection of detection results from throughout the dataset confirmed that the detector was performing as tested during the performance trials. We analyzed the results to test for the significance of the variance in the number of detected fin whale

TABLE II. Parameter values used in Raven's band-limited energy detector to automatically detect fin whale 20 Hz song notes. The detector was applied to 238 days of acoustic data from one MARU in each recording array in Massachusetts Bay and New York Bight. The performance of the detector was measured on a dataset containing 5281 validated 20 Hz notes under varying, representative noise conditions from both areas.

Detector parameter	Value
Minimum frequency	15.5 Hz
Maximum frequency	21.0 Hz
Minimum duration	0.2 s
Maximum duration	6.0 s
Minimum separation	0.5 s
Minimum occupancy	50%
Block size	2.0 s
Hop size	0.5 s
Maximum memory heap size	1 GB
Percentile	20.00%
Detector performance	**Value**
% True positives	78.66
% False positives	19.67
% False negatives	21.34

20 Hz notes between geographic regions, years, and months, with a 3-way ANOVA without interaction in JMP 9.0 (SAS Institute, Cary, NC).

III. RESULTS

A. Seasonal presence of fin whales in the western North Atlantic

Fin whale 20 Hz notes were identified on all 266 days of recording in New York Bight between February 2008 and March 2009. In Massachusetts Bay, 20 Hz notes were identified on 814 of the 817 analyzed days of recording between October 2007 and March 2010 (99%); 20 Hz notes were not detected on 28 January 2008, 20 January 2009, and 20 February 2009.

B. Geographic and annual differences in 20 Hz note acoustic features

When we compared the peak frequency, center frequency, low frequency, high frequency, and bandwidth feature measurements of 20 Hz notes between Massachusetts Bay and New York Bight and between years, there were significant differences in two of the features. The high frequency feature of a 20 Hz note is 0.4 Hz greater in Massachusetts Bay than in New York Bight (2-way ANOVA, $F_{(2,607)} = 5.57$, $P = 0.004$), and the bandwidth feature was 0.3 Hz greater in 2009 than 2008 (2-way ANOVA, $F_{(2,607)} = 5.03$, $P = 0.0068$). The differences between the means for the selection-based high frequency and bandwidth features were less than our measurement precision of 0.977 Hz.

To examine if the frequency resolution of the spectrogram affected these high frequency and bandwidth feature measurements, we used a sub-sample of 86 songs from the 610 analyzed songs to compare the high frequency and bandwidth measurements based on a FFT at 8192 points (0.244 Hz resolution) and a FFT at 2048 points (0.977 Hz resolution). There were significant differences between the frequency measurements for high frequency (2-tailed paired t-test, DF = 85, $t = 3.6580$, $p < 0.0004$) and bandwidth (2-tailed paired t-test, DF = 85, $t = 7.5316$, $p < 0.0001$) features. When we compared the high frequency features of 20 Hz notes between Massachusetts Bay and New York Bight measured with a FFT at 8192 points, the high frequency feature was 1.31 Hz higher in Massachusetts Bay (2-way ANOVA, $F_{2,83} = 7.5796$, $p = 0.0009$), a similar result when measured with a FFT at 2048 points. The bandwidth of 20 Hz notes measured with a FFT at 8192 points was 1.5 Hz higher in Massachusetts Bay (2-way ANOVA, $F_{2,83} = 8.7709$, $p = 0.0004$), but not significantly different between years, as measured with a FFT at 2048 points. Therefore, the differences between years or regions in bandwidth may be due to changes measured in high frequency or measurement uncertainty. However, the differences in high frequency features between regions are not due to measurement uncertainty.

C. Seasonal changes in INIs

The most variable song measurement was INI, which changed significantly at two times within a year and repeated in both years of the study (Fig. 3). The INI was 0.5 s longer in 2009 than 2008 (2-way ANOVA, $F_{(2,607)} = 3.47$, $P = 0.032$),

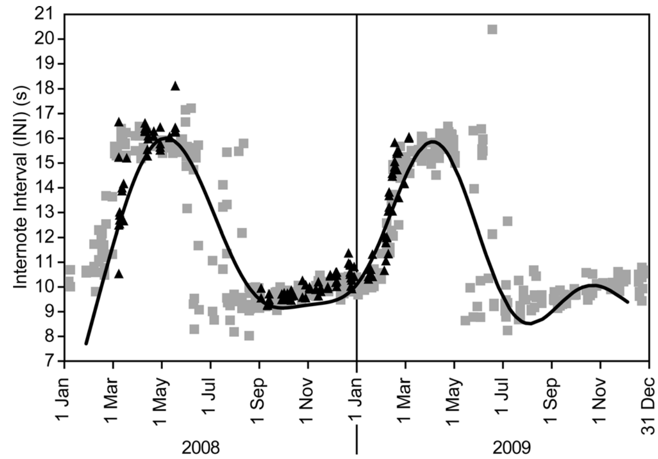

FIG. 3. INI of fin whale 20 Hz song notes measured for 1 January 2008–31 December 2009 in Massachusetts Bay (gray squares, $N = 481$ songs) and New York Bight (black triangles, $N = 129$ songs). The generalized additive model (black line) explains the seasonal changes in INI, where the short-INI season occurs in September–January, the long-INI season occurs in March–-May, and February and June–August are transitional months.

but there was no significant difference between geographic regions. A generalized additive model explained 79.9% of the deviance over time across both regions (Table III). Following this model, we defined the "short-INI" season as the period including September through January, where the average INI was 9.6 (±0.02 SE, $N = 268$). We defined the "long-INI" season as the period including March through May, where INI was 15.1 s (±0.11 SE, $N = 161$). Since the INIs in February gradually increased over time, and the INIs in June, July, and August were highly variable, we defined these as transitional-INI months.

D. Seasonal abundance of 20 Hz notes in the western North Atlantic

The number of 20 Hz notes automatically detected on each day over two years for both Massachusetts Bay and New York Bight varied throughout the year, with significant differences between months (3-way ANOVA, $F_{(13,225)} = 7.50$, $p < 0.001$). However, there was no significant difference in the number of

TABLE III. Summary of generalized additive model for 20 Hz INI from fin whale songs, 1 January 2008 through December 2009 ($N = 610$, ***$p < 0.001$).

Family	Gaussian
Link function	identity
Formula	INI ~ date
Parametric coefficients	
Intercept	11.69 (±0.05 S.E.)
t value	234
p-value	<2e-16 ***
Significance of smooth term: Date	
edf	8.954
Reference DF	8.999
F	263.5
p-value	<2e-16 ***
Deviance explained	79.9%

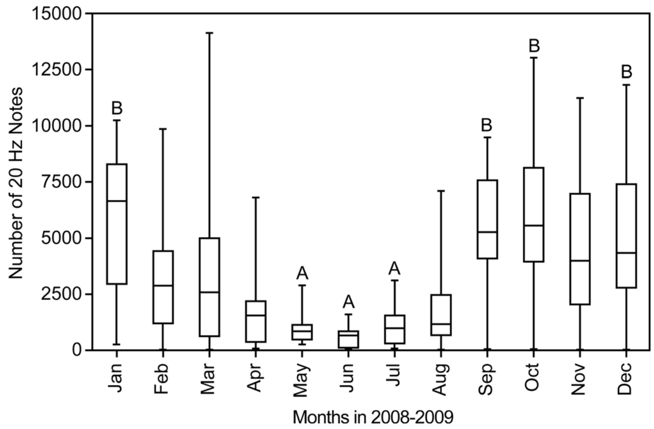

FIG. 4. Monthly distribution of the daily number of detected 20 Hz notes in both regions, combined over both years ($N = 238$ days), where the vertical lines show the maximum and minimum number of detections, the top of the box represents the 75th percentile value, the bottom of the box represents the 25th percentile, and the center horizontal line represents the median value. 20 Hz notes are significantly less abundant in the months of May–July (marked with *A*) than in September–October and December–January (marked with *B*).

daily 20 Hz note detections between Massachusetts Bay and New York Bight or between years. To explain the changes throughout the year, a *post hoc* test showed that 20 Hz note abundance was significantly lower in the months of May–July than in September–October and December–January (Tukey-Kramer, $q^* = 3.30$, $P < 0.05$; Fig. 4). The months with highest 20 Hz note abundance correspond to the short-INI months, and the months with the lowest 20 Hz note abundance correspond to the long-INI and the transitional-INI months. There is a statistically significant linear relationship between the average daily INI and the daily abundance of 20 Hz notes (linear regression, $R^2 = 0.06$, $p = 0.0002$), where daily 20 Hz abundance decreases with increasing INI.

IV. DISCUSSION AND CONCLUSIONS

Singing fin whales were recorded year-round in Massachusetts Bay and New York Bight, and the abundance and INI of fin whale 20 Hz notes showed intra-annual variation. Given that (i) the INIs do not differ between the two regions, (ii) INIs steadily increase in February, transitioning from the short-INI (9.6 s) season to the long-INI (15.1 s) season, and (iii) the distinct short-INIs and long-INIs do not co-occur, we conclude that these annual changes in INI are occurring within the same fin whale population. Therefore, fin whale singers in these two regions cannot be distinguished as separate management stocks on the basis of their 20 Hz song note features (*sensu* Delarue *et al.*, 2009; Castellote *et al.*, 2012).

The distinct seasonal pattern of INI may be associated with changes in reproductive and/or feeding contexts. These results show that the short-INI (9.6 s) season, from September–January, co-occurring with high 20 Hz note abundance, overlaps the reported reproductive season, between November and March (Lockyer, 1984; Watkins *et al.*, 1987; Watkins *et al.*, 2000; Croll *et al.*, 2002). In contrast, the long-INI (15.0 s) season and lower 20 Hz note abundance occurs from March–May. Given that fin song features (e.g., INI variability) may communicate information about available food resources (Croll *et al.*, 2002), changes in INI variability may also indicate changes in resource availability within the context of this male acoustic reproductive display.

The changing relative abundance of 20 Hz notes throughout the year may result from the change in INI, where the rate of 20 Hz note production increases as INI decreases. However, given that the daily 20 Hz note abundance was highly variable, the relative abundance of notes could indicate changes in the duration of singing, changes in the numbers of singing males, or relative numbers of fin whales in an area. The rate of singing males or the relative number of singing males in a population has not been measured, so we cannot determine the cause of the changes in 20 Hz note abundance.

Although we cannot determine the underlying cause(s) of these pronounced seasonal changes in fin whale 20 Hz note features and abundances, song note types and patterns of singing are behavioral or physiological states that can change seasonally. This phenomenon has been documented in a variety of other vocally active taxonomic groups beyond mammals, such as birds and anurans (e.g., Radwan and Schneider, 1988; Leitner *et al.*, 2001; Kunc *et al.*, 2005). Frequently, seasonal changes in vocal behavior patterns are related to changes in reproductive state, where the acoustic behavior serves a courtship advertisement function. In whales, behavioral states may be communicated through changes in the rate of calling (e.g., Tervo *et al.*, 2009), call types (e.g., Oleson *et al.*, 2007), or varying patterns in song (e.g., Tervo *et al.*, 2009).

The slightly higher high-frequency feature of 20 Hz notes in Massachusetts Bay than in New York Bight may demonstrate that fin whales modify the frequency features of their 20 Hz song notes to communicate information to conspecifics. However, it is unclear if the difference measured in this study is biologically significant because the difference is less than 2 Hz. For blue whale song notes in the 17–25 Hz range, McDonald *et al.* (2009) found average annual decreases of around 0.1 Hz over periods of 15–50 yr, but whether or not the whales perceive such difference is unknown. Although the resolution of frequency discrimination for mysticetes has not been measured, *Tursiops truncatus* can detect changes of 0.2% in frequency (Thompson and Herman, 1975). Thus, it is possible that fin whales can perceive the measured frequency differences, but further work is required.

Given the obvious and consistent pattern of seasonal INI variability, when acoustically defining management stocks, one must consider possible seasonal changes in vocal behavior patterns and the associated acoustic properties. Future research could explore the seasonal changes in fin whale song of other populations to understand if patterns similar to those observed in Massachusetts Bay and New York Bight occur in other regions or populations, and to identify the behaviors associated with these seasonal changes in fin whale 20 Hz song note INI.

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