First look at humpback whale (*Megaptera novaeangliae)* song structure from western South Africa

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Abstract

Humpback whales are known for their complex and well-structured song that is typically produced on low-latitude breeding grounds. However, there is increasing evidence of song production on migration routes and high-latitude feeding grounds. Within a breeding ground and season, males share songs that progressively change over time. Song production on migration routes leads to the cultural transmission and sharing of songs. This is the first assessment of song structure in humpback whales recorded near Cape Town, South Africa. Song was identified in recordings made between 9 September 2016 and 21 October 2016 on a moored hydrophone located in Fish Hoek, False Bay. Thirty-nine song sessions were recorded, consisting of nine distinct units, forming ten themes. Themes occasionally overlapped in time, indicating multiple simultaneous singers. They were repeated on multiple days with consistent patterns in theme transition, demonstrating song sharing amongst individuals. Convergence on a similar song structure suggests singing whales originate from the same breeding stock. We propose that an unknown proportion of these whales continue to sing beyond the recognised breeding season. These data support previous studies that found that singing is not restricted to low-latitude breeding sites.

Keywords: breeding, singing, suspended migration, vocalisation

Introduction

The song produced by male humpback whales (*Megaptera novaeangliae*) is considered one of the most unique forms of communication in the animal kingdom, because of its complex characteristics, rapid evolution and cultural transmission within and between populations (Payne and McVay 1971; Darling et al. 2006; Garland et al. 2011; Garland et al. 2013). Humpback whale song is highly stereotypical and based on a hierarchical structure; units are repeated in a fixed sequence to make a phrase; repeated phrases comprise themes. Sequences of themes in a specific order make up a song (Payne and McVay 1971; Cholewiak et al. 2013). Males repeat songs during a song session, which can continue for up to eight hours (Payne and Payne 1985; Garland et al. 2013). Song units are highly variable in frequency range, with most energy concentrated in the 100 Hz to 4 000 Hz band (Tyack and Clark 2000). However, low frequency components at 30 Hz and harmonics as high as 24 000 Hz have been documented (Payne and Payne 1985; Au et al. 2006).

The function of humpback whale song is not fully understood (Herman et al. 2013; Herman 2017), though its production is strongly linked to breeding behaviour (Payne and McVay 1971; Cerchio et al. 2001; Cholewiak 2008). Although song is extensively produced at

breeding grounds, there are increasing reports of singing behaviour on low-latitude feeding grounds and during annual migrations when breeding is not observed (Gabriele and Frankel 2002; Clark and Clapham 2004; Vu et al. 2012; Garland et al. 2013; Gridley et al. 2018; Magnúsdóttir and Lim 2019). Within breeding grounds, song largely conforms to a single type, with only minor individual variation (Payne and Payne 1985; Helweg et al. 1992; Garland et al. 2013). However, at the same time the song is also constantly evolving (Payne and Payne 1985). Different populations show similarities in song type, i.e. a sharing of units and phrases, with the extent of shared song content being relative to the geographical distance of separation (Helweg et al. 1998; Cerchio et al. 2001; Garland et al. 2013, 2015; Rekdahl et al. 2018). Therefore, in addition to traditional methods, such as, photo identification, genetic sampling and satellite tracking (Barendse et al. 2011; Rosenbaum et al. 2014), detailed analysis of song structure may provide a contemporary and cost-effective indicator of population structure and interchange (Rekdahl et al. 2018).

In the Southern Hemisphere, humpback whales are typically observed spending summer months feeding in high-latitude Antarctic waters, migrating north to low-latitude breeding grounds during the winter months (Kellogg 1929; Barendse et al. 2011; Best 2011; Findlay et al. 2017). The coastal waters of southern Africa are used as a migration path, with the west coast population referred to as Breeding stock B (BSB), split into two subpopulations BSB1 (Gulf of Guinea) and BSB2 (west South Africa), and the east coast population as Breeding stock C (BSC) (IWC 1998).

The International Whaling Commission's moratorium on commercial whaling (introduced in 1982, effective by 1985), has been a huge conservation success for humpback whales, with many stocks growing markedly in abundance since the moratorium was put in place (Wedekin et al. 2017), including BSB (IWC 2012). As stock sizes change, there have been remarkable behavioural shifts within humpback whale populations (Mobley et al. 1999; Félix and Haase 2001). The cold, nutrient rich upwelled water of the Benguela current off the west coast of southern Africa has long been recognised as a potentially important feeding ground for migrating whales. In this area animals have been observed feeding well after the typical southern migration period (October–November), in what has been termed a 'suspended migration' (Best et al. 1995; Barendse et al. 2011). Along the west coast of South Africa, large feeding aggregations of whales have been documented in the past eight years, with 'super-groups' of animals in excess of 200 individuals feeding for hours at a time (Findlay et al. 2017; Gridley et al. 2018). Song was recently documented from recordings of humpback whales feeding in super-groups (Gridley et al. 2018); however, very little other information about the singing behaviour of whales on the west coast of southern Africa exists. Studying song may provide insight into the population structure and movements along this migratory corridor. Here we conducted a preliminary investigation into song occurrence and structure within western South African waters to investigate song convergence. We demonstrate the viability of passive acoustic monitoring in near shore waters of the West coast of South Africa to acoustically monitor humpback whale behaviour and presence over time.

Materials and methods

The data analysed in this study were collected as part of a broader project focusing on coastal dolphin distribution in False Bay, South Africa (34.2° S, 18.7° E). False Bay is a shallow sloped, sandy-bottomed bay roughly 30 × 30 km in extent. Four SoundTrap hydrophones (Ocean Instruments NZ, Auckland, New Zealand), were deployed at sites within False Bay in water depths of 30 m or less between September 2016 and January 2018 (Figure 1). Hydrophones were set with a high gain preamplification mode and acoustic data saved as SUD raw files through lossless compression. Because the original project goal was to record dolphin presence, an intermittent duty cycle of 5 min on and 5 min off was

used, with acoustic data sampled at 96 000 Hz. This had implications for the consistent identification and description of whale song structure, outlined below.

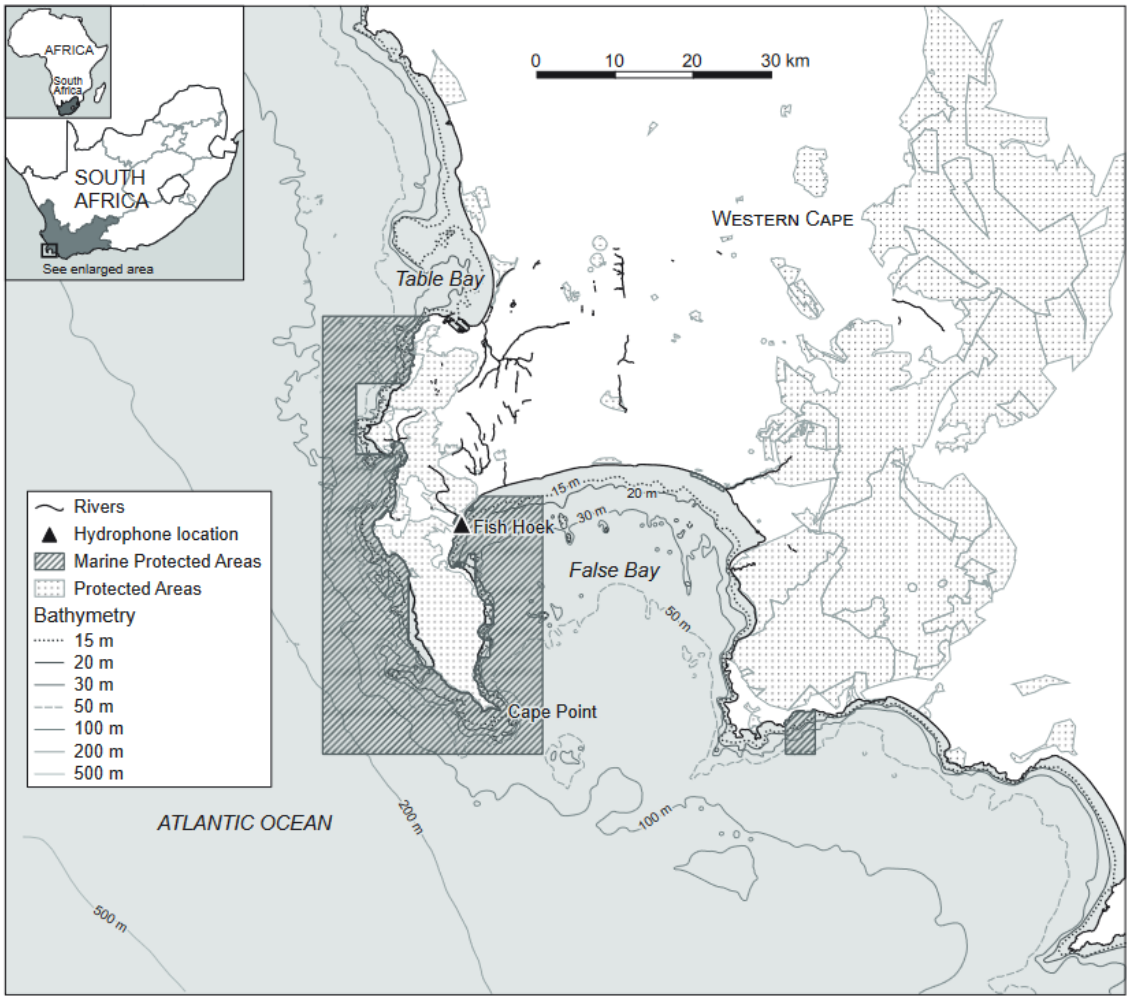

Figure 1: Map of the study area showing hydrophone location at Fish Hoek

Acoustic data were converted to Long-Term Spectral Averages (LTSAs) using the MATLAB based program Triton (Matlab v.2017b, Triton v. 1.93.20160524) with a time and frequency resolution of 5 s and 50 Hz, respectively. A manual analysis (author AP) searching for dolphin vocalisations scanned the LTSAs at a 30 min time window, confirming dolphin encounters by selecting the signal of interest and viewing the full resolution spectrogram with a time window of 10 s. During this process, it became clear that whale song was present during several recordings corresponding to the austral spring in 2016, for which incidental observations were logged.

A complementary study, Ross-Marsh et al. (2020) documents the long-term presence of song from the four sites. The current study, however, focuses only on whale song recorded at Fish Hoek (34°14' S, 18°44' E), over one deployment spanning 9 September 2016 to 21 October 2016. Fish Hoek is located in the north-west corner of False Bay. All logged song was confirmed by inspecting a full resolution spectrogram with the expand function in Triton (frequency bandwidth 0 to 6 000 Hz, time window of 30 s, FFT 8192, 50% overlap, brightness of 25 to 30 dB and contrast of 100%) and by using the audio-playback feature to confirm signal classification. We systematically went through recordings and built

a catalogue of units, phrases and themes, using the standard hierarchical methodology applied to humpback whale song (Payne and McVay 1971). Signal to noise ratio (SNR) was visually assessed by the author (JH) and songs of low quality (i.e. units unclear or faint) were discounted from the detailed analysis section. Because songs can change in SNR over the song cycle, it is impractical to quantify the SNR for all units and visual assessment of SNR is typical in humpback song research (Cholewiak et al. 2013; Garland et al. 2015; Herman 2017). As can be seen by the sample sizes, we distilled the data to the best possible song sessions (six sessions out of 39 used) so that we could be confident in our results. Units were labelled with numbers and phrases/themes were labelled with letters. Because of the intermittent nature of the acoustic duty cycle, it was not possible to conduct a full analysis of continuous song structure. However, we used the data to describe song characteristics and investigated similarities in song type between song sessions indicative of signal convergence. Song separated by quiet periods exceeding one hour were defined as separate song sessions.

We investigated song structure by looking at patterns in theme and phrase transitions identified within the six high quality song sessions. This was the only effective way to analyse similarities in song type, because of the limitations of the five-minute duration recordings. Theme transitions were defined as the change from one theme to another (e.g. A-C or B-A for example). The theme transitions from each song session were pooled to identify if there were similarities in song type between the song sessions identified. Regarding song stability, previous studies have found phrase duration to be a stable feature of song that is more consistently produced within and between individuals (reviewed in Cholewiak et al. 2013), while theme duration is more variable (Payne and Payne 1985). Phrase duration was measured following Cholewiak et al. (2013), including the period of silence between phrases, and measuring from the onset of the first unit in one phrase to the analogous unit in the subsequent phrase. Investigating theme duration was problematic, because of the duty cycle. However, where the whole theme could be resolved we made a conservative measure of theme duration. Phrase and theme duration were compared using the coefficient of variation CV) expressed as a percentage (CV = SD/mean × 100) to provide a standardised measurement of variation. Because of sample size constraints, CVs were calculated from duration data pooled over sessions and compared for phrases/themes

Results

In total, 490 hours of recordings were available from just less than 42 consecutive days between 9 September 2016 and 21 October 2016. The first song session was recorded on 9 September, and the last song session was recorded on 16 October 2016. During this period, we identified 39 song sessions lasting between 5 min and 8 h (mean 1 h 43 min ± 2 h 5 min SD). Songs consisted of nine distinct units, forming ten phrases, repeated into themes. Although uncommon, observations of overlapping song occurred in three song sessions, indicating the presence of multiple singers.

Of the song sessions identified, six (3, 23, 26, 30, 34 and 35) were visually assessed as having a high signal-to noise ratio and were used for detailed analysis. Out of the six song sessions selected, two pairs were close in time: session 23 and 26 were separated by 12 h 38 min and session 34 and 35 separated by 1 h and 49 mins. All others were separated by one to seven days. The same themes were identified within different recording sessions, with theme A, B, and C recorded in all song sessions, theme D recorded in four of the six song sessions and E and F in three of the six (Figure 2, Table 1). Of the 10 themes recorded in total, four themes were rare and not recorded within the songs selected for detailed analysis, with subsequent results focusing on the most common themes, A to F. Overall 93% of the 407 theme occurrences documented were classified as either themes A (38%), B (23%) or C (32%), indicating high levels of similarity between the structure of songs

recorded. Within song sessions, the proportion of themes of different types was also very similar (Table 1).

A-C only.

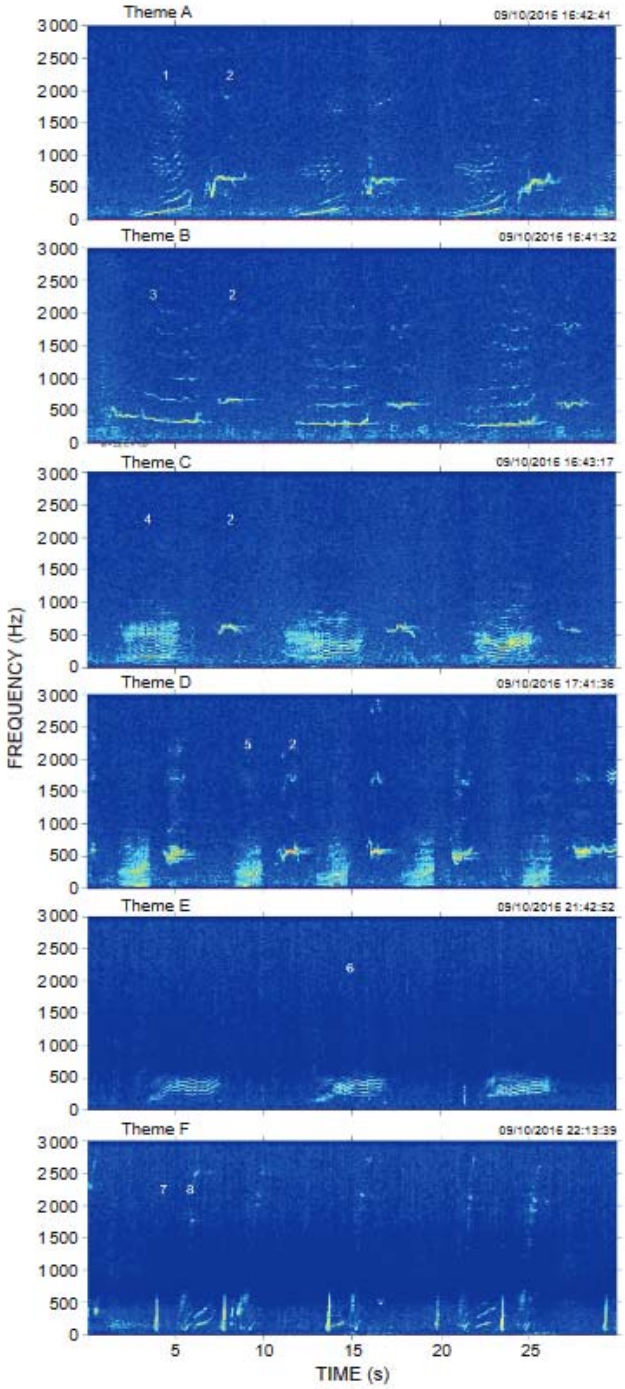

Figure 2: Spectrogram of the most frequently occurring song themes, from humpback whales recorded in Fish Hoek (10 September 2016). The best example of units within themes are labelled in white text

Table 1: Summary of song occurrence (date/ time, duration) and breakdown by theme (count with percentages shown) for different humpback whale song sessions analysed. Songs were recorded in Fish Hoek, False Bay, South Africa, between 9 September and 16 October 2016

Song session	Start	End	Duration (h:min:s)	A	B	C	D	E	F
3	2016/09/10 16:40:34	2016/09/11 00:20:54	07:40:20	54	33	52	1	1	0
				38%	23%	37%	1%	1%	0%
23	2016/09/18 19:30:34	2016/09/19 02:22:14	06:51:40	44	23	34	3	0	3
				41%	21%	32%	3%	0%	3%
26	2016/09/19 15:00:44	2016/09/19 17:14:34	02:13:50	17	9	7	0	0	4
				46%	24%	19%	0%	0%	11%
30	2016/09/21 20:33:09	2016/09/21 23:24:39	02:51:30	21	15	20	12	1	0
				30%	22%	29%	17%	1%	0%
34	2016/09/23 10:00:34	2016/09/23 12:20:39	02:20:05	17	12	11	1	0	1
				40%	29%	26%	2%	0%	2%
35	2016/09/23 14:10:19	2016/09/23 14:54:34	00:44:15	4	1	6	0	2	0
				31%	8%	46%	0%	15%	0%
Total				157	93	130	17	4	8
%				38%	23%	32%	4%	1%	2%

In total, 18 theme transition combinations were documented and within song sessions there were generally consistent patterns in theme transition (Figure 3, Figure 4). The most frequent theme transitions were A to C (30%) and B to A (22%). Transition B to C (10%) was also common and present in all song sessions, excluding session 35. There was only sufficient data to resolve meaningful duration information for the most common themes A, B, and C. Of these, A was the longest (mean 1 min 38 sec ± 52 sec SD), then theme C (mean 1 min 16 sec ± 43 sec SD) and finally theme B (mean 56 ± 27 sec SD, Figure 5), which also showed less variability in duration. The duration for themes D to F was much shorter than the main themes, but measurement was based on much smaller sample sizes. The duration of themes sung was more variable than phrases (Figure 5) with the CV of theme duration for A, B and C being 54%, 49% and 57%, respectively. For comparison, the CV for phrase duration was 15%, 17% and 20% for A, B and C, respectively.

In summary, we documented substantial singing activity in humpback whales over this 42-day period and a strong similarity in song type between the six discrete song sessions analysed.

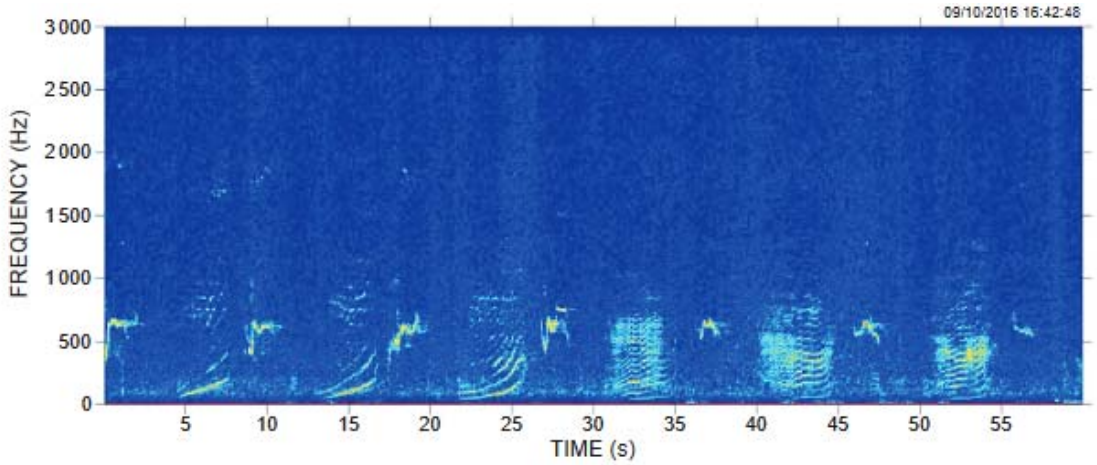

Figure 3: Spectrogram of phrase transition A to C

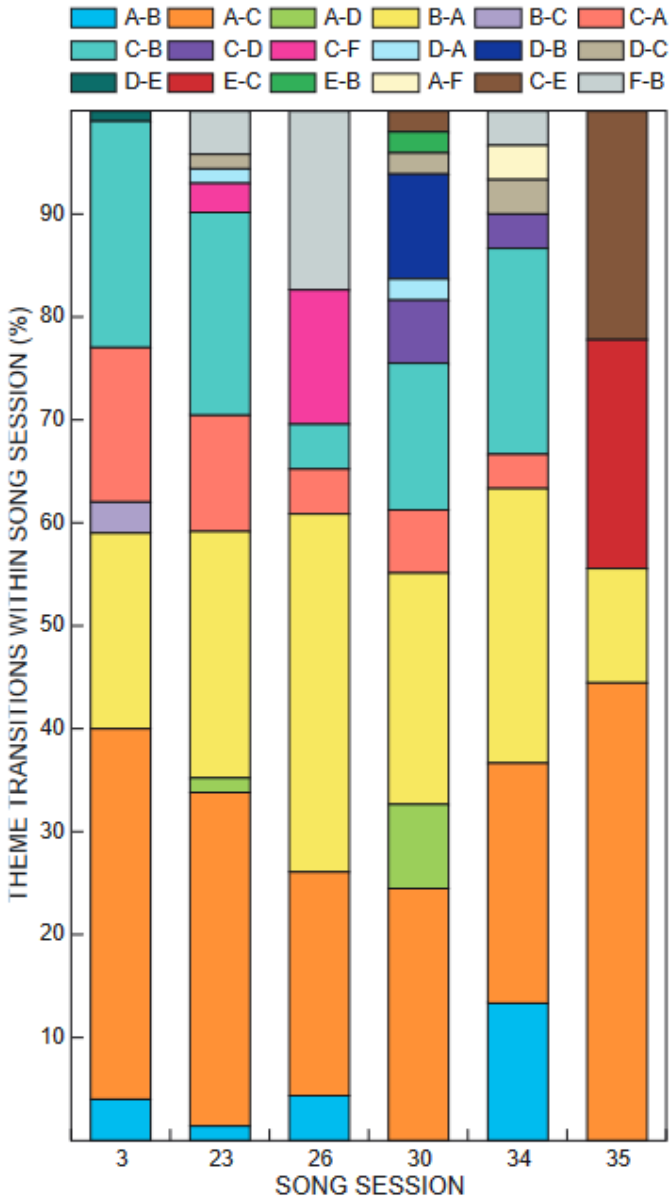

Figure 4: Stacked bar chart showing frequency of humpback whale song theme transition as a proportion of each song session of whales recorded in Fish Hoek, South Africa, between 9 September and 16 October 2016. The figure demonstrates overall similarity in the structural composition of the songs identified

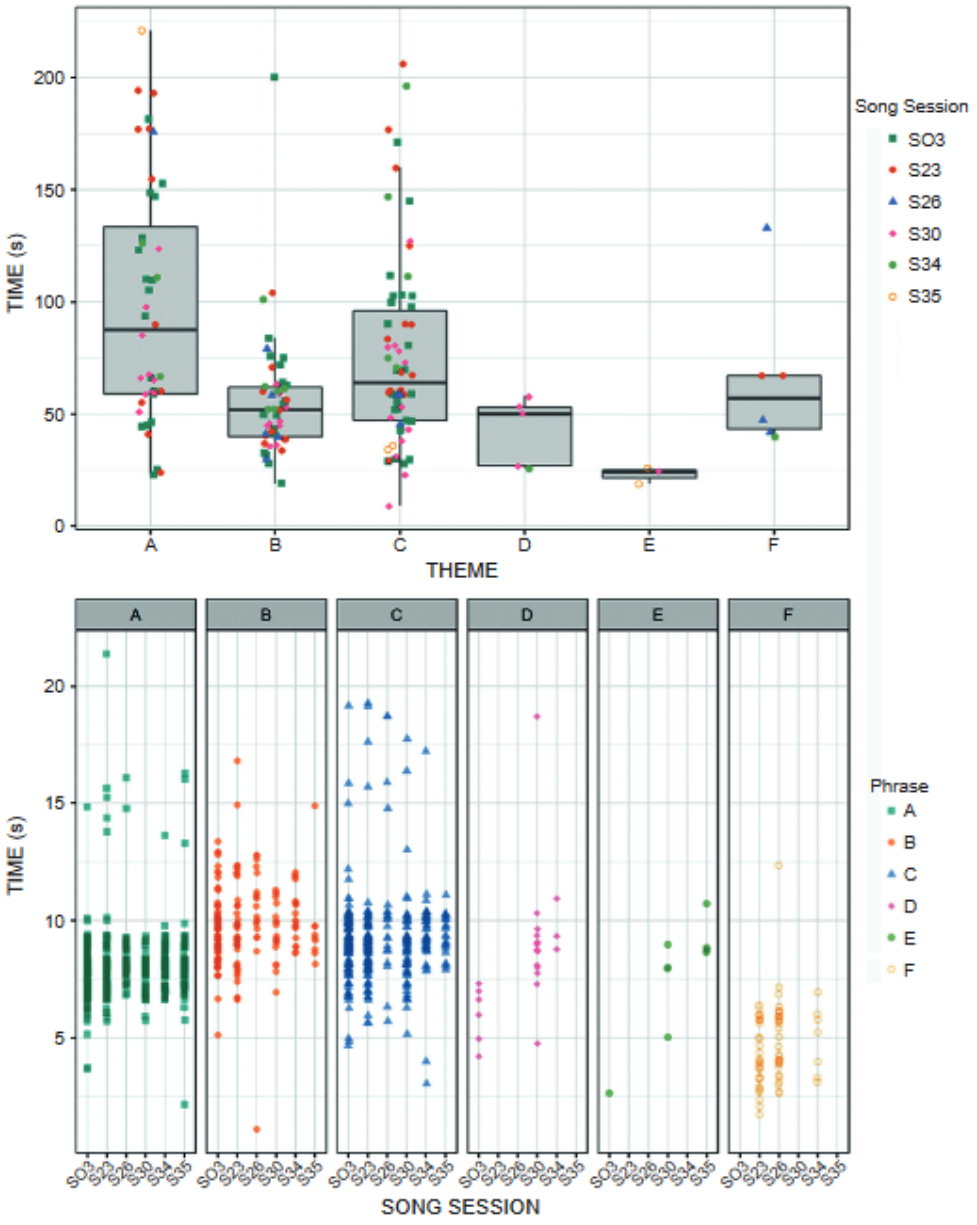

Figure 5: Average duration(s) of song phrases and themes identified from Fish Hoek, South Africa, between 9 September and 16 October 2016

Discussion

In this study we provide a first description of the song structure of humpback whales recorded in South Africa. We detected a substantial amount of song at Fish Hoek during September and October, sometimes produced by multiple animals. The analysis of theme occurrence, proportions, transitions and phrase durations indicates convergence in song type between individuals, with themes A, B and C the most commonly occurring in the songs identified. As with early descriptions of humpback whale song (Payne and McVay 1971; Payne and Payne 1985), we found that song sessions could last multiple hours, with consistent structure and sequence of themes. Themes A, B and C were the most common

(Table 1) and the order in which they were sung was structured. The transitions A-C and B-A were common to all song sessions. Other transitions, such as A-B or C-A, were comparatively rare. As in other studies (reviewed by Cholewiak et al. 2013), phrase duration was more consistent than theme duration (Figure 4). The number of themes identified (10), was also similar to that identified in other populations (for example, Payne and Payne 1985 typically found 5–9 themes in any given year).

In general, humpback whale song is very well studied (reviewed in Parsons et al. 2008; Herman 2017). In the South Pacific, for example, there have been extensive studies of the cultural transmission of song between different regional populations where some phrases were found to be common to all populations (Helweg et al. 1998; Garland et al. 2015). Although based on limited sample sizes, a comparison between song characteristics of West (BSB) and East (BSC) African coastal stocks demonstrated similarities within most years, indicative of song sharing (Rekdahl et al. 2018). In addition, humpback whales breeding in Angola show similarities in song type when compared with whales recorded off Brazil in the south-west Atlantic Ocean, suggesting seasonal mixing and sharing of song components on the winter feeding grounds in the Antarctic (Darling and Sousa-Lima 2005). However, there is very little information on the acoustic behaviour of humpback whales inhabiting or migrating through South African waters with no confirmed observations of singing whales within the study area. Singing whales may travel slowly (Noad and Cato 2007), or be characterised by a downward facing position (Au et al. 2006). In South Africa, Gridley et al. (2018) documented song produced by or near to feeding whales, and Ross-Marsh et al. (2020) documented the seasonal and diel patterns in song. However, no detailed analysis on song structure has been conducted in South African waters. Our study demonstrates similarities in song structure between sessions over a 42-day period and is the first step in describing the song of migrating whales in South African waters. During passive acoustic monitoring in the near shore waters of False Bay, we were able to record extensive song and multiple singers, demonstrating the potential for this region to be an area of song exchange and transmission between the various stocks breeding around Africa.

Our study raises questions on individual singing behaviour, the source population of the singers and the purpose of such extensive song on what is currently believed to be a southbound migration route. Although there are documented similarities in the song of humpback whales between separate breeding stocks (Darling and Sousa-Lima 2005; Garland et al. 2017), including between the west and east coasts of southern Africa (Rekdahl et al. 2018), the relatively discrete timing of song production (September to October) and similarity in song suggests that the singers detected were from the same breeding stock. All these song sessions were recorded in September, a time of year when there are large numbers of humpback whales occurring in coastal South African waters. In most cases, there were sufficient intervals between songs to indicate different singers were recorded, however, in cases of songs sessions occurring close in time (23/26, and 34/36), the repeated recording of the same individual cannot be discounted.

The South African coast largely acts as a migration corridor for humpback whales and the study site lies near the southern limit of the coastline and just to the east of known feeding grounds in the southern Benguela (Barendse et al. 2011; Findlay et al. 2011). The location and timing of whale presence in this area suggests that the animals detected are most likely from the West coast BSB population, but could also be from the East coast BSC population (Vinding et al. 2015).

The recordings analysed in this study were made during the expected southern migration period for animals observed in this region, but given the timing and the distance from the known breeding ground, the extent of song recorded was unexpected. These data indicate that an unknown proportion of the humpback whale populations using the west coast of South Africa as a migratory corridor and feeding grounds continue to sing beyond the documented breeding season (June-August) and that singing is not restricted to the known low-latitude breeding sites. Whether singing whales are from BSB and engaged in southwards migration, originated from the BSC population, or have remained in South African waters without migrating to the breeding grounds is currently unknown. Our information adds to the growing body of evidence, indicating that humpback whale singing is not restricted to breeding grounds, and that breeding display behaviour may be common on migration routes and feeding grounds, year round (McSweeney et al. 1989; Clapham and Mattila 1990; Clark and Clapham 2004; Stimpert et al. 2012; Gridley et al. 2018). Alternatively, as sexually immature males may engage in singing (Herman et al. 2013), it is also possible the animals detected were non-breeding animals that had not completed the full northwards migration.

This study highlights the potential opportunity to monitor the evolution of song on the migration route. Of particular interest is the potential cultural transmission of song components between BSB1 and BSB2 on the west coast. Additional investigation of horizontal cultural transmission of song types between the east coast (BSC) and west coast (BSB) populations is also warranted. Continuous multiyear passive acoustic monitoring within South African waters and at breeding grounds of BSB and BSC (and substocks) is therefore recommended to enable detailed analyses of song structure and evolution over time, such as those conducted in other locations (Payne and Payne 1985; Noad et al. 2000; Garland et al. 2013, 2015), and to investigate stock structure using acoustic methodology (Darling et al. 2014).

Summary

Long-term passive acoustic monitoring from fixed locations provides a new research method in this study area for the collection of population level data on humpback whale occurrence and behaviour (Ross-Marsh et al. 2020, Thomisch et al. 2019). Although not directly representative of abundance, the data collected indicates the presence of humpback whales and is far superior in temporal coverage than the limited sightings data that are currently available. Year-round acoustic monitoring for humpback whale song and social sounds will undoubtedly provide important information on the occurrence and breeding behaviour of the growing whale population, while providing insight into population and substock dynamics over time, as well as cultural transmission of song. Additional data collection could provide a unique opportunity to link song to behaviour on this migratory route for the first time.

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Ethics approval

The following approvals were obtained: Animal ethics committee approval under project (EC074-15), SANParks permit CRC/2016-2017/026-2015/V2 and a Government research permit (DEA/DAFF) for 2016: RES2016/86.

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