Song recorded near a super-group of humpback whales on a mid-latitude feeding ground off South Africa

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Abstract: Humpback whales (*Megaptera novaeangliae*) are well known for their complex song which is culturally transmitted and produced by males. However, the function of singing behavior remains poorly understood. Song was observed from 57 min of acoustic recording in the presence of feeding humpback whales aggregated in the near-shore waters on the west coast of South Africa. The structural organization of the song components, lack of overlap between song units, and consistency in relative received level suggest the song was produced by one "singer." The unusual timing and location of song production adds further evidence of plasticity in song production.

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1. Introduction

Humpback whales (*Megaptera novaeangliae*) are renowned for their characteristic song (Payne and McVay, 1971; Winn *et al.*, 1981) produced by males (Darling *et al.*, 2006; Smith *et al.*, 2008). Linked to breeding behavior, singing activity peaks during the winter season on low-latitude breeding grounds (Winn and Winn, 1978; Helweg *et al.*, 1992). However, a growing body of evidence details singing during migration (Norris *et al.*, 1999; Noad and Cato, 2007) and on high latitude feeding grounds (e.g., Mattila *et al.*, 1987; Clark and Clapham, 2004; Stimpert *et al.*, 2012; Vu *et al.*, 2012; Garland *et al.*, 2013; Magnúsdóttir *et al.*, 2014), suggesting a flexible use of song.

The International Whaling Commission (IWC, 1998) has designated the west coast of southern Africa as a migratory corridor for Breeding Stock B (BSB) humpback whales. BSB is made up of two stocks: BSB1, breeding in the Gulf of Guinea from Angola northwards and BSB2 whose breeding locality remains unknown (Best, 2018). The number of whales in the Benguela Current Ecosystem on the west coast of South Africa peaks from June to July, coincidental with the northward migration toward Southern Hemisphere winter breeding areas. A second peak from October to December is concurrent with the southward movement to high latitude summer feeding grounds (Barendse *et al.*, 2010; Best and Cherry, 2010; Elwen *et al.*, 2014).

In general, humpback whale numbers have increased since the international ban on commercial whaling and the BSB population is increasing (IWC, 2012). The Benguela upwelling ecosystem is an extremely nutrient rich environment (Fréon *et al.*, 2009). Recently (2011 onwards) large numbers of whales have been observed forming aggregations exceeding 20 animals per group, termed "super groups" (Findlay *et al.*, 2017). These whales are abundant from October to February (Barendse *et al.*, 2011) and are feeding on euphausiid shrimp (*Euphausia lucens*) (Barendse *et al.*, 2010; Findlay *et al.*, 2017). The number of humpback whales feeding in super-groups is highly unusual

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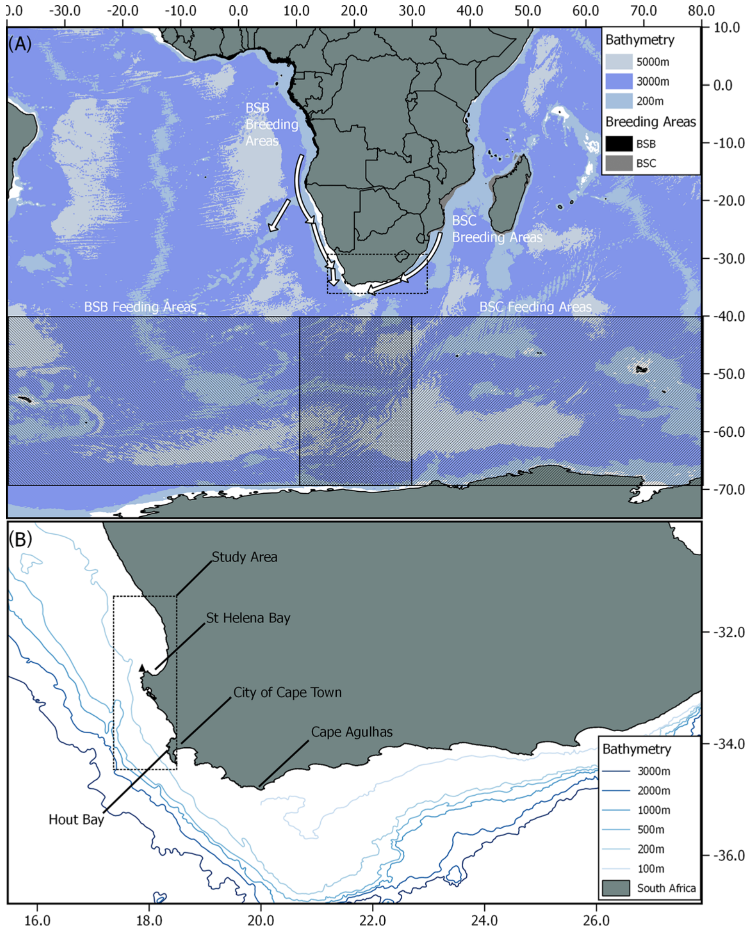

Fig. 1. (Color online) (A) Map showing the location of known breeding and feeding grounds for BSB and BSC humpback whales on the shelf waters of West Africa and East Africa and associated islands. White arrows show typical migration routes used by animals passing around the coast of southern Africa en route to Southern Ocean breeding grounds (offshore migration routes not shown). Box shows zoomed in area in lower map. (B) Map of south-western South Africa showing the study area, locations referred to in text including the recording location indicated by a black triangle near St Helena Bay.

in mid- to low-latitudes, with estimated group sizes of up to 200 individuals reported from western South Africa (Findlay *et al.*, 2017). It may be that some BSB humpback whales suspend their southward migration to feed in South African waters in the spring and summer months (Best *et al.*, 1995). Alternatively, feeding aggregations may comprise a non-breeding migration of young, physically immature animals or represent the immigration of young non-breeding animals from IWC Breeding Stock C (BSC) during their southward migration (Findlay *et al.*, 2017, Fig. 1).

Here we investigate an occurrence of humpback whale song recorded at this mid-latitude feeding ground in late spring (November). Humpback whale song was first described by Payne and McVay (1971) and is recognised by the structural repetition of sound features. The most basic are song units (uninterrupted sounds) which are stereotyped and combined to form a phrase. An unbroken sequence of similar phrases is termed a theme, with several distinct themes combining to form a song. We identified song following this widely recognised paradigm. This work forms part of a larger project investigating the acoustic behavior of humpback whales in western South Africa.

2. Methods

Acoustic and surface behavioral data were collected in South Africa during 2015 and 2016 as part of an ongoing project to investigate the social (i.e., non-song) sounds of humpback whales. Several small research and commercial vessels were used to locate whales during both dedicated scientific surveys and trips to undertake commercial film work. Super-groups of humpback whales were located off the west coast of South Africa within a 180 km range from St Helena Bay (32° 38′ S, 17° 54′ E) in the north to Hout Bay (34° 05′ S, 18° 19′ E) in the south from October to February (Fig. 1). Throughout this study, recordings were made using either a HTI-96-MIN (High Tech

Inc.) dipping hydrophone (frequency response: 2 Hz to 30 kHz, sensitivity: −165 dB re: 1 V/μPa, deployment depth: 3–6 m, 24 bit .wav files) connected to a SONY D50 (JAP) digital recorder or an Ocean Instruments Sound Trap 300 (NZ) autonomous underwater recorder (frequency response: 20 Hz to 60 kHz ± 3 dB, sensitivity: −171.5 dB re: 1 V/μPa, deployment depth: 10 m, saved as 16 bit compressed SUD files which convert to .wav files without loss). In both cases, a sample rate of 96 000 Hz was applied. Additional recordings were collected using the dipping hydrophone setup during focal follows with smaller groups of humpback whales (one to four animals) during scientific research surveys in the near short waters close (<20 km) to Cape Town. In general, we aimed for 1 h of acoustic recording per day in the vicinity (<100 m) of humpback whales. Decisions to start and end recordings were based primarily on the proximity to whales, group movement, and environmental conditions, rather than any underwater acoustic cues.

Recordings were down-sampled to a 22.05 kHz sampling rate for analysis. Aural and visual inspection of the recording spectrogram generated in Adobe Audition CS5.5 took place to identify the occurrence of humpback whale song and non-song social sounds within the dataset. All sounds attributed to humpback whales were manually identified and verified by the authors (T.G. and M.S.). The start and end time of all sounds and the quality was visually assessed based on the relative signal-to-noise ratio (SNR) and whether or not the sound was masked by concurrent, overlapping noise (often attributed to surface water noise). Song was identified in one recording (November 1, 2016) which forms the basis of this report. From this, song units, phrases, and themes were identified. We measured the received level of selected song units within the recording to infer possible movement (i.e., toward or away from the research vessel) during the recording session from consistent shifts in song intensity. Song units were measured using the selection function in Raven Pro 64 1.5 (Cornell Bioacoustic Research Program, 2011) and the relative received power of song units was expressed as dB_{re} 1 dimensionless sample unit.

3. Results

In total, we collected acoustic data from 20 encounters with humpback whales over 16 days between October 2, 2015 and November 4, 2016. From these, 12 encounters were with super-groups of humpback whales, of which eight groups were engaged in feeding. Encounters with super-groups were limited to the months of October and November, with additional recordings from smaller groups of whales (two to four animals) made in February.

The humpback whale song was recorded on one occasion in late spring (November 1, 2016, 9:13 am onwards) using the HTI-96-MIN hydrophone configuration. The recording was made in the presence of approximately 25 feeding whales, located 6 km from shore (32° 40.71′ S, 17° 52.05′ E) and in a water depth of approximately 35 m. In total, 953 sounds attributed to humpback whales were identified within this 56 min 56 s duration recording, of which 464 (49%) were identified as units involved in song and 74 (8%) were identified as possible song units. Non-song social sounds were detected throughout the recordings, with 179 (19%) social sounds identified, including wops, grumbles, and tonal sounds which have been described in other humpback whale populations (Dunlop *et al.*, 2007). Although poor resolution (low SNR, or masked), the majority of the remaining 236 (25%) uncategorized sounds were also likely to be social sounds, as song units were stereotyped in form and temporal production, making them straightforward to identify even at poor resolution.

Song units arranged into phrases were clearly visible throughout the available recording duration (engine noise lasting 10 min 56 s intersects the recording at time 13 min 40 s). A conservative estimate of nine different types of song unit were identified (named numerically) with short, more variable sub-units produced in a sequence identified for unit 4 (Fig. 2). Units were organized into seven song phrases (Fig. 2, Mm. 1–Mm. 7), which were organized into themes A to G (Table 1). Of these, phrase A (Figs. 2 and 3) was recorded with the greatest clarity and was highly stereotyped (Fig. 3).

Mm. 1. Song phrase A. This is a file of type .wav (525 KB).
Mm. 2. Song phrase B. This is a file of type .wav (525 KB).
Mm. 3. Song phrase C. This is a file of type .wav (525 KB).
Mm. 4. Song phrase D. This is a file of type .wav (525 KB).
Mm. 5. Song phrase E. This is a file of type .wav (525 KB).
Mm. 6. Song phrase F. This is a file of type .wav (525 KB).
Mm. 7. Song phrase G. This is a file of type .wav (589 KB).

The relatively short recording duration and associated noise interference (wave and engine) obstruct a full sequence analysis of themes and complete song structure. An

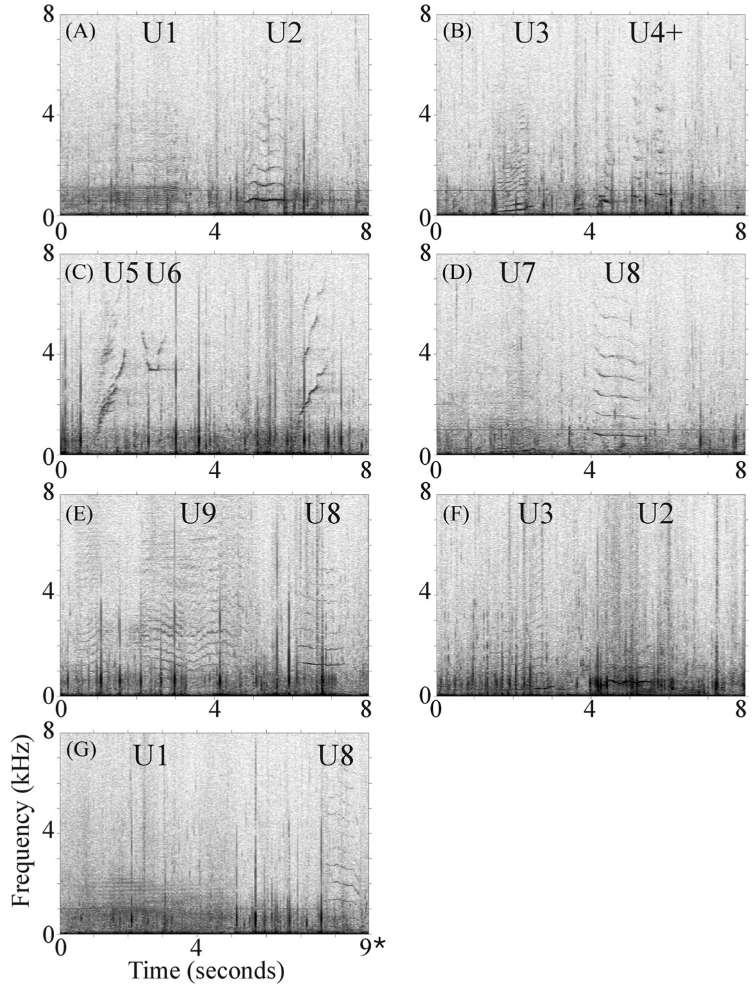

Fig. 2. Stereotyped song phrases were observed throughout the recording of humpback whales on November 1, 2016, which were repeated to form themes [(A)–(G)]. Units are identified numerically on each spectrogram. Unit 4 consists of a series of subunits, indicated by a "+" sign. Spectrograms are displayed on a standard *x* axis time scale of 0–8 s, apart from G which is on a 0–9 s time scale, as indicated by "*." Frequency range shown 0–8 kHz, sampling rate 22.05 kHz, fast Fourier transform (FFT) 2056.

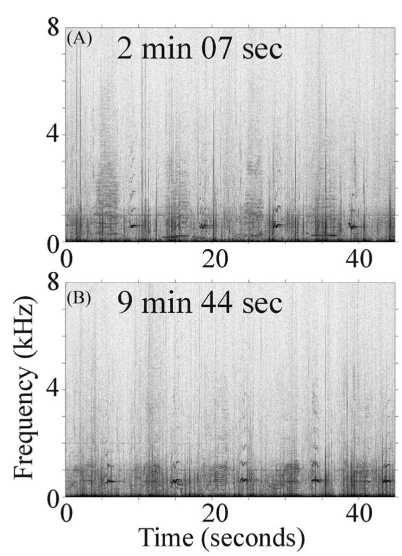

Fig. 3. Examples of repeated phrases forming theme A, which was highly stereotyped and clearly observed throughout the recording. High stereotypy in unit frequency and temporal production are illustrated here in examples (A) and (B) with the recording time relative to session start time indicated. Spectrograms are displayed on a standard *x* axis time scale of 0–45 s. Frequency range shown 0–8 kHz, sampling rate 22.05 kHz, FFT 2056.

Table 1. Summary statistics for the song components, detailing the sample size for each theme identified in the 57 min recording, range in the number of phrases repeated per theme, and typical unit sequence for the phrase. Unit ID numbers in parentheses indicate units which were likely to be repeated and the order.

Theme code	Sample size (no.)	Phrases per theme (range min-max)	Typical unit sequence
A	9	5 to 11	1,2 (2)
B	7	1 to 17	3,4 (4)
C	1	11	5 or 5,6
D	2	2 to 4	7,8
E	5	2 to 8	9 (9),8 (8)
F	7	2 to 8	3,2
G	3	2 to 3	1,8 (8)
Unpatterned	20	2 to 18	n.a

analysis of theme order revealed no consistent patterning in transitions between one theme and the next. However, we did note that between stereotyped themes, there often occurred "unpatterned themes" (Payne and Payne, 1985) whereby the stereotypy in phrase production ceased and the units appeared less stereotyped and somewhat jumbled in presentation. Unpatterned themes contained a variable number of units (2 to 18). Following this, the next theme with stereotypy in unit and phrase production was reinstated.

We did not observe or acoustically localise a singing whale, consequently we cannot determine with certainty whether it was located within the focal super-group and actively feeding, or whether we were coincidentally recording an outlying whale engaged in another type of behavior. However, song units were non-overlapping, stereotyped in structure and temporal production, and relatively consistent in received level throughout the recording, indicating that they originated from one animal. For example, song unit 2 (a tonal call with a fundamental frequency between 600 and 800 Hz) was the most commonly found unit and dominated the session, being clearly identified 123 times. This unit was recorded with a high received level SNR throughout recording, with a relative peak power which changed little during the recording. At 10 min 18 s, i.e., close to the recording start, the received peak power was 70.9 dB and at 43 min 41 s, i.e., close to the recording end, it was 70.0 dB. Overall, the relative peak power of song units ranged between 41.7 and 71.1 dB. Social calls were identified throughout the recording and these occasionally overlapped the song units in time and sometimes frequency, in an unsystematic manner.

4. Discussion

Here we report the occurrence of song at a mid-latitude feeding ground in South African waters. In general, the production of song in humpback whales is strongly linked to breeding behavior, with structured song most ubiquitous at low-latitude, warm water breeding grounds (reviewed in Helweg *et al.*, 1992). However, we recorded song in late spring, after the completion of the breeding season in Angola and Gabon, and in an area where breeding is not thought to occur (Barendse, 2011; Findlay *et al.*, 2017). Although singing during migration toward feeding grounds (e.g., Norris *et al.*, 1999) and on feeding grounds (e.g., Stimpert *et al.*, 2012) is well documented, this is the first time it has been documented in western South Africa.

Humpback whale song can travel several kilometres (Helweg *et al.*, 1992; Frankel *et al.*, 1995; Clark and Clapham, 2004), with distant song detected up to hundreds of kilometres away (Risch *et al.*, 2012; Gong *et al.*, 2014). On breeding grounds, singing males are usually solitary and stationary at depths of 15 to 25 m (Au *et al.*, 2006). Our recording could therefore originate from a lone singing whale located a distance from the super-group. Humpback whales have also been recorded singing while actively migrating at speeds of up to 7 km per hour with faster bursts of movement possible during song production (Noad and Cato, 2007). However, the relatively constant received level of the most ubiquitous song unit (unit 2) indicates the animal did not move a long distance during the nearly 1 h of recording. Acoustic tagging studies indicate that humpback whales may continue to sing whilst engaging in active feeding, including diving deeper than 100 m and lunging (Stimpert *et al.*, 2012). However, Stimpert *et al.* (2012) acknowledged that the song they documented may have originated from a close by conspecific and not an actively feeding animal. Consequently, the singing animal we recorded may have been located within the super-group and engaged in feeding activity, singing from a stationary position or moving within the vicinity of the actively feeding whales.

Complete analysis of the song was not possible due to the relatively short recording duration and interruption due to boat repositioning. However, our data could successfully be analysed within the song framework first proposed by Payne and McVay (1971) of units, phrases, and themes. In addition, we identified unpatterned themes (Payne and Payne, 1985). A less stereotyped form of song has been reported from feeding grounds (Stimpert *et al.*, 2012), where unidentified phrases, periods of poorly refined song (i.e., no obvious pattern), and periods of non-song production have been documented. In our recording, the high incidence of unpatterned themes and the apparent inconsistencies in theme transitional order may indicate lower stereotypy in song on this migration and feeding area compared to song on the breeding grounds. Additional high quality recordings obtained from more individuals will help better elucidate the repertoire of song phrases and song structure from individuals on the west coast of Southern Africa.

Song production at high latitude feeding grounds may facilitate the cultural transmission of acoustic signals between stocks (Garland *et al.*, 2013), with song novelty thought to convey a breeding advantage to an individual (Noad *et al.*, 2000; Parsons *et al.*, 2008). Findlay *et al.* (2017) recently suggested that super-groups of whales on the west coast of South Africa may contain humpback whales from BSC, usually located on the east coast of South Africa. If so, a detailed comparison of song structure from BSB and BSC together with song recorded in the presence of super-groups may provide information on the origin of these feeding whales. These data are currently being obtained for such a comparison.

In explaining the occurrence of song on feeding grounds, Clark and Clapham (2004) suggest that breeding extends geographically and temporally into feeding grounds in spring and early summer. Elevated testosterone levels could also promote singing activity into shoulder seasons (spring and autumn) (Clark and Clapham, 2004; Vu *et al.*, 2012), which could explain singing in the absence of clear breeding behaviour or opportunities. The potential for animals to switch between feeding and display behaviour at feeding grounds has been further highlighted by tagging studies (Stimpert *et al.*, 2012). Although we did not observe mating behaviour, the possibility that song is used within a breeding context by animals engaged in feeding or associated with prey patches on the west coast of South Africa cannot be discounted. The suggestion that whales forming super-groups may be young animals (Findlay *et al.*, 2017) is not counter to the observation of singing activity as Herman *et al.* (2013) provide evidence that some immature males also sing. However, if singing does originate from the immature animals observed in super-groups, this could explain the lack of observed breeding behaviour.

Understanding why we detected song at this mid-latitude feeding area requires considerable further information on the identity of singing whales, the prevalence and context of singing behavior, as well as the social dynamics of animals aggregated within super-groups or associated with them. Further research is underway to address these questions for humpback whales utilising waters on the west coast of South Africa.

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