

**Singing in South Africa: Monitoring the occurrence of humpback whale
(*Megaptera novaeangliae*) song near the Western Cape**

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Abstract

Humpback whales (*Megaptera novaeangliae*) are highly vocal, producing a wide repertoire of sounds often organised into song. Song is prolific at breeding sites but also documented along migration routes and at feeding sites, including along the west coast of South Africa (28° to 34°S). Here we examine the occurrence of humpback whale song within False Bay, South Africa, using intermittent recording periods from moored hydrophones spanning September 2016 to January 2018. Recordings from four locations were scrutinised for humpback whale vocalisations using long-term spectral averages (LTSAs). In total, 7205 hrs were examined, with song identified in 3% (211 hrs) of recording hours. Song was exclusively documented in September and October 2016 and was more prevalent at the most westerly sites. Diel patterns of song presence were modelled, showing the likelihood of detection was higher in the early morning and late evening (GAM: $p < 0.05$). On 15 occasions, two or more singers were detected with temporally overlapping song components. These results indicate prevalent, albeit seasonal, song production by humpback whales off the coast of South Africa and highlight the utility of passive acoustic monitoring to indicate their presence and behaviour, and potential population linkages in the region.

Keywords

Megaptera novaeangliae, humpback whale, acoustic monitoring, song, Western Cape, migration

Introduction

Humpback whales produce a wide variety of sounds broadly divided between internally produced ‘vocalisations’, such as song or non-song calls, and surface generated noises, such as tail slaps (Au et al. 2006; Dunlop et al. 2008; Darling, 2015; Fournet et al. 2018a). Of their vast vocal repertoire, humpback whales are most well-known for the complex, often long-lasting songs that males produce abundantly during the breeding season (Clark and Clapham 2004; Payne and McVay 1971). While historically believed to only occur in the breeding season, singing behaviour by male humpback whales has been increasingly reported outside of the breeding season during migration and at feeding locations (Noad et al. 2000; Stimpert et al. 2012; Gridley et al. 2018). Thus, monitoring song occurrence could provide insight into whale occurrence, movement patterns and behaviour throughout their range.

Although the precise function of humpback whale song still remains uncertain (Herman 2017; Darling et al. 2019), the structure of song has been well studied (Au et al. 2000; Parsons et al. 2008; Cholewiak et al. 2013). The first description of song was given by Payne and McVay (1971) where it was described as the structured repetition of sound features. The shortest continuous sound is termed a ‘unit’, several units sung together form a ‘phrase’, repeated phrases form a ‘theme’, and several distinct themes combine to form a ‘song’ (Payne and McVay 1971). Within a population and a time period, humpback whale males will converge on a song type (Sterelny 2009; Garland et al. 2011) through a process thought to be mediated by vocal production learning and cultural transmission (Janik 2009; Garland et al. 2013; Herman 2017). Therefore, inter-population variation in song patterns (Noad et al. 2000; Garland et al. 2011) is often present and can help identify separate populations or stocks (Darling et al. 2019). However, the sequence, structure, and even duration of songs sung within a population are constantly being modified (Winn and Winn

1978; Payne and Payne 1985; Mercado et al. 2003; Vu et al. 2012; Allen et al. 2018, Rekdahl et al. 2018). Populations occurring in the same oceans may show some similarity in their song due to some level of spatial overlap in their range where song may be exchanged (Rekdahl et al. 2018, Darling et al. 2019).

Humpback whale song is both well-described, stereotyped and generated at high source levels, making it an obvious and easily identifiable sound in long-term recordings made within acoustic range of singing animals. As such, passive acoustic monitoring (PAM) is a powerful tool for detecting the seasonal presence of these animals using song occurrence (Stafford et al. 2007; Stimpert et al. 2011). In the past, acoustic monitoring has detected singers on their migration route between feeding and breeding grounds (Clark and Clapham 2004; Noad and Cato 2007; Vu et al. 2012; Garland et al. 2013) and has been used to determine whether different breeding populations are using the same feeding grounds (Hazevoet et al. 2011).

Humpback whales occurring off the west coast of Africa are designated as Breeding Stock B (BSB) by the International Whaling Commission (IWC 1998), which is made up of two stocks, BSB1 who breed in the Gulf of Guinea from Angola northwards, and BSB2 which migrate past and feed off western South Africa, but whose breeding site remains unknown (Best 2011). Despite a large amount of research effort to date and the accepted consensus by the International Whaling Commission (IWC 2012), the exact nature of the stock structure of humpback whales along the western African coast remains uncertain. Although some level of feeding in the Benguela ecosystem has long been known (Best et al. 1995; Findlay and Best 1995; Barendse et al. 2010, 2011), there has recently (2011 onwards) been a rapid increase in the numbers of whales observed forming dense feeding aggregations

of well over 20 animals per group (Findlay et al. 2017) with feeding whales most abundant from October to February (Barendse et al. 2011, Findlay et al. 2017). It has previously been assumed that whales feeding in the southern Benguela represent some, or all, BSB2 individuals which suspend their southward migration to feed while *en route* to the Southern Ocean (Best et al. 1995). However, more recent data from feeding aggregations off west South Africa do not support this. Feeding aggregations appear to comprise mainly a non-breeding component of the population made up of young, physically immature animals and may even include a component of young non-breeding animals from Breeding Stock C, originating from the east of southern Africa, during their southward migration (Findlay et al. 2017).

In this study we monitor the occurrence of humpback whales and specifically singing whales, using song recorded from four coastally located moored hydrophones situated in False Bay, on the south-west coast of South Africa. We quantify the amount of song (measured as hours with positive song detection) as well as seasonal and spatial variation in song detected at four sites. We note basic song features such as the duration, signal to noise ratio (SNR) and occurrence of simultaneous singers which provides indicators about the possible location of singing whales. This is the first study to investigate humpback whale singing behaviour from multiple acoustic receivers in South African waters and provides an important baseline from which future acoustic monitoring programmes for this species can be developed.

Methods

Underwater acoustic recordings were made using autonomous recorders (Ocean Instruments SoundTrap 300, New Zealand, frequency response: 20 Hz to 48 kHz \pm 3 dB, sensitivity: between 120 – 121 dB re: 1V/1 Pa). Instruments were deployed at four sites around False Bay South Africa, namely Smitswinkel Bay (SM), Fish Hoek (FH), Strandfontein (ST) and Rooi Els (RE) (Figure 1). All recording sites were located in coastal waters within two kilometres of shore and at depths ranging from 14 to 25 m. The recording period spanned September 2016 to January 2018, including several recording periods of simultaneous recordings across sites (Table 1).

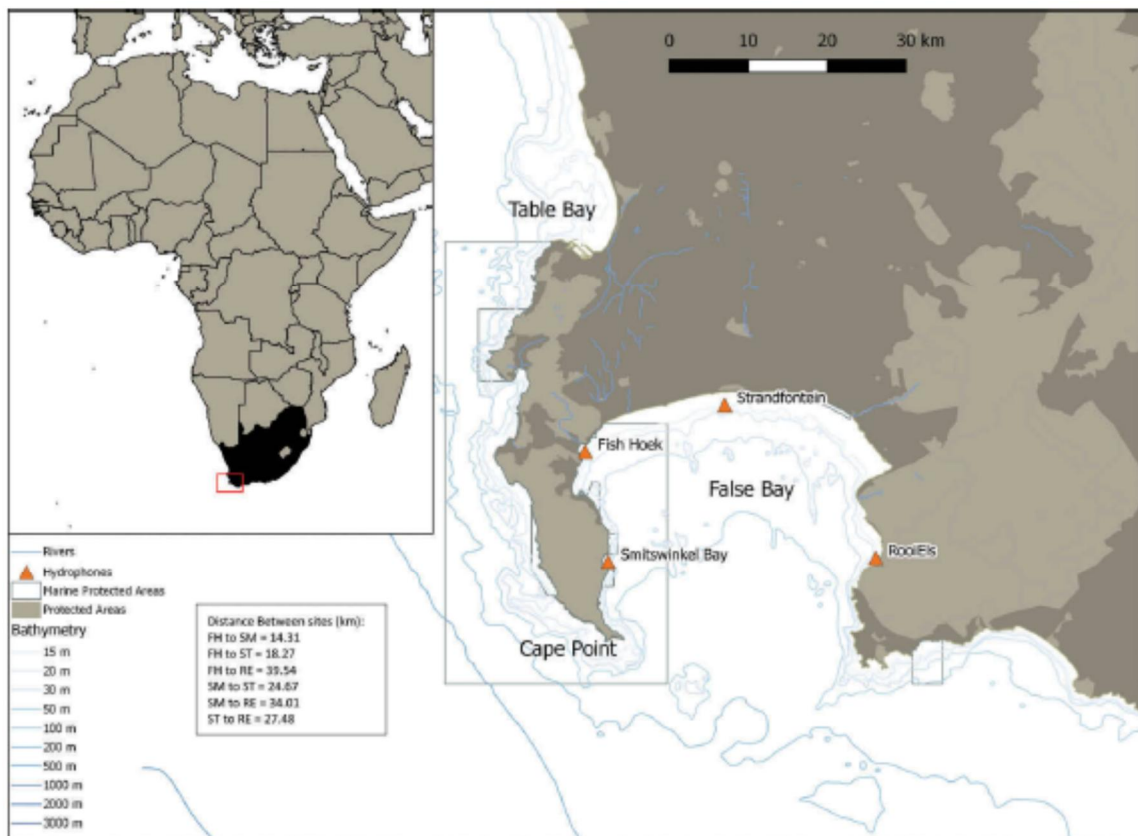
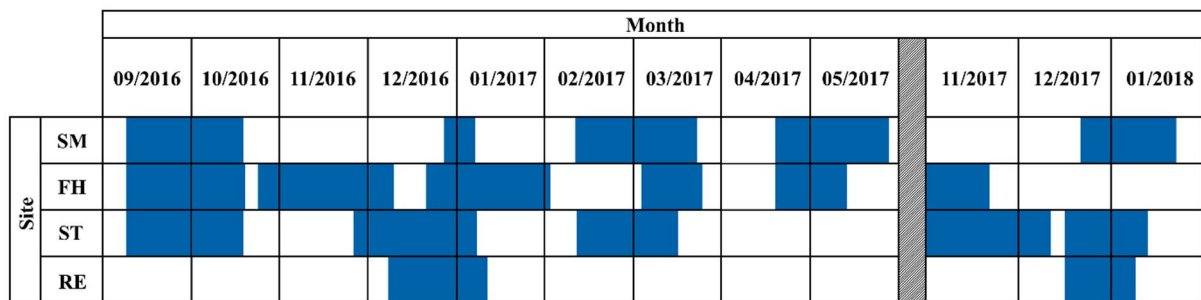


Figure 1. Map of False Bay in South Africa showing the location of three hydrophones used in this study (orange triangles). Distances between hydrophones are shown. Bathymetry and Marine Protected Areas (MPAs) are also indicated.

Table 1. Gantt chart summarising recording effort (blue) from four sites within False Bay from September 2016 to January 2018. SM: Smitswinkel Bay, FH: Fish Hoek, ST: Strandfontein, RE: Rooi Els. Only the first deployments for SM (09/09/2016 – 19/10/2016), FH (09/09/2016 – 21/10/2016) and ST (09/09/2016 – 18/10/2016) recorded humpback whale vocalisations and were analysed in this study. During the period between May and November 2017 (crosshatch) no hydrophones were deployed.



Hydrophones were deployed on fixed moorings with sub-surface buoys, with the instrument attached at 15 m above the bottom or at the mid-water column in shallower deployments, to keep the instrument away from kelp and reef-associated noises. Recordings were made at a sampling rate of 96 kHz and saved as 16-bit compressed SUD files which convert to .wav files using equipment specific software (<http://www.oceaninstruments.co.nz/>). The hydrophones were deployed for a project focusing on coastal dolphin movements and the recording schedule (duty cycle) was optimised for detecting dolphin presence while maximising deployment duration such that recordings were made for 5 min and off for 5 min. This generated six five-minute files per recording hour, with 30 min of recording effort spread across an hour.

Long-term spectral averages (LTSA) were created using the MATLAB based programme Triton (<http://cet.uscd.edu/>, 5 sec time resolution and 50 Hz frequency) and used to visualise the data. Triton generates an LTSA which can be used to view a long time series of acoustic recordings on one screen (from hours to weeks or more) with the option of

expanding the view to zoom in on times of interest. All occurrences of song were identified manually. LTSA's were viewed and scanned at 0.5 hrs resolution looking in the frequency band 0 to 3 kHz (30 dB contrast, jet view) for the occurrence of humpback whale song. Songs were defined in accordance with the definition provided in Payne and McVay (1971), i.e. a stereotyped set of units sung in a specific order to create phrases, which were then repeated two or more times to generate themes. Probable song seen in the LTSA was inspected in detail using the 'Expand' feature in Triton to generate a standard spectrogram view. For this, spectrograms were created with a time window of 30 sec and frequency band of 0 to 3 kHz, with a Fast Fourier Transform (FFT) of 8192, 75% overlap, Hanning window, brightness at 30 dB and contrast of 100%. The present study did not focus on song structure, but rather the presence or absence of any humpback whale song. Therefore, song was defined as a stereotyped vocalisation, including song fragments as defined by Kowarski et al. 2019 (containing at least one repeated phrase). Once song was confirmed the song session duration was calculated. Sessions were defined as continuous periods of song separated by 1 hr or more of silence. The recording duty cycle prevented identification of separate song within song sessions and limited analysis applied to the data. A single song was assumed to be sung by the same singer if there were no overlapping of sound units and the stereotypy of the song was maintained throughout the song session. Overlapping songs for concurrent singers were identified on occasions when units and phrases overlapped in time (Figure 2)

Spectrograms were investigated to determine if the song was simultaneously recorded on two or more recorders located at the different sites. On a song by song basis, each song was cross-checked for its entire duration against the same recording period at another site. To match songs, the frequency modulation pattern of each potential song unit was compared within the context of the phrase seen, and unit by unit matching for at least one minute of the

recording was necessary to confirm a match and to account for potential clock drift between instruments.

Diel patterns in song occurrence were investigated for Smitswinkel Bay where song sessions were most frequently detected. Song presence-absence was counted for every hour of every day when the acoustic recorder was active. Periods of song separated by more than one hour (30 minutes of recording time) were treated as separate song sessions. Presence counts for each hour (00:00 to 23:00) were then divided by the total number of days that the recorder was active (41 days) to determine the proportion of song present for each hour of the day over this period. The influence of hr on song presence-absence was investigated using a binomial generalized additive model (GAM) analysis, completed in RStudio (R Core Team 2019; RStudio Team 2015) using the ‘mgcv’ (Wood 2017) and ‘nlme’ (Pinheiro et al. 2019) core packages. Presence-absence were further grouped into five broader day periods within the day using time information from Time and Date.com (<https://www.timeanddate.com/sun/south-africa/cape-town>). The 24hr day was divided into Dawn (nautical dawn to sunrise), Morning (sunrise to solar noon), Afternoon (solar noon to sunset), Dusk (sunset to nautical dusk) and Night (nautical dusk to nautical dawn, when sun altitude is between 0° and 12°). Due to the varied nature of these times during the study period, time intervals were averaged to determine a generalised start and end time for an average day resulting in Dawn = ~1 hr, Morning = ~ 6 hr, Afternoon = ~6 hr, Dusk = ~1 hr, and Night = ~10 hr). Presence-absence were then determined for each day period and modelled using a binomial GAM (methods and packages as above) to determine potential diel patterns.

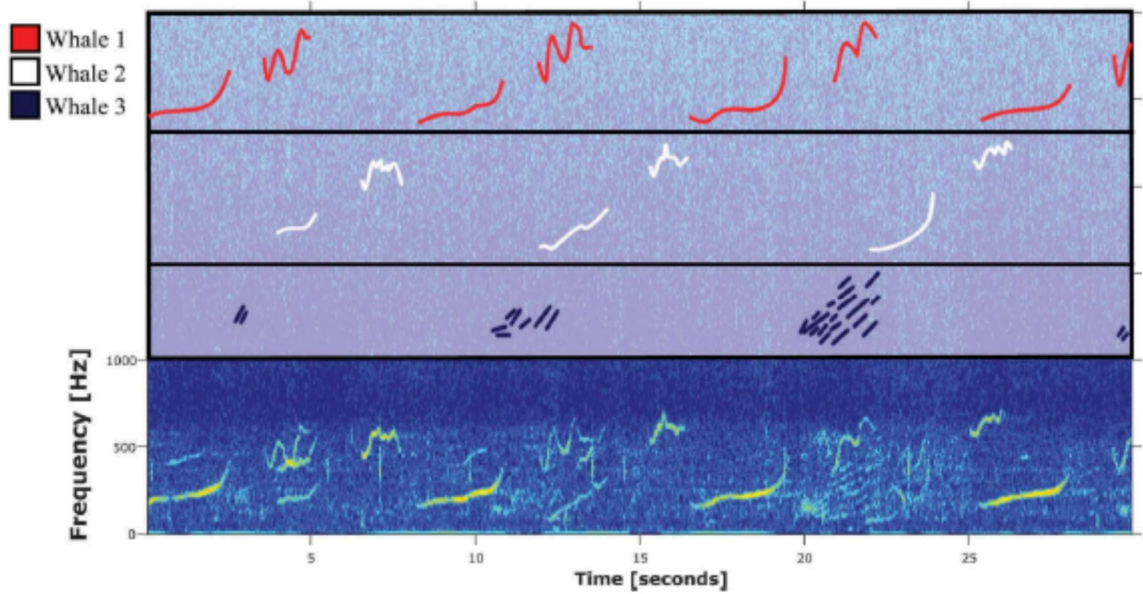


Figure 2. A schematic of a spectrogram with multiple whales singing simultaneously clarifying overlapping phrases recorded at Smitswinkel Bay at 04:42:24 am on 13/09/2016. Song from three different simultaneous singers overlap on the spectrogram and have been traced and mirrored in a schematic (black boxes) in the top half of the spectrogram to clarify overlapping phrases. The first singer (traced in red) has a much higher signal to noise ratio compared to the second (white) and the third (dark blue).

Non-song calls were identified, many of which matched previously identified non-song calls from this population (Silva 2017; author's unpublished data) and others (Dunlop et al. 2008; Stimpert et al. 2011; Rekdahl et al. 2017; Fournet et al. 2018a). These were easily distinguishable from song as their production was non-stereotyped in comparison to the characteristic repetitive structure of song which lasted up to several hours (Figures 3 and 4; Payne and McVay 1971).

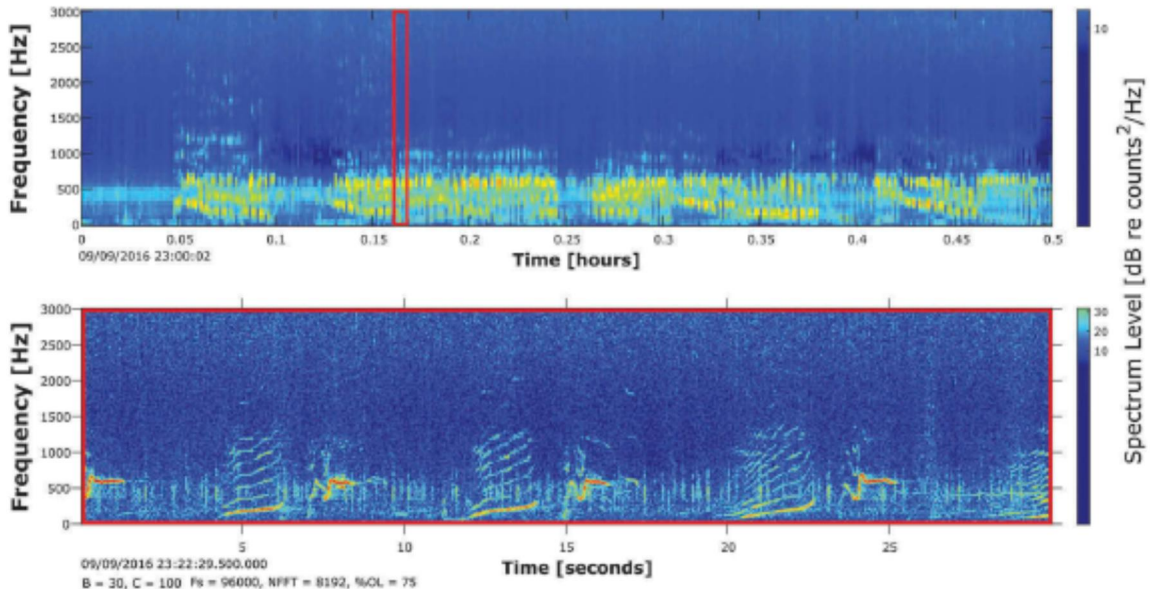


Figure 3. Long term spectral average (LTSA) of probable song (top panel). LTSA's were created using 5 sec time resolution and 50 Hz frequency resolution. These were viewed with a 0.5 hr time window, scanning the 0 to 3 kHz frequency bandwidth (LTSA viewer settings: 30 dB contrast, jet view). The area outlined in red in the LTSA is confirmed as likely song by identification of repeated phrases (bottom panel) in the spectrogram view (spectrogram settings: time window of 30 sec, frequency band 0 - 3 kHz, FFT = 8192, 75% overlap, Hanning window, brightness and contrast set to 30dB/ 100%).

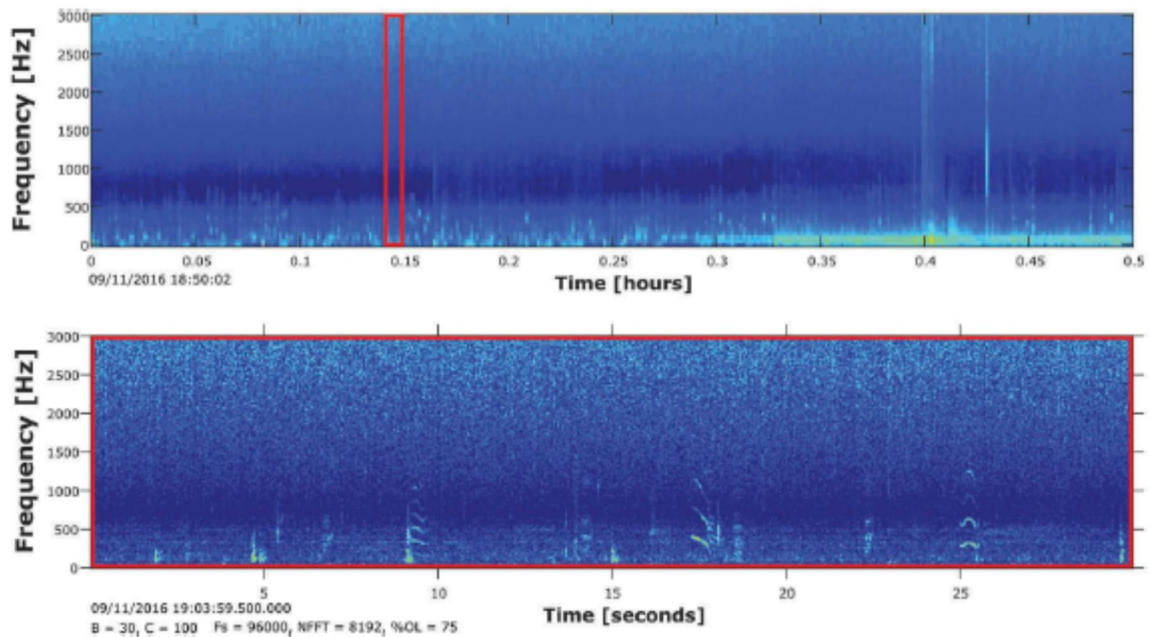


Figure 4. LTSA of probable non-song calls (top panel). A 30 sec spectrogram of the area in red reveals likely non-song humpback whale calls (bottom panel).

Results

Acoustic data recorded in False Bay at all four sites totalled 7205 hrs over 606 recording days from September 2016 to January 2018 (Table 2). Recording effort varied considerably between the locations (range 60 to 201 days, 701 to 2371 hrs), with the greatest effort towards the southwestern side of the bay (Fish Hoek) and least at the eastern side (Rooi Els). Simultaneous recording effort at all four sites was rare, due to logistical constraints of hydrophone deployment and intermittent recording faults. For Rooi Els, the eastern-most location, only two recording periods were possible in December 2016 to January 2017 and December 2017 to January 2018. However, for the three western sites recording effort was reasonably spread across recording dates and there were 10 simultaneous recording days.

Table 2. Recording effort per site together with information on location, song detection (song positive days and hours), and song characteristics (number and duration)

| Location | Deployment location (lat and long) | Recording effort (days) | Recording effort (hrs) | Song positive days (%) | Song positive hrs | No. of song sessions | Average song duration (hrs \pm SD) |
|-----------------|------------------------------------|-------------------------|------------------------|------------------------|-------------------|----------------------|--------------------------------------|
| Smitswinkel Bay | -34.267°S 18.147°E | 162 | 1885 | 29 (96.7) | 156 | 40 | 3.91 (\pm 2.87) |
| Fish Hoek | -34.141°S 18.444°E | 201 | 2371 | 14 (46.7) | 44 | 19 | 2.32 (\pm 2.55) |
| Strandfontein | -34.088°S 18.636°E | 183 | 2244 | 4 (13.3) | 11 | 4 | 2.76 (\pm 1.04) |
| Rooi Els | -34.263°S 18.847°E | 60 | 701 | 0 (0) | 0 | 0 | 0 (\pm 0) |
| Total | | 606 | 7201 | 30 (100) | 211 | 63 | 3.35 (\pm 2.79) |

Overall, song was identified on 5% ($n = 30$) of recording days and 3% ($n = 211$) of recording hours with a total of 63 separate song sessions detected. However, the occurrence of song differed substantially between sites, with occurrence decreasing from west to east (SM = 40 sessions, FH = 19 sessions, ST = 4 sessions; RE = 0 sessions). The greatest song occurrence (in terms of song positive days, hours and number of song sessions) was found at the most south-westerly site, Smitswinkel Bay, while no song was recorded at the most easterly site, Rooi Els, where recording effort was lowest (Table 2). However, the pattern in declining detection of song from west to east remains clear even if only the three sites with higher recording effort are considered (Figure 5). The longest duration of song presence recorded during this study was 13 hrs 4 min at Smitswinkel Bay and song durations were generally longer in the west than the east (Figure 5). Smitswinkel Bay and Fish Hoek showed no significant difference in their song duration (Mann-Whitney U test $p = 0.6$), however, on average songs sessions recorded at Smitswinkel Bay ($3.9 \text{ hr} \pm 2.9 \text{ SD}$) were longer than those recorded in Fish Hoek ($2.3 \text{ hr} \pm 2.6 \text{ SD}$).

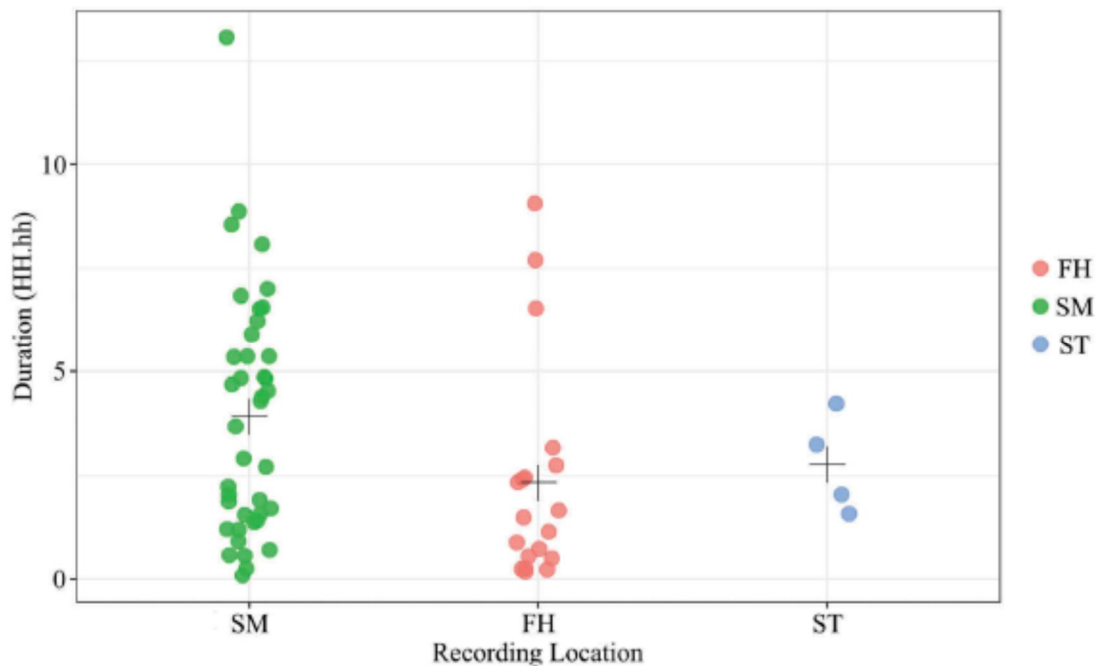


Figure 5. Duration of songs recorded at three locations (SM = Smitswinkel Bay, FH = Fish Hoek, ST = Strandfontein). The (+) indicates the mean value for each category. Points were adjusted to remove overlap.

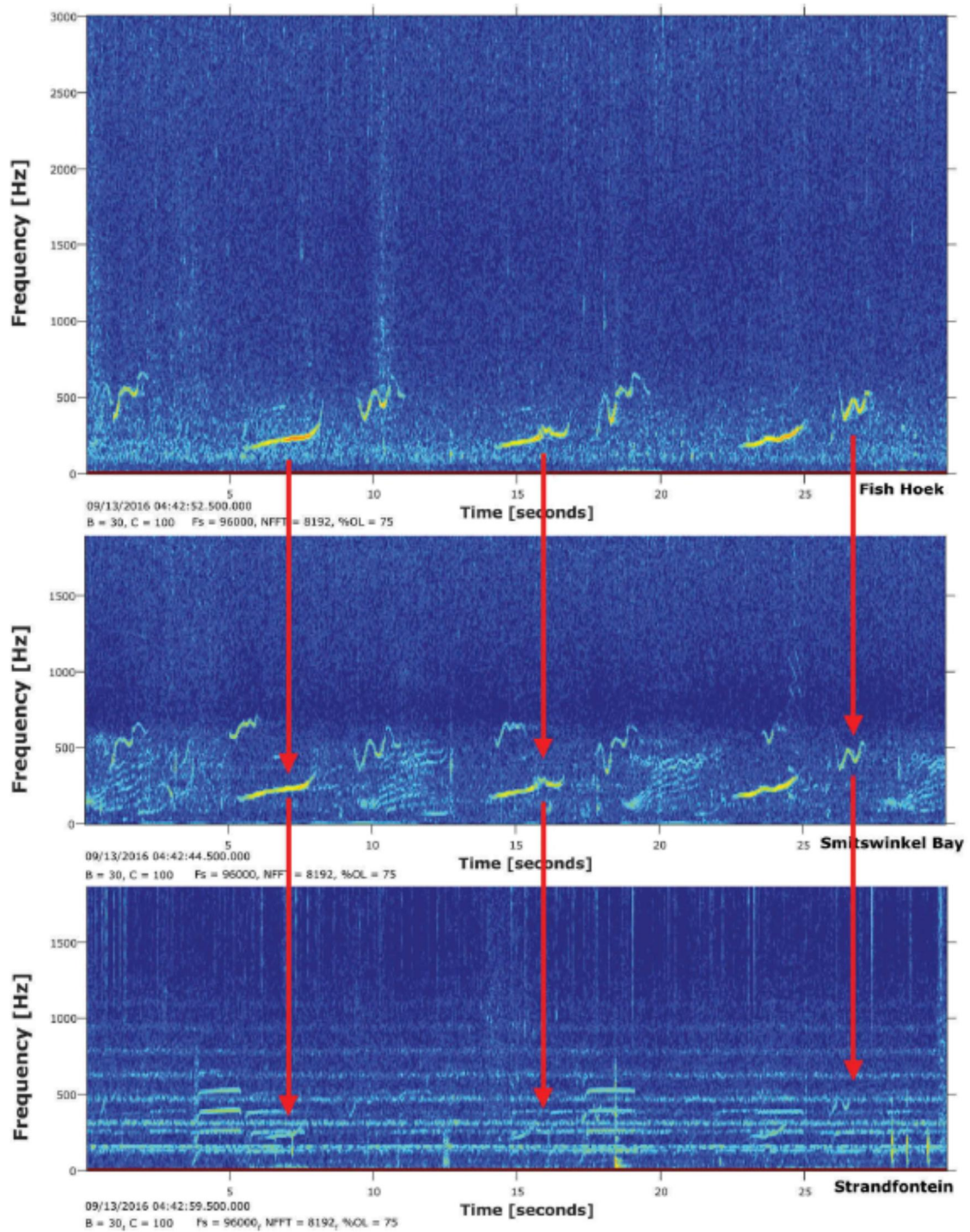


Figure 6. Simultaneous song recorded at Smitswinkel Bay (top panel), Fish Hoek (second panel), and Strandfontein (bottom panel), 10 and 46 seconds later respectively. Strandfontein is roughly 26km from Smitswinkel (the presumed source) within False Bay. Arrows show matched identifying points.

Consistent non-overlapping units indicated that in most cases, only a single singer was likely to be producing each song. However, on 15 occasions (24% of song sessions),

there was strong evidence for two, in one instance three, individuals singing simultaneously as song units overlapped in time (Figure 2). Of these 15 instances, 14 were seen in Smitswinkel Bay and one in Fish Hoek.

Song was never detected on all four recorders simultaneously as song was not detected at the Rooi Els site. However, on 11 separate occasions, song was detected simultaneously on the three western hydrophones (Figure 6). In all but one instance of simultaneous detection, song was initially detected at Smitswinkel Bay then Fish Hoek several seconds later (average $19.3 \pm \text{SD } 10.6$ sec). In only one instance was song recorded at Fish Hoek first and then at Smitswinkel Bay 27 sec later. These sites are separated by a 14.3 km. On the 13th and the 19th of September, song was detected at all three western sites, first at Smitswinkel Bay, then at Fish Hoek (7 sec later) and finally at Strandfontein (15 sec later, 24.7 km from Smitswinkel Bay, Figure 6). Unit by unit matching of the frequency modulation pattern and sequence of units detected across hydrophones supports the finding that song transmitted across False Bay. Further, the song was detected simultaneously at different hydrophones with a time lag contingent with the time taken for sound to propagate within the environment (see Figure 6). Song detected at Smitswinkel Bay and Fish Hoek often showed instances of very clear and loud song, with high SNR, while song recorded at Strandfontein was often faint with low SNR. Most songs recorded would start faintly and gradually become louder and clearer with an increase and subsequent gradual reduction in signal to noise ratio, although, on several occasions, an abrupt start or finish of a song occurred within a continuous 5 min recording.

Humpback whale song was recorded only in September (163 positive hrs, 77% of total song positive hrs) and October (48 positive hrs, 23% of total) in 2016 indicating a strong

seasonal trend in occurrence coinciding with austral spring. The number of hours per day that song was detected ranged from zero to 17 hrs (Figure 7). A detailed assessment of the diel patterns in song occurrence was conducted for the Smitswinkel Bay site where song was most frequently detected. Here, song was detected at least once in all hours of the day, however, song was recorded more often in the night-time hours and less so during midday. This strong diel pattern of song presence-absence was supported by a generalized additive model with hr as a predictor (Figure 8). Probability of detecting song was higher in the early morning and late evening hours ($p < 0.05$). This was further supported when day period was investigated, as Dawn and Night were the only significant predictors ($p < 0.05$) of song presence.

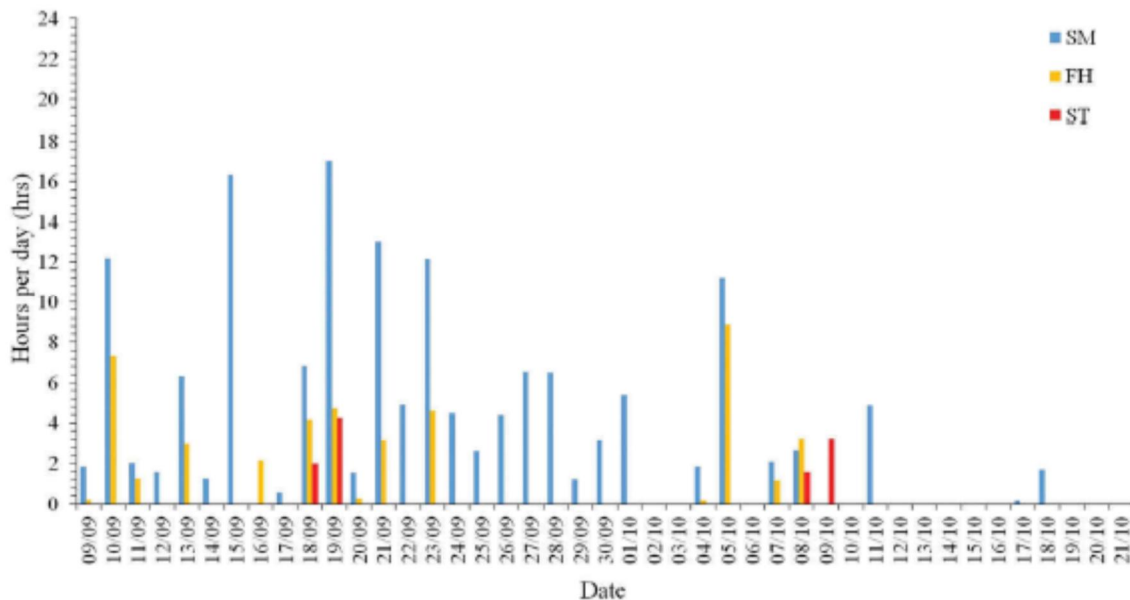


Figure 7. Song positive hours per day shown for song positive days during the time of the study for all three locations where song was detected; Smitswinkel (SM; blue), Fish Hoek (FH; yellow) and Strandfontein (ST; red). Song was only detected in September and October 2016 and was thus not detected in Rooi Els.

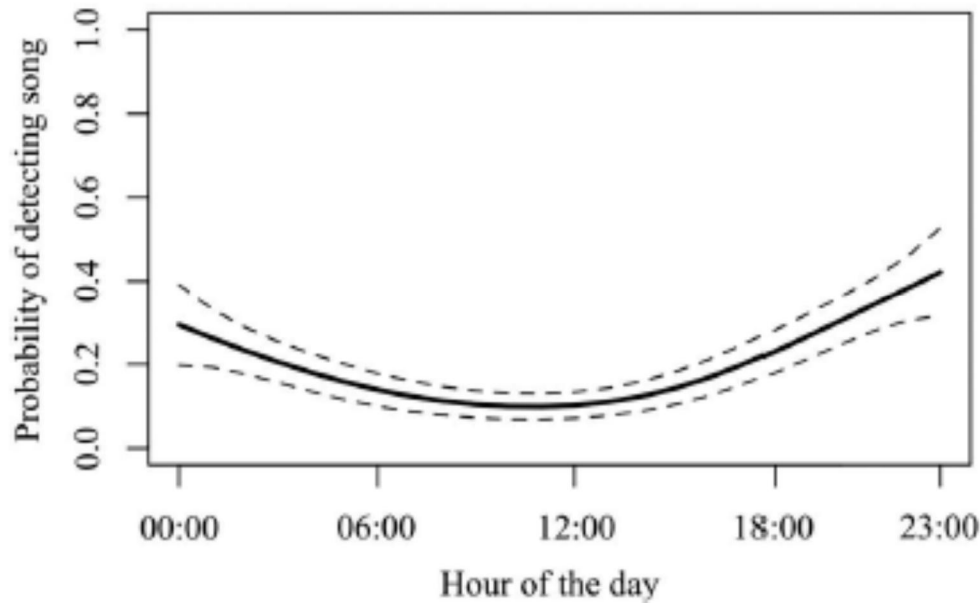


Figure 8. Results of a binomial GAM showing the probability of detecting humpback whale song presence-absence at a specific hour of the day. The dotted lines show the 95% confidence bands.

In addition to humpback whale song, low-frequency, high intensity sounds presumed to be generated by fishes, and often detected in bouts, were also detected throughout recordings and particularly at the Fish Hoek and Strandfontein sites. Although recorded with a high SNR and found within the same frequency band as song, these did not adversely affect song detection. Other biological sound sources, including echolocation clicks and tonal whistles of dolphin species, and low-frequency underwater calls of unknown cetacean species possibly Bryde’s whales (*Balaenoptera brydei*) or southern right whales (*Eubalaena australis*), were also detected. Snapping shrimp were heard at all four locations in all hours of recordings. In addition to biological sounds, anthropogenic sources were also detected within recordings. On several occasions, song was masked by distant low-frequency ship noise and the transient signature of presumably smaller, and faster, motorised vessels passing by.

Discussion

This study is the first to report the regular occurrence and timing of song from humpback whale males off the coastal waters of South Africa. The limited research of humpback whale vocal behaviour in South African waters is perhaps because the coast of South Africa is largely regarded to be a migratory route with animals passing by (Best and Allison 2010; Barendse et al. 2011) and not engaging in mating activities when song is typically expected to occur. However, the recent documentation of large scale feeding events (Findlay et al. 2017) and first reports of singing (Gridley et al. 2018) indicate a more complex behavioural repertoire and habitat use than previously acknowledged.

The coastline of South Africa is of biogeographical importance as it lies between, and essentially divides, the migration routes of humpback whales associated with the eastern Atlantic and western Indian Ocean breeding grounds. Data for the current study were collected over a 17 month period in False Bay, which lies immediately to the east of Cape Point and ~150 km west of Cape Agulhas, the southernmost point of the African continent. Recording effort was spread across these months, with coverage best between September and January. However, all occurrences of song were between 9 September and 21 October 2016, with the frequency of song detection declining rapidly after the 11th of October. Singing behaviour was, therefore, tightly coupled with the timing of the expected southern migration of humpback whales (October - November) following the end of their winter breeding season, and may represent the occurrence of a discrete cohort of southward migrating males who continue to sing during the period immediately following their departure from the breeding ground, as observed in other geographic areas (Norris et al. 1999; Noad and Cato 2007; Kowarski et al. 2019). The presence of song during this portion of migration may occur for several reasons, but two hypotheses stand out. Firstly, males that were unsuccessful in

mating may be attempting to extend their reproductive efforts into the migratory period and even onto the feeding grounds (Clark and Clapham 2004), and secondly, if singing is influenced by testosterone levels, continued singing after the breeding season may be associated with a gradual reduction in testosterone in the migrating males as they move to their feeding grounds (Clark and Clapham 2004; Vu et al. 2012; Kowarski et al. 2019). Thus, song detected in False Bay is likely made by males moving southwards from their breeding grounds north of Namibia or even Mozambique.

The amount of song detected during the course of this study was surprising and indicates the possibility that migrating males may be lingering in the area due to opportunistic feeding. There are regular occurrences of high densities of feeding humpback whales along the west coast of South Africa between October and January (Barendse et al. 2010, 2011; author's unpublished data) with the recent documentation of 'super-groups' just 10s of km from the south-western tip of False Bay (Findlay et al. 2017). Some of these animals may also engage in singing (Gridley et al. 2018) and in other areas, song has been recorded on feeding grounds (Clark and Clapham 2004; Vu et al. 2012; Garland et al. 2013) and during times where group members were engaged in active feeding behaviour (diving, feeding lunges: Stimpert et al. 2012). Therefore, it is premature to conclude that song presence only reflects the occurrence of male humpback whales as they pass by while migrating southward, as it might also reflect whales engaged in feeding behaviour, particularly if song is documented in conjunction with non-song feeding calls. Indeed, non-song calls were occasionally found within the same day or hour as song and sometimes simultaneously. Further, if the western coast of South Africa is emerging as an important feeding area, it may also represent a potential area for song exchange between breeding stock B and C, as evidence from recent satellite tagging shows overlap in distributions these two stocks on the

west coast of South Africa (DEA 2016). The potential use of this area by different breeding stocks (BSB and BSC), as well as a cohort of migrating post-breeding animals and potentially semi-resident feeding animals at different and overlapping time periods, produces a confusing picture which will require considerably more effort to fully resolve.

The aim of this study was to use available acoustic monitoring data to investigate the presence and timing of humpback whale males in False Bay, an area that has not been well studied to date. The closest and most recent data-set of humpback sightings to which we can compare the timing of our acoustic detections derives from Kleinbaai (<80 km east of our study site). Data in that study came from a whale watching boat operating year-round and showed a clear but small peak in numbers in June and July (Vinding et al. 2015). No clear southward peak was seen except for a small number of sightings in late November and December (Vinding et al. 2015), which aligns with the west coast ‘feeding season’. Additionally, a small but clear northward migration peak has been reported near Saldanha Bay (~150 km north of our study site) showing a clear male-bias in animals biopsied during this period (May to June; Barendse et al. 2010). As both studies indicate humpback whales occurring in South African waters in May to June, it is surprising that no song at all was detected during the May recording periods, as males will sometimes engage in singing or produce song fragments while migrating towards their breeding grounds (Clark and Clapham 2004; Kowarski et al. 2019). Although, as male humpback whales are usually amongst the last animals to migrate to a breeding ground (Rizzo and Schulte 2009), any occurrences of song made while migrating northwards may only have occurred during the period (June to August 2017) where recordings did not take place.

Between the start of recording effort (9 September 2016) and the day song was last heard (18 October 2016), the average number of song positive hours per day was approximately 3 hrs, peaking to 17 hrs on the 19th of September. The maximum number of song positive hours is not unusual, as some studies have reported over 20 hrs of singing in one day during their spring migration (Vu et al. 2012) with a similar number of song positive hours per day observed on breeding grounds (Kowarski et al. 2018). Humpback whale song was, however, substantially more prevalent in the dataset than anticipated given the low numbers of animals reported less than 80 km to the east of our study site by Vinding et al. (2015) between the months of September and October. However, lack of visual detection does not itself mean animals are not present. The nature of humpback whale singing behaviour, where males sing for long periods (Winn and Winn 1978) and surface on average every 14 min (Chu 1988), can make them difficult to detect visually, while the acoustic characteristics of humpback whale song can allow detection of individuals over distances of 32 km or more (Norris et al. 1999). Further, the vast majority of detected song was recorded on the western-most hydrophone located at Smitswinkel Bay in False Bay despite having the lowest recording effort of the three sites where song was recorded. On rare occasions, song would start or end abruptly during the course of a continuous 5 min recording, perhaps indicating that singers were stationary as they sang. However, in the majority of cases, most song sessions would start faintly and gradually become clearer and louder. This suggests that we were detecting whales moving into False Bay from the south-west, perhaps attempting to continue to follow the coast during their southward migration. Cape Point is the south westernmost piece of land these animals encounter before being forced into a completely oceanic journey towards their feeding grounds. As song progressively diminished from west to east and no song was detected at our most easterly location, Rooi Els, it seems that, if entering False Bay, animals did not move across the bay to the east.

Although humpback whale song can travel vast distances underwater, song transmission will be far less effective in shallower waters than deeper waters (Whitehead and Moore 1982). In our study, song propagated at least the 25 km between Smitswinkel Bay and Strandfontein, where it was weakly received. However, how true the distance and whether the animals were located within False Bay or just to the south or south-west of Cape Point (i.e. near or approaching the true ‘west coast’) when signing cannot currently be determined. The one occasion when song was first detected at the Fish Hoek site (located further inside False Bay) and then later at Smitswinkel Bay site does suggest that at least some singing is taking place within the bay. The internal clocks within SoundTraps were synchronised on deployment, however, these results should be treated with caution as differential drift in the timekeeping of these units could potentially invalidate this result. Deployment sites were matched in depth and placement was away from commercial harbours and analysis was not impacted by excessive anthropogenic noise sources. However, it remains possible that environmental conditions and topographic features at deployment locations had an unquantified impact on detection radii which could be investigated in future studies through modelling procedures and simulations (Mercado and Frazer 1999; Helble et al. 2013; Binder and Hines 2019).

Of all four sites, Smitswinkel Bay was the only site where song was recorded during every hour of the day (00:00 to 23:00) throughout the period when song was present in False Bay (September – October 2016). An analysis of the diel patterns in song detection from this location revealed that song was more prevalent in the night-time hours than during the day, being least detected at midday. Singing whales from various populations globally have also been observed to show this behaviour both in winter and on the breeding grounds (Au et al.

2000; Kowarski et al. 2019). Due to the widespread nature of this phenomenon (Hawai'i, Au et al. 2000; Angola, Cerchio et al. 2014; Canada, Kowarski et al. 2018) it is reasonable to suggest that this diel trend is one common to the species (Kowarski et al. 2019). Further, Au et al. (2000) suggested that a trend for night-time calling may be a result of animals relying more on acoustic displays, as visual cues become harder to receive. This idea was proposed in terms of mating strategies (Au et al. 2000) but may also be true of maintaining group cohesion during migration.

Passive acoustic monitoring provides a powerful tool for detecting the presence of vocalising cetaceans (Dudzinski et al. 2009). This dataset has provided a proof of concept for the use of PAM to study humpback whales in the coastal waters of southern Africa. However, some sounds are easier to detect than others. Other than song, humpback whales produce a diverse repertoire of foraging and social sounds (Dunlop et al. 2007; Fournet et al. 2018a), although these are generally fainter than song (Au et al. 2006; Dunlop 2018; Fournet et al. 2018b) and do not occur in extended bouts (Rekdahl et al. 2015) making them harder to detect. Detailed investigations of non-song vocalisations recorded from sites in the Western Cape would potentially provide more information on the presence and behaviour of humpback whales, particularly feeding whales, within this study area (Stimpert et al. 2011; Vu et al. 2012; Van Opzeeland et al. 2013; Fournet et al. 2018a). Therefore, a broader scale array of hydrophones along both the east and west coasts with year-round temporal coverage would be invaluable to better understand these animals along this important section of their range. Further, dedicated investigation is necessary to help elucidate the function of song by whales on the western South African coastline and the detection radius of singing whales in these waters.

Acknowledgements

This publication is an output of the Sea Search Research and Conservation non-profit group and was largely funded by contributions from the National Research Foundation (NRF, Grant 93689 to SE 2015 - 2018) which contributed funds for fieldwork, equipment and salary (for AP). SE was funded by an NRF salary grant 91459 (2014-2019). E R-M was funded through the NRF Internship scheme (2018-19). TG was funded by the Claude Leon Foundation (2015 - 2017), a University of Stellenbosch Biological Sciences fellowship (2019) and an ASAB small research grant (2019). We would like to thank all of our colleagues who assisted in data collection through the provision of sea time on their boats or effort in deploying/retrieving hydrophones and conducting surveys, especially Chris Wilkinson, Monique Laubscher and Els Vermeulen. Research was conducted under a series of research permits issued by the Department of Environmental Affairs to SE and colleagues at the Mammal Research Institute (RES 2015/94, 2016/86, 2017/50), the South African National Parks for work in the Table Mountain National Park MPA (CRC/2015-2016/026--2015/V3 and renewals) and under ethics clearance from the University of Pretoria Animal Use and Care Committee permit (EC074-15).

Declaration of Interest Statement

We hereby declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere.

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We

further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

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References

Allen JA, Garland EC, Dunlop RA, Noad MJ. 2018. Cultural revolutions reduce complexity in the songs of humpback whales. *Proc R Soc B*. 285(1891): 20182088.

Au WW, Mobley J, Burgess WC, Lammers MO, Nachtigall PE. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Mar Mam Sci*. 16(3): 530-544.

Au WW, Pack AA, Lammers MO, Herman LM, Deakos MH, Andrews K. 2006. Acoustic properties of humpback whale songs. *J Acoust Soc Am*. 120(2): 1103-1110.

Barendse J, Best PB, Thornton M, Elwen SH, Rosenbaum HC, Carvalho I, Pomilla C, Collins TJQ, Meyer MA, Leeney RH. 2011. Transit station or destination? Attendance patterns, regional movement, and population estimate of humpback whales *Megaptera novaeangliae* off West South Africa based on photographic and genotypic matching. *Afr J Mar Sci.* 33(3): 353-373.

Barendse J, Best PB, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC. 2010. Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *Afr J Mar Sci.* 32(1): 1-22.

Best PB. 2011. Where is the breeding ground for humpback whales from Breeding Stock B2? Paper SC/63/SH17 submitted to the Scientific Committee of the International Whaling Commission. 1-8.

Best PB, Allison C. 2010. Catch history, seasonal and temporal trends in the migration of humpback whales along the west coast of southern Africa. *International Whaling Commission: IWC SC/62/SH5.*

Best PB, Sekiguchi K, Findlay KP. 1995. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Mar Ecol Prog Ser.* Oldendorf. 118(1): 1-12.

Binder CM, Hines PC. 2019. Range-dependant impacts of ocean acoustic propagation on automated classification of transmitted bowhead and humpback whale vocalisations. *J Acoust Soc Am.* 145(4): 2480-2497.

Cerchio S, Strindberg S, Collins T, Bennett C, Rosenbaum H. 2014. Seismic surveys negatively affect humpback whale singing activity off northern Angola. *PloS One*. 9(3): e86464.

Cholewiak DM, Sousa-Lima RS, Cerchio S. 2013. Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. *Mar Mam Sci*. 29(3): E312-E332.

Chu KC. 1988. Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). *Can J Zoo*. 66(6): 1322-1327.

Clark CW, Clapham PJ. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proc R Soc Lond [Biol]*. 271(1543): 1051-1057.

Darling JD. 2015. Low frequency, ca. 40 Hz, pulse trains recorded in the humpback whale assembly in Hawaii. *J Acoust Soc Am*. 138(5): EL452-EL458.

Darling JD, Acebes JMV, Frey O, Urbán RJ, Yamaguchi M. 2019. Convergence and divergence of songs suggests ongoing, but annually variable, mixing of humpback whale populations throughout the North Pacific. *Sci Rep*. 9(1): 7002.

[DEA] Department of Environmental Affairs. 2016. State of the oceans and coasts around South Africa 2017 Report card based on research and monitoring observations. Verheye H,

Huggett J, Crawford R, editors. Pretoria (RSA): Department of Environmental Affairs (RSA).
Report No.: 15-RP348/2016.

Dudzinski KM, Thomas JA and Gregg JD. 2009. Communication in marine mammals. In:
Perrin WF, Würsig B, Theewissen JGM, editors. Encyclopaedia of marine mammals. 2nd ed.
[place unknown]: Academic Press; p. 260-269.

Dunlop RA. 2018. The communication space of humpback whale social sounds in wind-
dominated noise. *J Acoust Soc Am.* 144(2): 540-551.

Dunlop RA, Cato DH, Noad MJ. 2008. Non-song acoustic communication in migrating
humpback whales (*Megaptera novaeangliae*). *Mar Mam Sci.* 24(3): 613-629.

Dunlop RA, Noad MJ, Cato DH, Stokes D. 2007. The social vocalization repertoire of east
Australian migrating humpback whales (*Megaptera novaeangliae*). *J Acoust Soc Am.* 122(5):
2893-2905.

Findlay KP, Best PB. 1995. Summer incidence of humpback whales on the west coast of
South Africa. *Afr J Mar Sci.* 15(1): 279-282.

Findlay KP, Seakamela SM, Mejer MA, Kirkman SP, Barendse J, Cade DE, Hurwitz D,
Kennedy AS, Kotze PG, McCue SA, Thornton M. 2017. Humpback whale “super-groups” – a
novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (*Megaptera
novaeangliae*) in the Benguela Upwelling System. *PloS one.* 12(3): e0172002.

Fournet ME, Matthews LP, Gabriele CM, Mellinger DK, Klinck H. 2018a. Source levels of foraging humpback whale calls. *J Acoust Soc Am.* 143(2): EL105-EL111.

Fournet ME, Gabriele CM, Culp DC, Sharpe F, Mellinger DK, Klinck H. 2018b. Some things never change: multi-decadal stability in humpback whale calling repertoire on Southeast Alaskan foraging grounds. *Sci Rep.* 8(1): 13186.

Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole MM, Robbins J, Noad, MJ. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr Biol.* 21(8): 687-691.

Garland EC, Noad MJ, Goldizen AW, Lilley MS, Rekdahl ML, Garrigue C, Constantine R, Daeschler Hauser N, Poole, MM, Robbins J. 2013. Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale. *J Acoust Soc Am.* 133(1): 560-569.

Gridley T, Silva MFP, Wilkinson C, Seakamela SM, Elwen SH. 2018. Song recorded near a super-group of humpback whales on a mid-latitude feeding ground off South Africa. *J Acoust Soc Am.* 143(4): EL298-EL304.

Hazevoet CJ, Gravanita B, López Suárez P, Wenzel FW. 2011. Seasonality of humpback whale *Megaptera novaeangliae* (Borowski, 1781) records in Cape Verde seas: evidence for the occurrence of stocks from both hemispheres. *Zool CV.* 2(1): 25-29.

Helble TA, D'Spain GL, Hildebrand JA, Campbell GS, Campbell RL, Heaney KD. 2013. Site specific probability of passive acoustic detection of humpback whale calls from single fixed hydrophones. *J Acoust Soc Am.* 134(3): 2556-2570.

Herman, L.M., 2017. The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biol Rev.* 92(3): 1795-1818.

[IWC] International Whaling Commission. 1998. Report of the Scientific Committee. Annex G. Report of the sub-committee on comprehensive assessment of Southern Hemisphere humpback whales. [Place unknown]: International Whaling Commission. 48:170– 182.

[IWC] International Whaling Commission. 2012. Report of the Scientific Committee. Annex H: report of the subcommittee on other Southern Hemisphere whale stocks. *J Cetac Res Manage.* 13. Suppl: 192–216.

Janik VM. 2009. Whale song. *Curr Biol.* 19(3): R109-R111.

Kowarski K, Evers C, Moors-Murphy H, Martin B, Denes SL. 2018. Singing through winter nights: seasonal and diel occurrence of humpback whale (*Megaptera novaeangliae*) calls in and around the Gully MPA, offshore eastern Canada. *Mar Mam Sci.* 34(1): 169-189.

Kowarski K, Moors-Murphy H, Maxner E, Cerchio S. 2019. Western North Atlantic humpback whale fall and spring acoustic repertoire: insight into onset and cessation of singing behavior. *J Acoust Soc Am.* 145(4): 2305-2316.

Mercado E III, Frazer LN. 1999. Environmental constraints on sound transmission by humpback whales. *J Acoust Soc Am.* 106(5): 3004-3016.

Mercado E III, Herman LM, Pack AA. 2003. Stereotypical sound patterns in humpback whale songs: usage and function. *Aquat Mamm.* 29(1): 37-52.

Noad MJ, Cato DH. 2007. Swimming speeds of singing and non-singing humpback whales during migration. *Mar Mam Sci.* 23(3): 481-495.

Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KCS. 2000. Cultural revolution in whale songs. *Nature*, 408(6812), p.537.

Norris TF, McDonald M, Barlow J. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *J Acoust Soc Am.* 106(1): 506-514.

Parsons ECM, Wright AJ, Gore MA. 2008. The nature of humpback whale (*Megaptera novaeangliae*) song. *J Mar Anim Ecol.* 1(1): 22-31.

Payne RS, McVay S. 1971. Songs of humpback whales. *Science.* 173(3997): 585-597.

Payne K, Payne R. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. *Z. Tierpsychol.* 68(2): 89-114.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019. nlme: linear and nonlinear mixed effects models. R package version 3.1-140, <URL: <https://CRAN.R-project.org/package=nlme>>.

R Core Team. 2019. R: a language and environment for statistical computing. Austria: R Foundation for Statistical Computing. URL: <http://www.R-project.org/>.

RStudio Team .2015. RStudio: integrated development for R. Boston (MA): RStudio, Inc. URL: <http://www.rstudio.com/>.

Rekdahl ML, Dunlop RA, Goldizen AW, Garland EC, Biassoni N, Miller P, Noad MJ. 2015. Non-song social call bouts of migrating humpback whales. J Acoust Soc Am. 137(6): 3042-3053.

Rekdahl ML, Garland EC, Carvajal GA, King CD, Collins T, Razafindrakoto Y, Rosenbaum H. 2018. Culturally transmitted song exchange between humpback whales (*Megaptera novaeangliae*) in the southeast Atlantic and southwest Indian Ocean basins. R. Soc. open sci. 5: 172305.

Rekdahl, M, Tisch C, Cerchio S, Rosenbaum H. 2017. Common non-song social calls of humpback whales (*Megaptera novaeangliae*) recorded off northern Angola, southern Africa. Mar Mam Sci. 33(1): 365-375.

Rizzo LY, Schulte D. 2009. A review of humpback whales' migration patterns worldwide and their consequences to gene flow. J Mar Biol Assoc UK. 89(5): 995-1002.

Silva M. 2017. Investigating the social sounds of humpback whales (*Megaptera novaeangliae*) from Southern Africa [master's thesis]. Belgium: Ghent University.

Stafford KM, Mellinger DK, Moore SE, Fox CG. 2007. Seasonal variability and detection range modelling of baleen whale calls in the Gulf of Alaska, 1999–2002. *J Acoust Soc Am.* 122(6): 3378-3390.

Sterelny K. 2009. Peacekeeping in the culture wars. In: Laland KN, Galef BG, editors. The question of animal culture. Cambridge, MA: Harvard University Press; p. 288–304.

Stimpert AK, Au WW, Parks SE, Hurst T, Wiley DN. 2011. Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *J Acoust Soc Am.* 129(1): 476-482.

Stimpert AK, Peavey LE, Friedlaender AS, Nowacek DP. 2012. Humpback whale song and foraging behavior on an Antarctic feeding ground. *PLoS One.* 7(12): 51214.

Van Opzeeland I, Van Parijs S, Kindermann L, Burkhardt E, Boebel O. 2013. Calling in the cold: pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. *PLoS One.* 8(9): e73007.

Vinding K, Bester M, Kirkman SP, Chivell W, Elwen S.H. 2015. The use of data from a platform of opportunity (whale watching) to study coastal cetaceans on the southwest coast of South Africa. *TME.* 11(1): 33-54.

Vu ET, Risch D, Clark CW, Gaylord S, Hatch LT, Thompson MA, Wiley DN, Van Parijs SM. 2012. Humpback whale song occurs extensively on feeding grounds in the western North Atlantic Ocean. *Aquatic Biol.* 14(2): 175-183.

Winn, H.E. and Winn, L.K., 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar Biol.* 47(2): 97-114.

Whitehead H, Moore MJ. 1982. Distribution and movements of West Indian humpback whales in winter. *Can J Zool.* 60(9): 2203-2211.

Wood SN. 2017. Generalized additive models: an introduction with R. 2nd ed. Chapman and Hall/CRC.