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Variability in Temporal Characteristics of the South Eastern Indian Ocean Pygmy Blue Whale Song

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Abstract – The temporal characteristics of whale song are considered to be amongst the most stable elements of song production, though very few studies have looked at the timing of discrete sounds or the silences between them. This study indicates that the temporal characteristics of the song of the southeast Indian Ocean pygmy blue (SEIOPB) whale are highly variable. While the song repetition interval, or inter-song interval (ISI), appeared to remain consistent within a song event, defined as a consistent bout of singing presumed to come from an individual animal, it was found to be variable between song events. Song structure was a confounding factor in the analysis of variability in ISI with songs comprised of longer phrases naturally having a longer song repetition interval. The songs of the SEIOPB whale are characteristic of the species with only three primary song types. The three-unit song (units I, II and III) has the longest mean ISI of ~ 200 s, approximately twice that of songs composed of only two units (II and III) at a mean of ~ 100 s ISI which is approximately twice the ISI of a one-unit song (unit II only). The results of this study suggest that variability in ISI cannot be attributed to change in one element of a song but is driven by temporal changes in all elements of the song including phrase structure, unit duration and the length of the intervals between song units. Thus, the temporal characteristics of blue whale song appear to be under the control of the animal and may vary between individual whales, and within songs of an individual. It is concluded that the temporal characteristics of song potentially encode contextual information about the singer and may be influenced by audience effects, including audience composition and singer density.

Keywords – Blue whale, Song interval, Song variability, Bioacoustics, Behavior, Whale song

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Singing is an important behavioral display for many species. Marine mammals rely heavily on sound for social and communicative purposes. Song is recognized as a cultural element of whale behavior and just as with birds, is a learned rather than inherited trait (Hammond et al., 2017; Jolliffe et al., 2019; Mercado et al., 2005; Rendell & Whitehead, 2001). Thus, studies of whale song can provide important information about the cognitive capabilities of the species as well as further understanding of vocal behavior. The mechanisms that permit animals to acquire, process and store information from their environment make up cognition (Sewall, 2015). It is thought that navigating complex social environments requires superior levels of cognition, which are likely required for other behaviors such as migration and navigation of the open ocean (Sewall, 2015; Seyfarth & Cheney, 2015; Wiggins et al., 2015). While communication and cognition are often considered separately in research, communication is essential for the transmission of social information and mediation of interactions with other animals, and vocal complexity may be an indicator of cognitive capacity, thus cognition and communication are inherently linked (Sewall, 2015). There is evidence to support the notion that whales communicate information through vocal displays (Cazau et al., 2016; Dunlop, 2017), and it is plausible to consider that this information is potentially communicated through changes in the frequency or duration of calling whales' vocalizations (Cazau et al., 2016). When considering information encoded within animal songs, it is possible that not just the order of discrete sounds or units is important, but that information may exist in the general and relative timing of the units within the sequence.

There are many synergies in the characteristics and contexts of song production by both whales and songbirds, though studies of songbirds naturally lend themselves to better observation. It has been found that the songs of birds, and indeed many other terrestrial animals, conform to well-studied linguistic laws. An example is Menzerath's law, which suggests that as the length of a sequence increases, the length of the units within the sequence decreases (Mačutek et al., 2017). Menzerath's law reflects mathematical principles of compression, which is argued to be a universal theory relevant to the animal behavior and biological systems more broadly (Favaro et al., 2020; Gustison et al., 2016; Heesen et al., 2019; Mačutek et al., 2017). While it is not clear whether the same linguistic laws apply to the songs and vocal behavior of marine mammals, it is not unreasonable to hypothesize that this would be the case. Particularly given the highly structured songs of whales show strong rhythmicity. Inter-pulse interval is a commonly used metric for measuring temporal variability in a song as variability in pulse intervals can encode information about individual fitness and identity, or species identification (Hauser et al., 1998; Randall, 1989, 1997). While evidence of variations in song structure, including the song duration and repetition interval, in the songs of mysticete whales continues to grow, the cause of such variation is harder to define (Fristrup et al., 2003; Kershenbaum & Garland, 2015; Ronald et al., 2015). It is not understood whether the drivers of this variability are background noise conditions including those driven by higher densities of singing animals, changes in behavioral state, changes in some other aspect of the singer's situation or environment, or a complex combination of these factors (Cazau et al., 2016; Dunlop, 2017).

Whale songs are broadly recognized as being comprised of identifiable units that are clustered together in phrases or themes, which are repeated to form a song (Baptista & Keister, 2005; Handel et al., 2009; Mercado et al., 2005; Payne & McVay, 1971). Vocal complexity can be expressed at different levels including the diversity paradigm (e.g., repertoire size) and repetition paradigm (e.g., temporal variability) (Kershenbaum et al., 2016; Macdougall-Shackleton, 1997). Information encoded in acoustic sequences can be classified by the paradigms of diversity such as ordering, combination, overlapping and timing (Kershenbaum et al., 2016). In the songs of many animals, song diversity or complexity may be related to sexual selection, for example female zebra finches (*Taeniopygia guttata*) prefer longer songs with a greater variety of syllables (Neubauer, 1999; Searcy & Andersson, 1986). Discrete units are generally identified by periods of silence but can also be delineated by change in acoustic properties, and due to the perceptual limits to gap detection, periods of silence may not be perceived that way by the receiver (Handel et al., 2009). Complexity in the composition of whale songs varies between species and populations (Cantor & Whitehead, 2013; McDonald et al., 2006). For some species, such as blue whales (*Balaenoptera musculus* spp.), songs are typically comprised only of one phrase that is repeated and so the phrase length is generally synonymous with inter-song interval (ISI), however hybrid song variants that are the repetition of two phrase types in sequence do occur (Jolliffe et al., 2019). While species specific songs appear to be governed by structural rules, long term changes in song characteristics are well documented across several species of whale (Helweg et al., 1998; Leroy et al., 2018; Miksis-Olds et al., 2018; Parks et al., 2008). However, until recently, the temporal structural of song was considered to be the most stable. Recent studies of humpback whales have found that while most songs conform to high degrees of temporal regularity within a song, there is significant variability in the timing of sounds and temporal characteristics between song bouts (Schneider & Mercado, 2019).

Variability in song production is well documented in marine species for which considerable research effort has been expended. Numerous studies have documented the ability of whales to alter their acoustic behavior in response to environmental disturbances or audience effects providing evidence that variability in temporal structure is under the control of the individual and not a result of errors in song learning (DeRuiter et al., 2017; Fristrup et al., 2003; Goldbogen et al., 2013; Guazzo et al., 2020). Within the songs of the humpback whale (*Megaptera novaeangliae*), while phrase duration has been found to have the lowest level of variability between singing animals and within an animal's song (Cholewiak et al., 2013), significant differences have been found in the average length of a song (comprised of multiple phrases) from an individual singer, as well as a high degree of variability in song length between vocalizing animals (Cholewiak et al., 2018). Variability in the singing behavior of an individual whale, particularly the source level of vocalizations, has been linked to acoustic disturbances, including low frequency sonar and vessel noise, as well as variability in background noise conditions

(Cholewiak et al., 2018; Dunlop et al., 2010, 2014; Fristrup et al., 2003; Guazzo et al., 2020; Thode et al., 2020). Blue whales have been observed to alter vocalization rates in response to acoustic disturbances, with an increase in vocalization rate for D calls, believed to be contact or social calls, reported in the presence of ship noise (Melcón et al., 2012). Low frequency sonar has also been found to influence blue whale behavior, with blue whales ceasing to vocalize in the presence of low frequency sonar (Melcón et al., 2012). Additionally, there are several studies demonstrating changes in bowhead whale calling rates and dive behavior in response to seismic sound (Blackwell et al., 2015; Blackwell et al., 2017; Robertson et al., 2013). Variability in whale songs may also have environmental or social drivers. Fin whales (*Balaenoptera physalus*) are thought to use songs to indicate prey availability and location, potentially through variability in inter note intervals (Morano et al., 2012; Payne & McVay, 1971). The inter note interval in fin whale calls has been found to transition from short to long duration over the course of a season without reverting to a short duration (Morano et al., 2012; Weirathmueller et al., 2017). Further, in that study, the short duration inter-note interval was observed to coincide with the breeding season when the caller density was at its highest (Morano et al., 2012), highlighting the potential for animal density to influence song intervals. Density specific calling behaviors are well reported in terrestrial species, where the shortening of vocalization intervals is often observed in response to increased background noise, including where the increase in ambient noise comes from high densities of vocalizing conspecifics (Dorado-Correa et al., 2018; Hedwig et al., 2015). For example, birds, such as red-throated ant-tanagers (*Habia fuscicauda*), have been observed to increase their song rate in noisier environments (Simpson & McGraw, 2018).

This paper investigates variability in the temporal characteristics of the South Eastern Indian Ocean pygmy blue (SEIOPB) whale (*Balaenoptera musculus brevicauda*) song, and whether there is a rhythmicity to the song. The SEIOPB whale has several distinct song and phrase variations with songs composed of one, two or three units (Jolliffe et al., 2019). The “traditional” SEIOPB or “Australian” song type is a repeated three-unit phrase comprised of type I, type II, and type III units. Variability in the structure of the SEIOPB whale song is explained in detail in Jolliffe et al. (2019), and it can be summarized as either the traditional three-unit (*P3*), or shortened two-unit (*P2* – type II and III units only) or one-unit (*P1* – type II unit only) phrases. Generally, a song is comprised of only one phrase repeated over and over with the song type reflecting the name of the repeated phrase. There are at least three variations in the composition of songs, combining multiple phrase structures, termed *P3A*, *P3B* and *P2A* songs (Jolliffe et al., 2019). It is expected that the prevalence of different song variations within the population will likely be a driving factor in the variability of inter-song-interval or the time between repetition of consecutive song units. However, noting that the temporal characteristics of song may be used to communicate important information about an individual or their context, understanding the song repetition rate, defined as the ISI, as well as the finer scale temporal structure of songs may reveal important information about the cognitive capabilities of blue whales and further our understanding of vocal behavior.

Methods

Ethics Statement

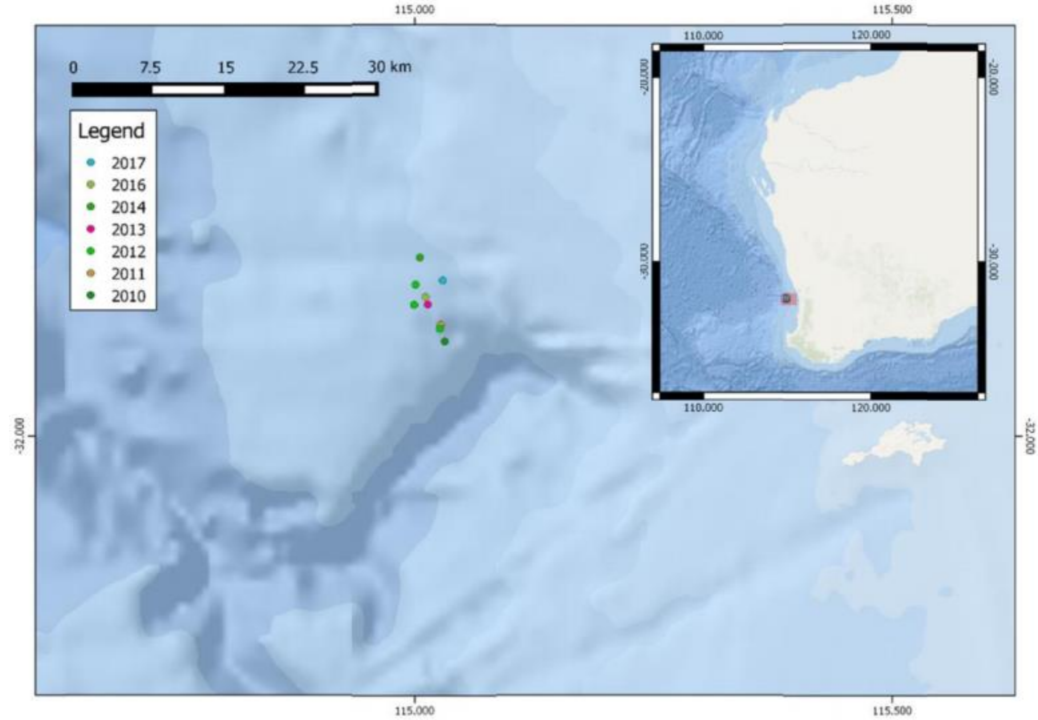
This research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number # AEC_2013_28 - Passive acoustic recording of marine animal (mammal and fish) vocalization.

Data Collection

Long term data were collected from the Perth Canyon, Western Australia (Figure 1), located to the west of Rottnest Island in the Indian Ocean. The Perth Canyon is a submarine canyon that supports a hot spot of productivity on a largely oligotrophic coastline (Rennie, 2005; Rennie et al., 2009). In some years the Perth Canyon is a known feeding area for pygmy blue whales that aggregate in the canyon area between March and June annually. A passive acoustic observatory, consisting of between one and four underwater sound recorders, has been deployed in the Perth Canyon for nearly two decades (Figure 1). The underwater sound recorders were Curtin University CMST-DSTO autonomous underwater sound recorders, as described in McCauley et al. (2017). White noise of a known Power Spectral Density (PSD) level was used to calibrate the recording system response with frequency, including the hydrophone in the circuit, pre and post deployment. Calibration data used the hydrophone sensitivity and system frequency response to correct the frequency spectra or waveform of signals of interest. Calibrated data was available from 1 Hz to the Nyquist frequency. Where possible, underwater sound recorders were deployed in a triangle with sides of approximately 5 km, with a fourth recorder in the center.

Figure 1

Location of Noise Receiver Deployments in the Perth Canyon, Western Australia



Note. Three logger deployments in 2012 and 2014, and one in all other years, none of the sample years used in this study had four deployments. Chart not to be used for navigation purposes.

Underwater sound recorders were deployed at depths of 430 to 490 m. Recorders were decoupled from the main mooring to reduce noise, with a ground line of approximately twice the water depth from the instrument to a dump weight and acoustic release (EdgeTech ORE, CART). Hydrophones used were Massa TR 1025-C or High Tech HTI U90. Recorders sampled at 6 kHz sample rate, with recordings of 300 to 500 s of underwater noise starting every 15 min, a 2.8 kHz anti-aliasing filter, and a gentle high-pass filter with roll off below 8 Hz to flatten the low frequency noise curve. A total of five sample years from the Perth Canyon were included in this analysis between 2011 and 2017 as per Table 1. Where samples ran over two years, the sample year was defined as the year within which the pygmy blue whale foraging season in the Perth Canyon (e.g., March – June) was sampled.

Table 1

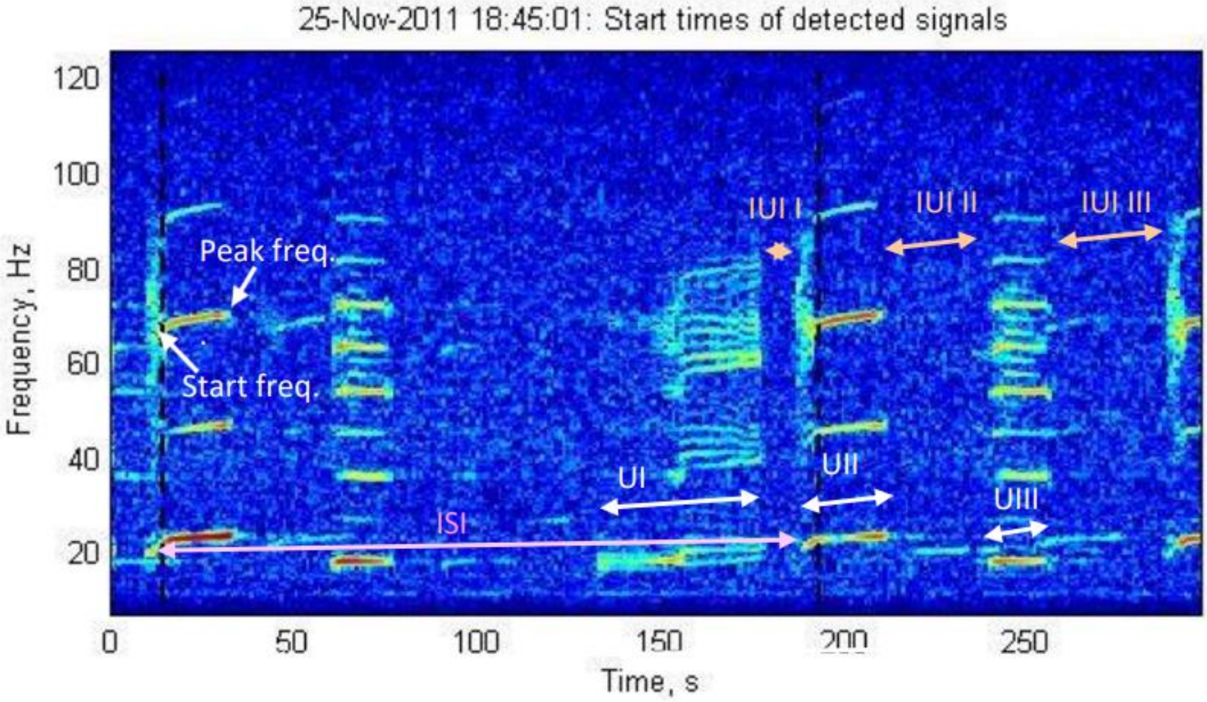
Data Collection Years, Sample Regime, and Recording Equipment for the Perth Canyon Data Set

Data Set	Sample Year	Start Date	End Date	Deployment Lat (°’S)	Deployment Lon (°’E)
3006	2012	14-Jul-2011	18-Jun-2012	31° 51.98’	115° 0.05’
3154	2013	10-Aug-2012	14-Jun-2013	31° 53.05’	115° 0.81’
3376	2014	28-Nov-2013	03-Nov-2014	31° 50.53’	115° 0.82’
3445	2016	05-Jan-2016	30-Dec-2016	31° 52.66’	115° 0.66’
3444	2017	23-Sep-2016	26-Aug-2017	31° 51.77’	115° 1.74’

Data were pre-processed and explored in the MATLAB environment using long term spectrograms or spectrograms calculated from each recording. The SEIOpygmy blue whale full song contains three 'units', a unit being a relatively consistent sound type. A full song (termed P3 here) has three units which always occur sequentially and are termed units I, II, and III, as shown on Figure 2. The song can contain variants where unit I is dropped (leaving unit II and III only, P2 song) or unit I and III are dropped, leaving unit II only (P1 song) (Jolliffe et al., 2019). The grouping of units is termed a phrase throughout (or the particular song type). Pygmy blue whale songs were searched for with an automatic detection algorithm that searched for the type II unit which occurred in all song types (Gavrilov & McCauley, 2013). The algorithm: 1) used spectrogram correlation; and 2) compared the energy in frequency bands corresponding with the type II unit with the energy in surrounding frequency bands to identify the presence of the song unit in sound recordings. The algorithm is described in detail in Gavrilov and McCauley (2013), and has misdetection and false detection rates of less than 5%.

Figure 2

Definition of Inter-unit Interva (IUI)l, Inter-song Interval (ISI), Start Frequency, and Peak Frequency Measurements for a Full Three-Unit Song Phrase



Note. The start and peak frequency are measured on both the fundamental and third harmonic, though are only labelled on the third harmonic in this figure for clarity.

Spectrograms of recordings containing pygmy blue whale songs were visually inspected to confirm detection and enable visual inspection of song characteristics. Spectrograms from which manual measurements were made used a 1 kHz sample rate, 2048 point fast Fourier transform (FFT) and an 80% overlap, to give a 0.488 Hz and 0.41 s frequency and time resolution, respectively. Only songs with a signal-to-noise ratio of > 3 dB were used in analysis to ensure that signals were of a high enough quality for manual analysis. When the signal-noise ratio is poor, the ‘quieter’ parts of the song, including unit I became difficult to observe visually in the spectrogram. Signal-to-noise ratios of song used in analysis were calculated by: 1) downsampling the 6 kHz samples to 1 kHz; 2) bandpass filtering the sample using a 15 Hz high pass and 200 Hz low pass filter; 3) identifying the type II unit, surrounding this in time (total of 30 s centered on the signal extracted); 4) calculating the calibrated dB value of the mean squared pressure of the unit II signal; and 5) subtracting the lowest of 1 s of the dB value of mean squared pressure from before or after the signal. Call parameters, including song length or ISI, unit length, and the time between units (end to start), were measured from the spectrogram. Inter-unit intervals, unit intervals, and repetition rate were measured using traditional techniques (Randall, 1989), whereby periods of silence between sounds and signals > 3 dB above background noise were measured.

Manual sampling of spectrograms to calculate temporal and spectral characteristics was only possible where spectrograms were of a high quality. Where signal-to-noise ratio was low, or multiple animals were singing at once, it was not possible to generate accurate measurements, consequently, samples were sorted to identify those suitable for analysis. A subset of 1,812 suitable song events, defined as a consistent bout of singing where there is a reasonable certainty song comes from a single individual due to consistency in received level and spectrogram appearance (Beck, 2019), with a high enough signal noise ratio for accurate manual measurements, and those for which one entire song repetition without overlapping signals from other animals was captured within the sample window, were selected for use in this analysis and were sorted by song type. ISI refers to the length for a complete repetition of a song type. For many songs, this is synonymous with phrase length as songs for the *P3, P2 and* P1 song types are comprised only of a single phrase repeated over and over. However, for hybrid song types, ISI is the product of the two phrase types that are combined to form a song (Jolliffe et al., 2019). Inter song interval is measured as being between the start of the first unit in a song and its start in the immediately following song and was measured for all samples and outputs used to explore annual and seasonal trends in ISI between song variants.

Randomized sampling was then used to select 120 of the *P2* and 120 of the *P3* song events for further detailed analysis. The length of each song unit was measured as well as the time between the end of one unit (a continual sound type within a song) and the start of the next unit, defined as inter-unit interval (IUI), and the time between phrase (or song) repetition (ISI), as defined in Figure 2. The starting and maximum frequency of the 60-70 Hz third harmonic of unit II were also manually measured using cross hairs to align the start and end point of the signal with the frequency axis from the spectrogram (Figure 2). The third harmonic was used as it is typically the target for automatic detection algorithms and past studies of long-term frequency decline in the SEIOPB song. Due to the confounding nature of song structure influencing ISI, song types were separated by season and month to look for patterns of inter and intra annual change in ISI. All analyses presented in this paper use data manually derived from spectrograms of complete song phrases.

The introduction of unit breaks in later sample years provided the opportunity for further comparison of temporal characteristics. As defined in Jolliffe et al. (2019) a unit break was classified as an interval of greater than two seconds in the middle of unit production that was observed consistently within a song sequence (Figure 3). Further analysis of songs with unit breaks was carried out on the subset of 240 song events across the two major song variants (120 *P3* songs and 120 *P2* songs).

Environmental Noise Calculations

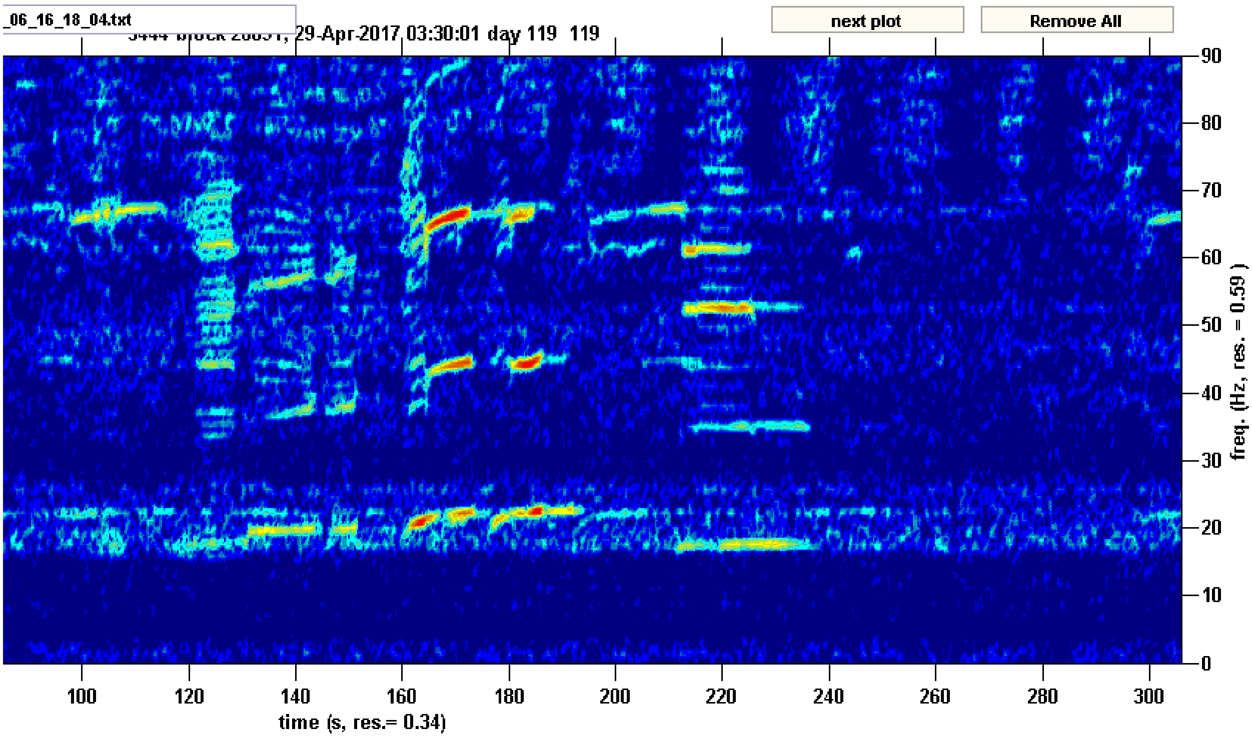
Background noise conditions were calculated and averaged for each month of peak pygmy blue whale presence across all sample years. Background noise conditions were quantified by calculating power spectral density (PSD) levels in 1/12–octave frequency bands for the 50th percentile value using the CHORUS software (Gavrilov & Parsons, 2014) which corrects for the frequency characteristic of receivers using calibration data. This corresponds to the median spectrum level of noise. PSD analysis was conducted, with peaks in the PSD curve indicating intense and persistent sound sources in the acoustic environment.

Data Analysis

Statistical analysis was carried out in the R software environment (R Development Core Team, 2010). Linear models were tested to investigate any potential annual relationship in the variability of song repetition interval. Differences in ISI between sample years were analyzed to investigate the existence of any significant relationships using a type II analysis of variance (ANOVA) run in the ‘car’ package of R (R Development Core Team, 2010), that accounted for song structure as an influential variable. A Bartlett test was conducted to test for homogeneity of variances. Further statistical modelling was carried out using the PMCMR package in the R statistical environment (R Development Core Team, 2010). A Kruskall-Wallis test was used to determine whether significant differences existed in the prevalence of song structures and ISI length between sample years. A post-hoc Tukey and Kramer (Nemenyi) test with Tukey-Dist approximation for independent samples was used to make pairwise comparisons.

Figure 3

Spectrogram of SEIOPB Song Unit Showing a Unit Break at Unit II at 160 s Split into Two Discrete Parts



Results

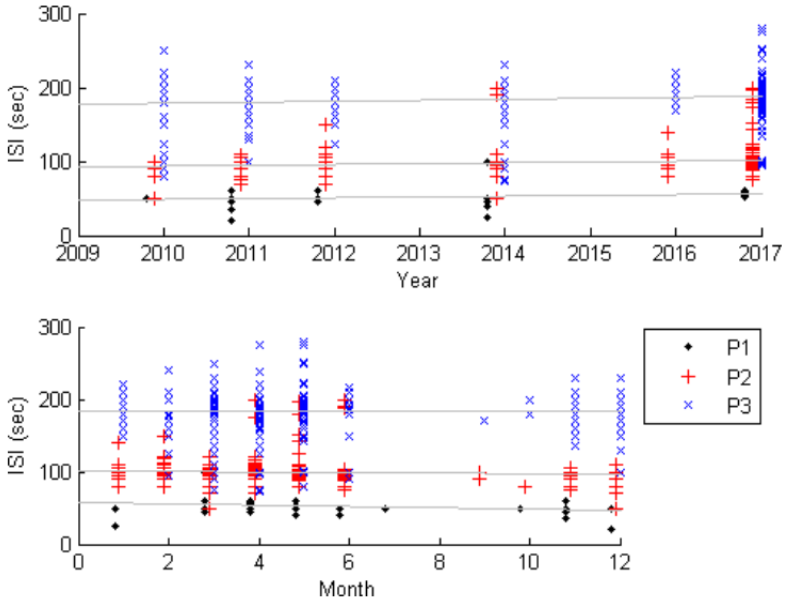
A total of 1,812 song events were recorded and classified for use in this analysis. Signal-to-noise ratios of song used in analysis ranged from a mean of 3 to 10 dB for the different data sets used, with an average of 7 ± 0.8 dB. Phrase length, termed here ISI, was averaged across all song types and plotted across sample years showing a decreasing trend when not accounting for song type and considering only the mean value. This trend for shorter ISI with time was driven by an increased prevalence of shorter songs comprised of shorter phrases (P2 songs) in later sample years. The range in ISI varied between years, and as expected mean ISI was higher in sample years where songs comprised of longer phrase types (*P3* songs) were more prevalent. To remove the confounding factor of phrase structure, song events were grouped by song type for analysis revealing a slight upward trend in the ISI of all song variants between 2010 and 2017; however, the range in ISI for each song type was variable between years (Figure 4). ISI was consistently lower with less variability in 2016 and 2012 (Figure 4). While there are no clear seasonal trends in ISI, the maximum values of ISI peak in April and May, then drop off in June back to similar length to January for *P3* and *P2* songs (Figure 3). Mean ISI appeared to be more variable in years and months with a higher number of song events (2011, 2014, and 2017), with an overall increase in the ISI of *P2* observed between 2010 and 2017 (Figure 4).

Analysis of the distribution of song variants throughout sample years shows that *P2* song variants were generally predominant representing an average of 48.6% (95% CI ± 3.87%) of all songs analyzed, while *P3* songs on average represented 38.8% (95% CI ± 3.77%) of all songs analyzed, with a peak of 45.2% in 2016 where they were the dominant song type (Table 2). The less common song variants, as described in Jolliffe et al. (2019), were variable in their occurrence peaking in random sample years (2016 for *P3A*, 2014 for *P2A*, and 2011 for *P3B*). The shorter song variants were most prevalent in 2014, with the highest proportion of *P3*S (1.3%), *P1* (6.3 %), and *P3B* (5.8%) song events.

This sample year also had the lowest proportion of long variants, with only 35.3% *P3* and 2.8% *P3A* song events (Table 2). The longer song variants, *P3* and *P3A*, were prevalent in 2016 representing 45.2% and 8.4% of all songs respectively (Table 2), coinciding with the lowest prevalence of the shortest *P1* song variant. When considering song variants overall, the prevalence of shorter song variants (*P2*, *P1*, *P2A*, *P3S)* were generally higher within the same sample years 2011, 2012, 2014, and 2017, with the exception of *P2A* which was low in 2017.

Figure 4

Temporal variability in the ISI of SEIOPB whale songs



Note: Top: ISI (s) measured from SEIOPB whale songs in the Perth Canyon separated by song structure across all sample years. Each symbol corresponds to a single sample. Bottom; ISI (s) from SEIOPB whale song events across sample months. Data points are clustered by sample year (top) and month (bottom), grey lines represent a linear fit to assess seasonal and annual trends in ISI.

Table 2

Distribution of song variants by sample year

		P3	P3S	P2	P1	P3A	P2A	P3B
2017	Total	352	0	492	42	44	2	0
	%	37.77	0	52.79	4.51	4.72	0.21	0
2016	Total	151	0	145	8	28	2	0
	%	45.21	0	43.41	2.40	8.38	0.60	0
2014	Total	140	5	193	25	11	23	0
	%	35.26	1.26	48.61	6.30	2.77	5.79	0
2012	Total	129	0	179	20	12	5	0
	%	37.39	0	51.88	5.80	3.48	1.45	0
2011	Total	224	0	272	33	42	13	2
	%	38.23	0	46.42	5.63	7.17	2.22	0.34

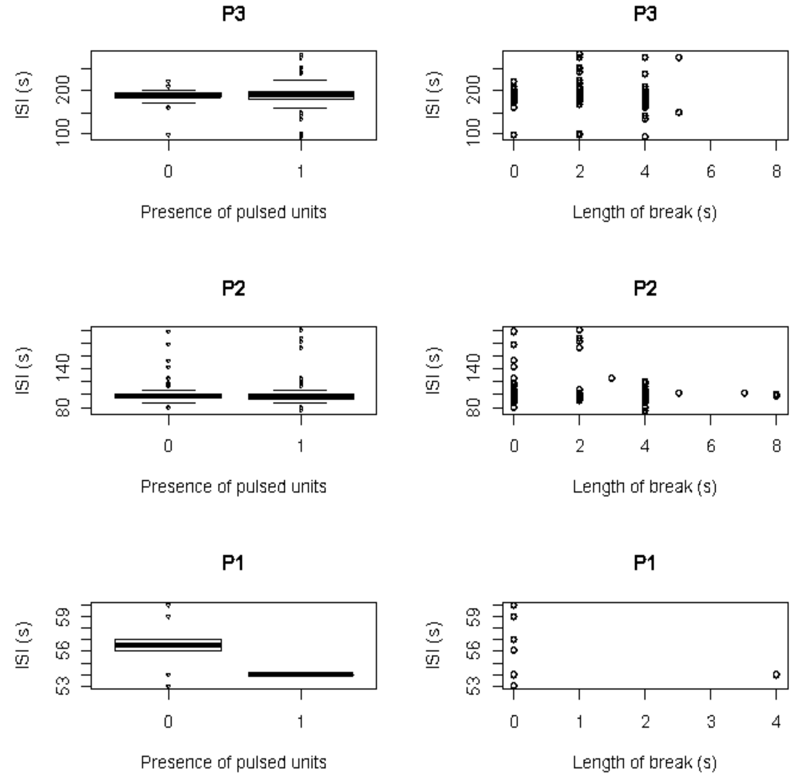
Note. Number of song events for each song variant with the distribution of song variants among sample population represented by a percentage. The dominant song variant is highlighted in red for each year, whilst the peak in less common song varieties is highlighted in yellow.

Plots of the residuals for the ANOVA model indicated that further testing was needed to validate the appropriateness of the model due to a non-random distribution of residuals. A Bartlett test indicated the variances were non-homogenous ($p < .001$, $K^2 = 26.426$) violating the standard assumption of a normalized distribution. Consequently, a Kruskall-Wallis test was used to confirm that there was a statistically significant difference in the proportions of song structure between years ($p < .001$). A post-hoc pairwise test indicated a significant increase in *P2* songs between 2010 and 2017. A significant difference was also seen in the mean ISI between years ($p = .036$). A Chi Square test was used to validate the ANOVA model, the output of which indicated that the difference in ISI and song type prevalence between years are not due to chance ($p = .025$ and $p < .001$ respectively).

Investigation of the influence of unit breaks on ISI provided conflicting results with unit breaks contributing to a slight increase in mean ISI in *P3* songs and *P2* songs (Figure 5). However, a slight decrease in ISI was seen for *P1* songs potentially due to the low number of *P1* song events with unit breaks (Figure 5). There was no indication of a relationship between the length of a break in sound production mid unit and ISI for any song type (Figure 4). The ANOVA model indicated that the apparent relationship between ISI in songs with and without unit breaks was statistically significant for *P3* ($F(1, 119)$, $p = .012$) but not *P2* ($F(1,119)$, $p = .381$) song types. A statistically significant relationship also existed for *P1* songs ($F(1, 49)$, $p = .039$), though the direction of the relationship was opposite to what was expected with *P1* songs with unit breaks having a shorter ISI than those without. This is likely due to the rarer occurrence of this song variant biasing the measurements.

Figure 5

Influence of Unit Breaks on Inter-song-interval (ISI)

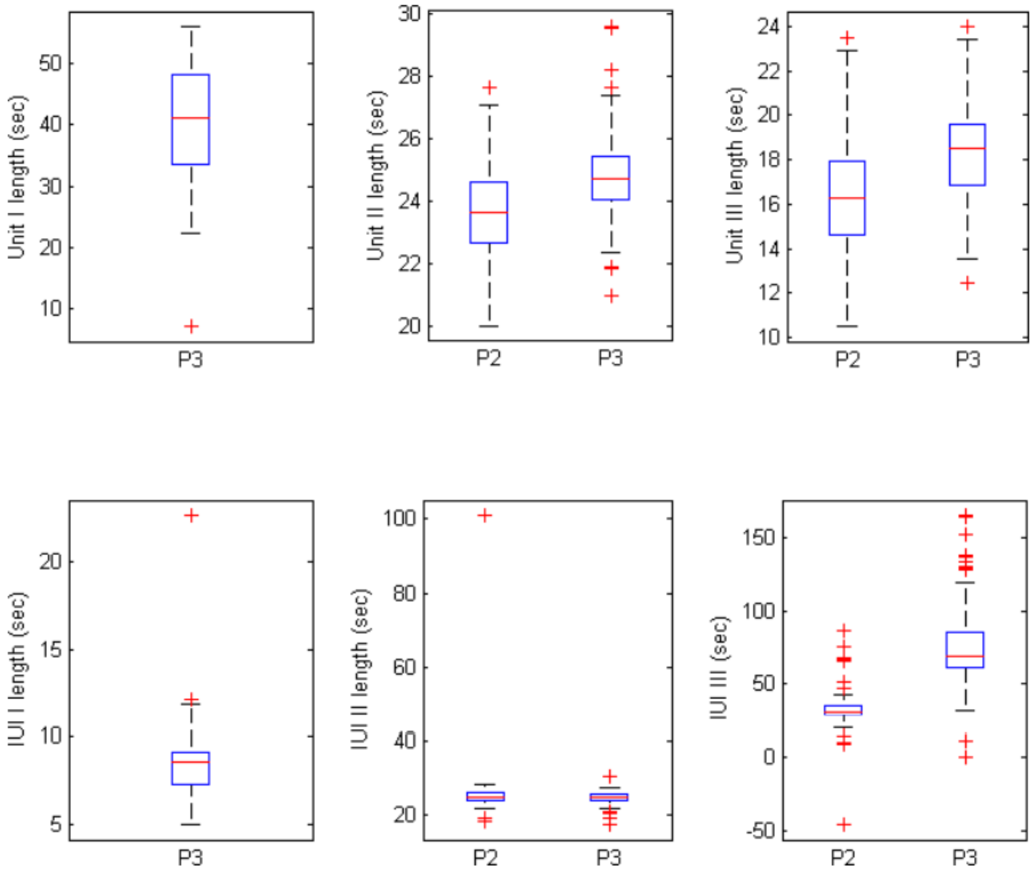


Note. The influence of unit breaks on ISI (seconds) for each of the three main song structures (P3-top, P2-middle and P1-bottom). Left: Mean ISI between normal (0) and song with unit break units (1). Right: ISI for song units with breaks of varying lengths (seconds) in one or more song units.

A subset of *P3* and *P2* songs was used for fine scale measurements of the length of individual song units as well as the spacing between successive units, referred to as the inter-unit interval (IUI). For *P3* songs the length of unit I, IUI-I, unit II, IUI-II, unit III and IUI-III were manually measured from spectrograms in that order. For *P2* songs, unit II, IUI-II, unit III and IUI-III were measured. The results of these measurements are displayed as box and whisker plots to assess the level of variability in each element that may contribute to the overall variability in ISI between singers (Figure 6). The results demonstrate that some elements of song structure are more variable in length than others. Unit I, only present in *P3* songs, was found to be highly variable in length, ranging in general from very short (~20 s) to very long (~60 s) units which could contribute considerably to the variation in ISI of *P3* songs (Figure 5).

Figure 6

Variability in the Length of the Song Units and Inter-Unit-Intervals (IUI)



Note. Box plots showing the median, interquartile range, and range of song units and inter-unit intervals for the subset of P3 and P2 songs that were used for further analysis. Top row, from left: Length of unit I (P3 songs only), inter-unit interval I (P3 songs only), length of unit II. Bottom row, from left: Length of inter-unit interval II, unit III, and inter-unit interval III (or the break before the commencement of the next song).

Table 3

Comparison of the Length of the Song Units and Inter-Unit-Intervals (IUI) Common to P2 and P3 Song Types

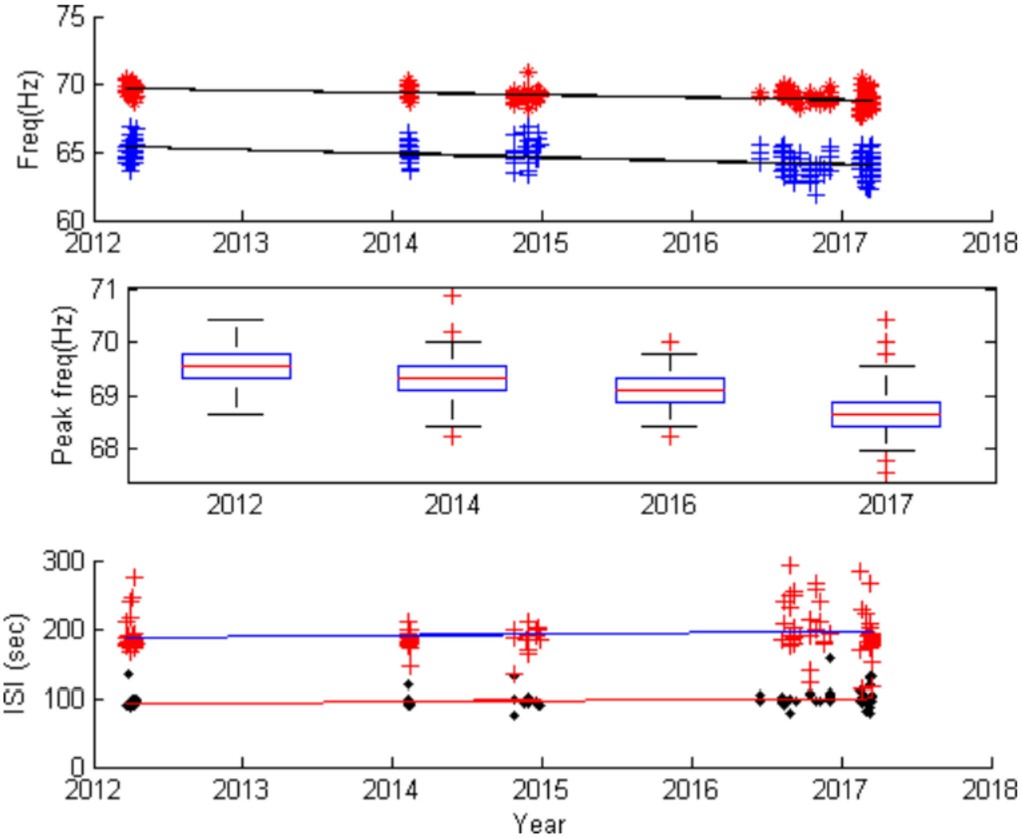
		Unit II	IUI-II	Unit III	IUI-III
P2	Mean 95% CI	23.66 s ± 1.69 s	24.59 s ± 1.72 s	16.25 s ± 2.42 s	32.37 s ± 13.05 s
P3	Mean 95% CI	24.74 s ±1.44 s	25.61 s ± 7.12 s	18.18 s ± 2.11 s	75.39 s ± 27.81 s
Ratio	P2 / P3	0.96	0.96	0.89	0.43

The length of the IUI between unit I and unit II in *P3* songs was also variable, with unit II found to be generally longer in *P3* songs than that in *P2* songs (Table 3). The length of IUI between unit II and unit III was the most consistent (Figure 6), though it was more variable in *P3* songs as opposed to

P2 songs (Table 3). Unit III length was highly variable though it was on average shorter in *P2* songs as opposed to *P3* songs (Table 3). The greatest level of variability was found in IUI-III between the final unit of a phrase (unit III) and the start of the next phrase (either unit I or unit II for *P3* or *P2* songs respectively; Table 3) and within song structures (Figure 6). Overall, there was a high level of variability in unit and IUI length between songs, with some elements more variable than others (Figure 6). The length of *P3* songs was the most variable, with length of unit I and IUI-III driving the greatest level of variability to ISI. Similarly, the length of IUI-III contributed the most to variability in the ISI of *P2* songs. It is evident that the comparatively shorter ISI of *P2* songs is not solely due to the omission of the first song unit, but that the production of all song units and intervals between units are also comparatively shorter than for *P3* songs (Table 3). This means that the difference in song construct between *P2* and *P3* is not purely a difference in the number of units, but in the timing of the units themselves.

Figure 7

Comparison of Changes in Frequency and Inter-song Intervals (ISI) in Song Events



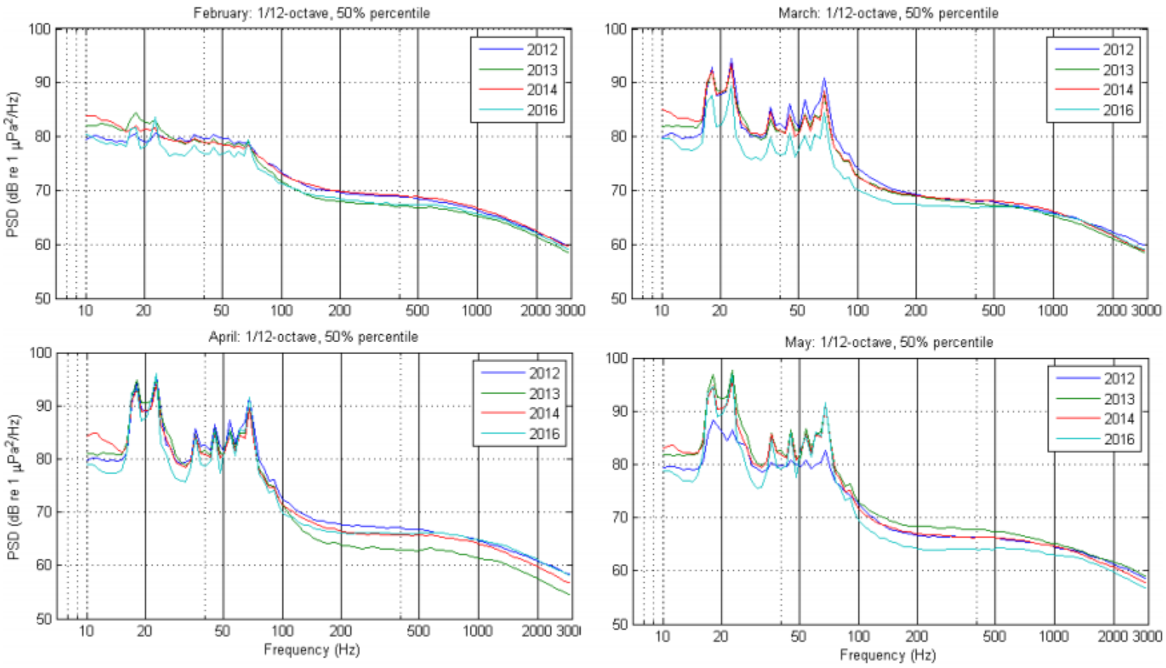
Note. Top: Peak (red) and start (blue) frequency of the third harmonic of type II song unit across sample years for P2 and P3 songs (P1 songs were not included due to the low overall number of song events), samples are clustered by year and the black lines represent the fit of a linear model to indicate overall trends in the peak and starting frequency. Middle: Box and whisker plot showing the median, range and interquartile range (25 to 75 %) of the peak frequency for the third harmonic of type II song units. Bottom: ISI of P2 (black) and P3 (red) songs across sample years, song events are clustered by sample year, and lines indicate linear models to assess overall trends in ISI.

A comparison of the starting and ending frequency for the third harmonic of the type II unit across the subset of *P3* and *P2* songs showed a continuation of the previously detected trends (Gavrilov et al., 2011) of declining tonal frequency (Figure 7). The ending and starting frequency decreased across sample years, and a fitted linear model indicated a decrease in tonal frequency of 0.26 Hz per year (Figure 7). Comparison of ISI across sample years indicates an increase in maximum ISI, and a very slight increase in mean ISI (Figure 7), as well as higher ISI in the sample months of March, April and May (Figure 4). There does, however, appear to be a greater range in ISI for both main song types in later sample years (2016 and 2017), with more overlap in the ISI ranges of *P2* and *P3* songs. A type II analysis of variance (ANOVA) found there to be a significant decrease in frequency between sample years ($F(4, 1807) = 125.0659$, $p = < .001$), however there was no significant effect of ISI on frequency change ($F(1, 1811) = 0.6368$, $p = .4275$,) suggesting there is no strong relationship between ISI and frequency. The residuals of the ANOVA model were normally distributed indicating an appropriate fit of the statistical model.

Analysis of the mean background noise levels in the Perth Canyon using power spectral density plots averaged across each month of pygmy blue whale presence indicates that environmental noise has remained consistent across the sample years but varies at the monthly time scale (Feb $M = 82 \pm 1.25$ dB re 1μPa^2/Hz at 20-21 Hz, Mar $M = 93 \pm 2.35$ dB re 1μPa^2/Hz at 20-21 Hz, Apr $M = 96 \pm 0.63$ dB re 1μPa^2/Hz at 20-21 Hz, May $M = 95 \pm 5.01$ dB re 1μPa^2/Hz at 20-21 Hz). Environmental noise between 20 and 70 Hz is dominated by pygmy blue whale vocalizations (Figure 8), and consequently higher level of ambient noise in these frequency bands corresponds to a higher calling density of pygmy blue whales. Higher occupancy of the Perth Canyon by pygmy blue whales from March to May is reflected in the peaks of the 50th percentile PSD curves in all years (Figure 8). Pygmy blue whale vocal presence was consistently high across all sample years for March and April, though appears to have increased from 2013 onwards for the month of May, indicating a higher level of vocal activity later in the season (Figure 8).

Figure 8

Ambient Noise Levels During Peak Months of Pygmy Blue Whale Presence in the Perth Canyon



Note. PSD of 50th percentile of sea noise spectrum level in 1/12-octave bands for months of peak pygmy blue whale presence in the Perth Canyon area across four sample years.

Discussion

Inter-annual variability in song characteristics has been documented for several marine mammal species (Garland, Rendell, Lamoni et al., 2017; Garland, Rendell, Lilley et al., 2017; Lewis et al., 2007), though the drivers of this variability remain poorly understood. Timing is an important structural element of song, though little research has been conducted to date on the variability in the temporal characteristics of pygmy blue whale songs. Inter song intervals for the SEIOPB whale, defined as the time between successive type II song units, were found in this study to be highly variable at both inter- and intra-annual timescales. When considering variability between sample years, the overall decreasing trend in ISI that was observed within this study appears to be driven by an increasing prevalence of songs comprised of shorter phrase structures. However, when considering the song types in isolation across all sample years, there was a slight increase in the average length of songs within each phrase structure. The ISI appeared to remain consistent within song events, as determined by visual analysis of spectrograms and consistent received levels (see Jolliffe et al., 2019) but varied considerably between song events of the same phrase structure within the same year. Unlike other species, such as fin whales, where variability in temporal characteristics follow a consistent seasonal trend (Morano et al., 2012), there were no apparent monthly or seasonal trends in ISI suggesting that variability is not likely to be linked to physical environmental factors. The temporal characteristics of songs were highly variable between song events and thus more likely driven by the context of the individual (for example, size, age, status, cognitive capacity, dive depth, behavior) than longer term factors.

Songs comprised of longer phrase structures unsurprisingly were most variable in their temporal structure with more units and IUIs for variability to occur within, while shorter phrase structures had the lowest level of temporal variability. Within the phrase structure, some units and IUIs were more stable in their temporal characteristics than others. The greatest variability for *P2* and *P3* songs comes from the IUI between the end of unit III and the start of the next phrase (unit I for *P3* songs or unit II for *P2* songs). For *P3* songs, the length of unit I was also found to be highly variable contributing to the large variability in ISI for *P3* songs. Variability in the temporal structure of unit II and III was greatest between song events with different phrase structures, rather than the song events of the same phrase structure. This may indicate that certain units, and the intervals between them serve different communicative purposes or convey specific information about the individual or their behavioral context.

Song complexity has long been considered to be a factor in animal sexual selection, with females presumed to prefer males with more complex songs (Creanza et al., 2016; Garland, Rendell, Lilley et al., 2017; Macdougall-Shackleton, 1997; Wiggins et al., 2015). Such sexual selection is believed to drive the evolution in whale song as males use complex vocal displays to compete for females, as well as mediate interactions with competing males (Cholewiak et al., 2018; Creanza et al., 2016; Garland, Rendell, Lilley et al., 2017). While complexity is recognized as being an important factor in sexual selection, song length is also hypothesized to influence female preference, with female zebra finches showing a preference for longer songs, as well as those comprised of heterozygous syllables (Neubauer, 1999). Within the songs of the SEIOPB, the first unit is the most complex, but also the least transmissible as given by the fact it does not appear for long range signals due to sound propagation losses and its lower source level compared to the other units (3 to 10 dB lower than unit II, McCauley et al., 2001). Where high levels of background noise result in a poor signal-to-noise ratio, the first unit of the SEIOPB is barely visible in spectrograms even when the second and third units are perfectly clear (Jolliffe et al., 2019). Perhaps while this unit adds favorable complexity, it does not contain critical information about the singer and hence is dropped to maximize singing efficiency when background noise conditions are high, or there are higher densities of singing whales, as hypothesized in Jolliffe et al. (2021).

Interestingly, this study found that the difference in the ISI of a song was not driven solely by the number of units in the phrase but the temporal characteristics of the units themselves, including the spaces between unit production (i.e., inter-unit interval). While it was previously assumed that the only difference between a *P2* and a *P3* song was the addition of unit I, this study found that both units II and III were distinctly shorter in *P2 s*ongs as opposed to *P3* songs (ratio *P2/P3* length of 0.96 and 0.89 of units II and III respectively; Table 3), contributing to the overall shorter ISI in the *P2* songs compared to the *P3* songs. Consequently, to shift from a *P3* to a *P2* song, an animal would not only have to omit the first unit from the song sequence but would also have to change the temporal structure of the other two units. Given that animals can shift between song structures (Beck, 2019; Davenport et al., 2022), this suggests that the vocal production of song units is adaptable indicating that variability in ISI is not due to differences in the learned song of blue whales. The findings of this study also suggest that songs adhere to some sort of production rules and that the similar rules and theories that apply to the acoustic communication of terrestrial animals also apply to marine animals. The fact that a change in phrase composition leads to a subsequent change in temporal duration that is a close multiplier of the other construct (e.g., 1 part phrase 50 s, 2 part 100 s, 3 part 200 s) that is not solely linked to the length of the additional unit itself implies there is some sort of temporal template constraining how songs can be structured.

Linguistic law suggests that the length and complexity of units within a sequence are related to the length of the sequence itself. However, the shortening of units in shorter phrases is contrary to common linguistic laws that have been shown to apply not only to human linguistics but to a variety of terrestrial animal vocal sequences as well (Favaro et al., 2020; Gustison et al., 2016; Heesen et al., 2019). Specifically, Menzerath's law suggests that shorter sequences should have longer components, and the longer the sequence, the shorter its constituents (Favaro et al., 2020; Gustison et al., 2016; Heesen et al., 2019). While it was hypothesized that linguistic laws would be relevant to the temporal structure of whale song, it is plausible that if information in whale song is encoded not only in the units themselves, but in the timing and spaces between, then variability in the vocal sequences may not be explainable by a linguistic law. Further, there may be potential energetic tradeoffs in the overall investment of effort between phrases. As noted above, some units are more transmissible than others and perhaps the units serve different functions based on the information they communicate. If this is the case, different units may be relevant to different potential receivers and thus audience composition may influence singing behavior with singers allocating more effort to the units that are of greatest importance depending on the audience (Fedurek et al., 2017). Studies have shown that audience composition, including whether adult male whales are already singing, is an important factor influencing the singing behavior of humpback whales (Dunlop & Noad, 2016). It is not clear exactly how whales are able to discern audience composition, but as singing whales are unlikely to be within visible range of each other it is likely that information about individual context is conveyed in vocal cues. Further, noting that breathing constraints likely apply to the singing bout, singers may benefit by allocating greater effort to specific units (e.g., the most transmissible ones) in periods of high background noise or high caller density, depending on the specific circumstance and context of the singer (Fedurek et al., 2017).

This study found a high level of variability in the temporal characteristics of song between singing bouts. Based on key characteristics in the spectrogram (see Jolliffe et al., 2019), it is reasonable to assume that a singing bout comes from an individual whale, though it is not possible to ascertain whether each singing bout is a different whale. Thus, there is a possibility that a whale could cease singing and recommence singing a song with different temporal characteristics. The high level of variability in the temporal characteristics of song units and IUIs supports the notion that the song may be used to convey important information about the singer or the singer's context. This could include the physical or behavioral context of the singer such as their dive depth (Davenport et al., 2022). Temporal stability of song structure within a singing bout could well be attributed to the relative consistency of a singer's context over the duration of a singing bout. It is not clear however, exactly what the drivers of this variability were, especially given the lack of consistent seasonal or annual trends. Blue whales are known to sing while they travel and migratory dives are relatively consistent in their depth (Lewis et al., 2018; Owen et al., 2016). It is hypothesized that blue whales likely migrate at a depth at which they are neutrally buoyant and thus the depth of migratory dives is likely to be influenced by the size of the animal as well as environmental variables (Oleson et al., 2007; Woodward et al., 2006). It is possible that dive parameters such as depth and time may be linked with the temporal structure of song which would in turn likely be influenced by both environmental factors as well as the physical characteristics of the individual. Ambient noise conditions may also influence vocal behavior by driving trade-offs between the production of complex song units that may be preferred by females, and the transmissibility of song units, as has been observed in silvereyes (*Zosterops lateralis*) singing in urban environments (Potvin et al., 2013). As suggested in Jolliffe et al. (2021), it is possible that important information about an individual animal is conveyed through songs, with some level of variability in structure being driven by a tradeoff between increasing vocal complexity and improving the energetic efficiency of song production. For blue whales, additional complexity has been observed in songs through the addition of breaks and pauses in song unit production (Jolliffe et al., 2019). The presence of unit breaks only appeared to influence the ISI for *P3* song structures, with the length of the break itself not having any influence on ISI. With the number of observed unit breaks increasing in later sample years, such unit variations are likely to have an influence on temporal trends in song variability into the future. The level of variability in the temporal structure of individual song units, as well as phrase and song structures, indicates that temporal elements of song may encode information about the singers themselves or their environment, as has been documented for other whale and bird populations (Dunlop, 2017; Job et al., 2016).

Overall, this study found that in the Perth Canyon, when all major song types were considered, there was a shortening in the temporal structure of song production through the preference for shorter song phrases with increasing time (years). Song structure was a confounding factor in ISI analysis with the length of the song depending largely on phrase structure. The prevalence of shorter song structures such as *P1*, *P2* and *P2A* songs, as well as longer song structures such as *P3* and *P3A* shaped the range of ISI for each sample year as well as having a significant influence on the mean ISI. Consequently, statistical methods used for analyzing song repetition intervals need to take diversity in song structure into consideration. When grouping data by song type, it is evident that ISI is more variable within some song types than others. Contrary to what we expected, a relationship between the range in ISI and sample size was not observed, and the absence of such a relationship could be a reflection of short-term changes to background noise in the environment (Cholewiak et al., 2013; Fristrup et al., 2003). For example, as suggested in Jolliffe et al. (2021), if singing is influenced by background noise levels, then it would be expected that when background noise is highest, whales produce songs comprised of the shortest variants. Noting that noise in the frequency bands of blue whale songs recorded here is primarily dominated by the chorus of co-specific singing blue whales, it may be that in years with the highest density of whales, ISI variability is at its lowest as whales favor the more transmissible shorter song variants (Jolliffe et al., 2021). However, noting that females are likely to prefer longer songs, there is sexual selection for longer phrase lengths even when singing shorter song variants. This could potentially explain the large range of ISI in the relatively small 2010 data set (Melcón et al., 2012; Parks et al., 2008). Background noise analysis indicates that there has been no statistically significant increase in background noise conditions across the years sampled and consequently it is unlikely that this was driving the observed differences in ISI. However, while there are no consistent directional trends, inter- and intra- annual fluctuations in background noise may be related to song length. This can be seen in the higher background noise levels indicated by PSD curves for 2014 and 2016 which also had large ranges in ISI and higher mean ISI values. Further, ISI was seen to increase in March, April and May corresponding with higher ambient PSD levels in these months, as well as the peak of the migration season. Notably these peaks in background noise correspond with the frequency bands of SEIOPB song and are caused by an increased density of vocalizing SEIOPB whales. This indicates that SEIOPB appear to decrease their song length in response to increasing levels of background noise by favoring songs comprised of shorter phrases even though they increase the phrase duration with longer repetitions of shorter song types (i.e., *P2* and *P1* songs) when background noise conditions are higher. Given the wide body of literature indicating an influence of background noise conditions on song rate and length (Dorado-Correa et al., 2018; Fristrup et al., 2003; Job et al., 2016), it is possible that the relationship between song rate and background noise is more complex than that assumed here and thus it is recommended that future song repetition studies consider more in-depth analysis of environmental conditions.

Song variability over time showed an increased occurrence of *P1* song events while the percentage of *P3* and *P2* events remained relatively consistent (Jolliffe et al., 2019). However, variability in ISI cannot be explained solely by changes in song structure prevalence and is likely influenced by other factors. A comparison of song structure prevalence across sample years indicates non-directional inter annual trends. There is a noticeable shift to shorter song variations in the 2014 sample year, including *P3*S, *P2A* (a *P2* and *P1* phrase combination) and *P1* which all occurred in the highest proportions for that sample year, while long songs such as *P3* and *P3A* (a *P3* and *P2* phrase combination) song variants occurred in their lowest proportions. Conversely 2016 presented the lowest proportion of shorter song variants (*P1*, HB and *P3*S) and the highest proportions of long song variants (*P3* and HA). Interestingly, these findings coincide with the significant 2014 to 2016 El Nino event that dramatically disrupted the climate and sea surface temperature (SST) patterns in Western Australia (Crimp et al., 2018). Changes in the physical properties of the water column may have an influence on song production and sound transmission (Chu et al., 2017; Luo et al., 2014) resulting in these anomalies in song variability, though this is speculative and does not explain inter-annual variability.

It is also plausible to consider that variability in ISI may be linked to other elements of song production including the frequency, as discussed in Jolliffe et al. (2019). A number of studies have described the worldwide decline in frequencies of whale sounds (Gavrilov et al., 2012; Leroy et al., 2018; Oleson et al., 2014), and this phenomenon has been documented for the type II SEIOPB whale sound (Gavrilov et al., 2011). It is not clear whether the decline in frequency is due to environmental factors, or whether lower frequency songs are favored by females noting they may give the impression of a larger animal. If low frequency calling is preferred by females but is more costly, a relationship between number and duration of calls and the frequency would be expected whereby the song rate decreases (increased song duration) with decreasing frequency (Linhart et al., 2012). It is possible that a decline in average frequency of song units may influence their duration, though the likely effect would be an increase in duration which is supported by the findings of this paper as well as Jolliffe et al. (2021). This would suggest that there may be a trend towards increasing ISI if song frequency continues to decline inter-annually, despite the intra-annual variability observed in ISI. This study indicated a weak, but not statistically significant, inverse relationship between ISI and frequency, with interannual decrease in fundamental frequency and a slight increase in mean ISI. A larger sample size with respect to the number of song events analyzed may reveal a more significant relationship between ISI and frequency. Similar concurrent studies of frequency and ISI should be conducted into the future as trends in song duration may be too small to be detected in the manual analysis conducted in this study. While manual analysis has the benefit of quantifying combination phrase structures and is accurate for the classification of song types, it is time consuming resulting in smaller sample sizes than automatic analysis methods such as the feature space analysis presented in Jolliffe et al. (2019).

Conclusion

The results of this study identify that there is a distinct level of variability in the temporal characteristics of SEIOPB whale song with preliminary findings suggesting a relationship between the increased density of vocalizing animals (as shown by higher background noise levels) and the temporal structure of individual song types. Thus, call rates are not necessarily an immediate proxy for abundance or relative abundance as song repetition interval decreases with singer density. Based on the results of this, and past studies by Jolliffe et al. (2021), individual whales may switch to shorter song types in periods of higher singer density, biasing call rates up. This supports the hypothesis that whales make trade-offs between increasing song complexity and maximizing vocal transmission, with the introduction of unit breaks in later sample years perhaps an innovation to reintroduce complexity without compromising song transmission. The oceans are becoming noisier, meaning the production of more complex songs in the form of the longer, more intricate three-part song, may come at a cost given that longer songs effectively have a lower song rate and the first unit is not particularly transmissible when the signal to noise ratio is low. The key finding of this study is that it confirms that differences exist in the temporal characteristics of each song type, outside of the inclusion or omission of particular song units, with the units, and unit breaks within songs comprised of shorter phrases being shorter in duration. Such a finding suggests that the transition from songs comprised of different phrase structures appears to involve not only the omission of song units but a shift in the temporal characteristics of unit production, that is in itself highly structured, but also is contrary to common linguistic laws. It is hypothesized that important information about an individual’s context or social environment may be encoded within the temporal characteristics of song, including both the units and the breaks between the units. Temporal characteristics may also be influenced by changes in physical context, such as dive depth, increased background noise produced by chorusing whales, or audience composition. In order to elucidate any links that may exist between individual context, density effects and song repetition intervals, further studies are necessary. It is recommended that future studies incorporate in situ measurements of background noise, as well as visual observations of singing behavior of whales.

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References

Baptista, L. F., & Keister, R. A. (2005). Why birdsong is sometimes like music. *Perspectives in Biology and Medicine*, *48*(3), 426-443. https://doi.org/https://10.1353/pbm.2005.0066

Beck, C. D. (2019). *Vocal behaviour of the eastern Indian Ocean pygmy blue whale and its changes over time and between aggregations* [Unpublished doctoral dissertation]. Curtin University.

Blackwell, S. B., Nations, C. S., McDonald, T. L., Thode, A. M., Mathias, D., Kim, K. H., Greene, C.R., Macrander, A. M. (2015). Effects of airgun sounds on bowhead whale calling rates: Evidence for two behavioral thresholds. *Plos One*, *10*(6), e0125720. https://doi.org/10.1371/journal.pone.0125720

Blackwell, S. B., Nations, C. S., Thode, A. M., Kauffman, M. E., Conrad, A. S., Norman, R. G., & Kim, K. H. (2017). Effects of tones associated with drilling activities on bowhead whale calling rates. *Plos One*, *12*(11), e0188459. https://doi.org/10.1371/journal.pone.0188459

Cantor, M., & Whitehead, H. (2013). The interplay between social networks and culture: Theoretically and among whales and dolphins [Review]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120340. https://doi.org/10.1098/rstb.2012.0340

Cazau, D., Adam, O., Aubin, T., Laitman, J. T., & Reidenberg, J. S. (2016). A study of vocal nonlinearities in humpback whale songs: From production mechanisms to acoustic analysis. *Scientific Reports*, *6*, 31660. https://doi.org/10.1038/srep31660

Cholewiak, D. M., Cerchio, S., Jacobsen, J. K., Urban-R, J., & Clark, C. W. (2018). Songbird dynamics under the sea: Acoustic interactions between humpback whales suggest song mediates male interactions. *Royal Society Open Science*, *5*(2), 171298. https://doi.org/10.1098/rsos.171298

Cholewiak, D. M., Sousa-Lima, R. S., & Cerchio, S. (2013). Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. *Marine Mammal Science*, *29*(3), E312–E332. https://doi.org/10.1111/mms.12005

Chu, P. C., McDonald, C. M., Kucukosmanoglu, M., Judono, A., Margolina, T., & Fan, C. (2017). Effect of inter- and intra-annual thermohaline variability on acoustic propagation. *Ocean Sensing and Monitoring IX*, *10186* ,171-190. https://doi.org/10.1117/12.2258687

Creanza, N., Fogarty, L., & Feldman, M. W. (2016). Cultural niche construction of repertoire size and learning strategies in songbirds. *Evolutionary Ecology*, *30*(2), 285-305. https://doi.org/10.1007/s10682-015-9796-1

Crimp, S., Nicholls, N., Kokic, P., Risbey, J. S., Gobbett, D., & Howden, M. (2018). Synoptic to large-scale drivers of minimum temperature variability in Australia – long-term changes. *International Journal of Climatology*, *38*, e237-e254. https://doi.org/10.1002/joc.5365

Davenport, A. M., Erbe, C., Jenner, M.-N. M., Jenner, K. C. S., Saunders, B. J., & McCauley, R. D. (2022). Pygmy blue whale diving behaviour reflects song structure. *Journal of Marine Science and Engineering*, *10*(9), 1227. https://doi.org/https://doi.org/10.3390/jmse10091227

DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., & Southall, B. L. (2017). A multivariate mixed hidden 227arkov model for blue whale behaviour and responses to sound exposure. *Annals of Applied Statistics*, *11*(1), 362-392. https://doi.org/10.1214/16-aoas1008

Dorado-Correa, A. M., Zollinger, S. A., & Brumm, H. (2018). Vocal plasticity in mallards: Multiple signal changes in noise and the evolution of the Lombard effect in birds. *Journal of Avian Biology*, *49*(1), Article UNSP e01564. https://doi.org/10.1111/jav.01564

Dunlop, R. A. (2017). Potential motivational information encoded within humpback whale non-song vocal sounds. *Journal of the Acoustical Society of America*, *141*(3), 2204-2213. https://doi.org/10.1121/1.4978615

Dunlop, R. A., Cato, D. H., & Noad, M. J. (2010). Your attention please: Increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences*, *277*(1693), 2521-2529. https://doi.org/10.1098/rspb.2009.2319

Dunlop, R. A., Cato, D. H., & Noad, M. J. (2014). Evidence of a Lombard response in migrating humpback whales (*Megaptera novaeangliae*). *The Journal of the Acoustical Society of America*, *136*(1), 430-437. https://doi.org/10.1121/1.4883598

Dunlop, R.A., & Noad, M.J. (2016). The "risky" business of singing: tactical use of song during joining by male humpback whales. *Behavioral Ecology and Sociobiology*, *70*, 2149–2160. https://doi.org/10.1007/s00265-016-2218-8

Favaro, L., Gamba, M., Cresta, E., Fumagalli, E., Bandoli, F., Pilenga, C. Isaja, V., Mathevon, N., & Reby, D. (2020). Do penguins' vocal sequences conform to linguistic laws? *Biology Letters*, *16*(2), 20190589. https://doi.org/10.1098/rsbl.2019.0589

Fedurek, P., Zuberbühler, K., & Semple, S. (2017). Trade-offs in the production of animal vocal sequences: Insights from the structure of wild chimpanzee pant hoots. *Frontiers in Zoology*, *14*(1), 50. https://doi.org/10.1186/s12983-017-0235-8

Fristrup, K. M., Hatch, L. T., & Clark, C. W. (2003). Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. *Journal of the Acoustical Society of America*, *113*(6), 3411-3424. https://doi.org/10.1121/1.1573637

Garland, E. C., Rendell, L., Lamoni, L., Poole, M. M., & Noad, M. J. (2017). Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), 7822-7829. https://doi.org/10.1073/pnas.1621072114

Garland, E. C., Rendell, L., Lilley, M. S., Poole, M. M., Allen, J., & Noad, M. J. (2017). The devil is in the detail: Quantifying vocal variation in a complex, multi-levelled, and rapidly evolving display. *Journal of the Acoustical Society of America*, *142*(1), 460-472. https://doi.org/10.1121/1.4991320

Gavrilov, A. N., & McCauley, R. D. (2013). Acoustic detection and long-term monitoring of pygmy blue whales over the continental slope in southwest Australia. *The Journal of the Acoustical Society of America*, *134*(3), 2505-2513. https://doi.org/10.1121/1.4816576

Gavrilov, A. N., McCauley, R. D., & Gedamke, J. (2012). Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. *Journal of the Acoustical Society of America*, *131*(6), 4476-4480. https://doi.org/10.1121/1.4707425

Gavrilov, A. N., McCauley, R. D., Salgado-Kent, C., Tripovich, J., & Burton, C. (2011). Vocal characteristics of pygmy blue whales and their change over time. *Journal of the Acoustical Society of America*, *130*, 3651–3660. https://doi.org/10.1121/1.3651817

Gavrilov A.N. and Parsons M.J.G. (2014). A MATLAB tool for the characterisation of recorded underwater sound (CHORUS). *Acoustics Australia*, *42*(3), pp. 190-196.

Goldbogen, J. A., Southall, B. L., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Hazen, E. L., Falcone, E. A., Schorr, G. S., Douglas, A., Moretti, D. J., Kyburg, C., McKenna, M. F., & Tyack, P. L. (2013). Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B-Biological Sciences*, *280*(1765), 20130657. https://doi.org/10.1098/rspb.2013.0657

Guazzo, R. A., Helble, T. A., Alongi, G. C., Durbach, I. N., Martin, C. R., Martin, S. W., & Henderson, E. E. (2020). The Lombard effect in singing humpback whales: Source levels increase as ambient ocean noise levels increase. *Journal of the Acoustical Society of America*, *148*(2), 542-555. https://doi.org/10.1121/10.0001669

Gustison, M. L., Semple, S., Ferrer-i-Cancho, R., & Bergman, T. J. (2016). Gelada vocal sequences follow Menzerath's linguistic law. *Proceedings of the National Academy of Sciences*, *113*(19), E2750-E2758. https://doi.org/10.1073/pnas.1522072113

Hammond, P., Heinrich, S., Hooker, S., & Tyack, P. (2017). *Whales: Their Biology and Behavior*. Comstock Publishing Associates. https://books.google.com.au/books?id=cynOAQAACAAJ

Handel, S., Todd, S. K., & Zoidis, A. M. (2009). Rhythmic structure in humpback whale (*Megaptera novaeangliae*) songs: Preliminary implications for song production and perception. *Journal of the Acoustical Society of America*, *125*(6), EL225-EL230. https://doi.org/10.1121/1.3124712

Hauser, M. D., Agnetta, B., & Perez, C. (1998). Orienting asymmetries in rhesus monkeys: The effect of time-domain changes on acoustic perception. *Animal Behaviour*, *56*(1), 41-47. https://doi.org/10.1006/anbe.1998.0738

Hedwig, D., Mundry, R., Robbins, M. M., & Boesch, C. (2015). Audience effects, but not environmental influences, explain variation in gorilla close distance vocalizations-A test of the acoustic adaptation hypothesis. *American Journal of Primatology*, *77*(12), 1239-1252. https://doi.org/10.1002/ajp.22462

Heesen, R., Hobaiter, C., Ferrer-i-Cancho, R., & Semple, S. (2019). Linguistic laws in chimpanzee gestural communication. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1896), 20182900. https://doi.org/10.1098/rspb.2018.2900

Helweg, D. A., Cato, D. H., Jenkins, P. F., Garrigue, C., & McCauley, R. D. (1998). Geographic variation in South Pacific humpback whale songs. *Behaviour*, *135*, 1-27. https://doi.org/10.1163/156853998793066438

Job, J. R., Kohler, S. L., & Gill, S. A. (2016). Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation. *Behavioral Ecology*, *27*(6), 1734-1744. https://doi.org/10.1093/beheco/arw105

Jolliffe, C. D., McCauley, R. D., Gavrilov, A. N., Jenner, C. S., Jenner, M. N., & Duncan, A. (2019). Song variation of the Eastern Indian Ocean pygmy blue whale population. *Plos One*, *14*(1), e0208619. https://doi.org/10.1371/journal.pone.0208619

Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, C., Backus, G., Bee, M. A., Bohn, K., Coa, Y., Carter, G., Cäsae, C., Coen, M., DeRuiter, S. L., Doyle, L., Edelman, S., Ferrer-i-Cancho, R., Freeberg, T. M., Garland, E. C., Gustison, M., Harley, H. E., Huetz, C., Hughes, M., Bruno, J. H., Ilany, A., Jin, D. Z., Johnson, M., Ju, C., Karnowski, J., Lohr, B., Manser, M. B., McCowan, B., Marcado III, E., Narins, P. M., Piel, A., Rice, M., Salmi, R., Sasahara, K., Sayigh, L., Shiu, Y., Taylor, C., Vallejo, E. E., Waller, S., & Zamora-Gutierrez, V. (2016). Acoustic sequences in non-human animals: A tutorial review and prospectus. *Biological Reviews*, *91*(1), 13-52. https://doi.org/10.1111/brv.12160

Kershenbaum, A., & Garland, E. C. (2015). Quantifying similarity in animal vocal sequences: Which metric performs best? *Methods in Ecology and Evolution*, *6*(12), 1452-1461. https://doi.org/10.1111/2041-210x.12433

Leroy, E. C., Royer, J.-Y., Bonnel, J., & Samaran, F. (2018). Long-term and seasonal changes of large whale call frequency in the southern Indian Ocean. *Journal of Geophysical Research: Oceans*, *123*(11), 8568-8580. https://doi.org/10.1029/2018JC014352

Lewis, L. A., Calambokidis, J., Stimpert, A. K., Fahlbusch, J., Friedlaender, A. S., McKenna, M. F., Mesnick, S. L., Oleson, E. M., Southall, B. L., Szesciorka, A. R., & Sirović, A. (2018). Context-dependent variability in blue whale acoustic behaviour. *Royal Society Open Science*, *5*(8), 180241. https://doi.org/10.1098/rsos.180241

Lewis, T., Gillespie, D., Matthews, L. J., Danbolt, M., Leaper, R., McLanaghan, R., & Moscrop, A. (2007). Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003. *Journal of the Marine Biological Association of the United Kingdom*, *87*(1), 353-357. https://doi.org/10.1017/s0025315407054896

Linhart, P., Slabbekoorn, H., & Fuchs, R. (2012). The communicative significance of song frequency and song length in territorial chiffchaffs. *Behavioral Ecology*, *23*(6), 1338-1347. https://doi.org/10.1093/beheco/ars127

Luo, J., Koselj, K., Zsebok, S., Siemers, B. M., & Goerlitz, H. R. (2014). Global warming alters sound transmission: Differential impact on the prey detection ability of echolocating bats. *Journal of the Royal Society Interface*, *11*(91), 20130961. https://doi.org/10.1098/rsif.2013.0961

Macdougall-Shackleton, S. A. (1997). Sexual selection and the evolution of song repertoires. In: Nolan, V., Ketterson, E.D., Thompson, C.F. (eds). *Current Ornithology*. Current Ornithology, vol 14, pp.88-144. Springer, Boston, MA. https://doi.org/10.1007/978-1-4757-9915-6_3

Mačutek, J., Čech, R., Rovenchak, A., & Hernández-Fernández, A. (2017). The Menzerath-Altmann Law in synctactic dependent structure. Proceedings of the Fourth International Conference on Dependency Linguistics, 2017, 100-107. Pisa,Italy. Linköping University Electronic Press. De Gruyter Mouton.

McDonald, M. A., Hildebrand, J. A., & Mesnick, S. L. (2006). Biogeographic characterization of blue whale song worldwide: Using song to identify populations. *Journal of Cetacean Research and Management*, *55*. https://doi.org/10.47536/jcrm.v8i1.702

Melcón, M. L., Cummins, A. J., Kerosky, S. M., Roche, L. K., Wiggins, S. M., & Hildebrand, J. A. (2012). Blue whales respond to anthropogenic noise. *Plos One*, *7*(2), e32681. https://doi.org/10.1371/journal.pone.0032681

Mercado, E., Herman, L. M., & Pack, A. A. (2005). Song copying by humpback whales: Themes and variations. *Animal Cognition*, *8*(2), 93– 102. https://doi.org/10.1007/s10071-004-0238-7

Miksis-Olds, J. L., Nieukirk, S. L., & Harris, D. V. (2018). Two unit analysis of Sri Lankan pygmy blue whale song over a decade. *Journal of the Acoustical Society of America*, *144*(6), 3618-3626. https://doi.org/10.1121/1.5084269

Morano, J. L., Salisbury, D. P., Rice, A. N., Conklin, K. L., Falk, K. L., & Clark, C. W. (2012). Seasonal and geographical patterns of fin whale song in the western North Atlantic Ocean. *Journal of the Acoustical Society of America*, *132*(2), 1207-1212. https://doi.org/10.1121/1.4730890

Neubauer, R. L. (1999). Super-normal length song preferences of female zebra finches (*Taeniopygia guttata*) and a theory of the evolution of bird song. *Evolutionary Ecology*, *13*(4), 365-380. https://doi.org/10.1023/A:1006708826432

Oleson, E. M., Calambokidis, J., Burgess, W. C., McDonald, M. A., & LeDuc, C. A. (2007). Behavioural context of call production by eastern North Pacific blue whales. *Marine Ecology Progress Series*, *330*, 269-284. https://doi.org/10.3354/meps330269

Oleson, E. M., Slrovic, A., Bayless, A. R., & Hildebrand, J. A. (2014). Synchronous seasonal change in fin whale song in the North Pacific. *Plos One*, *9*(12), *18*, e115678. https://doi.org/10.1371/journal.pone.0115678

Owen, K., Jenner, C. S., Jenner, M. N. M., & Andrews, R. D. (2016). A week in the life of a pygmy blue whale: Migratory dive depth overlaps with large vessel drafts. *Animal Biotelemetry*, *4*(1), 17. https://doi.org/10.1186/s40317-016-0109-4

Parks, S. E., Clark, C. W., & Tyack, P. (2008). Short- and long-term changes in right whale calling behaviour: The potential effects of noise on acoustic communication. *Journal of the Acoustical Society of America*, *122*(6). https://doi.org/10.1121/1.2799904

Payne, R. S., & McVay, S. (1971). Songs of humpback whales. *Science*, *173*(3997), 585-597. https://doi.org/10.1126/science.173.3997.585

Potvin, D. A., Mulder, R. A., & Parris, K. M. (2013). Acoustic, morphological, and genetic adaptations to urban habitats in the silvereye (*Zosterops lateralis*). In *Avian urban ecology* (pp. 171-180). Oxford University Press.

R Development Core Team. (2010). *R: A language and environment for statistical computing (V4.3.1)*. [Computer program]. The R Project for statistical computing. https://www.r-project.org/

Randall, J. A. (1989). Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis*. *Animal Behaviour*, *38*(4), 620-630. https://doi.org/10.1016/S0003-3472(89)80007-7

Randall, J. A. (1997). Species-specific footdrumming in kangaroo rats: *Dipodomys ingens*, *D. deserti*, *D. spectabilis*. *Animal Behaviour*, *54*(5), 1167-1175. https://doi.org/10.1006/anbe.1997.0560

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins [Review]. *Behavioral and Brain Sciences*, *24*(2), 309-+. https://doi.org/10.1017/s0140525x0100396x

Rennie, S. (2005). *Oceanographic processes in the Perth Canyon and their impact on productivity* [unpublished doctoral dissertation]. Curtin University.

Rennie, S., Hanson, C. E., McCauley, R. D., Pattiaratchi, C., Burton, C., Bannister, J., Jenner, C. & Jenner, M.. (2009). Physical properties and processes in the Perth Canyon, Western Australia: Links to water column production and seasonal pygmy blue whale abundance. *Journal of Marine Systems*, *77*, 21-44. https://doi.org/10.1016/j.jmarsys.2008.11.008

Robertson, F. C., Koski, W. R., Thomas, T. A., Richardson, W. J., Würsig, B., & Trites, A. W. (2013). Seismic operations have variable effects on dive-cycle behavior of bowhead whales in the Beaufort Sea. *Endangered Species Research*, *21*(2), 143-160. https://doi.org/10.3354/esr00515

Ronald, K. L., Skillman, T., Lin, A., Li, Q. L., Fernandez-Juricic, E., & Lucas, J. R. (2015). Watch your tone: Social conditions modulate singing strategies. *Ethology*, *121*(11), 1104-1115. https://doi.org/10.1111/eth.12425

Schneider, J. N., & Mercado, E. (2019). Characterizing the rhythm and tempo of sound production by singing whales. *Bioacoustics-the International Journal of Animal Sound and Its Recording*, *28*(3), 239-256. https://doi.org/10.1080/09524622.2018.1428827

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, *17*(1), 507-533. https://doi.org/10.1146/annurev.es.17.110186.002451

Sewall, K. B. (2015). Social complexity as a driver of communication and cognition. *Integrative and Comparative Biology*, *55*(3), 384-395. https://doi.org/10.1093/icb/icv064

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, *103*, 191-202. https://doi.org/10.1016/j.anbehav.2015.01.030

Simpson, R. K., & McGraw, K. J. (2018). Multiple signaling in a variable environment: Expression of song and color traits as a function of ambient sound and light. *Biotropica*, *50*(3), 531-540. https://doi.org/10.1111/btp.12528

Thode, A. M., Blackwell, S. B., Conrad, A. S., Kim, K. H., Marques, T., Thomas, L., Cornelia, S., Oedekoven, D. H., & Broker, K. (2020). Roaring and repetition: How bowhead whales adjust their call density and source level (Lombard effect) in the presence of natural and seismic airgun survey noise). *Journal of the Acoustical Society of America*, *147*(3), 2061– 2080. https://doi.org/10.1121/10.0000935

Weirathmueller, M. J., Stafford, K. M., Wilcock, W. S. D., Hilmo, R. S., Dziak, R. P., & Tréhu, A. M. (2017). Spatial and temporal trends in fin whale vocalizations recorded in the NE Pacific Ocean between 2003-2013. *Plos One*, *12*(10), e0186127. https://doi.org/10.1371/journal.pone.0186127

Wiggins, G. A., Tyack, P., Scharff, C., & Rohrmeier, M. (2015). The evolutionary roots of creativity: Mechanisms and motivations. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *370*(1664), 129-137, Article 20140099. https://doi.org/10.1098/rstb.2014.0099

Woodward, B. L., Winn, J. P., & Fish, F. E. (2006). Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology*, *267*(11), 1284-1294. https://doi.org/10.1002/jmor.10474