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Humpback Whales in the Western Indian Ocean

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Editorial Note

Humpback whales are well known especially for their very long migration routes and also because of the songs that males emit during the breeding season. In 1971, in their famous article published in the journal ‘Science’, Payne and McVay describe these songs as “a series of surprisingly beautiful sounds”! Since 1971, more acoustic data have been collected and more knowledge generated; we now know that the song ‘leitmotiv’ is different from one geographic area to another, and from one year to the next. We also now know how they produce these sounds from their respiratory system.

In the last two decades, different techniques have been deployed to observe humpback whales in all the oceans. Not only have passive acoustic monitoring techniques been used, but also visual observations, electronic devices, and genetics. The objectives of these studies have been to better understand whale activities, behaviors, and also the underwater environment in which they live, and the potential effects of anthropogenic activities on their societies. This has involved many different research teams, with their own skills, methods and programmes. Results have been published in the scientific literature and presented at different international conferences.

However, three things have recently become apparent: Firstly, the study of humpback whales is a wide subject requiring people with complementary skills. It was apparent that it was necessary to bring these people together to discuss this species of whale for several reasons: a) because it would highlight the major results obtained thus far; b) because it would be interesting to share experiences (especially on the data and methods used, but also on common challenges); c) to co-design future projects and identify priorities; and d) because it would provide an opportunity to start new collaborations.

Secondly, before 2015, no international scientific conference or workshop existed with regular annual sessions especially dedicated to this species of Mysticeti whales. In order to address this, we initiated the creation of the Humpback Whale World Congress (HWWC, http://www.hwwc.mg/). The first session was held in Madagascar in 2015 and the second in La Réunion Island in 2017. Our idea was to bring together researchers and technicians from universities, research institutes, government organizations, and industry, dealing with all aspects of the biology, ethology, genetics, ecology, acoustics, signal processing, pattern recognition, mathematics, and computer sciences applied to the study of the humpback whales and their environment, and the potential effects of anthropogenic activities on the species. The goal of the HWWC is to provide a forum for exchange of new results obtained from the latest advances in instrumentation and methods.

Thirdly, during the BaoBaB project I led from 2012 to 2014, it became apparent that the extensive movement of humpback whales, even during the breeding season (with more than 100 km being covered per day), resulted in the same individuals being observed from the east coast of Africa to the Mascarene Islands. Because of this remarkable characteristic of this baleen whale species, it was obvious that we needed to encourage collaboration at a regional level, and we envisaged a consortium of people who work collaboratively on the Southwestern Indian Ocean humpback whale population.

During the international HWWC we were very pleased by the quality of the work shared by different teams, and the strong motivation to exchange information and work together. For this reason, we requested some colleagues to describe their projects in full papers, to put them together, and publish this unique special issue.

I would like to thank all the authors and co-authors, all the persons who contributed to this special issue, and more strongly the Cetamada Team who currently does such amazing work on these humpback whales!

Enjoy reading!

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Recurrent acoustic patterns produced by a singing humpback whale (*Megaptera novaeangliae*)

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Abstract
Humpback whales (*Megaptera novaeangliae*) often sing continuously for multiple hours. Little is known about how individual singers vary the acoustic features of their songs within such prolonged song sessions. Here, a case study analysis of a seven-hour singing bout was performed to clarify the consistency with which global acoustic features can be produced by an individual singer. Analyses of 44 consecutive songs within a multi-hour sample revealed that: (1) songs of similar duration may be repeated for at least an hour; (2) frequency content and sequencing can be produced stably for several hours; and (3) multiple, narrow-band tonal streams, possibly song-generated, may co-occur within a song session. These analyses of intra-individual variations in acoustic features within a song session revealed the precision with which a singer can control acoustic fields, raising new questions about the predictability of acoustic variations in songs across different contexts and environmental conditions. The finding of spectral stability over hour-long periods further supports a potentially important functional role for song-generated reverberation and provides a baseline for future quantitative comparisons of song acoustics within and across individual singers.

Keywords: acoustics, mysticete, propagation, reverberation, song.

Introduction
One of the most unique qualities of humpback whales (*Megaptera novaeaengliae*) is their vocal prowess and perseverance. Humpback whales produce patterned sound sequences ("songs") at all times of day and night (Au *et al.*, 2000; Sousa-Lima and Clark, 2008), throughout most of the year (Clark and Clapham, 2004; Watkins *et al.*, 2000), and in a wide range of behavioral and environmental contexts (Darling and Berube, 2001; Stimpert *et al.*, 2012; Tyack, 1981). The sequential structure of songs varies across populations and years (Garland *et al.*, 2011; Payne and Payne, 1985; Payne *et al.*, 1983; Winn *et al.*, 1981), as do several acoustic features of songs (Cato, 1991; Mercado *et al.*, 2005; Payne and Payne, 1985). Variations across consecutive songs produced by individuals also occur (Chu, 1988; Perazio *et al.*, 2017), but most of the acoustic features that a singer might vary while singing (e.g., distribution of peak frequencies or unit durations) have yet to be analyzed in any detail. Characterizing intra-individual variations in song production is critical to assessing when and why humpback whales sometimes sing non-stop for many hours, as well as for determining how consistently and precisely humpback whales control sound production during such prolonged singing bouts.

Many hypotheses of humpback whale song function assume that listening whales are able to judge the location and relative sexual fitness of singers at kilometer distances (Frankel *et al.*, 1995; Helweg *et al.*, 1992; Parsons *et al.*, 2008). However, song features can become distorted as they travel long distances (Mercado and Frazer, 1999; Mercado *et al.*, 2007), in ways that could confound assessment of singer quality or position by listening whales. Even at shorter distances, song qualities depend on a specific whale's singing skills. Large intra-individual variations in song production might thus further complicate cross-singer comparisons. For instance, if song duration indicates a singer's fitness (Chu, 1988), then large within-session variations in song duration would make comparing the capabilities of different singers based on song duration difficult. Conversely, highly consistent song production might provide listeners with honest indicators of a singer's vocal control capacities and overall fitness (Cazau *et al.*, 2016). It is not a given, however, that the most effective humpback whale singers will be those that produce the most consistent songs. Singers with the ability to flexibly adapt acoustic features of their songs to account for variations in environmental and social factors might be more successful than singers that do not adequately account for such factors. Because current functional hypotheses for humpback whale songs only weakly predict how singers should vary song elements over time, descriptions of singing by individual whales are important for identifying the kinds of information that their songs may provide.

Surprisingly little is known about the factors that determine when and how humpback whales sing. Humpback whales of most ages sing (Herman *et al.*, 2013). There are indications that the probability of singing may vary with time-of-day and/or stage of the lunar cycle (Au *et al.*, 2000; Seger *et al.*, 2016; Sousa-Lima and Clark, 2008). Some individuals have been observed singing continuously for 10+ hours (Payne *et al.*, 1983; Winn and Winn, 1978), but it is unclear how prevalent such long-lasting song sessions are. Most past studies of singing humpback whales have focused exclusively on singers recorded opportunistically during the day. It is also not yet known what proportion of each day/week/month individuals spend singing, or how this distribution varies over time and across individuals. Humpback whales are known to produce songs more often at certain times of the year (particularly during the breeding season), but this could be either because more whales are singing at such times, or because a fixed number of whales increase the amount of time they spend singing. Analyses of prolonged song sessions, especially those occurring at night, can potentially provide new clues about the factors that determine how long any given humpback whale is likely to persist in singing.

Singing humpback whales can stably repeat rhythmic patterns of sound for periods of at least 40 minutes (Schneider and Mercado, 2018; Thompson, 1981). Individual singers vary the rate and rhythm of songs, suggesting flexible control of production mechanisms (Schneider and Mercado, 2018). Initial analyses of spectral energy patterns within song sessions suggest that the timing and order of spectral content may be consistent across whales (Mercado, 2016), despite changes in the absolute frequencies of units (Green *et al.*, 2011). Specifically, humpback whale singers often gradually shift from mid-range (300-500 Hz) to lower frequency content (<200 Hz) while singing (Mercado, 2016; Mercado and Handel, 2012; Mercado *et al.*, 2010). The acoustic properties of units (Au *et al.*, 2006; Mercado *et al.*, 2005), and sequences of units (Payne and McVay, 1971; Winn and Winn, 1978) have been extensively described, whereas interspersed silences between units have received little attention. Inter-unit intervals sometimes contain discrete echoes from units (Winn and Winn, 1978), as well as song-generated reverberation (Mercado, 2016). Reverberation can appear as narrow-band "tails" that may persist until a similarly reverberant unit is repeated, resulting in continuous bands of reverberant energy that collectively last several minutes across a sequence of repeated units. How often such reverberation occurs within song sessions is unknown. Because such reverberation is singer-generated (in combination with the environment), intra-individual variations in song production can also drive variations in reverberation. Exploring relationships between the stability of song repetitions and their reverberant consequences can provide new clues as to whether singing humpback whales are actively modulating reverberation.

The objective of the current study was to describe acoustic features produced by a distant humpback whale singing for several hours during the night, focusing particularly on the consistency with which temporal and spectral properties were repeated. Characterizing singer behavior in this way can potentially lay the groundwork for detailed assessments of prolonged singing bouts across individual whales and can facilitate the development and testing of hypotheses regarding why humpback whales sing continuously for such long periods.

Materials and methods

An existing archival database of continuous recordings collected off the coast of California between September 1, 2001 and November 14, 2001 was used in the current study (available at http://abdus.sfsu.edu/pioneer/scanpeg.html). These recordings were originally collected from the Pioneer Seamount Underwater Observatory, which was setup by NOAA, the Pacific Marine Environmental Laboratory (PMEL), and San Francisco State University; they have previously been used in analyses of blue whale (*Balaenoptera musculus*) songs (Hoffman *et al.*, 2010). The sample of sounds in these recordings is unbiased in that the position of the recording array was not selected to record humpback whales and was not moved or adjusted based on any detections of singing humpback whales.

A vertical array of hydrophones was anchored ~1000 m below the surface, near the peak of Pioneer Seamount. Recorded signals were transmitted to the shore via a communications cable and digitized at a sampling rate of 1000 Hz. Consequently, the frequency range of the recording is limited to signals below 500 Hz and does not span the full range of frequencies produced by singing humpback whales, which is ~20-8000 Hz (Mercado *et al.*, 2005; Payne and Payne, 1985), with some harmonics reaching 20 kHz (Au *et al.*, 2006). Recordings from one channel of the vertical array was made available within the online database. Archival sound files were stored in MP3 format and sped up by a factor of 10; three-minute long, unaltered samples from each 15 minutes of recording were also available in the database.

Spectrograms of recordings were visually scanned to identify segments that contained features consistent with singing humpback whales (e.g. repetitive production of sounds with energy between 100-500 Hz). The presence of singing humpback whales was then verified through aural analyses. The goal of this subjective approach was to identify extended periods when one or more singers were vocalizing. From this sample of singing bouts, one song session was selected for detailed acoustic analyses based on its duration and visual clarity in spectrograms (which was a function of ambient noise levels and the presence of other singers or overlapping anthropogenic noise sources).

The selected song session was manually divided into spectrographic segments that depicted similar visual patterns to provide an estimate of the duration of song-like cycles within the session. Spectral peaks were measured from a single three-minute sample taken from each hour of recording based on signal strength. Peaks were identified by creating a spectrum for each sample (FFT size = 22979, 75% overlap, giving .5 Hz resolution) using Raven Pro 1.5, Beta version. Continuous bands of narrowly focused spectral energy consistent with song-generated reverberation were also acoustically analyzed to determine their duration and focal frequencies. The spectral properties of these bands were subsequently compared with the peak frequencies within song cycles.

This methodological approach differs from those typically applied in past analyses of humpback whale songs (reviewed by Cholewiak *et al.*, 2013) in that no attempt was made to identify phrases or themes within song sessions, and no comparisons were made between songs produced by different whales. The approach corresponds more closely to a case study in that it focuses on describing the singing behavior of an individual whale. Rather than identifying behavior that is representative of any particular group of singing humpback whales, the goal of the current case study was to establish what it is possible for a singing humpback whale to do over an extended period.

Results

Humpback whale singing was visually detectable in recordings from 65 of the 75 days evaluated. Of those 65 days, individual singers were clearly visible on 16 days; in some recordings, noise levels made it difficult to determine whether singers were present. A single continuous song session recorded on October 28th and 29th was selected for analysis. This song session lasted at least eight hours. The exact duration of continuous singing could not be determined, because it is possible that the individual was singing before he became detectable on the recording array, and because later songs in the session possibly overlapped with the songs of another singer. The segment of the recording analyzed began at 9:15 PM and continued until 3:30 AM (Fig. 1).

Temporal structure

The analyzed singing bout was segmented into 44 visually comparable cycles. Most spectrographic cycles likely correspond to "songs," defined as one progression through a predictable sequence of sound patterns ("themes"). However, it is impossible to determine this from analyses of a single session from an individual singer (Cholewiak *et al.*, 2013). The starting and ending times for each cycle were selected by identifying where the sound energy was the strongest and using this to determine start and end points (see horizontal white bar in Fig. 1). This approach to segmenting a song session is similar to that used by Fristrup *et al.* (2003), where the least energetic points in recordings (typically associated with surfacing) were used to measure song duration within a series of songs. Fig. 2 summarizes the sequence of cycle durations, rounded to the nearest minute. The median and mode cycle duration were both 9 min. The median and mode difference in duration across successive cycles was 1 min.

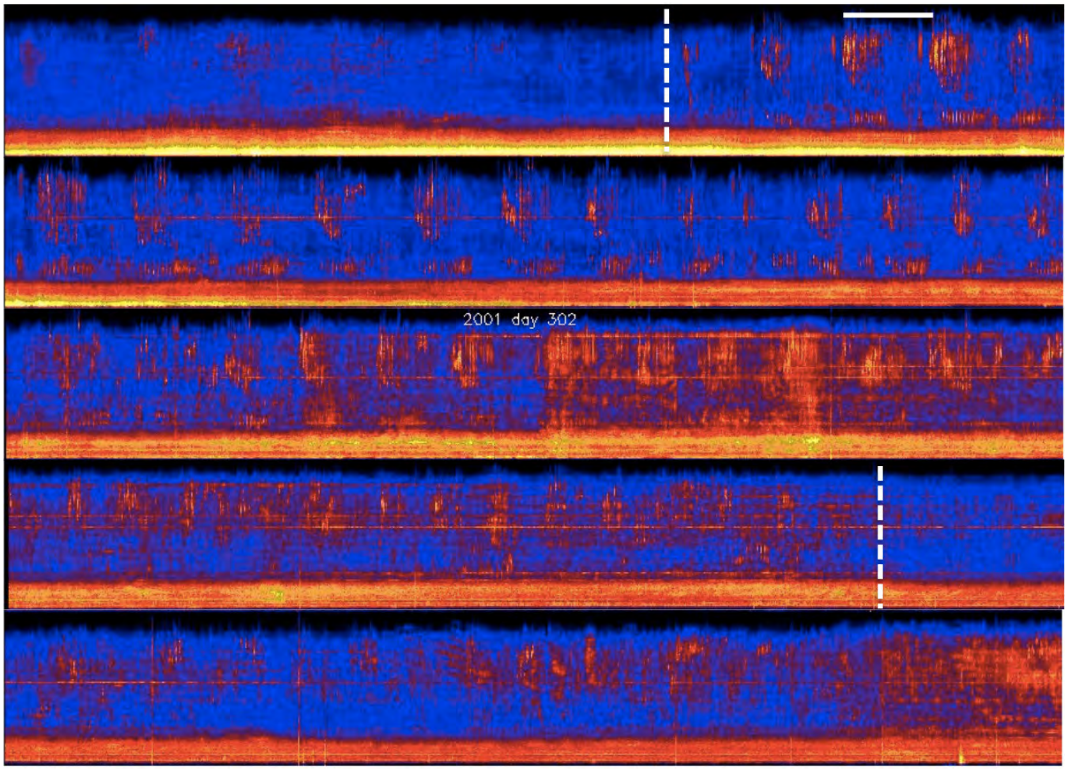

Figure 1. Spectrogram of analyzed song cycles. Each row encompasses two hours. The frequency range (vertical axis) for each row is 0-500 Hz. Vertical dashed lines indicate the section of recorded singing that was analyzed. The horizontal white bar in the top row indicates the duration of one song cycle (9 min). Tonal bands (horizontal red lines) that are correlated with the most energetic frequencies generated by the singer began to emerge after the first hour of singing.

Spectral properties

The first 24 song cycles within the analyzed singing bout showed a consistently alternating spectro-temporal pattern within each cycle in which energy was first concentrated in two bands (100-150 Hz and 200-400 Hz), before shifting primarily into the lower band (Fig. 1 and 3). Within the first half of this alternating pattern, minimum frequencies within each of the two bands gradually decreased (Fig. 3). Later cycles (25-44) showed less clear alternation, with energy primarily focused in the upper band. This difference in the observed spectral patterns of later cycles may have resulted either from changes produced by the singer, changes in the position of the singer relative to the hydrophone that led to greater signal attenuation, or changes in the recording system. Consistencies in spectral patterning over time, however, likely reflect stereotypy in sound production and/or diving patterns of the singer.

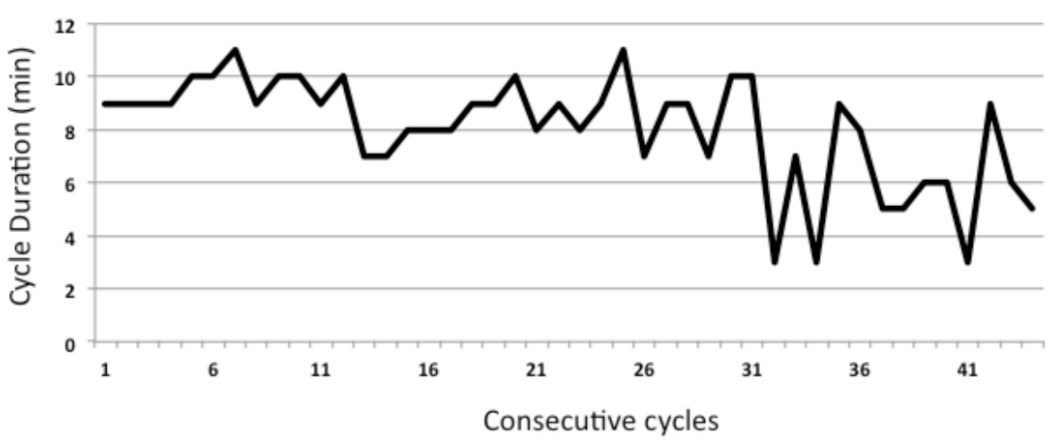

Figure 2. Durations of acoustic cycles measured from spectrograms show that most consecutive cycles change in duration by one minute or less. Shorter duration (3 min) cycles later in the sequence are likely to correspond to repeats of cycle segments rather than shorter duration songs.

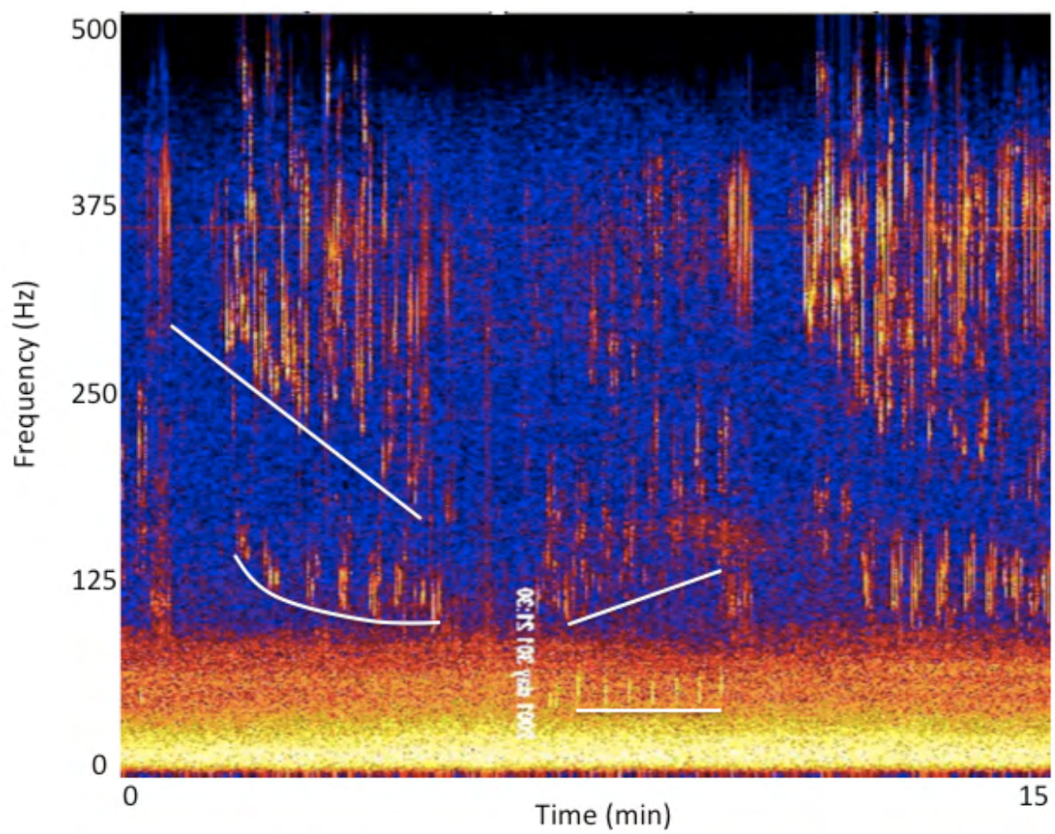

Figure 3. Spectrogram of a song cycle. White lines highlight gradual changes in the frequency content of sounds within a cycle produced by the singer. The singer repeated this general pattern of frequency modulation consistently for multiple hours.

Analyses of peak frequencies from three-minute samples within each hour of the song session showed exceptionally high consistency of frequency usage throughout the session (Fig. 4). Broad peaks were consistently found in three bands: 100-180 Hz; 200-420 Hz; and 400-500 Hz. The peak frequency of the lowest band was between 123-128 Hz for five of the seven hours analyzed. The peak in the highest band ranged between 423-433 Hz for the three hours that a peak was evident. The most energetic frequencies were consistently in the mid-range band for six of the seven hours analyzed. The specific frequencies with maximal energy were more variable over time in the mid-range band than in other bands, ranging from 252-351 Hz. In all three bands, additional narrow peaks were evident, with energy slightly less than was present at the maximum peak frequency; these secondary peaks were most prominent in the mid-range band, which showed 2-6 narrowband peaks (ranging from 208-380 Hz) in addition to the maximal peak for each sample.

Reverberant features

Individual sounds within three-minute samples showed evidence of generating both discrete echoes and reverberant tails (Fig. 5). However, not all sounds generated echoes and even fewer had reverberant tails. Reverberant tails could last significantly longer than the duration of the sound that generated them (Fig. 5), but none lasted longer than a few seconds.

Multiple, persistent narrow bands of energy appeared as the song session progressed, none of which were evident prior to the beginning of the analyzed singing bout (Fig. 1). The first band appeared after five song cycles, was centered at 295 Hz, and was continuously present for about two hours. A second band appeared in the third hour of the bout, focused at 271 Hz, which lasted over four hours. Two more tonal bands emerged in the subsequent hour, centered at 123 and 405 Hz. Finally, a fifth band emerged, five hours into the song session, focused at 305 Hz. Because these narrow tonal bands appeared to be correlated with the frequencies being used by the singing whale and were similar in certain respects to long-duration, reverberant bands sometimes produced by singing whales (Mercado, 2016), the focal frequencies of these bands were compared to the peak frequencies within song cycles (Fig. 4). The lowest tonal band exactly matched the lower peak frequency produced by the singer, and the highest tonal band was about 30 Hz less than the

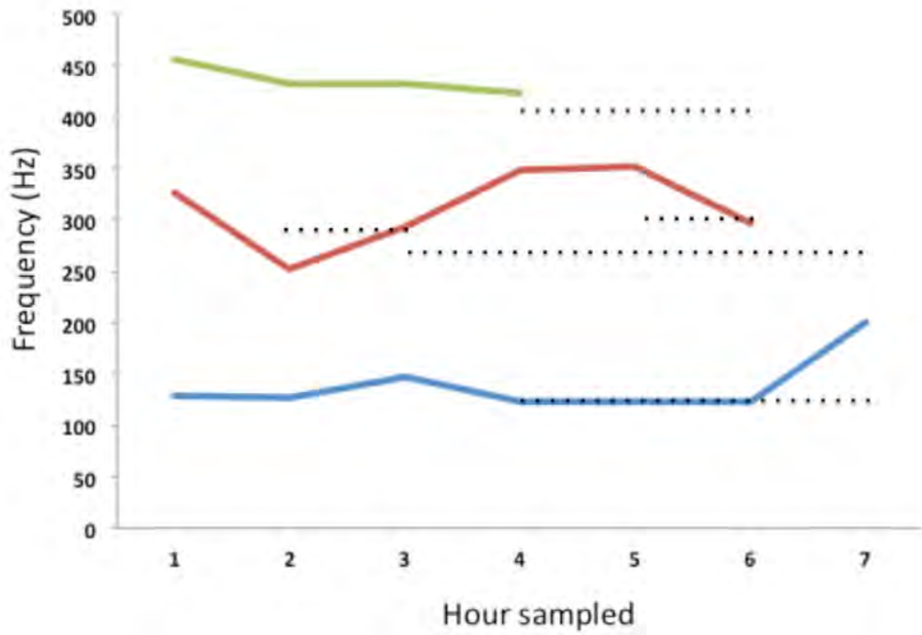

Figure 4. Peak frequencies measured from three-minute samples within each hour of the analyzed segment. Three broad spectral peaks were present for the earliest song cycles in the sample. Later cycles showed fewer peaks. Colored lines show changes in frequencies with peak energy across the song session. Dotted lines show the focal frequencies and the lengths of these lines correspond to the durations of tonal bands present during singing. The focal frequencies of extended tonal bands were correlated with the peak frequencies being used by the singer, but time-lagged relative to song production. The bands persisted during periods when the singer did not appear to be generating units with spectral energy focused at the frequencies within the bands (see Fig. 1).

highest peak frequencies produced by the singer. The mid-range tonal bands were within the range of peak frequencies produced by the singer but did not match the peak frequencies of sampled song segments as closely as in the lower and higher bands. The transitions between tonal band focal frequencies did, however, follow the pattern of changes observed in mid-range peak frequencies produced by the singer.

Discussion

The singing episode described here conforms with several global properties noted in earlier descriptions of songs recorded on several different breeding grounds, including the durations of song cycles (Fristrup *et al.*, 2003), and the distribution of spectral content within songs (Mercado, 2016), providing preliminary evidence that songs produced at night are acoustically comparable to those produced during the day (see also Seger *et al.*, 2016). Songs recorded at a distance, and at a time when the singer was likely migrating, retain acoustic features evident in close recordings collected from breeding groups. Additionally, this case study of a singing humpback whale established that singers may consistently repeat the timing and frequency content of consecutive songs for several hours, and confirmed earlier reports that singers may consistently alternate between two main frequency bands (Mercado *et al.*, 2010). These replications of earlier observations increase confidence that the focal song session analyzed in this study is not an outlier in terms of its acoustic properties, and thus that it can provide a reasonable baseline for evaluating variability in prolonged song sessions.

Temporal and Spectral Dynamics

Fristrup *et al.* (2003) reported that the duration of songs (measured as the interval between inferred surfacing events) for whales singing off the coast of Hawaii averaged 13.8 min, with an average difference in successive songs of 2.5 minutes. Song durations reported by Fristrup *et al.* (2003) closely match earlier measures of singer dive times (MN = 13 min, Chu, 1988). Thompson (1981) measured the duration of 219 songs (defined as a complete cycle through subjectively identified themes) from multiple populations and found that most of them were between 6-12 min long (see also Payne *et al.*, 1983, who reported a range of 6-17 min). Cycle durations measured in the current study ranged between 3-11 min. If the shorter duration cycles are interpreted as corresponding to repeated theme transitions (Darling and Sousa-Lima, 2005), this would give a range of within-session song cycle duration of between 6-12 min.

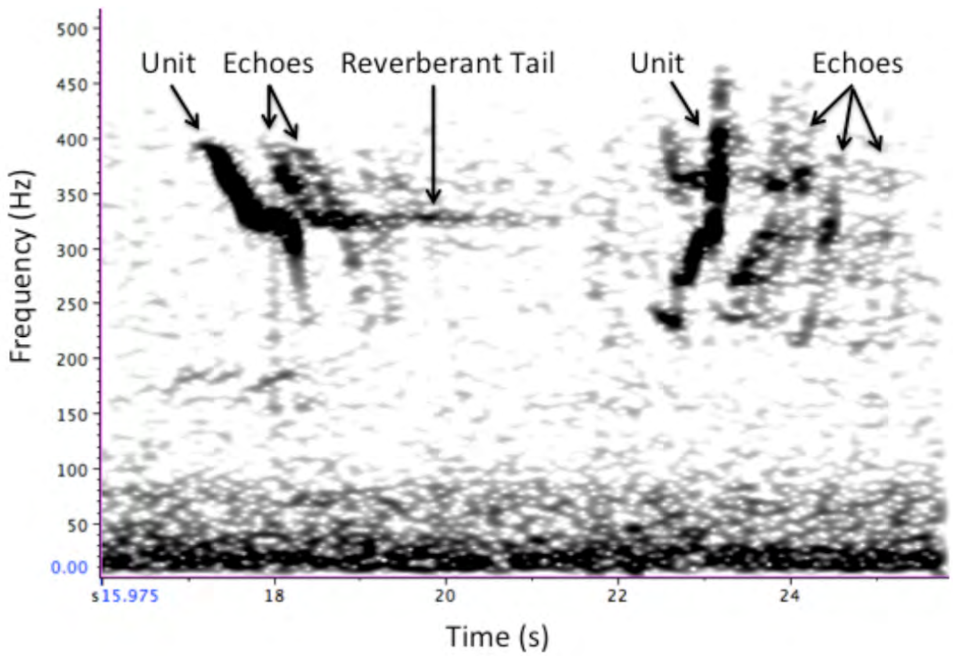

Figure 5. Spectrogram of individual sounds (units) produced by the singer within the song session showing evidence of both discrete echoes and reverberant tails.

The longest song series analyzed by Fristrup *et al.* (2003) consisted of 13 consecutive songs, compared with 44 consecutive song cycles analyzed in the current study. Fristrup *et al.* (2003) noted significant differences in song duration across individual singers but did not report on how any individual singer varied song duration. Thompson (1981) analyzed 132 consecutive song pairs and found that nine showed less than a 1% change in duration. One percent of a 10 min song is a six second difference, less than the duration of a typical song phrase. Finding nine pairs of consecutive songs that differed by such a small interval provides strong evidence that singers do sometimes repeat songs quite precisely (see also Schneider and Mercado, 2018). Frumhoff (1983) found that songs were less variable in duration than their constituent themes, leading him to suggest that song duration may be more constrained than the specific sequences (theme durations) produced within songs. Chu (1988) also noted that there was more variation in dive times between singers than within the dives of any particular singer. The current analysis found that most consecutive cycles (64%) differed in duration by a minute or less. The observed trajectory of cycle durations suggests that the singer gradually shifted to shorter duration cycles over time. Measures of song duration trajectories within song sessions may be more informative than measures of variance in duration across songs of multiple singers, if singers are gradually adjusting or maintaining song/dive durations. For instance, systematic changes in song duration trajectories may correlate with changes in diving patterns (Chu and Harcourt, 1986) and/or activity levels and the swimming behavior of a singer.

Past quantitative analyses of sequential frequency content within songs suggest that singing humpback whales often progressively switch between producing sounds with energy focused at higher frequencies to producing sounds with energy concentrated at lower frequencies (Mercado, 2016; Mercado and Handel, 2012; Mercado *et al.*, 2010). This pattern was previously found in songs from Hawaii, Puerto Rico, Madagascar, Columbia, and Brazil. The current analysis of consecutive cycles showed consistent repetition of a “hi-lo” frequency pattern for many of the cycles analyzed. Mercado and Handel (2012) previously suggested that this pattern might be a side-effect of gas exchange occurring while a singer is submerged, in combination with periodic changes in a singer’s depth associated with surfacing. Alternatively, this pattern may reflect a stereotyped progression through song elements that in some way contributes to song functionality. For instance, song sounds with different frequency content will generate different patterns of constructive and destructive interference (Mercado and Frazer, 1999; Mercado *et al.*, 2007), such that a singer gradually sweeping through a broad range of frequencies may more fully ensonify the kinds of shallow water habitats frequented by singing humpback whales.

Despite cyclical shifts in the frequency content of the songs analyzed here, the frequencies with peak energy stayed remarkably stable across many song repetitions. Maximal energy was reliably found in a band between 200-400 Hz, consistent with past analyses of sound production (Mercado *et al.*, 2010), and with earlier work suggesting that frequencies in this band often propagate optimally within humpback whale habitats (Mercado and Frazer, 1999). The peak frequencies within song cycles identified in the current study also correspond closely to those of "drone units", which are individual sounds within songs that recur at regular intervals and that are prone to generating reverberant tails (Mercado, 2016). The lower frequency spectral peaks within song cycles were particularly consistent, varying by 3 Hz or less over multiple hours. High-energy, mid-range peak frequencies varied more over time than both higher and lower peak frequencies, suggesting that singers may more flexibly modulate the frequency content of sounds within this range.

Persistent Tonal Bands

There was little evidence of individual sounds generating persistent reverberant tails within the analyzed song session. The reverberant tails that were identified generally lasted less than three seconds. Initial analyses of song-induced reverberation similarly found that only some recordings show individual sounds generating persistent narrowband reverberation (Mercado, 2016). Multiple discrete echoes followed many recorded sounds, establishing that the recording system was sufficiently sensitive to detect narrowband reverberant tails if they had been present.

A surprising finding of the current analysis was the presence of long-duration bands of narrowly focused acoustic energy coinciding with song production. These bands did not appear until well after singing was evident and appeared to be correlated with the frequency content of songs. It is impossible to discount the possibility that these tonal bands are some type of recording artifact. But, it is unclear what the mechanism of such an artifact might be, especially given how the focal frequencies remain stable despite changes in the spectral content of overlapping songs, as well as changes in their received levels. The fact that the tonal bands emerge and then dissipate over hour-long periods, and are focused at various frequencies, suggests that they probably are not caused by any direct interaction between the recording system and the signals being recorded. Visual inspections of other recordings from the database revealed that tonal bands were not always coincident with song production, suggesting that they may be either some form of intermittent background signal or may result from some type of environmental resonance phenomenon. However, given the close correspondence of the focal frequencies within these bands to those being produced by the singer, it seems that either the singer may be selecting frequencies that in some way correspond to these bands (prior to the occurrence of the bands), or that song production (either by the recorded singer or by choruses of distant singers) is in some way driving the emergence of the bands. The acoustic similarity of these tonal bands to previously identified streams of continuous song-generated reverberation is particularly intriguing, but could be coincidental.

Many more observations may be needed to identify the nature and origins of these tonal bands and their relationship (if any) to singing by humpback whales. The existence of persistent, song-generated, narrowband reverberation escaped the attention of bioacousticians for many years, and it was only after the discovery of similar reverberant bands in bird songs (Mercado *et al.*, 2017), that long-lasting reverberant tails were sought for and found in recordings of humpback whale songs. Further evidence that song-generated reverberation might play an important role in humpback whale songs came from the finding that consecutive units within songs were often spectrally interleaved, such that successive units minimally masked ongoing reverberation (Mercado, 2016). Might it be possible that regular repetition of phrases in some way contributes to the persistence of acoustic energy at particular frequencies above-and-beyond the boosts that are already delivered by the regularly timed production of reverberating drone units? If so, what might be the necessary conditions for such a phenomenon to occur? The current analysis cannot adequately address such questions, but at a minimum suggests that this issue is worth considering more closely in future analyses of humpback whale songs.

Limitations and Future Directions

The current case study serves to highlight aspects of singing that previously have received little attention, and thus may act as a catalyst for future hypothesis development and scientific research. By design, this study cannot address issues related to typical singer behavior, the functional role of songs, or the factors that determine when and how humpback whales produce songs. The recorded signal analyzed in this study differs from those encountered by humpback whales in that it only includes frequencies below 500 Hz and was recorded at a depth of ~1000 m. The positions and movements of the singer relative to the recording hydrophone are unknown, but it is almost certain that the singer was at least a kilometer away from the recording array. In the ideal case study, a recording device would have been placed on the singer for multiple days and the singer would have been surrounded by a large array of hydrophones positioned at depths similar to those inhabited by humpback whales at a variety of distances from the singer. Such a recording configuration would make it possible to more fully evaluate how the acoustic properties of received sounds relate to produced sounds, and to more precisely measure the consistency of singing by an individual singer.

Neither surfacing events nor thematic structure could be reliably identified in the current study, although there were regular, short-duration "gaps" within song cycles that may correspond with the signal attenuation that often occurs when a singer surfaces (Fristrup *et al.*, 2003). Consequently, it is difficult to assess whether the measures of cycle duration used in the current study are directly comparable to past measurements of song duration. The sample analyzed here does not constitute a complete song session, because there were traces of song elements evident both before and after the analyzed segment (Fig. 1). Winn and Winn (1978) mention a 22-hour recording of continuous singing, which probably also was not a complete song session. They suggested that song sessions might extend for several months. More recent studies suggest that, instead, humpback whales most likely switch between singing and other activities (Herman, 2016). The maximum durations of continuous song production, the typical duration of song sessions, and the proportion of time humpback whales spend singing each day are all unknown. Recordings of individuals collected continuously at the source over periods of weeks or months will be needed to more fully assess the consistency and precision of song production by individuals over time.

Long-term acoustic recordings collected from the bodies of singing humpback whales (Sousa-Lima *et al.*, 2003; Stimpert *et al.*, 2012; Stimpert *et al.*, 2007) can provide more detailed information about intra-individual variations in song production. But, these need to be combined with long-range recordings to gain a complete picture of the acoustic fields that singers generate. Additionally, long-term analyses of song variations produced by singers in different geographic and social contexts may reveal different dynamics from those produced by a lone singer. More detailed measurements of temporal structure within song sessions may also prove useful in characterizing intra- and inter-individual differences in song production. Understanding what individual singers normally do can potentially provide behavioral insights that would not be revealed by traditional analyses of prototypical structural qualities of songs, or by analyses of how songs vary within and across populations.

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