

**School of Earth and Planetary Sciences**

**Centre for Marine Science and Technology**

**Vocal Behaviour of the Eastern Indian Ocean Pygmy Blue Whale and Its  
Changes over Time and Between Aggregation Areas**

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**This thesis is presented for the Degree of**

**Doctor of Philosophy**

**of**

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## Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). 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) vocalisations.

Signature:

Date: 29 Mar 2019

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## Abstract

This study investigates the calling behaviour of the eastern Indian Ocean pygmy blue whale. This subspecies has previously been termed the Australian or South East Indian Ocean stock, however is referred to here as the Eastern Indian Ocean subspecies (EIOPB) or simply as pygmy blue whales. The EIOPB whale is vocally distinguishable from other subspecies of blue whale by their production of what will be referred to hereafter as the EIOPB song type. In accordance with the broader body of whale song literature, a song is defined as repeated phrases which are made up of individual sounds called units. The composition of units into phrases and subsequent repetition of these phrases are described as song structure. Understanding variability in the calling behaviour and song structure within the EIOPB population is precursory to any future efforts to census the population using acoustic techniques. Acoustic techniques for measuring abundance rely on a thorough understanding of the song structure and length, as well as the presence and movement of animals within the detection range of the acoustic recorders. In order to build upon the existing understanding of pygmy blue whale singing behaviour, six years of acoustic data from the Perth Canyon, Western Australia ( $\sim 32^\circ$  S,  $115^\circ$  E) and four years of acoustic data from Portland, Victoria, South Eastern Australia ( $\sim 38.5^\circ$  S,  $141^\circ$  E), were analysed. Through the use of a combination of automatic detection algorithms and manual spectrogram verification, a number of variations to the previously described three unit phrase or song were found, including two phrase variations comprising one or two units repeated, plus three new song patterns. Additionally, in recent years, further variability in the form of split or broken song units has appeared. Variability in the song structure of the EIOPB whale has been described in the EIOPB whale song catalogue and validated using a Fleiss unweighted Kappa test to measure inter-observer agreement. To explore drivers of song structure variability, the difference in singing behaviour between feeding aggregations in the Perth Canyon and Portland was investigated. All song variants were found to be present at the Perth Canyon and Portland sample sites. However, two unit phrases ( $P2$ ) were found to be most prevalent in the songs recorded at the Perth Canyon sample site ( $P2$  - 46% singing EIOPB,  $P3$  - 36% singing EIOPB), while three unit phrases ( $P3$ ) were most prevalent in the songs recorded at the Portland sample site ( $P2$  - 24% singing EIOPB,  $P3$  - 61% singing EIOPB). The presence of all song variants and similar levels of diversity between sample locations support the conclusion of previous genetic studies that the feeding aggregations belong to the same breeding stock. Further, these findings support the idea that song

structure is not specifically linked to cohorts of animals. The high level of variability in song structure was not constrained to the organisation of song units but extended to the temporal structure of songs. Analysis of song repetition interval, commonly referred to as Inter-Song Interval (ISI), found a high degree of variability existing within and between sample sites. The ISI of songs was confounded by phrase structure, with a trend towards shortened phrase (*P2* and *P1*) variants, with a shorter ISI observed within the Perth Canyon. Song length was also found to vary at annual timescales. The background noise conditions, which were dominated by pygmy blue whale vocalisations during peak months of pygmy blue whale presence, were found to vary between sample locations and years, with an indication that the production of shorter phrase variants may be correlated with higher levels of background noise. This was suggested by consistently higher background noise levels in the frequency bands corresponding to the fundamental frequencies of EIOPB song units at the Perth Canyon site ( $92 \pm 4.5$  dB re  $1 \mu Pa^2/Hz$  at 20 – 21 Hz), compared to that at Portland ( $80 \pm 1.2$  dB re  $1 \mu Pa^2/Hz$  at 20 – 21 Hz). The level of variability in ISI and song structure observed in this study presents a challenge for acoustic abundance estimation by complicating the application of cue counting techniques that utilise a measure of the number of signals within a particular time frame to estimate relative abundance.

A tracking array of acoustic receivers was used to localise vocalising animals in the Perth Canyon over two sample years. Vocalising animals were localised by measuring the time difference of arrival of a signal at each of four receivers. Source of successive signals were localised and linked together in tracks based on a set of tracking criteria derived from spatial and behavioural variables. A total of 383 'tracks' were analysed ranging from two successive song phrase localisations to ten or more. Movement patterns were classified into circular or directional movement. Circular movement, described as milling behaviour, was deemed to indicate area restricted search behaviour synonymous with feeding behaviour whereas directional movement was deemed to indicate travel behaviour. While previous studies have suggested that blue whales tend to vocalise while travelling rather than when exhibiting feeding behaviours (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007), a large proportion of tracks (~ 50% of tracked animals) exhibiting circular movements, particularly between the months of March and April, indicated that EIOPB sing while staying within feeding areas.

Given the high level of variability in the songs of the EIOPB whale, it was suspected that differences may exist in the song characteristics between individual animals. Songs were analysed using an algorithm which detected and distinguished the slowly increasing tones

of the second song unit to measure the frequency change over time. The results indicated that very slight differences in signal production exist between individual animals. Such a finding indicates that there may be the potential for individual animals to be recognised by the frequency curve of their vocal cues. In addition, fine scale analysis of song structure revealed a link between the frequency and temporal aspects of unit production. The frequency of the upper harmonic of the second song unit was found to be decreasing at a continuous rate over sample years, with this decline in tonal frequency supporting the findings of previous studies on this population as well as other populations of baleen whale globally. Visual inspection of the relationship between the frequency change and the length of the type II song unit suggested that the latter might increase with the frequency decline, however the relationship was not statistically significant (Spearman's  $R^2 = 0.18$ ). The length of each song unit was measured, and variability in the length of the first song unit as well as the pause between the end of one song sequence and the start of the next, was found to have the greatest influence on song length. The level of song complexity was observed to increase post 2015 with the appearance of song units containing a break or pause in signal production, that were defined as unit breaks. The most noticeable of these variations was the unit break in the second song unit that lasted for between two and eight seconds and often resulted in the second song unit broken into two shortened unit II song elements. The discovery of additional levels of complexity in later sample years suggests that the EIOPB song type is constantly changing.

Variability in the EIOPB song type has occurred rapidly across the sample years of this study, with high levels of diversity maintained across sample years. Such rapid innovation indicates changes in song structure are not defined by genetics but rather governed by behavioural processes. It is postulated that pygmy blue whales have the ability to vocally learn and may be capable of changing between song structures based on background noise conditions. This hypothesis is supported by studies indicating the presence of cognitive structures in the brains of great whales, as well as genes which are believed to function in vocal learning. The possibility that EIOPB whales may not only have the capacity for vocal learning, but potentially exhibit vocal behavioural plasticity has widespread consequences for any attempt to acoustically assess population abundance that is applicable to all blue whale populations. At present, it is assumed that most species of great whale, including blue whales, fin whales and right whales, produce stereotypical song sequences. The high level of variability that has been found in the song production of the EIOPB whale is cause to reassess assumptions related to song production in other species. The research

contained within this thesis highlights and quantifies the variability in song production of the eastern Indian Ocean pygmy blue whale and questions the efficacy of traditional acoustic techniques for abundance assessment. It is postulated that behavioural plasticity in song production provides a distinct fitness advantage to species adapted for long range communication allowing them to balance the trade-off between producing favourable complex songs, and maximising signal transmission amidst the din of other vocalising EIOPB whales. With the threat of global climate variation, increasing anthropogenic noise due to growing shipping, assessing the abundance of critically endangered species such as the blue whale is of high importance. Understanding the vocal behaviour of these animals is fundamental in developing cost-effective and efficient acoustic techniques for the management of these populations.

## Dedications

*“... An understanding of the natural world and what's in it is a source of not only a great curiosity but great fulfillment ...”*

*David Attenborough*

*We all have dreams, but in order to make dreams come into reality, it takes an awful lot of determination, dedication, self-discipline, and effort.*

This thesis is dedicated to my husband, without whose patience and support this dream could not have come into actuality.

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### *The Official*

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Ambient sound recordings used for analysis in this thesis was sourced from the Integrated Marine Observing System (IMOS, 2008-2017) and collected with the support of the Australian Department of Defence and Curtin University (2003-2007). The IMOS observatory is supported by the Australian Government through the National Collaborative Research Infrastructure Strategy and is publicly available through the IMOS portal <https://acoustic.aodn.org.au/acoustic/> or can be requested from <https://portal.aodn.org.au/>.

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### *The Unofficial*

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*A pygmy blue whale surfacing in the Perth Canyon – photo courtesy of Curt & Micheline Jenner, CWR.*

## *Publications*

Publications arising from this thesis:

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## *Statement of Candidate Contributions*

This thesis is presented as a series of manuscripts, each in journal format, in addition to a literature review, with a general introduction and discussion.

These manuscripts were primarily developed from my own ideas and approaches with support and guidance of my supervisors. The methodology of the studies was designed in collaboration with my co-authors, my supervisors assisted in the development of GUIs for analysing noise logger data. I then carried out the subsequent data analyses and constructed relevant statistical models. Professor Robert McCauley assisted in providing long term acoustic data for analysis, the development of code for acoustic and tracking analysis and provided regular guidance and feedback on the written chapters. Professor Alexander Gavrilov assisted in the development of code for acoustic and tracking analysis, as well as code for analysis of background noise, and provided guidance on data analysis and methodology. Curt and Micheline Jenner provided visual data and assisted in the deployment and retrieval of Curtin noise loggers.

I wrote all chapters with feedback from Professor Robert McCauley and Professor Alexander Gavrilov.



Capri Beck

(student)



Professor Robert McCauley

(Supervisor)

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## Chapter 1 General Introduction

### 1.1 Background

Throughout the twentieth century, many large cetacean species, primarily baleen whales, were hunted to near extinction. The portrayal of whales since the earliest records as a mythical kind of beast to be feared, garnered public support for whaling, which provided the oil to fuel the industrial revolution. Whale oil was used to fuel everything from machines to lamps and street lights, giving whaling companies a similar level of pull and power in society as modern day oil and gas companies (Graham-Rowe 2005; Gordinier 2009). Despite the International Whaling Commission's ban on commercial whaling in 1986 (IWC 2019), many of these species' populations are still heavily depleted and continue to face a number of anthropogenic threats (Kelly et al. 2010; Thomas, Reeves, and Brownell 2016). Ironically, while whale oil is no longer an essential commodity, the shift to fossil fuels may pose indirect threats to whale populations through environmental impacts (Graham-Rowe 2005). In many cases, data on the pre-exploitation population status of cetacean species is scarce or non-existent, making it difficult to assess the health of the current population (Lewis et al. 2007). Consequently, ongoing abundance studies for large cetaceans are important for the management and protection of these populations.

Passive acoustic techniques are important for the management and study of sound producing marine mammal species as they present a non-invasive, cost-effective and efficient means of monitoring their populations (Benoit-Bird, Dahood, and Wursig 2009; Gavrilov et al. 2012; Au and Hastings 2008; Mellinger et al. 2007). The potential for passive acoustic observatories to be deployed year round without being restricted by weather conditions makes them particularly useful for studying long term trends in abundance, vocal behaviour and spatial patterns in presence (Mellinger et al. 2007). One aspect of passive acoustics that presents useful applications for the management of cetacean populations is the potential to track vocal animals. The ability to track vocalising animals allows for the study of cetacean behaviour including as a monitoring tool to identify exposure of animals to anthropogenic noise and dangers associated with busy shipping lanes or industrial activity (White et al. 2006). Passive acoustic monitoring is a valuable tool

for assessing the density, range and utilisation of different geographical areas by vocal marine mammal species. Several successful studies have been conducted utilising passive acoustics to yield population density estimates, however the accuracy of such techniques relies in part on a thorough understanding of the vocal behaviour of the species in question (Balcazar et al. 2017; Marques et al. 2009; Marques et al. 2013; Kusel et al. 2011). In order to extrapolate the use of passive acoustic methods to abundance studies, there exists a need for consolidated research into the vocal behaviour, range and migratory patterns of marine mammal species.

In the space of 65 million years, whales have evolved from small, hoofed, wolf like animals to the whales we know today (Rose 2001). Such a comparatively rapid evolution in morphology and physiology would likely be coupled with exceptional development of cognitive structures and associated functioning (Galef 2001; Rose 2001). The communication systems of all whales are known to be well developed, and baleen whales commonly use low frequency, high intensity sounds to communicate over vast distances (Marques et al. 2013; Stafford, Nieukirk, and Fox 1999; Moore et al. 2006). The purpose of these vocalisations remains uncertain, though it is thought that complex song structures are produced by males for reproductive purposes (Payne and Payne 1985; Tyack 1981; Mann et al. 2000; Wiggins et al. 2015; Clark 1990; Darling, Jones, and Nicklin 2006). In some cases, such as with blue whales, vocalisations are population specific with subpopulations defined by geographic range and song structure (McDonald, Hildebrand, and Mesnick 2006; Miller et al. 2014; Buchan et al. 2014; Balcazar et al. 2015; Barlow et al. 2018). As such the correct classification of song types is important for successful acoustic monitoring of populations. The detection of population specific song types may indicate the migratory timing of a population or individual whales with the potential for developing a better understanding of population structure and abundance (McDonald, Hildebrand, and Mesnick 2006; Miller et al. 2014; Sousa and Harris 2015) (Buchan et al. 2014). Studying the intra-specific communication of populations can provide valuable clues as to the evolution of vocal systems and mechanisms for vocal learning within a population. This is because changes to the vocal structure of a population can be indicative of large, and small scale processes that shape vocal repertoires at the species and population level (Rekdahl et al. 2013; Deecke, Ford, and Spong 2000; Janik 2014). These changes may be in the form of the loss or addition of vocal elements or the modification of existing vocal elements (Rekdahl et al. 2013; Cerchio, Jacobsen, and Norris 2001; Garland, Rendell, Lilley, et al. 2017; Janik 2014). Further, changes to vocalisation structure can be defined as changes to the duration

and timing of song intervals, composition, or frequency of units of the song (Rekdahl et al. 2013; Garland, Rendell, Lilley, et al. 2017; Gavrillov et al. 2011a; Janik 2014; McDonald and Hildebrand 2009). Several factors are thought to be responsible for shaping changes in song structure including physical processes such as increases in background noise and social changes such as cultural drift within the population (Janik and Slater 1997; Marler 1997; Rekdahl et al. 2013; Johnson et al. 2015; Mercado, Herman, and Pack 2005). Changes in song structure may also arise through genetic drift (Janik and Slater 1997). As yet, it is unclear whether small scale variations in call structure are part of population wide changes, or can be attributed to individual whales (Buchan et al. 2014). A better understanding of the driving factors behind changes to vocal repertoires may provide clues as to the purpose of particular vocal signals, such as whether they have a reproductive or social context (Deecke, Ford, and Spong 2000; Rekdahl et al. 2013). It is thought that vocalisations within a familial group produced in a social context are least susceptible to change whilst those with a reproductive context are most likely to change (Rekdahl et al. 2013).

Population specific vocalisations are useful in the monitoring and management of species that are difficult to study with visual techniques, such as the Antarctic blue whale (*Balaenoptera musculus intermedia*) and eastern Indian Ocean pygmy blue (EIOPB) whale (*Balaenoptera musculus brevicauda*). These sub-species of blue whale live in sympatry in Australian waters with overlapping geographic ranges (Attard and Moller 2013; Gedamke et al. 2007; Samaran et al. 2013; Tripovich et al. 2015). Whilst they are difficult to separate visually, they are easily distinguished by their vocal cues (Stafford et al. 2011; McDonald, Hildebrand, and Mesnick 2006). The recovery of the Antarctic blue whale stock has been slow, while the EIOPB stock remains largely unassessed (McCauley et al. 2018; McCauley and Jenner 2010b). Passive acoustic monitoring (PAM) provides a cost-effective means for monitoring cetacean species and the potential for long term abundance assessments. However, these methods require an adequate knowledge of the vocal repertoire and song structure of the species. Blue whale song types are categorised based on differences in song phrasing, inter unit time interval, frequency, duration, modulation and total song length (Stafford et al. 2011; McDonald, Hildebrand, and Mesnick 2006; Buchan et al. 2014). These elements of vocal repertoire are subject to change possibly as a result of sexual selection pressures that may be social or environmental. Understanding the drivers of changes in vocal repertoires may have implications for the conservation and management of species, especially if these changes are driven by environmental factors.

## 1.2 Characteristic Call Types

Sound is of critical importance to whales and dolphins, with songs and vocalisations being important for reproduction, hunting and migration (Mann et al. 2000; Tyack and Clark 2000). Many cetaceans, including blue whales can produce a repertoire of sounds, many of which are region or population specific (McDonald, Hildebrand, and Mesnick 2006). The acoustic distinction of populations may be of critical importance for reproduction and migration, as well as allowing geographically distinct populations to communicate at the optimum frequency for their specific environment. Blue whale calls are characteristically low frequency ( $< 100$  Hz), long duration (tens of s) and intense sounds ( $> 175$  dB re  $1 \mu\text{Pa}$  RMS source level; (Sirovic, Hildebrand, and Wiggins 2007; Samaran et al. 2010c). Aside from stereotypical songs there are also frequency modulated down-swept sounds, produced between approximately 25 and 90 Hz and commonly referred to as D calls, which occur across all populations and are common amongst feeding whales (Samaran et al. 2008). Based on calling behaviour, blue whales found in the Southern Hemisphere have been separated into six acoustically distinct populations, one of Antarctic blue whales, and five vocally distinct pygmy blue whale populations separated by song types into Sri Lankan, Madagascan, Chilean, “Australian” (referred to here as EIOPB) and most recently New Zealand (Samaran et al. 2008; Gavrilov et al. 2011b; Barlow et al. 2018; Branch, Monnahan, and Sirovic 2018; McDonald, Hildebrand, and Mesnick 2006).

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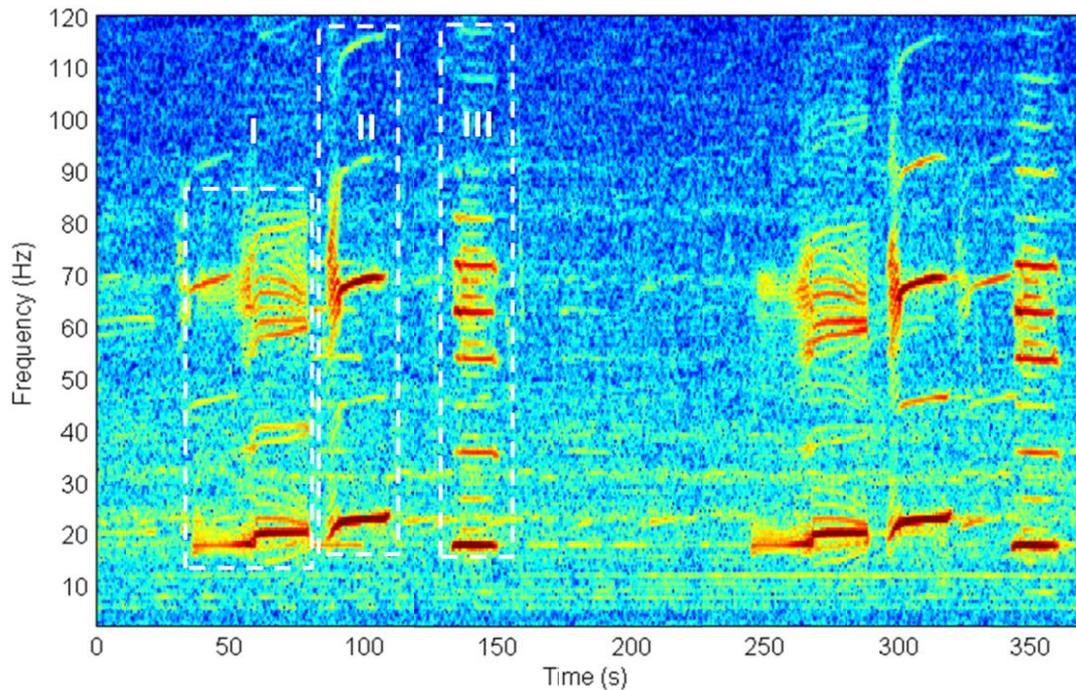


Figure 1.1 A spectrogram showing the EIOBP whale three part song. The dashed line boxes indicate the three distinct song units. A second repetition of the three unit song is seen from the 250 s mark.

The song type of interest to this study is the EIOBP song type, previously known as the “Australian” song type (McDonald, Hildebrand, and Mesnick 2006; McCauley et al. 2006), which is characteristic to the sub population of pygmy blue whales which is now known to roam from almost the equator (Double et al. 2014a), to around 55° S in the eastern Indian Ocean, hence they are termed here EIOBP (McCauley et al. 2006; McDonald, Hildebrand, and Mesnick 2006; McCauley et al. 2018). The song is characterised by a phrase of three harmonic units repeated in a song sequence (Figure 1.1) with approximately 200 seconds between phrases (McCauley, Bannister, Burton, Jenner, Rennie, et al. 2004; McCauley et al. 2001). The first unit is the longest with energy centred around 20 Hz and harmonics up to 80 Hz. Known as a type I unit, this song unit consists of a 19 Hz tone that lasts for 21 seconds before jumping to 21 Hz for further 22 seconds (McDonald et al. 2001; Stafford et al. 2011; McCauley, Bannister, Burton, Jenner, and Rennie 2004; McCauley et al. 2001) This is followed five to ten seconds later by the second unit, referred to as a type II unit. This unit is a frequency modulated up-sweep starting at about 20 Hz and increasing to 26 Hz over a period of 23 seconds. The energy is centred around 24.7 Hz with strong harmonics up to about 72 Hz. The type II unit is sometimes preceded by a “blip” tone between 62 and 93 Hz which was also recorded on its own and not as part of the three part characteristic song

(McCauley et al. 2001). The last portion of the phrase, the type III unit, follows about 23 seconds later and is a constant frequency tone between 18 and 19 Hz lasting between 26 and 48 seconds. This unit has strong harmonics with a secondary pulsed 60-65 Hz tone being produced at the same time (Samaran et al. 2008; McCauley et al. 2001).

### 1.3 Ecology and Behaviour of Pygmy Blue Whales

The EIOPB whale is an elusive species of whale, tending to remain in deep water, with limited surface activity and the capacity to dive for relatively long periods (Owen et al. 2016; Double et al. 2014b; McCauley and Jenner 2010b). As such, studies of their behaviour and ecology have been limited. Thought to be a solitary species by nature, large aggregations of pygmy blue whales are often observed in areas of high primary productivity, such as off the coast of Sri Lanka, and the southern and western coasts of Australia (Branch, Abubaker, et al. 2007; Attard and Moller 2013; Gill 2002). These highly productive areas have been associated with dense populations of krill species, the primary food source of pygmy blue whales (Branch, Abubaker, et al. 2007). A growing body of research into the migratory behaviour of the EIOPB whale suggests they follow a similar pattern to that of other great whales (Double et al. 2014b; McCauley and Jenner 2010b; McCauley et al. 2018; Gavrilov et al. 2018), migrating from lower latitude breeding grounds to high latitude feeding grounds (Attard and Moller 2013; Branch, Stafford, et al. 2007; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). Research suggests that from January through to June, pygmy blue whales aggregate in the Perth canyon area before continuing their journey north past the North West Cape and into what is thought to be breeding grounds in the Banda Sea and waters off Indonesia (Attard and Moller 2013; McCauley and Jenner 2010b; Double et al. 2014a; McCauley et al. 2018). Come October, the EIO subpopulation of pygmy blue whales begins its southward migration, which continues through to late December, partly through Geographe Bay and around the southern capes of Western Australia (Burton 2003). The Perth Canyon has been identified as an important opportunistic feeding area for the population during the whales' northern migration, with the observation of surface behaviour consistent with feeding, as well as krill streaming from the mouth of feeding whales and krill mouthparts identified in faecal samples collected from the area (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009). A number of

surface behaviours have been identified and classified from visual surveys of pygmy blue whales in the Perth Canyon area. Feeding behaviour was characterised by circular or zigzagging movement and dives of longer than seven minutes, followed by surfacing and eight to ten blows (McCauley, Bannister, Burton, Jenner, and Rennie 2004). An animal was assumed to be travelling if it followed a relatively straight track with dive times of less than six minutes. Competitive behaviour was also characterised on rare occasions, where two or more animals would engage in porpoising behaviour and high-speed travel at greater than 15 knots in what appeared to be a linear or circular 'chase' (McCauley, Bannister, Burton, Jenner, Rennie, et al. 2004). A deviation from this behaviour was a medium speed 'chase' with the lead whale defecating in the path of the follower (McCauley, Bannister, Burton, Jenner, and Rennie 2004). Interestingly, genetic sampling of animals within the canyon area indicates a sex bias with seven out of eleven animals sampled in 2001 being male, and all animals sampled in 2002 being male (McCauley, Bannister, Burton, Jenner, and Rennie 2004). Whilst the number of animals sampled genetically was not large enough to draw any significant conclusions regarding sex bias, it may represent variability in migratory behaviour and the utilisation of the canyon area by male and female animals. Sex segregation in the use of particular habitats, and bias in the sex ratio of whales on breeding grounds and along migratory corridors has been documented previously for humpback whales (Franklin et al. 2018; Brown et al. 1995; Heide-Jørgensen et al. 2007; Wade et al. 2011). Concurrent visual surveys over several years within the Perth Canyon area have identified 216 individual pygmy blue whales with 51 resights indicating the importance of the canyon region as a destination along the migratory route of the EIOPB whale (McCauley, Bannister, Burton, Jenner, and Rennie 2004). One whale that was identified in 1996 was resighted in the Perth Canyon in 2001 and 2004 suggesting individual animals may exhibit site fidelity in their migratory behaviour (McCauley, Bannister, Burton, Jenner, and Rennie 2004).

### 1.4 Vocal Behaviour of Pygmy Blue Whales

The behavioural context of vocalising or singing pygmy blue whales is poorly understood, with only a few relevant studies existing on the vocal behaviour of North Pacific blue whales and other baleen whales such as humpbacks (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Oleson 2005; Burtenshaw et al. 2004; Cholewiak, Sousa-Lima, and Cerchio 2013; Handel, Todd, and Zoidis 2012; Guinee and Payne 1988; Payne and Payne 1985). For the purpose of this study, all attempts have been made to utilise

nomenclature consistent with the wider body of cetacean vocalisation literature. As such, the term vocal behaviour or vocalising will be used hereinafter to refer to all kinds of pygmy blue whale vocalisations, while 'singing' or 'song' will be used to refer to the production of repetitive phrases. Peaks in pygmy blue whale vocal behaviour generally occur at dawn and dusk, with a high proportion of vocalisations during night hours, though detections are not limited to these times (McCauley and Jenner 2010b; Gavrilov and McCauley 2013). It is thought that up to approximately one third of a migrating population exhibits singing behaviour, based on studies of North Pacific blue whales, suggesting there likely exists a sex-bias in the context of song, with the possibility that only mature males produce song (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Lewis and Sirovic 2018). In order to discern the behavioural context of vocal behaviour a combination of visual and acoustic observations is needed, however the challenge is matching the acoustic recordings with visual observations of an individual animal behaviour (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Lewis et al. 2018). In recent studies, the use of acoustic recording tags (DTags) and Crittercam (Marshall et al. 2007) has made it possible to simultaneously monitor individual whales visually and acoustically. This method has been applied to studies of eastern North Pacific populations of blue whales with success, resulting in links between song type and behaviour (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). One such study, on North Pacific blue whales, found that all whales producing phrase units, either singularly or in the repetitive form of song were males, though male and female whales produced short duration frequency modulated sounds (Oleson, Calambokidis, Barlow, et al. 2007). The high statistical significance of these results provides strong evidence supporting the theory that only male blue whales produce song (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). As such it is highly likely that blue whales may sing for the purpose of attracting a mate or mediating male-to-male interactions, in the same way as humpback and fin whales (Frankel et al. 1995; Oleson 2005; Oleson, Calambokidis, Burgess, McDonald, LeDuc, et al. 2007; Cholewiak, Cerchio, et al. 2018). Further, it was found that all singing North Pacific blue whales were in a state of travel in a consistent direction and at a steady pace (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). Singing male whales appeared to be travelling alone with no closely associated whales within a kilometre radius (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). Singing whales also showed no evidence of feeding behaviour directly before, after or during singing (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007), a finding which is reflected in Lewis *et al.* (2018) who found a consistent shallow U shaped dive profile to be exhibited by singing North Pacific blue whales. Whales

were also recorded producing song units sporadically, but not in the repetitive form of song, and these were defined as singular calls. Whales producing singular calls were always in close proximity with other whales (within 1 km) and generally paired with one or more closely associated whales (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). These whales exhibited a variety of behaviours while vocalising, including foraging behaviour, lunge feeding, milling and resting. Tissue samples revealed that female whales were paired with those males producing singular calls (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). One whale was recorded making singular calls while paired with a female whale and then converted to a repetitive form of song after travelling away from its companion (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). This behaviour suggests a social context for many blue whale vocalisations, which may function to maintain contact with a mate once paired, but when separated by distance, the whale may shift into a song to call to its mate or to attract other potential mates. The down swept singular D call has been observed in all blue whale populations and recorded from male and female whales (Oleson 2005; Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Thode, D'Spain, and Kuperman 2000; McDonald et al. 2001; Recalde-Salas, Salgado Kent, et al. 2014; Saddler et al. 2017). Animals producing D calls have always been in the presence of other whales and were often engaged in feeding behaviour, making calls before and after diving (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007) . Interaction between whales making D calls has been observed, suggesting a social context to the production of this sound, though there has been no observation of any group feeding effort among whales making D calls (Thode, D'Spain, and Kuperman 2000; McDonald et al. 2001; Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007) .

Studies have found song production to be constrained to depths of less than 35 metres with no more than two metres change in depth over the course of a singing bout which would support the idea that there is an optimal depth to produce song sounds, as well as that singing behaviour is not possible during deeper foraging dives (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Lewis et al. 2018). As such it is assumed that singing and feeding behaviours are not conducive to each other, at least in the short term. Deep dives have however been observed prior to or following some vocalisations such as singular song units and D calls (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). Tagged whales generally vocalised from the horizontal position or with their heads tilted slightly down, and were recorded producing up to 15 singular D calls per dive and between three and ten song units (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). Whilst

vocalising whales spent a greater amount of time at shallower depths than quiet whales, their overall diving behaviour was similar, with vocalising whales engaging in lunge feeding behaviour at depths greater than 50 metres when not engaged in vocalising behaviour (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007). Thus, while singing behaviour may not be sympatric with feeding, singing behaviour tended to occur while whales were travelling, suggesting this is a technique to minimise the cost of singing by overcoming the trade-off between vocalising and feeding. A blue whale may travel greater than 100 kilometres per day in search of food (Mate, Lagerquist, and Calambokidis 1999) and utilising this transit time for singing would provide an energy efficient means of mate attraction or communication. Further, blue whales are neutrally buoyant at around 30 metres depth meaning that theoretically a whale could travel and sing at that depth with very little energy expenditure (Mate, Lagerquist, and Calambokidis 1999). Whilst the results of these studies have been useful in hypothesising the function of singing behaviour in the North Pacific population of blue whales, further study is required to determine whether EIOPB whales share these behavioural characteristics with their North Pacific counterparts.

This study will use long term acoustic data from the Perth Canyon area in Western Australia, in combination with data sets from Portland, Victoria to build an understanding of the song of the EIOPB whale. This includes the identification of characteristic phrase types, as well as long term variability in song structure, and the spatial movement of vocalising whales within the vicinity of an acoustic tracking grid. The down swept type D signals (Recalde-Salas, Kent, et al. 2014), while present in recordings of EIOPB in the Perth Canyon, are not considered here. Through comparison of long-term data and the tracking of individual vocalising animals, the function of singing behaviour will be investigated. Patterns in the timing and movement of whales within the canyon area will be compared with environmental data to isolate any trends or potential drivers of singing behaviour and presence. Detailed analysis of acoustic recordings and passive acoustic tracking analysis will be used to work towards methods for deriving abundance from passive acoustic data alone in future studies.

### 1.5 Knowledge Gaps

Despite a growing body of knowledge on the acoustic behaviour of humpback, right, and killer whales less is known about the acoustic behaviour of the EIOPB whales (McCauley,

Bannister, Burton, Jenner, Rennie, et al. 2004; McCauley et al. 2001; McCauley et al. 2006; Barlow et al. 2018). These animals are comparatively elusive, spending little time at the surface, making them difficult to study using visual observation methods. Unlike humpback whales that engage in conspicuous bouts of surface behaviour including breaching and pectoral slapping, blue whales spend considerably less time engaged in surface behaviours (Balcazar et al. 2017; Barlow et al. 2018; Gavrilov et al. 2012; Ichihara 1963; McCauley, Bannister, Burton, Jenner, and Rennie 2004; McCauley et al. 2006). For species such as this, acoustic methods of observation often provide the greatest insight into their behaviour and presence (Godo et al. 2013; Marques et al. 2013; Kershenbaum et al. 2016).

### 1.6 Aims and Objectives

The research contained within this thesis aims to contribute to the wider field of knowledge of the acoustic behaviour of baleen whales, as well as assist in assessing the status of the pygmy blue whale population world-wide. Each chapter of this thesis represents a discrete parcel of knowledge that has contributed to our understanding of pygmy blue whale singing behaviour, as well as building on techniques and methods for acoustic assessment of populations. Each chapter aims to focus on one of the following areas of research in the field of pygmy blue whale acoustics:

- Long term variability in the EIOBP whale song type;
- Comparing calling behaviour between two different feeding aggregations of pygmy blue whales to identify any site-specific acoustic behaviour;
- The potential for acoustic tracking of individual vocalising animals;
- Annual trends in frequency and song length;
- Identifying individual level variability in acoustic behaviour.

The objective of this thesis is to build an understanding of the acoustic habits and behaviour of the EIOBP whale, including describing the characteristic song structures and any levels of variability that exist within the songs of the population.

### 1.7 Significance

There is to date no accurate abundance estimate of pygmy blue whales making it impossible to assess their conservation status (Reilly et al. 2008). Pygmy blue whales were only recognised as a separate subspecies in 1961 and consequently many pygmy blue whales were recorded as Antarctic blue whales in historical whaling records (Ichihara 1961, 1966). Using all information currently available to separate stocks, Branch (2018) has attempted to assign historical 'blue' whale catches to sub species. Antarctic blue whales were heavily targeted by commercial whaling resulting in their population that has been decimated. Whilst not exploited to the same extent, pygmy blue whales likely suffered similar implications of dramatically reduced population numbers (Ichihara 1963, 1966; Attard and Moller 2013; Branch, Monnahan, and Sirovic 2018). Without a comprehensive record of catches and little idea of what the baseline population was, the pygmy blue whale has been listed as data deficient on the IUCN Red List (Thomas, Reeves, and Brownell 2016). Recent genetic surveys of blue whale populations in the Southern Hemisphere have found that the range of pygmy blue and Antarctic blue whales overlaps further south than previously expected in the waters of the Antarctic (Attard and Moller 2013). Whilst previously recognised as a sub-tropical species of blue whale, the overlap in geographical range could present increasing challenges for populations of blue whale competing for the same food resources. Further, genetic surveys suggest that habitat is not the only thing the two sub species of blue whale share, with the identification of hybrid animals in recent years in the waters off Antarctica (Attard and Moller 2013). Competition between blue whales and other species for resources as well as a decreased ability to respond to environmental change as a result of genetic bottlenecks are recognised as threats to cetacean populations, including blue whales (Mann 2017; Attard et al. 2018; Sousa et al. 2019).

Human impacts including vessel traffic and anthropogenic noise have been shown to impact on the behaviour and habitat use of cetaceans (Nowacek, Johnson, and Tyack 2004; Melcon et al. 2012; Thomas, Reeves, and Brownell 2016). Noise pollution is an area of increasing concern for the management of cetacean populations with the potential to impact the ability of animals to find a mate and locate conspecifics (Cholewiak, Clark, et al. 2018; Parks, Clark, and Tyack 2008; Clark et al. 2009) as well as increase stress and disrupt foraging behaviour (Rolland et al. 2012; Croll et al. 2001). In some cases, there is evidence to suggest animals will avoid particularly noisy habitats while other research indicates long term changes in vocal behaviour perhaps in response to increasing anthropogenic noise (Madsen et al. 2006; Fristrup, Hatch, and Clark 2003; Clark et al. 2009; Parks, Clark, and

Tyack 2008). Further, there is evidence to suggest that some anthropogenic sounds can cause physical damage to species of cetaceans (Southall et al. 2009; Southall, Finneran, et al. 2019), often as a result of behavioural changes in response to the sound (Southall, DeRuiter, et al. 2019), such as the associations between military sonar use and mass stranding events (Dalton 2006; Dolman, Parsons, and Wright 2011; Fahlman et al. 2014; Falcone et al. 2017; Harris et al. 2018). Human impacts are far reaching in the marine environment and as the use of key habitat areas increases, the potential implications for marine mammal species require research and mitigation (Mann 2017).

The Perth Canyon is an area of considerable ecological significance (Double et al. 2014b, 2014a; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009; McCauley, Bannister, Burton, Jenner, and Rennie 2004; McCauley and Jenner 2010b). Whale watching charters to the area occur, with a burgeoning interest in seeing the rarer species of whale such as blue whales. The Perth Canyon, with its unique bathymetry and oceanography is also of considerable significance to the military and as such an improved understanding of pygmy blue whale behaviour is essential to deconflict military activities with pygmy blue whale habitat use (McCauley, Bannister, Burton, Jenner, and Rennie 2004). Consequently, the research presented in this thesis is essential for the ongoing management and conservation of the EIOPB whale. Further, the findings presented here pertaining to pygmy blue whale behaviour, habitat use and vocal changes over time may be applicable to other populations of blue whale world-wide. With no current abundance measure for this population, it is intended that the information presented in this thesis will aid in future attempts to quantify the health and abundance of the EIOPB whale population, with the hope of allowing the IUCN species classification to be changed from Data Deficient to a quantifiable status.

### 1.8 How to read this thesis

This thesis has been written to explore the acoustic behaviour of the EIOPB whale, and work towards developing a robust set of acoustic methods to allow for long term abundance estimates to be conducted in a cost-effective manner. As such, the information presented in this thesis is designed to be a stepping stone for future research and methodology. Throughout the research process, several interesting observations on the singing behaviour of the EIOPB whale were made. Consequently, the chapters of this thesis have been written with the intention of later being adapted into publishable scientific

papers. A literature review has been provided to assess the current applications of passive acoustics for assessment of cetacean populations with a focus on blue whales, and the existing limitations and knowledge gaps. Further, the literature review serves to highlight the relevance of this thesis to the wider research context. A common methods chapter has been written in an attempt to limit duplication between chapters, with any specific data analysis or statistical methods provided in the relevant chapters. Attempts have been made to minimise duplication between chapters while maintaining a publishable and fluent structure.

Whilst a general introduction and methods section has been included, the chapters are presented as scientific papers, each with their own relevant introductions, methods and discussions. The data chapters presented in this thesis are as follows:

**Chapter 4. Song variation of the eastern Indian Ocean pygmy blue whale population in the Perth Canyon, Western Australia.**

Long term ambient sound recordings from the Integrated Marine Observing System (IMOS, <http://imos.org.au/>) in the Perth Canyon area were used to explore changes in song structure across sample years. A number of variations to the traditional three unit EIOPB whale song type were found and are described for the first time in this chapter. A song classification chart is constructed for the classification of song variants. A total of three song structures with an additional three patterns in song production are described. Trends in the prevalence and appearance of song variants are compared across years. This chapter was published in the journal PLoS One in January 2019.

**Chapter 5. Comparing the singing behaviour of the Eastern Indian Ocean pygmy blue whale at two Australian aggregation areas**

Feeding aggregations of pygmy blue whales have been described along the Bonney Coast, Portland Victoria, and in the Perth Canyon, off Western Australia. Whilst genetic studies of EIOPB whales feeding in the Perth Canyon and Bonney Upwelling have found them to belong to the same genetic population of EIOPB whales, their vocal behaviour has previously not been compared. Long term acoustic data were used to compare song structure and variability between locations to determine the level of similarity in the vocal behaviour of EIOPB at each location.

**Chapter 6. Tracking pygmy blue whales in the Perth Canyon using passive acoustic observatories**

Vocalising pygmy blue whales were localised within the area of a passive acoustic tracking observatory by calculating the time difference of arrival of a signal at four acoustic receivers. A set of rules were established to allow for vocal animals to be followed as they moved through the acoustic observatory. Patterns in movement and song structure were analysed to look for any relationship between singing and movement behaviour. Patterns in the locations of vocalising animals were compared between seasons indicating inter annual variability in distribution patterns.

**Chapter 7. Variability in the temporal characteristics of the Eastern Indian Ocean pygmy blue whale song.**

Song repetition rate, defined as the inter song interval (ISI), has been found to be highly variable. While a large degree of this variability is dependent on song structure, there is a considerable degree of variability within phrase and song structures. This chapter looks at patterns in ISI and analyses which units of the song are most subject to variability. Further, long term trends in ISI variability are compared with long term trends in frequency decline in the type II unit of pygmy blue whale song.

**Chapter 8. Investigating fine scale variability in the Eastern Indian Ocean pygmy blue whale Song.**

High levels of variability in the EIOPB whale song will complicate any attempt at an acoustic assessment of population abundance. In order to improve the efficacy of acoustic methods and better understand the calling behaviour of the population, fine scale variability within a sample year is explored. The potential for individual level variability in song structure was investigated with a detailed investigation of the primary elements of song structure.

**Chapter 9. General Discussion**

## Chapter 1. *General Introduction*

This thesis will conclude with a general discussion summarising the main findings of each chapter within the context of the wider field of pygmy blue whale research. Recommendations will be made for future research in the field, as well as how this research may be used to better inform studies on blue whale populations world-wide.

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## Chapter 2 Literature Review: Understanding variability in cetacean songs and the implications for acoustic monitoring

### 2.1 Overview

There is growing concern for the health of whale populations with an increase in anthropogenic threats and environmental stressors including ship strike, noise from ships, military sonar and seismic surveys, and global warming (Thomas, Reeves, and Brownell 2016; Mann 2017; Harris et al. 2018; Rolland et al. 2012). Sound is of critical importance for surviving in the ocean, being integral for foraging and reproductive fitness (Mann 2017). Whilst many ecological and behavioural characteristics of species such as the blue whale remain a mystery, the sounds they produce may assist in assessing the geographical range and health of populations, as well as provide insights into behaviour (Marques et al. 2013; Kusel et al. 2011). However, changes in the environment may drive changes in the acoustic behaviour of populations which presents challenges for ongoing acoustic monitoring (Noad, Dunlop, and Mack 2017). Continued research into vocal behaviour has the potential to improve the application of acoustic methods and subsequent management actions for cetacean populations, with the hope that rare species such as the blue whale may be censused with the acoustic methods alone in the future.

### 2.2 Biology and Life History of the Pygmy Blue Whale

The pygmy blue whale is a subspecies of blue whale that was identified in 1961 (Ichihara, 1961, 1963, 1966; Zemsky and Sazhinov, 1982). Pygmy blue whales are visually distinguishable from Antarctic blue whales by a proportionally shorter tail region, and a shorter maximum length, reaching sexual maturity at 19.2 m as opposed to 23.7 m for Antarctic blue whales (Ichihara, 1963, 1966; Branch et al., 2007a). Female pygmy blue whales are believed to reach sexual maturity at an age of approximately ten years and have a gestation period of ten months (Branch, 2008). It is commonly accepted that females will not breed whilst they are with a calf and weaning occurs after a minimum of seven months (Branch, 2008). Consequently, whilst a female could potentially calve every two years, the

calving interval may be longer as not every mating leads to a pregnancy and not every pregnancy will result in a live calf. As a result, the average calving interval for pygmy blue whales is estimated to be 2.5 years (Branch, 2008). Whilst it is believed that pygmy blue whales share many characteristics with Antarctic blue whales, currently little is known about their range, life history and population status.

The behaviour and ecology of blue whales is a topic of ongoing study and there is a growing body of research focused on uncovering more about the populations around the world (Jolliffe et al. 2019; Southall, DeRuiter, et al. 2019; Lewis and Sirovic 2018; Attard et al. 2018; Bedrinana-Romano et al. 2018; Barlow et al. 2018; Lewis et al. 2018; McCauley et al. 2018; García et al. 2018; Miksis-Olds, Nieukirk, and Harris 2018). While blue whales exhibit similar migratory pattern as other great whale species, with migration from high latitude feeding grounds to low latitude breeding grounds, it is thought that migration may be variable between individuals (Bailey et al. 2009). The large body size of the blue whale makes them vulnerable to perturbations in prey availability, meaning they need to balance the cost of finding prey and feeding, with resource availability (Croll et al. 2005; Croll et al. 2001). There is a cost-benefit to finding large patches of prey, with the energetic cost of transit decreasing with body size, and the ability to fast increasing (Croll et al. 2005; Croll et al. 2001). This may be why blue whales appear to be opportunistic feeders, with animals spending extended periods of time in areas of high productivity (Bailey et al. 2009). For a blue whale, the balancing act of finding and exploiting dense patches of krill may drive variable migratory and foraging behaviour (Hazen, Friedlaender, and Goldbogen 2015; Bailey et al. 2009). It is not surprising then that blue whales have demonstrated the ability to switch foraging strategies depending on prey availability (Hazen, Friedlaender, and Goldbogen 2015). Hazen *et al.* (2015) found that in areas of higher prey density, blue whales lunged more at depth, as opposed to less lunges of depth in areas of lower prey density. It is believed that, by adapting their foraging strategy, blue whales can exploit areas of high and low prey density while balancing the aerobic cost of feeding (Hazen, Friedlaender, and Goldbogen 2015). This is demonstrated through the use of oxygen conserving, or energy maximising foraging strategies in response to krill density (Hazen, Friedlaender, and Goldbogen 2015). This study reflects the behavioural plasticity of blue whales through the capacity to change their foraging strategy to maximise foraging efficiency.

Studies to assess the health of populations globally are ongoing, with the continued development of acoustic technology and modelling methodology to quantify population densities and relative abundances (Vernazzani et al. 2017; Hazen et al. 2016; Pardo et al. 2015). Whilst their breeding and calving habits remain a mystery, a number of recent studies suggest that blue whales may be capable of altering their song production based on environmental context (DeRuiter et al. 2017; Lewis et al. 2018). These studies suggest that blue whales are cognisant of their environment and can alter their vocal behaviour accordingly. Additionally, a number of studies indicate that blue whales may be sensitive to anthropogenic noise through assessment of their behavioural response to ship noise, sonar and seismic air guns (Southall, DeRuiter, et al. 2019; DeRuiter et al. 2017; Shabangu et al. 2017a; Derian and Alfadenata 2017).

### 2.3 Song Variability

One of the ways that blue whales and other cetaceans respond to anthropogenic sound is changing their vocal behaviour. This has been demonstrated in a number of species, including changes in song rate in bowhead whales in the presence of seismic sound (Blackwell et al. 2017). Blackwell *et al.* (2017) found that bowhead whales initially increased their calling rates in response to anthropogenic noise, however when sound levels increased above 127 dB their call rates decreased below normal levels and above 160 dB they ceased vocalising entirely. Similarly, humpback and blue whales have been shown to change their singing rate in response to anthropogenic noise (Melcon et al. 2012; Fristrup, Hatch, and Clark 2003). These responses to changes in ambient sound conditions are not limited to changes in song rate and may indicate that complex cognitive processes are involved in the interaction of cetaceans with their environment. For example, modelling studies have indicated that humpback whales may adapt their singing strategy by changing their singing depth or vocalisation frequency to overcome environmental constraints on sound transmission (Mercado and Frazer 1999).

Changes in the ambient sound conditions of the ocean, whether they are from anthropogenic, or natural sources, likely present an ongoing challenge for cetacean species that rely on sound for communication, navigation and foraging (Harris et al. 2018; Cholewiak, Clark, et al. 2018). As the ocean gets noisier, the communicative space for whale species gets smaller, and their ability to attract conspecifics, navigate, and find food may be

impacted (Hatch et al. 2012; Cholewiak, Clark, et al. 2018; Clark et al. 2009). The ability of animals to adapt their vocalisation strategies to maximise signal transmission likely presents a fitness benefit to animals and may be one of the key drivers of song variability in cetacean species (Lewis et al. 2018; Mercado and Frazer 1999).

## 2.4 Social drivers of changing vocal behaviour

The reason why baleen whales have developed complex vocal behaviour and produce songs is not fully understood, though it is commonly believed that vocalisations serve some sort of communicative purpose and so relate to cognition and behaviour (Cantor and Whitehead 2013b; Cholewiak, Cerchio, et al. 2018). Despite being considered less social than their odontocete counterparts, baleen whales live in the same complex and variable aquatic environment that favours acoustic forms of communication (Mann 2017). Given the increasing evidence for complexity in the songs of baleen whales, it is prudent to include here a discussion of the social context of baleen whale song, and potential mechanisms driving variability in vocal behaviour. The mechanisms that permit animals to acquire, process and store information from their environment make up cognition (Sewall 2015). It is thought that existing in complex social environments requires high levels of cognition, which may be required for other behaviours such as migration and navigation in the open ocean (Wiggins et al. 2015; Sewall 2015; Seyfarth and Cheney 2015). Whilst until now communication and cognition have been considered as separate traits, communication is essential for the transmission of social information and mediation of interactions with other animals, thus cognition and communication are inherently linked (Sewall 2015). The greater the sociality of the animal, in general the greater the ability of the animal to communicate and the more complex the vocal repertoire are (Mitchell 2016; Seyfarth and Cheney 2015). As such, it is thought the cognitive abilities of animals vary between and within species (Sewall 2015).

The ability of animals to use information provided by others to inform or change their own behaviour is widespread and allows animals to adapt to their environment faster than if they relied on personal information alone (Duboscq et al. 2016). It requires the perception of signals by the receiving animal which may then be linked to specific contexts or situations through contextual learning (Sewall 2015). Social information can influence where, when and how an animal feeds based on the behaviour of other animals and the

transmission of that information within the population (i.e. the simple assumption that the location where more animals are calling from contains more food). Whilst it is generally considered to be beneficial for an animal, social information can be maladaptive, as the trade-off for acquiring information from others is that it is less reliable than acquiring the same information individually (Duboscq et al. 2016). In addition, vocalisations have been hypothesised to contain social information about the status and class of an animal (Koren, Mokady, and Geffen 2008; Koren and Geffen 2009, 2011). Social diffusion or the transmission of social information has been studied extensively in terrestrial species but is more difficult to observe in marine species in the field. There have, however, been a number of cases, including the proliferation of specific behaviours in dolphin populations and widespread vocal change in humpback whale song, that exemplify social diffusion in marine mammals (Duboscq et al. 2016). The rapidly changing songs of humpback whale populations provide evidence of the capacity of baleen whales to vocally learn. Vocal learning is a mechanism for the spread of vocal cues or songs that suggests that vocalisations are learnt and not an inherent trait (Galef 2001; Deecke, Ford, and Spong 2000; Janik and Slater 2000; Janik and Slater 1997). Vocal learning is one of the elements that underpin the existence of a form of culture and the transmission of vocal behaviours throughout a population (Galef 2001; Cantor and Whitehead 2013b). The presence of vocal learning indicates the ability of animals to imitate and teach suggesting a level of self-awareness and a high level of cognition (Galef 2001; Cantor and Whitehead 2013b; Rendell and Whitehead 2001).

### 2.5 Abundance estimation

Assessing the abundance of large cetaceans is challenging and subject to large margins of error, often due to a lack of baseline knowledge on species distribution, ecology and behaviour (Marques et al. 2009; Thompson 2004). With relatively low densities, baleen whales are often hard to survey visually, however the low frequency sounds produced by many of these species makes them suitable candidates for acoustic surveys. Several passive and active acoustic techniques exist for detecting, tracking and censusing whales, though the field still requires substantial development to improve the applicability of results in biological and behavioural contexts. It is primarily the signal processing and analysis requirements, coupled with a lack of understanding of singing behaviour, which causes

problems in interpreting passive acoustic monitoring (PAM) data. In many cases, shortfalls in acoustic techniques are related to a lack of understanding of species' calling parameters which has serious implications for the measurement of abundance (Marques et al. 2013; Marques et al. 2009). With the aid of advancing technology, the field of acoustics is developing allowing for long term data to be collected passively with the potential for acoustic techniques to be used to census species that are hard to survey visually (Rayment et al. 2018; Norris et al. 2017; Nowacek et al. 2016).

A number of studies have attempted to census whale populations using acoustic techniques alone (Williams 2017; Vernazzani et al. 2017; Norris et al. 2017). Despite conjecture surrounding the reliability of results, or the inability to differentiate signals between animals without concurrent visual surveys (Sousa-Lima et al. 2013; Marques et al. 2013), these studies represent promising progress in the field of acoustics. Passive acoustic techniques have been successfully used not only to confirm the presence of animals, but also to differentiate between populations (Balcazar et al. 2015; Buchan et al. 2014), provide information on species range and geographical area use (Samaran et al. 2013; Cerchio, Jacobsen, and Norris 2001), and more recently to localise vocalising animals (Macaulay et al. 2017; Gavrilov et al. 2012; Kusel et al. 2017; Warner, Dosso, and Hannay 2017). Already, acoustic techniques are being used to provide real time, cost effective data to inform population management and assessment (Kane et al. 2018; André et al. 2011; Miller 2012; McDonald 2004). However, work still needs to be done to improve the accuracy of existing techniques, as well as improve the understanding of how animal behaviour and cognition may impact upon existing detection and abundance assessment techniques. This review will focus on highlighting some of the gaps in existing acoustic techniques, as well as highlighting the potential implications of changes in animal behaviour for acoustic assessments.

### 2.6 Acoustic techniques for assessing abundance

Cue counting is a valuable method for estimating density in populations where individuals are acoustically indistinguishable (Martin et al. 2013; Marques et al. 2013). This is the case with many species of baleen whale, where vocalisations are common at the population or even species level. In cue counting studies, the number of detected 'cues' is combined with information on cue production rate, or song length, to determine the number of animals

## Chapter 2. *Literature Review*

vocalising (Marques et al. 2013; Marques et al. 2009). The actual cue to be counted is specific to the study but is generally a distinct vocalisation such as a particular song unit, or a click used for echolocation (Marques et al. 2013).

This is a useful method for assessing population density as demonstrated by Marques et al. (2013), who used this method to estimate the population density of Blainville's beaked whales. The number of detected cues, in this case an echolocation click, was combined with information on the cue production rate, probability of detection of the click, and false positive rate to yield a density estimate (Marques et al. 2013). In this method, false negatives are defined as cues that go undetected or are incorrectly classified. This can lead to an underestimation of the number of cues detected which would cause an underestimation of population density. If using an automated search algorithm or detector, increasing the sensitivity can aid in avoiding false negatives, but may lead to an increase in false positives, which is misclassification of a sound as a cue (Martin et al. 2013). This leads to an overestimation of population density and is best corrected for by manually checking cue detections (Marques et al. 2013).

The effectiveness of cue counting as a population estimation tool relies heavily on the assumption that all individuals of the population are producing the same cue or song in the same sequence with no variability in vocalisation sequence or frequency (Mellinger et al. 2007). Whilst in the past it was commonly accepted that this was the case for most of the baleen whales, it is now becoming evident that many species may have population or even pod specific vocalisations, and further that a number of species such as humpback, bowhead and fin whales, change the characteristics of their song on an annual and even seasonal basis (Oleson 2005; Mercado, Herman, and Pack 2005; Oleson et al. 2014; Cerchio, Jacobsen, and Norris 2001; Payne and Payne 1985; Weirathmueller et al. 2017; Stafford et al. 2018). However, understanding individual differences in sound production may allow for individual call rates to be assessed which is necessary for estimating the population density (Saddler et al. 2017).

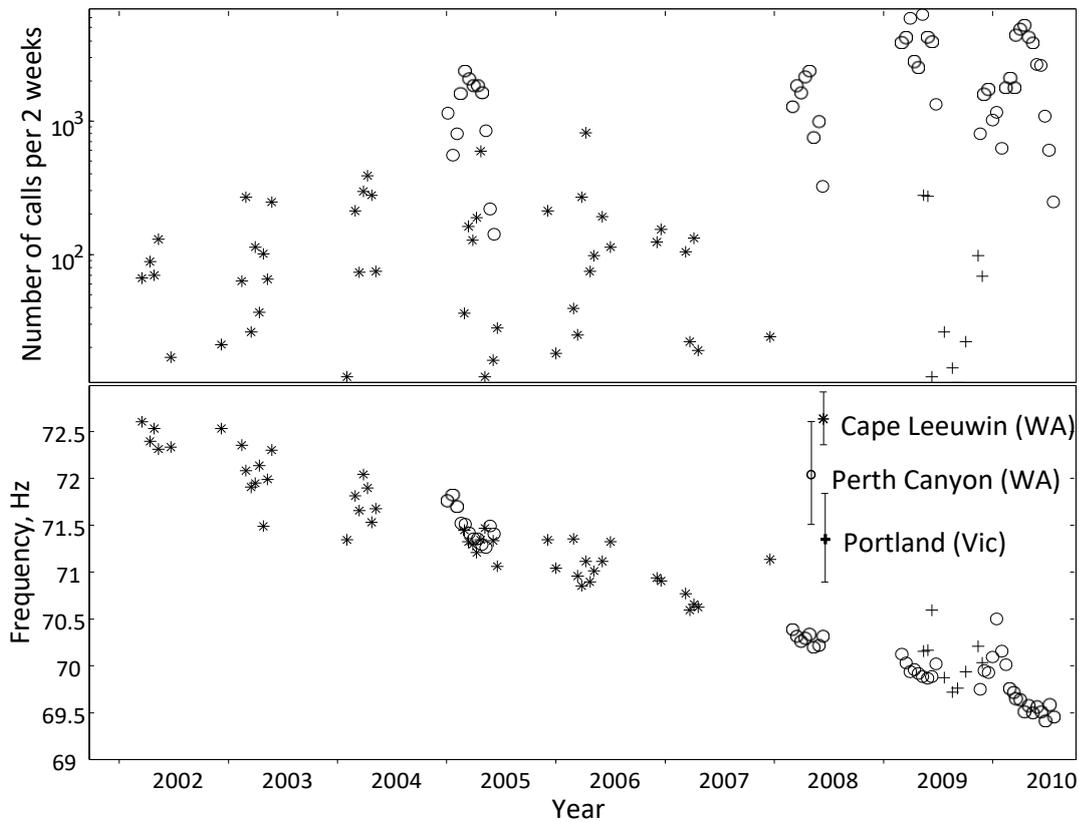


Figure 2.1 (From Gavrilov et al. 2011) Variation in the frequency of the 3rd harmonic of the type 2 sound produced by pygmy blue whales of the EIOBP population over the years 2002 to 2010 showing an increase in the number of vocalisations and a trend in decreasing frequency across all sample sites.

There is also evidence of long term decreases in the frequency of large baleen whale calls (Leroy et al. 2018; McDonald and Hildebrand 2009), such as the steadily dropping fundamental frequency and harmonics of the type 2 unit in the EIOBP whale song (Figure 2.1; Gavrilov et al., 2011). Thus, acoustic studies may need to incorporate flexible detection algorithms in order to account for inter-annual and intra-seasonal changes in song type or vocal frequency. Failure to adjust detection algorithms to changes in call characteristics could lead to false counts of calling whales. The cue counting method also fails to factor in the possibility of whales alternating between silent and vocal periods or the possibility of a vocalising animal lingering in the vicinity of the acoustic recorder. It is assumed that detected animals vocalise at a set rate continuously (Marques et al. 2009). This can lead to a gross misinterpretation of acoustic results such as an underestimation of the population

as a consequence of not factoring in silent whales, or worse overestimation by wrongly assuming that cues are produced from different whales due to a lack of information on cue rate, or the lingering presence of one vocal animal in the listening area (Efford, Dawson, and Borchers 2009; Warren et al. 2017).

Estimating animal density from acoustic samples requires knowledge of the area within which density is being measured as well as an idea of the cue production rate, unless cues can be identified to the individual level. In some cases, potentially through localisation of vocalising individuals, it may be possible to identify the number of groups of animals. If data on average group size is available, this can be used as a multiplier which is then divided by the probability of an animal vocalising to estimate the number of animals in the area (Marques et al. 2013). It is also important to consider that the context of vocal cues can be significant as the production of less regular social sounds may have direct links to animal density (Marques et al. 2013).

## 2.7 The importance of population monitoring into the future

Globally, it is considered that ship strike and bycatch are the greatest causes of direct mortality for baleen whales, though there is increasing concern for the long term impacts of acute sound sources of anthropogenic origin (Thomas, Reeves, and Brownell 2016). Acoustic threats can have long reaching impacts not only directly on marine mammals but through indirect processes as well (Rolland et al. 2012; Hatch et al. 2012; Cholewiak, Clark, et al. 2018; Blackwell et al. 2015; Blackwell et al. 2017). It is known that fisheries impact marine mammals not only through entanglement with fishing gear but also through trophic cascades by over fishing at one trophic level (Thomas, Reeves, and Brownell 2016; Tyack 2009). Additionally, fishing may have a cumulative effect by altering the marine ecosystem in such a way that it can no longer support the marine mammals that occupy higher tiers of the ecosystem food chain (Tyack 2009). Similarly, the threats posed by anthropogenic noise are not only direct through injury to the animal and temporary threshold shifts in hearing (Melcon et al. 2012; Gavrilov et al. 2011b; Tyack 2009; Southall et al. 2009; Southall, Finneran, et al. 2019), but noise pollution can have far reaching implications such as the exclusion of marine mammals from certain habitats including feeding and breeding sites (Tyack 2009; Thomas, Reeves, and Brownell 2016). It is postulated that increases in background noise may decrease the distance over which marine mammals can

communicate making it harder for them to find a mate, with negative implications for the recovery of populations (Tyack 2009; Thomas, Reeves, and Brownell 2016). It has been suggested that distant offshore seismic surveys increase background noise levels to such a level that fin and blue whales would experience a 29 to 40% reduction in communication potential (Gedamke et al. 2007; Thomas, Reeves, and Brownell 2016). Recent research has also indicated that exposure to intense sound sources, including those produced by military vessels and seismic surveys are associated with symptoms of chronic stress (Thomas, Reeves, and Brownell 2016; Tyack 2009). The long-term implications of exposure to acute noise threats is unknown but as with any animal, it is likely that increased stress levels would have negative impact on the health, fecundity and longevity of baleen whales (Harris et al. 2018; Thomas, Reeves, and Brownell 2016; Tal et al. 2015).

Rapidly changing climate and unstable environmental conditions may threaten the recovery and long-term health of baleen whale populations, many of which remain largely unassessed (Thomas, Reeves, and Brownell 2016; Simmonds and Isaac 2007). The oceans and climate are inextricably linked with long term climatic patterns such as the El Nino Southern Oscillation correlating with baleen whale occurrence in some areas (Thomas, Reeves, and Brownell 2016). As the Earth continues to 'warm up', reflective polar ice caps continue to melt into the deep blue ocean, resulting in an albedo effect where the reflectivity of the Earth's surface is decreased, and oceans absorb increasing amounts of solar energy (Ingram, Wilson, and Mitchell 1989). Already, a number of species from a variety of taxa have shifted their geographic range poleward in an attempt to escape increasingly warm waters (Thomas, Reeves, and Brownell 2016; Simmonds and Isaac 2007; Perry et al. 2005). Whilst the temperate species have several degrees of latitude to move through, those that already utilise the polar extremes, such as many of the baleen whales, have nowhere to go (Simmonds and Isaac 2007). As species shift their range towards the Antarctic or Arctic latitudes there is an increase in competition between species for resources (Moore and Huntington 2008), exposure to novel pathogens and parasites, as well as the potential for increased killer whale predation on young whales (Thomas, Reeves, and Brownell 2016). The threats of climate change may be amplified by ocean acidification which is likely to have negative implications on resource availability, as some of the life stages and reproductive success of krill due to the dissolution of calcium carbonate and changes in the acid-base balance of their body (Flynn et al. 2012). This is of particular concern in the Antarctic and Arctic oceans which are already deficient in calcium carbonate (Thomas, Reeves, and Brownell 2016).

Managing the recovery of marine mammal populations, particularly those of baleen whales, requires strict regulation and monitoring of industries that produce acoustic disturbance within the marine environment, such as oil and gas exploration, mining and shipping. There is a need to preserve known feeding and breeding grounds, and the migratory channels between these important sites (Thomas, Reeves, and Brownell 2016). Acoustic monitoring represents an effective tool for assessing the potential impacts to marine mammals from acoustic and physical disturbances. While legislation exists to protect marine mammals from direct acts of physical harm, there needs to be greater consideration in legislation for the maintenance of suitable environmental conditions in critical marine mammal habitats with one focus area on background noise, and the most critical area of concern being maintaining food stocks.

## 2.8 Passive acoustic tracking of vocalising whales

Patterns in the movement of animals can aid in identifying the drivers behind different animal behaviours as well as understanding how and why animals use certain areas and the threats they may face as a result (Whoriskey et al. 2017). This information can be used to inform management and conservation decision makers for specific areas and ecosystems. In aquatic ecosystems where visual observation of animal movement is often impossible, electronic telemetry techniques including acoustic positioning systems are becoming increasingly popular for generating time series of animal locations, or 'tracks' (Whoriskey et al. 2017). A breadth of studies have been carried out utilising acoustic recorders to localise and track vocalising animals (Miller 2012; Miller et al. 2013; García et al. 2018; Gavrilov et al. 2012; Gavrilov et al. 2018; Caudal and Glotin 2009; Clark 1995; Houegnigan et al. 2010; Kusel et al. 2017; Stanistreet, Risch, and Van Parijs 2013). The most common method for localising a vocalising animal uses an inversion based on an acoustical model relating time delays in received signals between recorders in a passive acoustic array to the position of the vocalising animal (Gavrilov et al. 2012; White et al. 2006). This process is complicated by variability in sound transmission conditions, sound refraction in the water column and multipath transmission of sound signals in the available ocean sound channel (White et al. 2006).

The possibility of tracking multiple animals with one passive acoustic array is an exciting application of acoustic studies with great value for behavioural studies. However, the

complication comes in differentiating between individual animals of species where the population produces the same vocal cue or song. There are a number of approaches to tracking individual and multiple animals but the one most applicable to this thesis is similar to that described in Nosal (2013) which separates animals by tracking slowly varying bearings. The study uses a model-based time-difference-of-arrival (TDOA) framework where the weighted least squares difference between actual and modelled TDOA is minimised. Tracking is then performed recursively by maximising a log-likelihood function for position given the associated TDOA (Nosal 2013). The derived locations are then combined with a clustering technique based on average swim speed and track duration to determine likely tracks by looking at the maximum change in TDOA. For example, based on a swimming speed of 10 km/h, the corresponding maximum change in TDOA would be 0.002 s/s. Points satisfying this criterion are chosen as the next point in the track. If no points exist satisfying the criteria, then the track is terminated (Nosal 2013; Guazzo et al. 2017). Such a method has been successfully applied in recent years to passive acoustic recordings to track the movement of grey whales in the North Pacific (Guazzo et al. 2017). While more work is needed to refine this technique, a number of behavioural models and software packages, including Markov Movement Models, exist to support the modelling of behaviour based on successive localisations of vocally active animals (Whoriskey et al. 2017; DeRuiter et al. 2017).

### 2.9 Future directions

The challenging task of monitoring abundance and distribution of marine mammals that have elusive behaviour with little surface activity, and poorly defined calling behaviour is an obstacle for the effective management of threatened cetacean species who live far offshore and occur in low densities. Keeping track of spatial and temporal variations in abundance is important not only for monitoring the recovery of species post whaling, but also for assessing the success of conservation actions taken by managing parties (Evans and Hammond 2004). Passive acoustic techniques have the potential to increase the accuracy, scope and efficiency of abundance surveys by allowing for observations to be collected year round, and utilising the favourable sound propagation properties of water which make acoustic observations more suitable than visual observations for animals that spend the majority of their time underwater (Mann et al. 2000; Oleson, Calambokidis, Barlow, et al.

2007; Stafford et al. 2011). Gaps exist in methodology to convert acoustic detections to measures of relative and absolute abundance, and the accuracy of such methods relies heavily on an in-depth understanding of species specific vocalisation rates and singing behaviour (Evans and Hammond 2004). Continued research into the behavioural context of vocalisations, as well as variability in vocal signals and song will improve the accuracy of acoustic techniques for abundance estimation. In this way, passive acoustic surveys may have the potential to yield abundance estimates for cetacean species whose populations remain unassessed, consequently resulting in better management and protection for threatened species (Thomas, Reeves, and Brownell 2016; Harris et al. 2018; Ward et al. 2012). Accurate acoustic localisation and tracking has the demonstrated potential to mitigate the exposure of cetacean species to anthropogenic threats and ship strike through real time tracking grids that can deconflict shipping and military operations with cetacean habitat usage (Miller 2012; André et al. 2011; Clark et al. 2005; Clark et al. 2007). Further, where passive acoustic sensors are fixed, there is the capacity for long term monitoring of trends in abundance leading to efficient management of recovering populations.

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## Chapter 3    Methods

## 3.1 Study Location

Data for this study were collected from two sample sites (Figure 3.1), the Perth Canyon, in the lower south west of Western Australia ( $\sim 32^\circ$  S,  $115^\circ$  E), and off Portland, Victoria ( $\sim 38.5^\circ$  S,  $141.2^\circ$  E) which lies on the South-Eastern edge of Victoria. Each receiver site was located on or immediately adjacent to the continental shelf edge allowing the site to be exposed to underwater sounds from the deep ocean. The Perth Canyon is a submarine canyon west of Rottnest Island, off the coast of Perth, Western Australia. It is a long narrow trench that functions as a hot spot of productivity along a largely oligotrophic coast (Rennie 2005). Upwelling along the edges of the canyon supports sufficient krill to feed seasonal aggregations of EIOPB whales around the canyon each year (Rennie 2005; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). Studies of the oceanography of the Perth Canyon have found that it is the interaction of the Leeuwin undercurrent with the bathymetric features of the canyon that is primarily responsible for the high productivity within the region (Rennie 2005; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). Upwelling occurs at the canyon's rims periodically while eddies within the canyon cause aggregations of krill to form at the head of the canyon (Rennie 2005). This corresponds with observations of the feeding behaviour of pygmy blue whales that are observed to aggregate around the head of the canyon (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Rennie 2005; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009), as well as in a particular gully immediately to the east of the passive acoustic receivers. This was unknown at the time the acoustic receivers were initially deployed. Productivity in the canyon is at its highest when the Leeuwin current is weak (Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009; Rennie, McCauley, and Pattiaratchi 2006), thus seasonal variations in the Leeuwin current, Leeuwin undercurrent and wind forcing lead to variability in the primary productivity, which may be reflected by trends in seasonal and annual pygmy blue whale abundance. (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009).

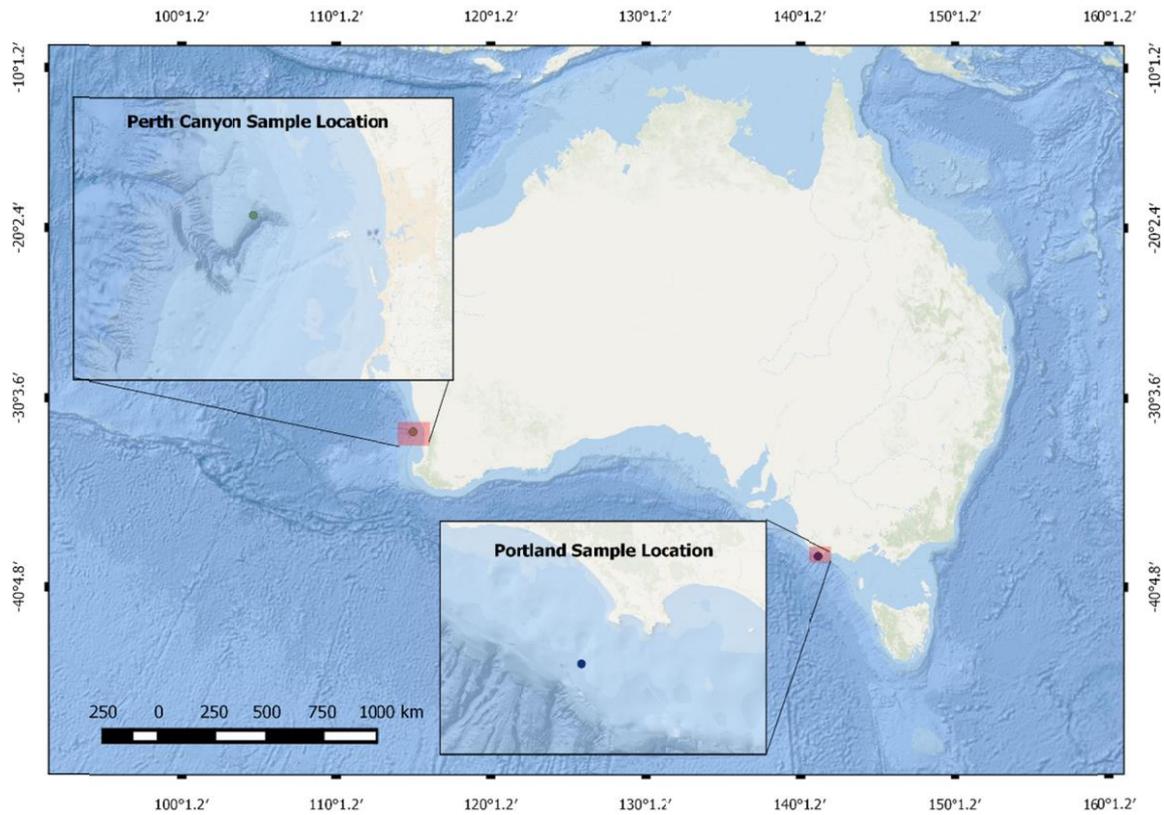


Figure 3.1. Sample locations in the Perth Canyon, Western Australia and Portland, Victoria. Inset; the location of the Perth Canyon and Portland sample sites with respect to Western Australia produced using ESRI World Ocean Base Map 2018.

The Portland sample site is located off the southern Victorian coastline, and is the site of an annual upwelling phenomenon, the Bonney upwelling (Middleton and Bye 2007). The Bonney upwelling is part of a chain of upwelling events along the southern coast of Victoria and South Australia driven by a subtropical atmospheric pressure ridge that sits south of the Great Australian Bight in summer (Middleton and Bye 2007). This atmospheric high pressure system is responsible for creating upwelling favourable conditions along the coast,

whereby prevailing south-easterly winds result in the offshore Ekman transport of surface waters and associated upwelling of cold nutrient dense shelf waters (Middleton and Bye 2007).

Passive acoustic observatories were deployed and maintained at the Portland and Perth Canyon sites since 2008 as part of the Integrated Marine Observing System (IMOS; [imos.org.au](http://imos.org.au)) providing long term data for analysis in this study.

### 3.2 Data Collection

Long term PAM data were collected from the IMOS observatories located at the Perth Canyon and Portland sites. The passive acoustic observatory consists of one to four Curtin University CMST-DSTO autonomous underwater sound recorders, referred to here as acoustic receivers (McCauley et al. 2017). All recorders were calibrated both pre and post deployment using white noise of known Power Spectrum Density (PSD) level applied to the hydrophone preamp in series with the hydrophone. Amplitude and spectra of ambient sound were corrected for system frequency response and hydrophone sensitivity using the calibration data. In some years, when this was possible, three or four instruments were deployed in a tracking configuration, with three instruments set in an approximately equilateral triangle array of about 5 km sides, and a fourth receiver in the centre of the triangle. The acoustic receivers were deployed on the seabed at a depth of 430 to 490 m and were mechanically decoupled from the main mooring by a ground line of approximately twice the water depth running from the instrument to a dump weight with an acoustic release (EdgeTech ORE, CART) and sub-surface floats. The receivers were programmed to sample underwater noise for 300 to 500 s every 900 s at a sample rate of 6 kHz with a low-pass cut off filter at 2.8 kHz and a low-order high-pass filter providing a roll off below 8 Hz to flatten the ambient sound spectra and so increase the dynamic range. While acoustic receivers were deployed in almost all years, various issues rendered some data sets unsuitable for analysis. Data collection years that were used for analysis are indicated in Table 3.1. Over a period of eight years, six years of data were analysed for the Perth Canyon region, and four years for the Portland sample region.

*Table 3.1. Data collection years for the Perth Canyon and Portland sample locations. The grey shaded boxes indicate years for which data were included in this analysis.*

	2010	2011	2012	2013	2014	2015	2016	2017
CANYON								
PORTLAND								

When using receiver arrays for passive acoustic tracking, the accuracy of sound source localisations depends largely on the accuracy of the receiver positions and internal clocks. The clocks of all receivers were synchronised to the GPS time pre-deployment but drifted inconsistently throughout the deployment period. The GPS locations of receivers were recorded upon their deployment; however, this is subject to error as the exact position of receivers on the seafloor at a water depth of more than 400 m cannot be determined by GPS measurements at the sea surface (Gavrilov et al. 2012). To determine the relative time offsets between the receiver clocks two methods were used. The first involved the implosion of eight light bulbs at 100 m ( $\pm 5$  m) below the sea surface in the vicinity of the array. The time difference of arrival (TDOA) of the shots at each of the receivers was used to refine the receiver locations and correct for the drift of the receiver clocks (Gavrilov et al. 2012). Each lightbulb implosion resulted in six TDOA measurements. The central receiver clock was chosen as a reference time and the position and offset of the other receivers calculated by minimising the difference between predicted and observed TDOA of lightbulb implosion shot in a least squares method (Gavrilov et al. 2012). The deployment location and a clock offset of zero were chosen as the starting point for the iterative least squares process. The resulting locations and clock offsets of receivers resulted in the TDOA of the lightbulb implosion shot at the receivers being within the satisfactory ( $\sim 10$  ms) range for accurate triangulation of sound source location from the receiver array (Gavrilov et al.

2012). The receiver clocks continued to drift at different rates throughout the deployment. A high-frequency (7.5 kHz) acoustic pinger set to transmit a series of pings over a few minutes every midnight was deployed along with the central receiver. All receivers were switched to a 22 kHz sampling rate during these time intervals to record the pings. The arrival of this ping at the different receivers was used to determine the rate of clock drift for each receiver. Determining the clock drift for each receiver allowed for continued alignment of the receiver clocks and subsequent recordings across the data set (Gavrilov et al. 2012). For a detailed description of these methods see Gavrilov et al. (2012a).

### 3.3 Maps

Maps for use in this thesis were produced using QGIS (QGIS Development Team 2018) and a variety of open source base layers. The source of map data is indicated in the figure labels for the maps in each chapter. The ESRI World Ocean Base Map (ESRI 2018) was the primary source of base layers for use in this thesis. All Australian charts displayed are based on the Australian Hydrographic Service chart series, obtained under Seafarer GeoTIFF Curtin University license No 2618SG.

### 3.4 Data Processing

Pre-processing and exploration of data were carried out in the MATLAB environment with PSD of recorded ambient sound calculated for each ambient sound sample (recording). Pygmy blue whale songs were detected using an automated search algorithm that searched for the type II unit of the three-part EIOPB song type. The algorithm had false positive and false negative detection rates of less than 5% and is described in detail in Gavrilov and McCauley (2013). The type II unit is the most intense and prolific, being present in all known variations of the EIOPB song (see Chapter 4). Energy in the frequency band of the type II unit is compared with the energy in surrounding bands of ambient sound allowing the algorithm to isolate this sound of the song (Gavrilov et al. 2012). Spectrograms of ambient sound samples containing detections were visually inspected to confirm the detection. For confirmed detections, the song structure, frequency, song interval and any

other distinctive characteristics were recorded and analysed. Where possible, song detections were attributed to individual singing animals.

An EIOPB whale song catalogue was devised to allow for the classification of song types based on the structure of the observed song (see Appendix 1). The characteristic EIOPB whale song is comprised of three units (Samaran et al. 2008; Stafford et al. 2011; McCauley et al. 2001). The first unit, termed a type I unit is the longest starting at 19 Hz for about 21 s then increasing to 21 Hz for nearly 22 s. The second unit, the type II unit, is a frequency modulated upsweep with the fundamental frequency varying from roughly 20 Hz to 26 Hz. The type II unit has three distinguishable harmonics and a fourth one often visible at short distances up to about 100 Hz. The fundamental frequency and the third harmonic contain more than 90% of sound energy (Gavrilov and McCauley, 2013). The third unit, or type III unit, follows by approximately 23 s and is a constant 18 to 19 Hz tone with several harmonics that lasts for 16 to 18 s. The presence and arrangement of these units determined the classification of phrase and song structure.

The nomenclature used here for song description is described in Table 3.2. The inter-song interval (ISI) was defined as the time in seconds for a full repetition of the song pattern or phrase, measured between the start of the first type II unit and the start of the next phrase's type II unit. The type II unit was used as the marker for measuring ISI as it is present in all known song variations. The ISI was variable between phrase structures and within song structures and was used in combination with other call parameters to delineate between singing animals.

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Table 3.2. *Phrase name, description of unit composition, and average ISI for all described EIOBP whale song types from Chapter 4.*

Name	Description	~ ISI (s)
<i>P3</i>	I, II & III repeated ('typical')	180-200
<i>P3L</i>	I, II & III with longer ISI to next	220-280
<i>P3S</i>	I, II & III with shorter ISI to next	120-160
<i>P1</i>	II only repeated	50
<i>P2</i>	II & III repeated	80-100
<i>HA</i>	I, II & III then II & III repeated	~ 300
<i>HB</i>	II & III then II repeated	~ 150
<i>HC</i>	I, II & III then I & II repeated	~ 280

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### 3.5 Localisation of whale signals

The ability to locate the source of sound from a signal has been refined over the years and is possible where multiple acoustic recorders are deployed in a suitable configuration. The IMOS observatory's tracking configuration consists of three or four receivers deployed in an approximately equilateral triangle configuration on the seafloor with a central fourth receiver in some deployments. Recordings from a full tracking configuration were only collected in some years due to the complexity and logistical difficulties involved. Tracking analysis was carried out on data collected in 2010 and 2011 in the Perth Canyon utilising a tracking algorithm in the MATLAB environment.

A brief description of the source localisation technique is given here. For a more detailed description of the methods, see Gavrilov *et al.* (2012). The basic process of sound source localisation relies on the correlation of the signal between receivers and the calculation of the TDOA to each pair of receivers. Spectrogram correlation was used for TDOA calculations in order to lessen the effect of multipath propagation (Gavrilov *et al.* 2012). All detections with inconsistent TDOA results were ignored to reject localisations with large errors. For localisation of the sound sources, it was assumed that all whales called at a depth of 30 m, the average calling depth of blue whales of the North Pacific population as reported by

Oleson *et al.* (2007b). Subsequent studies by Lewis *et al.* (2018) have found that North Pacific blue whales may call from depths as shallow as 15 to 20 m. The Levenberg-Marquardt method (Press *et al.* 1992) was used for localisation that seeks to minimise the following function:

$$\Psi(X_s, Y_s) = \sum_{i,j=1}^n [\Delta t_{ij} - (R_i - R_j)/C]^2, \quad \text{Equation 1}$$

where the distance of source to receiver  $i$  is

$$R_i = [(X_s - X_i)^2 + (Y_s - Y_i)^2 + (Z_s - Z_R)^2]^{1/2} \quad \text{Equation 2}$$

where the depth of the receiver is  $Z_R$ , and  $Z_s$  is the source depth. The presumed location of the singing whale is defined by the horizontal coordinates  $X_s$  and  $Y_s$ . For this equation, the sound speed  $C$  was assumed to remain constant along all direct paths to the receivers and equals to the mean value of the vertical sound speed profile. Errors in localisation were estimated in the form of error ellipses of chosen confidence (95%) from the covariance of the least squares solution of Equation 1 (Gavrilov *et al.* 2012).

Whale location results were ignored if an error ellipse had the maximum semi-axis of more than 0.5 km (each location returned a defined error ellipse). Data were sorted into 24-hour periods and viewed one day at a time. Spectrograms of each detection were viewed and checked manually to follow individual singers and allow for classification of song structure and measurement of ISI.

### 3.6 Tracking Methods

In order to determine the track of an individual animal, each detection localised from within an individual sound recording and temporally adjacent sound recordings, was compared with the last spatial event. Based on the signal characteristics from the spectrogram, such as the Sound Pressure Level (SPL), ISI and signal appearance, as well as the location of the detected vocalisation, it was manually determined whether it was likely to be the same vocalising animal or not. As it is impossible to tell without visual observation whether a localisation came from a single animal travelling alone or a group of animals, estimates were made based on likelihood criteria. This was deemed to be a suitable method for this study given the relatively low density of animals, and the small area within which signals could be accurately localised ( $\sim 20$  km from the array centre) (Gavrilov *et al.*

2012; McCauley, Bannister, Burton, Jenner, and Rennie 2004). As the average group size for pygmy blue whales in the Perth Canyon has been estimated to be 1.1 animals per pod (McCauley, Bannister, Burton, Jenner, and Rennie 2004), each localisation was treated as a single animal. It was assumed that the maximum normal travelling speed of a pygmy blue whale was 20 km per hour with an average speed of  $\sim 3$  km/h (Owen et al. 2016), whilst they are capable of speeds greater than this when disturbed (McCauley, Bannister, Burton, Jenner, and Rennie 2004). This was deemed to be a conservative estimate of the maximum speed of travel for use in this study. This was used to calculate the maximum distance an animal could have travelled between vocalisations over longer time scales and determine whether successive signal localisations of a continuous structure and song repetition interval were likely from one or multiple animals. The movement behaviour of individual animals was also considered, as animals travelling in straight lines were assumed to be likely to continue along a general bearing, while animals that appeared to be milling or engaging in area restricted search (ARS) behaviour were considered likely to continue with that behaviour. Localisations that were consistent with the track of a single whale, combined with a consistent song structure and common ISI amongst songs were used as a criterion for the likelihood of detections being from the same animal. Song intervals have been used in other studies to ascertain whether signals may be from one individual or not (Lewis et al. 2018). While this method relies on a number of assumptions and lacks the support of visual identification, the lower density of animals and generally solitary nature of EIOPB whales allowed for localisations to be allocated to individual tracks. Whale tracks were numbered chronologically and, where possible, were carried over from the previous ambient sound recording, with lapses in recording time taken into consideration when assessing likely localisations. Where a consistent signal was lost for more than one recording the successive vocalisation was classified as a new animal. The start and end time of each track, length of time calling, call type and direction and distance travelled was recorded for each whale track number. Manual analysis considered only events occurring at isolated points in time and it is recognised that individual animals may resume singing behaviour in the same area at a later time. It is also recognised that this methodology is based on a number of assumptions regarding the presence and behaviour of singing animals, and without concurrent visual observation or tagging there is no way to quantify the accuracy of following what is assumed to be one vocal animal in time.

### 3.7 Quantitative Data Analysis

Data were maintained in spreadsheets for use in a variety of statistical analysis techniques. Pygmy blue whale song detections, as well as the X and Y coordinates of whale tracking were saved in MATLAB data files for use in further analysis within the MATLAB environment. Quantitative analysis of population wide variability in song structure was carried out using the statistical program R (R Development Core Team 2010). Further data analysis and graphical representation of results was carried out in the MATLAB environment. Repeated measures multivariate techniques were used to test for significant differences in calling duration, song repetition interval and song structure between the sample years and locations. Specific data and statistical analysis methods are covered within the relevant chapters of this thesis.

### 3.8 Feature Space Analysis

An automated technique was used to assess the relative proportions of song types using all available data from the Perth Canyon and Portland sample sites. A brief summary is given here with a more in-depth description provided in the Supplementary Material of Chapter 4 (4.7 Supplementary Material S1). The search algorithm described in Section 3.4 was run across all data sets and each EIOPB whale detection (unit II) was assigned an arrival time. Arrival time was defined as the time at which the first 5% of the unit signal energy arrived. The sound pressure level of the third frequency harmonic of the type II song unit was derived by band pass filtering the recorded signal calibrated for frequency response of the sound recorder. Where more than one type II song unit were present within an ambient sound recording, the difference of received sound pressure level and arrival time of all units within the sample was derived. The same process was conducted for each ambient sound recording within a deployment period. This yielded a series of arrival time and sound pressure level difference values (which may potentially represent ISI values where the same song unit was repeated by an individual). The series of values formed a feature space and was gridded for counts of unit-to-unit time and level differences. A number of set bounds of time and level differences were defined (SPL difference of < 2.7 dB was applied), resulting from the difference in the sound level and time spacing of all combinations of type II units

within a sample, and the number of values within these bounds counted. Counts for values of less than 2.7 dB of type II to type II unit level differences were summed, allowing for curves of individual animal's song repetition intervals (termed ISI curves) to be derived for each season in the Perth Canyon and Portland respectively. Peaks in the ISI curves were a result of the mean ISI for each respective phrase type, as well as at values corresponding to multiple repetitions of shorter phrase types. These peaks corresponded to time windows of 30-60 s for *P1* phrases, 70 – 100 s for *P2* phrases, and 160 - 200 s for *P3* phrase types. As ISI was found to shift across years, the windows used to derive ISI values were relatively wide time spans. Small scale fluctuations seen as 'noise' in the ISI curves were smoothed with a running linear fit utilising  $\pm 5$  points either side of point in question.

The magnitude of peaks in the ISI curve combined with ambient sound recording length was used as an indicator of the proportion of song types encountered each year. Details are provided in the supplementary material of chapter 4 (4.7 Supplementary Material S1). In short, the magnitude of each peak was compared taking into consideration the expected number of calls with an ISI of that length within a single sample's time frame as well as multiples of shorter phrase types contributing to the longer ISI values. Models were used to verify how well the ISI analysis was able to predict the ratios of *P1*, *P2* and *P3* songs within data sets, including using simulated data sets analysed with the same set of six equations as the actual data set (see Supplementary Material S1). The model was run 100 times and the proportion of song types in the simulated data sets compared with that of the real data set to yield error estimates, with root mean squared errors of input ratios compared with derived ratios < 1% (full details provided in 4.7 Supplementary Material S1).

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## Chapter 4 Song Variation of the eastern Indian Ocean Pygmy Blue Whale in the Perth Canyon, Western Australia

Note. The full reference for this chapter is as follows,

Jolliffe, C. D., McCauley, R. D., Gavrilov, A. N., Jenner, K. C. S., Jenner, M-N M., Duncan, A. J. (2018). Song variation of the Eastern Indian Ocean pygmy blue whale population. PLOS One. Doi: 10.1371/journal.pone.0208619

### 4.1 Abstract

*Sea noise collected over 2003 to 2017 from the Perth Canyon, Western Australia was analysed for variation in the Eastern Indian Ocean pygmy blue (EIOPB) whale song structure. The primary song-types were: P3, a three unit phrase (I, II and III) repeated with an inter-song interval (ISI) of 170-194 s; P2, a phrase consisting of only units II & III repeated every 84-96 s; and P1 with a phrase consisting of only unit II repeated every 45-49 s. The different ISI values were approximate multiples of each other within a season. When comparing data from each season, across seasons, the ISI value for each song increased significantly through time (all fits had  $p \ll 0.001$ ), at 0.30 s/Year (95%CI 0.217-0.383), 0.8 s/Year (95%CI 0.655-1.025) and 1.73 s/Year (95%CI 1.264-2.196) for the P1, P2 and P3 songs respectively. The proportions of each song-type averaged at 21.5, 24.2 and 56% for P1, P2 and P3 occurrence respectively and these ratios could vary by up to  $\pm 8\%$  (95% CI) amongst years. On some occasions animals changed the P3 ISI to be significantly shorter (120-160 s) or longer (220-280 s). Hybrid song patterns occurred where animals combined multiple phrase types into a repeated song. In recent years whales introduced further complexity by splitting song units. This variability of song-type and proportions implies abundance measure for this whale sub population based on song detection needs to factor in trends in song variability to make data comparable between seasons. Further, such variability in song production by a sub population of pygmy blue whales raises questions as to the stability of the song types that are used to delineate populations. The high level of song variability may be driven by an increasing number of background whale callers creating 'noise' and so forcing animals to alter song in order to 'stand out' amongst the crowd.*

## 4.2 Introduction

Baleen whales commonly use low frequency, high intensity sounds to communicate over large distances (Mann 2017; Lewis and Sirovic 2018; Stafford et al. 2018; Payne and Payne 1985; Helweg et al. 1998; Noad et al. 2000; Clark and Clapham 2004). The purpose of these vocalisations remains uncertain and likely has multiple functions. In humpback whales the complex song structures are produced by males as part of reproductive displays (Noad et al. 2000; Cerchio, Jacobsen, and Norris 2001; Mercado, Herman, and Pack 2005; Darling, Jones, and Nicklin 2006), and it is likely that song serves some reproductive function in other baleen whale species as well (Wiggins et al. 2015; Ronald et al. 2015; Brunel-Pons, Alem, and Greenfield 2011). Vocalisations are population specific with subpopulations defined by geographic range and song structure (Garland et al. 2015; Tripovich et al. 2015; Cantor et al. 2015; McDonald, Hildebrand, and Mesnick 2006; Cerchio, Jacobsen, and Norris 2001). As such, the correct classification of song-types is important for successful acoustic monitoring of populations. The detection of specific song-types across protracted periods can indicate the migratory timing of individual whales or the population, and may allow an understanding of population structure and abundance (Adi, Johnson, and Osiejuk 2010). Studying the communication of populations can provide clues as to the evolution of vocal systems and mechanisms for vocal learning within a population (Garland, Rendell, Lamoni, et al. 2017; Cantor et al. 2015; Rendell and Whitehead 2001; Wiggins et al. 2015; Garland, Rendell, Lilley, et al. 2017; Cantor and Whitehead 2013a; Galef 2001). Changes to the vocal structure employed by a population can be indicative of large and small scale processes that shape vocal repertoires at the species and population level (Garland, Rendell, Lilley, et al. 2017). Changes in whale song may be in the form of the loss or addition of vocal elements or the modification of existing vocal elements (Garland, Rendell, Lilley, et al. 2017; Mercado, Herman, and Pack 2005; Payne and Payne 1985). Changes to existing vocalisation structure can be defined as changes to the duration and timing of song intervals, or composition and frequency changes in elements of the song (Garland, Rendell, Lilley, et al. 2017) above what normal variation can be expected. A number of factors are thought to be responsible for shaping changes in song structure including physical processes such as increases in background noise, social changes such as cultural drift within the population, or through genetic drift (Cerchio, Jacobsen, and Norris 2001; Mercado 2018; Janik and Slater 1997; Mann 2017). It is often unclear whether small scale variations in song structure are part of population wide changes or can be attributed to individual

whales (Buchan et al. 2014; Bottcher, Gero, and Beedholm 2018). A better understanding of the driving factors behind changes to vocal repertoires may provide clues as to the purpose of particular vocal signals, such as whether they have a reproductive or social context (Janik 2014; Janik and Slater 2000; Rekdahl et al. 2013; Dunlop 2017; Ronald et al. 2015). It is thought that vocalisations within a familial group with a social context are least susceptible to change whilst those songs with a reproductive context are most likely to change (Wiggins et al. 2015; Janik and Slater 2000; Rekdahl et al. 2013; Filatova et al. 2015).

Population specific vocalisations are useful in the monitoring and management of cryptic or offshore species such as the EIOPB whale population (*Balaenoptera musculus brevicauda*) or termed here, the Easter Indian Ocean (EIO) pygmy blue whale, a part of which traverses the Western Australia coast each year (Double et al. 2014a; McCauley and Jenner 2010b; McCauley et al. 2006). The use of passive acoustic monitoring (PAM) for assessing the abundance of pygmy blue whales in a quantitative fashion requires knowledge of the vocal repertoire, song structure and natural variability in the cue rate or proportion of animals vocalising. Blue whale song-types are categorised based on differences in song phrasing, inter song interval (ISI) or the time between phrase repetitions, unit frequency, duration, modulation or total song length (Ljungblad, Clark, and Shimada 1998; Stafford et al. 2011; Buchan et al. 2014; McDonald, Hildebrand, and Mesnick 2006). This paper explores the considerable on-going song variability found in the EIOPB whale song (referred to as pygmy blue whale hereafter for brevity). This variability in song structure has implications for passive acoustic census techniques and for understanding the social and external features which may drive song function, structure and variability. Relative abundance estimates are derived from passive acoustics data using some measure of song production per unit time across seasons. Underlying these measures is the assumption that song production, structure and song repeat intervals are persistent over years, but this is not quite the case, as demonstrated by this study.

### 4.3 Methods

#### Data Collection

Long term data were collected from a passive acoustic observatory located in the Perth

Canyon area to the north-west of Rottnest Island as part of the Australian, Integrated Marine Observing System (Figure 4.1). Data was collected under Curtin University Animal Ethics Committee permit AEC\_2013\_28 - Passive acoustic recording of marine animal (mammal and fish) vocalisations. Permits for deploying sea noise recorders were not required. Each passive acoustic observatory consisted of one to four Curtin University CMST-DSTO sea noise recorders (see [www.cmst.curtin.edu.au/products](http://www.cmst.curtin.edu.au/products) or (McCauley et al. 2017) for instrument and deployment details) set over 2003 to 2017 (Table 4.1). On occasion three or four instruments were deployed simultaneously in a tracking configuration, with three instruments in an approximate equilateral triangle of 5 km sides, and a fourth recorder in the triangle centre. The noise recorders were deployed on the seabed at a depth of 430 to 490 m. The recorders were set to collect ambient sound recordings of between 200-500 s every 900 s at a sample rate of 6 kHz with a low pass anti-aliasing filter at 2.8 kHz and a roll off applied below 8 Hz to flatten the sea noise spectra and so increase the effective dynamic range. All instruments were calibrated using white noise injection with the receiver in series to the noise generator output, allowing the full system frequency response to be corrected for in post processing (2 Hz to anti-aliasing filter frequency). The system clocks were set to UTC time before deployment and the clock drift was measured after recovery, allowing absolute time accuracy of  $\pm 0.25$  s, this driven by the jump in water temperature on deployment and recovery (see (McCauley et al. 2017) for calibration details). Sea noise recorders were deployed for between eight and twelve months at which point they were retrieved in order to upload data and change batteries. When using receiver arrays for passive acoustic tracking, the accuracy of sound source localisations depends largely on the accuracy of the receiver positions and internal clocks. The GPS locations of the touch-down positions were recorded upon deployment of the receivers while instrument clocks were synchronised in accordance with the procedures outlined in (Gavrilov et al. 2012).

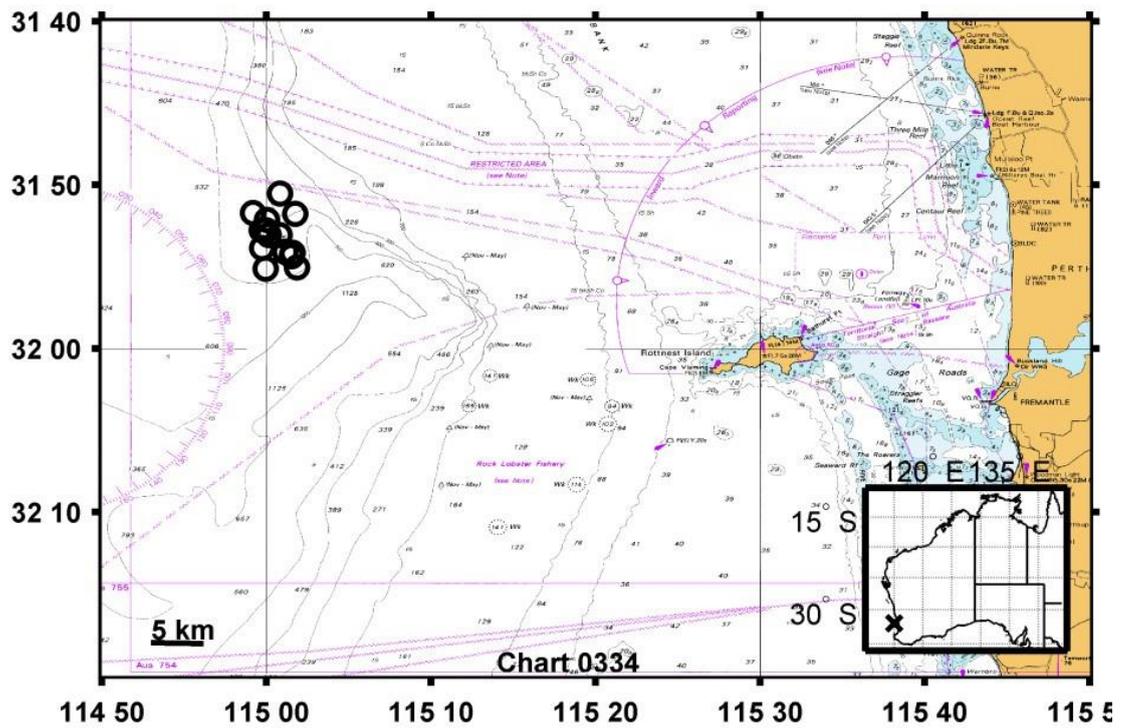


Figure 4.1. Location of sites sampled. The (black circles) are sampling sites in the Perth Canyon and (inset) the location of the Perth Canyon (black cross) within Western Australia. (Based on Australian Hydrographic Service chart, prepared under Seafarer GeoTIFF C)

Chapter 4. Song variation of the EIO pygmy blue whale

Table 4.1. Details of acoustic receiver primary deployments.

Set	Lat. (° ' S)	Lon. (° ' E)	Start	End	Len (s)
2615	31° 53.77'	115° 1.00'	18-Feb-2003	07-Jun-2003	205.3
2656	31° 50.86'	114° 59.92'	26-Feb-2004	14-Jun-2004	205.3
2672	31° 52.12'	115° 0.04'	30-Dec-2004	08-Jul-2005	205.0
2724	31° 54.08'	115° 1.14'	01-Jan-2007	25-Apr-2007	204.9
2802	31° 53.86'	114° 59.73'	26-Feb-2008	21-Apr-2008	204.9
2823	31° 54.47'	114° 59.08'	24-Feb-2009	11-Oct-2009	512.1
2884	31° 55.04'	115° 1.86'	13-Nov-2009	22-Jul-2010	460.9
2962	31° 54.14'	115° 1.61'	06-Aug-2010	08-May-2011	409.7
3006	31° 51.98'	115° 0.05'	14-Jul-2011	18-Jun-2012	307.3
3007	31° 53.07'	114° 59.96'	14-Jul-2011	16-Jun-2012	307.3
3004	31° 54.35'	115° 1.54'	14-Jul-2011	19-Jun-2012	307.3
3154	31° 53.05'	115° 0.81'	10-Aug-2012	14-Jun-2013	306.3
3376	31° 50.53'	115° 0.82'	28-Nov-2013	03-Nov-2014	307.3
3445	31° 52.66'	115° 0.66'	05-Jan-2016	30-Dec-2016	307.3
3444	31° 51.77'	115° 1.74'	23-Sep-2016	26-Aug-2017	307.3

Listed are: set number; Latitude (degrees and minutes S); longitude (degrees and minutes E); start day (UTC); end day (UTC); and sample length (s). All sets used a 6 kHz sample rate.

All samples were repeated every 15 minutes. Only one of the instruments used in the tracking grids is included.

Data analysis for this paper focused on the northern migration of pygmy blue whales from February to June, coinciding with peaks in acoustic presence in the Perth Canyon. Receiver deployments from all sample years cover these peak months making data suitable for comparison between years (Table 4.1).

All data sets were initially checked for major noise sources using an approach where 5-18 day spectrograms were produced and dominant sources identified [39]. Detection algorithms for pygmy blue whale signals were run across all data sets and the outputs of these manually checked. During the checking process the presence of all source types was noted.

Pygmy blue whale songs were detected using a search algorithm initially defined in (Gavrilov and Parsons 2014), which searches for the fundamental frequency of 20-23 Hz and the third harmonic of 60-70 Hz of the type II unit in the three unit pygmy blue whale phrase-type as shown in Fig 2 (McDonald, Hildebrand, and Mesnick 2006; Stafford et al. 2011; Gavrilov et al. 2011a; McCauley et al. 2006). The type II unit of the pygmy blue whale song was present in all song varieties. The detection algorithm had miss-detection and false-detection rates of less than 5% as described in (Gavrilov and Parsons 2014). The search algorithm isolated the signal by locating the frequency sweep based on a multivariate analysis of spectrogram features of the recorded signal (Gavrilov and Parsons 2014) . In many data sets (all from which manual song analysis was carried out) each detection was checked manually by viewing the spectrogram with detections marked. Song structure, duration and frequency were analysed for each detection where signals could be easily isolated from surrounding noise. Where continuity of song structure, duration, the animal's track (where available) and the ISI of songs was observed within a single recording, the signals were assumed to be produced by the same vocalising animal.

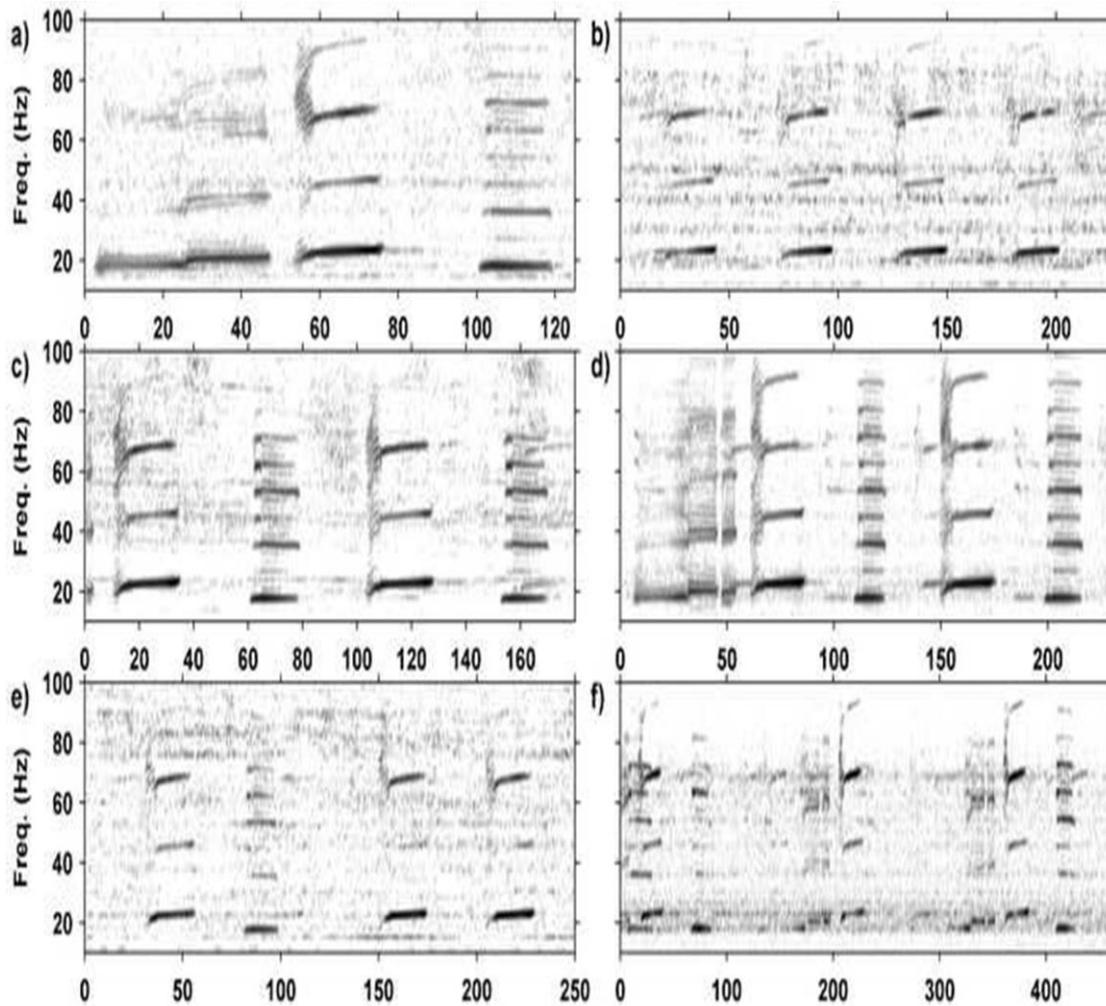


Figure 4.2. Spectrograms of pygmy blue whale song variants. All spectrograms made with 1024 point Fast Fourier Transform ( $\pm$ ), 0.8 overlap using a 1 kHz sample rate (0.977 Hz and 0.205 s frequency and time resolution, respectively). The x-axis is time, in s, the y-axis is common for all panels.

Shown are: a) one version of the normal, three unit song with the Type I (0-50 s), II (50-75 s) and III (100-125 s) units; b) the 'song' which repeats only the type II unit; c) the song which repeats only the type II and III units (*P2*); d) a *P3A* song-type displaying a three unit song sequence followed by a two unit song sequence; e) a *P2B* song structure showing a two unit

sequence followed by a lone type II unit and then another type II unit which marks the start of the next sequence; and f) a *P3B* song-type showing a three unit song sequence followed by a type I and type II unit and then another complete three unit phrase.

Classification of phrase structure was carried out using two approaches: the first was manually based by viewing spectrograms, and identifying the phrase based on hierarchical structure and presence or absence of particular units, as shown in Figure 4.3. The pygmy blue whale EIOPB song type has three units, type I, II and III as shown on Figure 4.2a. The sequence in which these units were repeated was used to classify phrase structure, and where repeated phrases were available for analysis, song structure was classified. For most songs, only one phrase structure was repeated in sequence, though combinations of phrase structures were repeated in hybrid song types. A *K* means cluster analysis was used in the R statistical environment to sort song events based on the type and order of the first three song units. Clustering analysis was run with a set seed of 20, and six categories. The resulting analysis sorted 3,239 song events into the six song structures with 100% accuracy. A song catalogue was subsequently produced describing each of the three known song units, the five phrase variations including three structural variations and two temporal variations, and six song sequence variations. The validity of this catalogue for classification of EIOPB whale song was assessed using an inter-rater reliability test, an established protocol for classification of cetacean vocalisations (Riesch, Ford, and Thomsen 2006; Janik 1999; Rehn, Teichert, and Thomsen 2007; Kershenbaum et al. 2014). A randomly selected subset of 22 signal spectrograms displaying different phrase and song variations was presented to five untrained observers. Spectrograms were produced with a 1024 FFT, Hanning window with no overlap, and 1 kHz sample rate. Each spectrogram was presented on a single slide and viewed by the observers in PDF format. All observers were supplied with a hard copy of the EIO PBW song catalogue and asked to classify the signals based on the appearance of the spectrographic contour, phrase organisation and duration (Janik 1999). A Fleiss unweighted Kappa analysis was used to statistically test the agreement of song classification between the five untrained observers (Siegel and Castellan 1988).

The time between successive phrase production, or ISI, was measured from manually derived data to classify the phrase structure, although there was a bias here as periods of high numbers of simultaneously calling pygmy whales could not be analysed manually because of the difficulty of identifying individual singers. For this reason, manual analysis was only carried out on song events where a solitary animal was vocalising. For the manual processing, data were pre-processed in the MATLAB environment to calculate the power

spectral density of sea noise for each ambient sound recording using the software package CHORUS [25]. Spectrograms were produced using a 6000 point FFT and Hanning window with no overlap. Spectrograms of each sample were stacked and displayed in batches of 5-20 days for quick perusal for pygmy blue whale presence, then perused individually where pygmy blue signals were present.

Starting Song Unit	Phrase Structure	Song Structure	Song Name
Unit I	P3 Unit I Unit II Unit III	P3 P3 P3 P3	P3
		P3 P2 P3 P2	P3A
Unit II	P2 Unit II Unit III	Unit I Unit II P3	P3B
		P2 P2 P2 P2	P2
	P1 Unit II	P2 P1 P2 P1	P2A
		P1 P1 P1 P1	P1

Figure 4.3. Song structure classification. The EIOPB whale song type has three defined units combined in different sequences to produce phrases that are then linked together in song. Phrases are categorised by the order that units appear with temporal variations in the length of phrase types. Songs are generally composed of the same phrase repeated over and over, though combination songs comprised of two different phrases in sequence have been observed.

A second analysis approach was used to study the ISI values and relative proportions of song types across each season. This technique used all data available from the Perth Canyon (thirteen seasons over 2003-2017, with 2006 and 2015 not sampled, Table 4.1). A brief summary of this technique is listed below; details are given in Supp. S1. The search algorithm for locating the type II unit of pygmy blue whale songs was run across all Perth Canyon data sets, with the detector output of several data sets fully manually checked. Each pygmy blue whale detection (the type II unit) was assigned an arrival time within a sample using a consistent technique to define arrival time (the time at which 5% of the whale unit energy arrived) and the sound pressure level derived for the type II upper frequency unit, by band pass filtering the calibrated data. If more than one pygmy blue whale type II unit was present within a single ambient sound recording, the difference of

received level and arrival time of all combinations of type II units in that sample was derived. The same process was repeated for each ambient sound recording and the time and level difference data assembled for all samples within each season. This gave a series of arrival time difference values (or potentially song repetition interval since the same unit in repeated songs may have been found) each with a level difference, for all type II to type II song unit combinations for each season. The set of values was treated as a feature space and gridded for counts of unit-to-unit time and level differences which fell within set bounds, that is bounds of level and time differences were set and the number of values within these bounds counted (Figure 4.4a). One would expect that for the same animal vocalising within a sample, the level difference of the repeat type II unit (song ISI) would be within a few dB of the prior type II unit and that the same unit-to-unit time differences would be similar between phrases. Thus, common inter-song intervals, as given by the type II separation for individuals, would sum in the feature space at small level differences while the time and level differences for different animals would essentially be random noise and so not sum. This was the case and is observed on Figure 4.4.

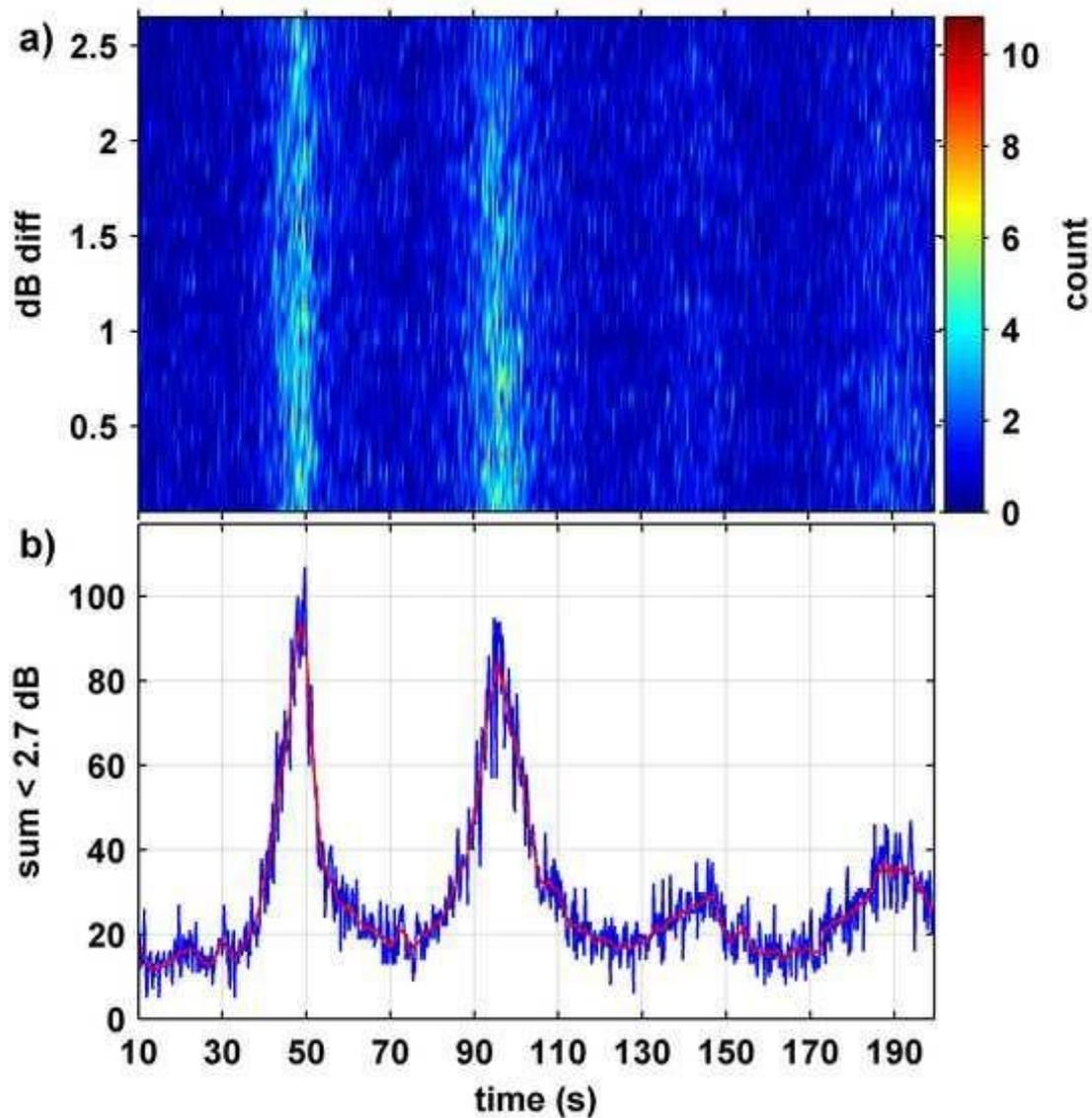


Figure 4.4. Inter-song-interval analysis. Density distribution (a) of song-to-song time and level differences for consecutive type II units, for 2016 with (b) the curve derived by summing data < 2.7 dB (blue is raw data, red is linearly smoothed data). Panel a) was derived using a 0.25 s and 0.1 dB time and level difference, respectively.

By summing counts for values less than 2.7 dB of type II to type II unit level differences in the gridded feature space, curves of song repetition intervals were derived for each season in the Perth Canyon (termed ISI-curves, with an example shown in Table 4.4b). Peaks in the ISI-curves occurred at the mean ISI for the respective phrase-type, and at multiple repetition intervals of the shorter phrase-types. The peak values in time windows of 30-60

s, 70-100 s and 160-200 s were found which gave the ISI for the three major phrase-types, noting that in Figure 4.4 the fourth peak at 140-150 s is a multiple of the first song type observed (i.e. the peak at 140-150 s represents the time between *P1* to *P1* to *P1* phrases, see Supp. S1 for elaboration of how this is dealt with). The windows used to derive ISI values were relatively wide time spans as the ISI spacing was found to shift across years. The ISI-curve peaks were gentle and had some 'noise' in terms of small scale fluctuations associated with them. To remove this 'noise' the ICI curves were smoothed, using a running, linear fit encompassing  $\pm 5$  points either side of the point in question, to give a smoothed value for that point. These smoothed curves were used for obtaining peak time and count values. A resolution of 0.1 s and 0.25 dB was used in the gridded feature space which derived these curves, with the respective x or y value for each 'bin' used to develop the 2D feature space, placed in the centre of the bin.

The magnitude of the ISI-curve peaks combined with the ambient sound recording length also gave information on the proportion of song-types encountered each year. Details of how this was done are given in Supp. S1. Briefly the technique compared the magnitude of the peaks of the ISI-curves, after accounting for the expected number of songs of that ISI length in that sample length, the 'noise' and by accounting for multiples of a shorter ISI song type adding into a longer ISI song-type. Several models were built to verify how well the ISI analysis technique was able to predict data sets with different ratios of *P1*, *P2* and *P3* songs present, with root mean squared errors of input ratios compared with derived ratios at < 1% (Supp. S1).

In order to better understand the movement patterns and presence of pygmy blue whales in the Perth Canyon area, vocalising animals were localised in space based on the time difference of arrival (TDOA) of the vocal signal at the noise recorders of the passive acoustic observatory. Tracking analysis could only be carried out for 2010, 2011 and 2012 where data sets had been collected successfully from four recorders within the observatory.

Localisation of pygmy blue whale vocalisations was based on the type II song unit as defined in (Gavrilov et al. 2012). Spectrogram correlation was used for TDOA estimates rather than waveform correlation in an attempt to lessen the effects of multipath

propagation. The Levenberg-Marquardt least square method was used for localisation and is explained in detail in (Gavrilov et al. 2012).

Whale localisation results were filtered to only include individual locations with errors of less than 0.5 km (an error ellipse was derived for each location). The filtered results were sorted into individual days and viewed one day at a time. Spectrograms of whale sounds for each localisation event were viewed, checked manually and classified based on song structure and song repetition interval. Each localised detection was compared with the previous localisation event and based on the signal characteristics from the spectrogram, as well as the location of the detected vocalisation, it was manually determined whether it was likely to be the same vocalising animal. It was assumed that the average swimming speed of a pygmy blue whale was less than 20 km per hour when comparing locations across longer time scales. A track consistent with a single whale combined with a common ISI amongst songs was used as a criterion for the likelihood of detections being from the same animal. Whale tracks were numbered chronologically and where possible were carried over from the previous sample. Where a consistent signal was lost for more than one sample (greater than 1800 s), or the location of the source did not fit the criterion above, the successive vocalisation was classified as a new vocal animal. The start and end time of each track, length of time calling, song-type, track direction and distance travelled was recorded for each whale track. While each song sequence was unique for an individual whale, many of the sequences were potentially produced by the same whale due to normal breaks in calling. Thus, the manual analysis considers events that occurred independently in time for an individual whale but which may have been replicated at a later time by the same individual.

Quantitative analysis of population wide variability in song structure was carried out using the statistical program R (R Development Core Team 2010). Repeated measures multivariate techniques were used to test for significant differences in calling duration, song repetition interval and song structure between the sampled years. Unless otherwise stated, errors about mean values are of 95 % confidence limits.

## 4.4 Results

### Song structure and variants

Across the five years of manually analysed samples (2010 to 2016), 2,627 song events from EIOPB whales were analysed and identified to song structure. No songs from pygmy blue whales of other Indian Ocean stocks were detected or noted. The highest number of song events analysed were in 2010 and 2011 with 509 and 598 records respectively (Figure 4.5). Peaks in the number of identified vocal events (Figure 4.5) were consistent with the northern (February to June) and southern (November to January) migratory pulses of the Eastern Indian Ocean pygmy blue whale, which occur along the Western Australian coast at this latitude (Double et al. 2014b; Gavrilov et al. 2018; McCauley and Jenner 2010b). The largest peak in pygmy blue whale song events was over March and April coinciding with the northern migratory pulse (Double et al. 2014b) where in some years animals are known to linger in the Perth Canyon engaging in feeding behaviour (Double et al. 2014b; Gavrilov et al. 2012; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009).

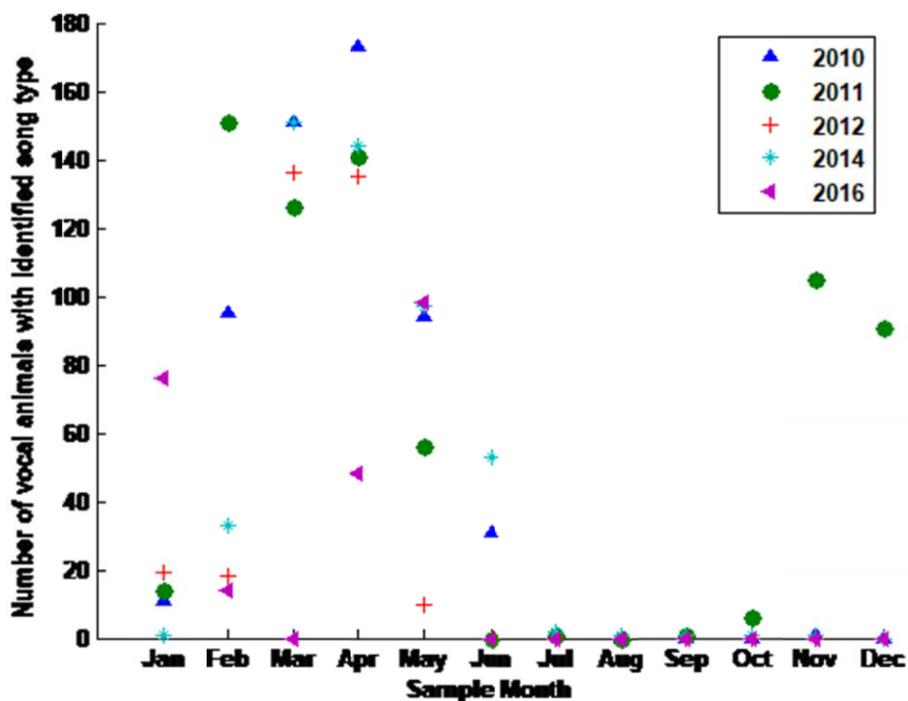


Figure 4.5. Identified singers per year. Distribution events where song structure was identified throughout the calendar year.

The full pygmy blue whale song or "typical" song, (termed here *P3*) consists of a phrase of three units (sounds) repeated in a sequence with approximately 180-200 s (the value differs amongst years, below) between the start of one phrase and the start of the next (the ISI value, Fig 2a). The first song unit (type I) is the longest with energy centred in the 20 Hz frequency band and harmonics up to 80 Hz. The type I unit starts with a 19 Hz tone that lasts for 21s before jumping to 21 Hz for a further 22 s. This is followed five to ten s later by the type II unit, a frequency modulated upsweep, which for example in 2010 swept upwards from 20 Hz to 26 Hz over a period of 23 s, with energy centred around 24.7 Hz and

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strong harmonics up to 72 Hz. The last unit of the song, type III, follows ~ 23 s later and is a constant frequency tone between 18 Hz and 19 Hz that lasts between 26 and 28 s. It is accompanied by strong harmonics and a secondary pulsed tone of 60 Hz-65 Hz. Of the total number of analysed song events with identified song-types in the manual analysis, 931 were classified as belonging to the *P3* variant (Table 4.2). This represented 35.4% of vocalising whales with recognisable song structures. Whilst there were no statistical differences in the proportion of song types between years, there appeared to be a slight decreasing trend in the number of whales producing this song-type through time in the manually processed data.

Table 4.2. Details of pygmy blue whale song variants described from manual analysis.

Code	Description	N	% of identified call type	~ ISI (s)
<i>P3</i>	I, II & III repeated ('typical')	931	35.4	180 - 200
<i>P3L</i>	I, II & III with longer ISI to next	11	0.4	220 - 280
<i>P3S</i>	I, II & III with shorter ISI to next	67	2.6	120 - 160
<i>P1</i>	II only repeated	91	3.5	50
<i>P2</i>	II & III repeated	1220	46.4	80 - 100
<i>P3A</i>	I, II & III then II & III repeated	263	10	~ 300
<i>P2A</i>	<i>P2</i> phrase then II repeated	41	1.6	~ 150
<i>P3B</i>	<i>P3</i> phrase then I & II repeated	3	0.1	~ 280

Given are: the code used throughout; a description of the phrase makeup with the song units involved (types). For *P1*, *P2* and *P3* songs the respective phrases are repeated in a song sequence; the number of occurrences of this song-type; the % of this song-type; and

the approximate inter-song interval (s) or the repeat time between type II to the next song-type II unit.

A number of variations to the pygmy blue whale *P3* phrase and song type were found. For the purpose of this study, a phrase was defined as one sequence of units where none of the units are repeated, while a song was two or more repetitions of any phrase structure. Songs that consisted of only one phrase type share the name of the phrase. Common variations included shortening of the phrase to a one (*P1*, unit II only) or two (*P2*, units II and III only) unit phrase and repeating the shortened phrase at a reduced ISI compared to that of the typical song. Combinations of different phrase structures were also identified and termed hybrid song-types. Hybrid song types were named based on the base phrase structure. In 2016 another variation was observed with different units of the song split or broken. Temporal variations to the *P3* song sequence in the form of long or short repetition ISI times were also observed. Details of the phrase and song variants are summarised in Table 4.2, and discussed below.

The complete *P3* song consists of a repeated phrase with three temporal variants: a) the normal variant; b) a variant with a longer repetition interval than the typical song (*P3L*); and c) a variant with a shorter than normal ISI (*P3S*). The long variation of the *P3* song followed the same basic structure but with 220 to 280 s intervals between the start of one sequence and the start of the next. The extra length of ISI in the song appeared in the length of time between the end of the previous phrase's type III unit and the beginning of the type I unit of the next phrase sequence. The time between the successive units within the sequence remained consistent between *P3L* and *P3* phrase. The *P3L* variation was identified on 11 (0.4%) occasions making it one of the least common song variants. *P3L* was only recorded in 2010 and 2011.

The *P3S* variation followed the same structure as the *P3* phrase but had only a 120 to 160 s interval between the start of one phrase sequence and the next. The phrase appears to be shortened in the type I unit and the time between the type I and type II units. The time between the end of the third and start of the first unit of the next sequence did not vary greatly from the repeated *P3* phrase structure. The *P3S* song was uncommon and only identified 67 (2.6%) times, occurring in the 2010, 2011, 2012 and 2014 datasets. The

production of *P3S* was limited to March, April and May, months with the highest number of song events analysed overall.

The one unit phrase variation (Figure 4.2b, *P1*) was the simplest variation with the shortest ISI with the first and last units of the *P3* phrase dropped leaving only the type II unit repeated in a sequence with ~ 50 s intervals. The *P1* phrase was one of the least common variations in the manually processed data, identified on 91 (4.3%) occasions. Comparisons across the sample years revealed that the number of *P1* song events appeared to increase between 2009 and 2011. In the manual data, after 2011 the number of whales producing the *P1* song remained relatively constant. Analysis of song structure by month showed the highest number of *P1* song events in March, April and May.

The two unit phrase (Figure 4.2c, type II and III units repeated, *P2*) was the most common variant of the *P3* phrase in the manual analysis. The subsequent *P2* song sequence is repeated at ~ 80 to 100 s ISI. There were 1,220 *P2* song events extracted from the manually analysed data, which represented 57.7% of sampled song events. The proportion of the *P2* song events remained stable across sample years with peaks in 2010 and 2014 coinciding with peaks in the number of song events recorded.

The appropriateness of song classification was tested with a Fleiss unweighted Kappa analysis on the classification of 22 spectrograms by five untrained observers. The analysis found substantial agreement between observers ( $K = 0.76$ ,  $z = 25.7$ ,  $p = 0$ ) based on the provided song catalogue. The greatest disagreement between observers was in identifying temporal variations of the *P3* phrase type, *P3S* where the *P3* phrase was repeated with an unusually short ISI value and *P3L* where the ISI between consecutive phrases was unusually long. When temporal variations were ignored, and observers were asked to classify signals into one of the three phrase structures or two song sequence variations, the agreement between observers was almost perfect ( $K = 0.83$ ,  $z = 23.4$ ,  $p = 0$ ). Based on the results of the Fleiss Kappa Analysis, it can be said that the classifications assigned to phrase and song variations are consistent and appropriate.

Aside from variations in the *P3* song arising from changes in song repetition interval and dropping off different elements, three hybrid song patterns were identified. The *P3A* song pattern (*P3A*, Figure 4.2d) is a combination of a *P3* phrase followed by a *P2* phrase. The song repetition interval for the *P3* & *P2* song is a combination of the repetition interval for each of the separate sequences, so roughly 300 s as the song comprises a *P3* phrase with ISI of approximately 200 s and a *P2* phrase with ISI of approximately 100 s. The *P3A* song was the most common of the hybrid song patterns with 263 detected whales (10.0%) producing this song variation. The *P3A* variant appeared to be increasing over years, with more than twice the number of occurrences in 2016 (189), compared with the other sample years combined (74). Instances of mixed *P3A* and *P3* song sequences were observed but were rare.

The *P2A* song pattern (Figure 4.2e, *P2A*) was first found in the 2014 data set and is a hybridisation combining the *P2* (type II & III), followed by the *P1* (type II only) phrase structure. The song repetition interval conforms to that of the *P2* and *P1* phrases with the time between type II units approximately 100 and 50 s respectively, resulting in a total song length of approximately 150 s. The *P2A* song variation is slightly less common than the *P3A* variant with 41 occurrences (1.6 %) of this song variant over the sample years. Where followed in time the *P2A* song was consistently repeated (*P2* & *P1* repetitions).

The *P3B* song pattern (Figure 4.2f, *P3B*) was the rarest song variation detected thus far, only found in the 2010 and 2011 data sets. Along with the *P1* phrase, the *P3B* song structure is the only other variant with the absent type III unit. The song consists of a complete *P3* phrase followed by a two unit sequence consisting of only the type I and type II unit. The length of the song is approximately 280 s, with the *P3* section lasting approximately 180 s and the following two units approximately 100 s. There have been very few occurrences of the *P3B* song variant (< 0.2%).

A breakdown of song variant production across all sample years from the manually processed data shows that the proportion of analysed song events containing the different phrase types remained relatively consistent year to year (Figure 4.6), though *P3* and hybrid song events appeared to be increasing in the 2016 data set. The greatest diversity in song

structure was found in the years with the largest sample sizes (Figure 4.6). The two and three unit songs were consistently the most prominent song variants in the manual analysis.

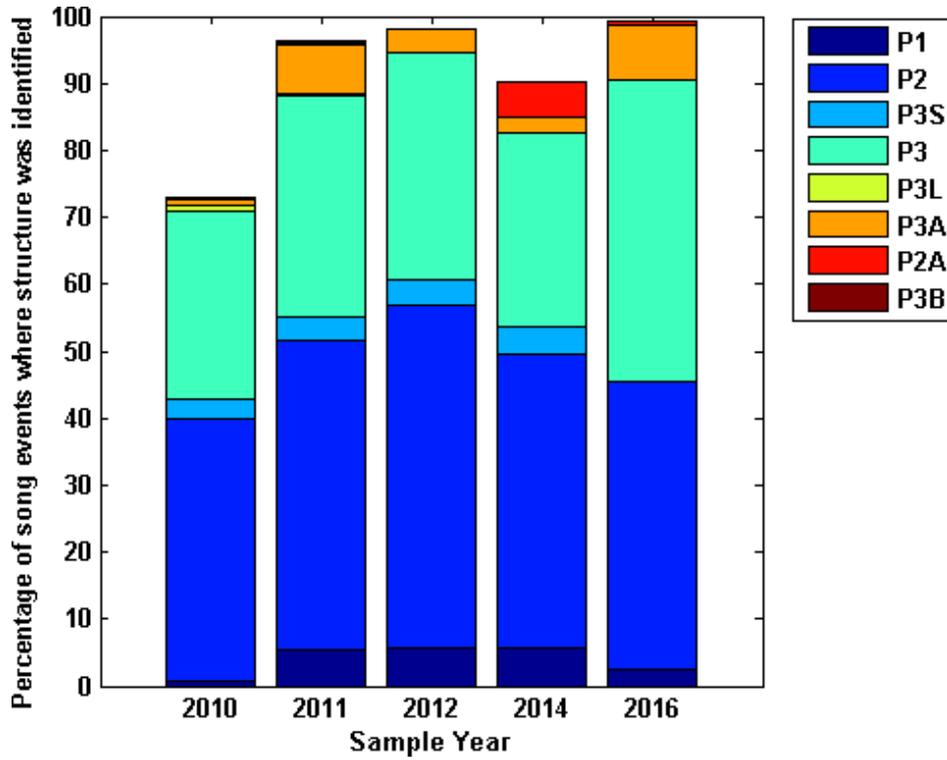


Figure 4.6. Proportion of song variants each year. Ratio of the number of vocal events displaying each song variant, as a proportion of all identified song events for the sample year. P3 refers to the three unit phrase song, P2 to the repeated phrase containing only the second and third units and P1 to a repeated type II unit only. P3A is a song combining the P3 and P2 phrases, while P2A combines the P2 and P1 phrase types. P3B is a unique combination of a P3 phrase and a single unit I and II. Unknown song events are those that are recognisable as EIOPB whale vocalisations but the signal is too poor or there are too many overlapping whale calls to identify the song structure.

There was no trend in the timing of different song variations throughout a season (

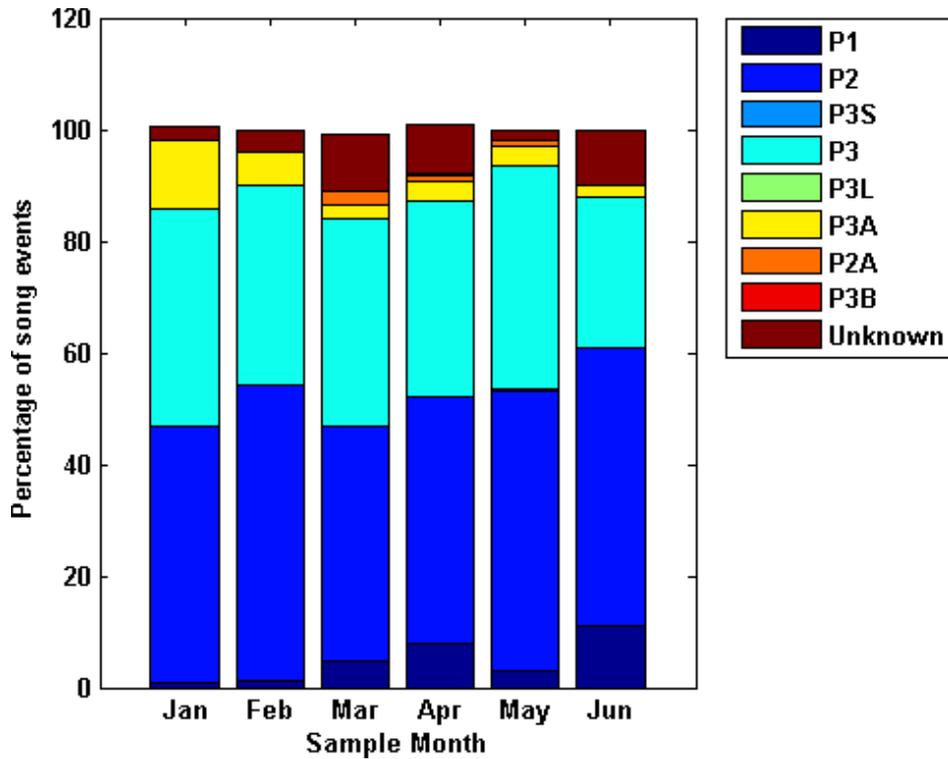


Figure 4.7). A larger number of detections of particular song variants in any given month were correlated with a larger sample size. Aside from an exceptionally large number of *P2* songs in 2014, likely due to the high sample number in this year, the number of vocal events identified manually to each song variant in each month of the year was consistent across all sample years.

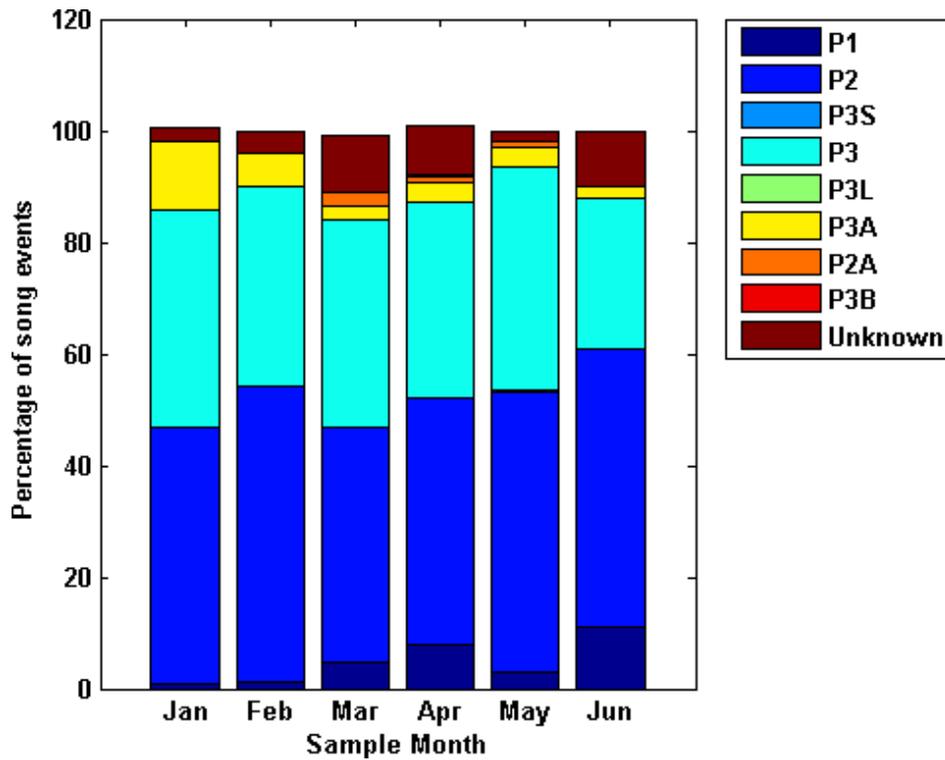


Figure 4.7. Proportion of song variants within a year. Distribution of song structures throughout the calendar year as a proportion of the total number of song events each month.

Post 2015, variations in pygmy blue whale vocal behaviour have extended to variability in the production of the song units themselves. All three extant song units were observed as being modified with breaks or pauses mid-way through the production of a unit in data from 2016 and 2017. The broken song units occurred across a variety of song structures, with one or more units in the phrase broken in two. The unit containing the break remained consistent within a song event, but varied between song events (i.e. Figure 4.8 a-d). Broken song units occurred in all observed song structures in 2016 and were not observed prior to 2016. The number of song events that were observed with a break in one or more song units compared with similar counts for song events without breaks is shown on Figure 4.9. Song units containing breaks were present in a large portion (~ 25%) of song occurrences regardless of structure. This trend in the occurrence of broken song units continued into 2017.

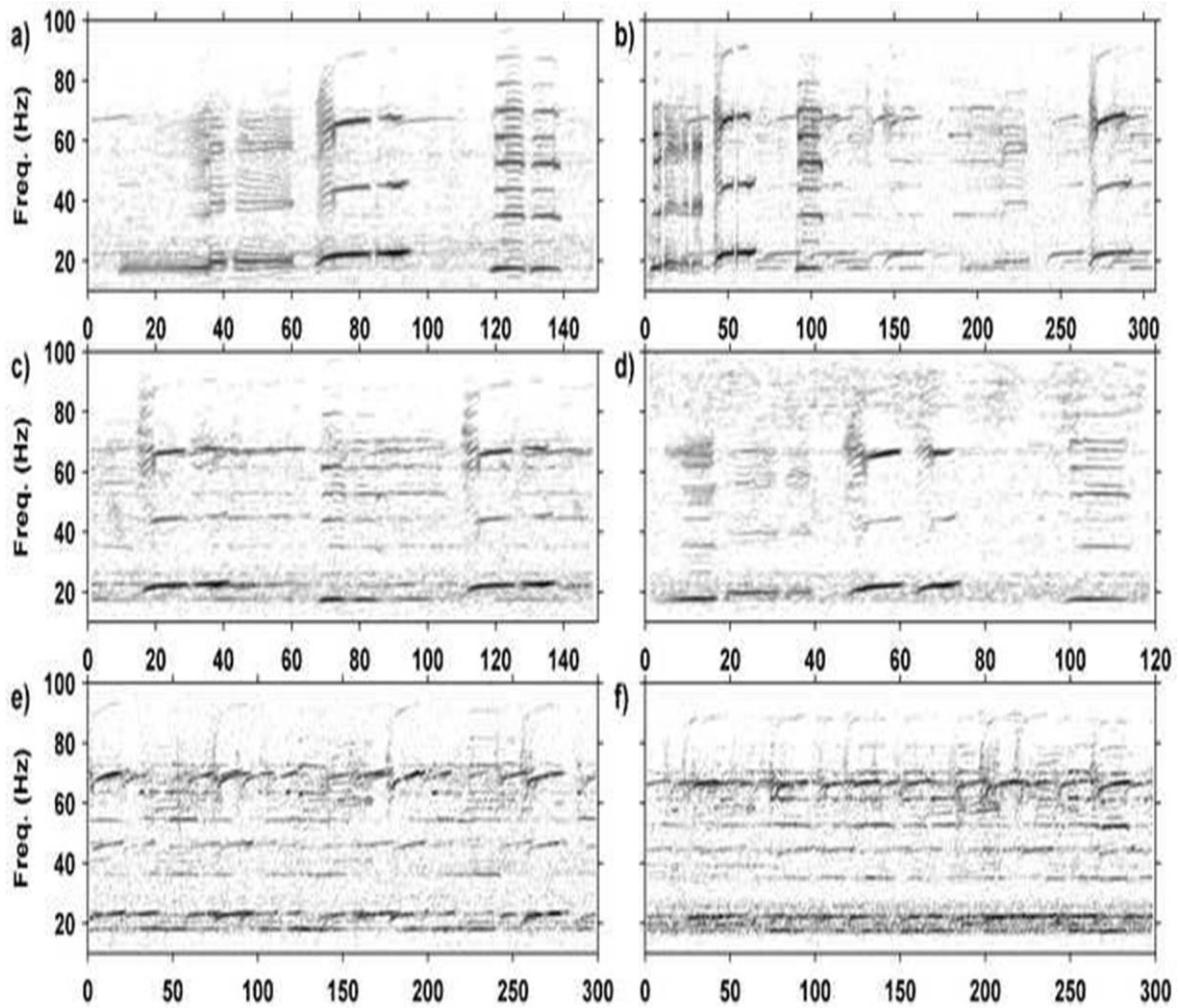


Figure 4.8. Spectrograms of pygmy blue whale song phrases showing broken units and periods of many singers. Spectrograms of pygmy blue whale song with broken units (a-d) and 5-7 overlapping callers (e-f), made with a 2048 point FFT, 0.8 overlap using a 1 kHz sample rate (0.488 Hz and 0.41 s frequency and time resolution, respectively). The x-axis is time in s, the y-axis is common for all panels. Shown are: a) a P3 phrase with all three song units broken; b) a P3 phrase variation with only the type I and type II units broken; c) a P2 phrase variant with units broken; d) a P3 phrase with the type I and II units broken; and e) and f) multiple singers (matched 300 s samples).

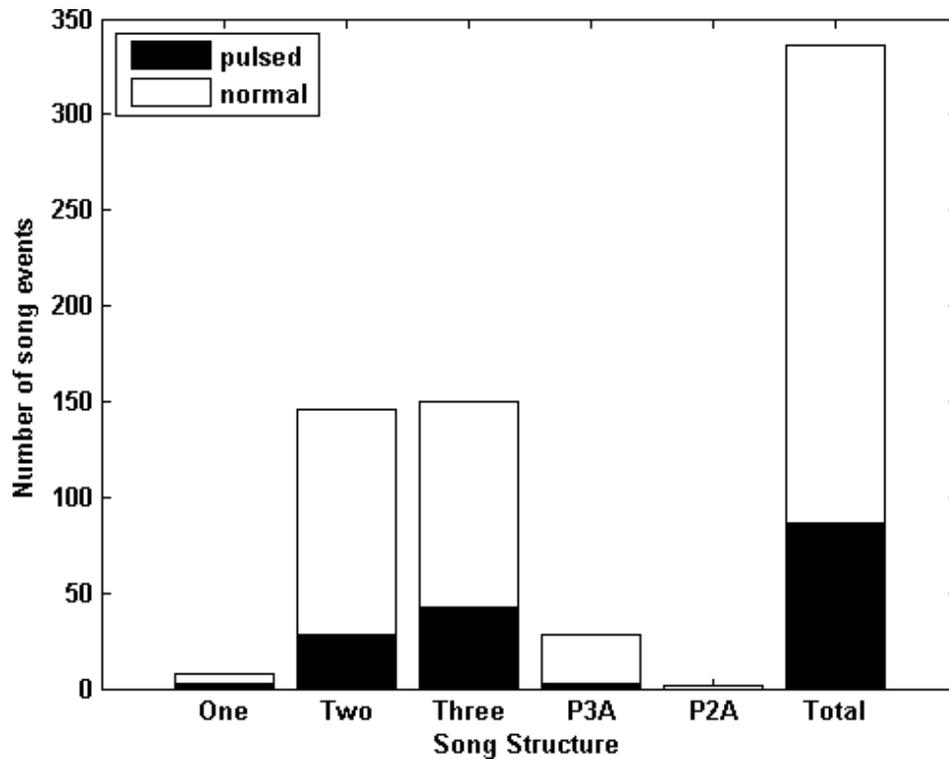


Figure 4.9. Comparison of phrase-types with normal or broken song units which appeared from 2015 onwards.

It needs to be noted that in the later years it became increasingly difficult to identify individual song events owing to the large number of whales calling and so overlapping song. Examples of samples with multiple callers (between 5-7 callers evident) are shown on Figs 4.8e and 4.8f. The high number of singers prevailed for several months and increased across seasons.

#### *Feature space song inter-song interval analysis*

When a season's data set was assembled and gridded using the time-level difference analysis, the technique discriminated ISI, as given by the peaks of time between repeat type II song units, for the three predominant pygmy blue whale song-types and multiples of the ISI of each. An example of the 2015 season's analysis of the ISI, as measured by time

differences between consecutive type II units, was shown on Figure 4.4a, where peaks at the repetition intervals of different song-types appear. By summing values in this time and level difference feature space for a type II unit to the next type II unit, with level differences of  $< 2.7$  dB, the ISI-curves shown on Fig 4b were derived. From the peaks in these curves the time intervals between the  $P1$ ,  $P2$  and  $P3$  unit songs were derived. The same analysis is shown for 2003-2017 on Figure 4.10a, with the ISI values derived from peaks in the summed curves for all years shown (Figure 4.10b). The thirteen-year analysis shown on Figure 4.10 involved 119,724 ambient sound recordings with multiple pygmy blue whale type II units and 545,607 type II to type II time and level difference pairs. The ISI value was increasing over time on Figure 4.10b for each song-type, at different rates (Table 4.3). The ISI values for each year along with the ratio of time between the combinations of song variants are listed in Table 4.3. The ratio between the  $P2$  and  $P1$ , ISI ( $P2/P1$ ) was consistent at 1.932 (95%CI 1.9113-1.9527) while the ratio between the  $P3$  and  $P2$  ISI ( $P3/P2$ ) was statistically the same, at 1.970 (95%CI 1.9401-1.9999). Thus, the ISI for the three songs ( $P1$ ,  $P2$  &  $P3$ ) were multiples of each other, each  $\sim 1.951$  times longer than the previous song-type according to the statistics. Given that the starting resolution was 0.1 s in the ISI-curve analysis technique, then the ISI of  $P2$  is approximately twice the length of  $P1$  while  $P3$  is approximately twice that of  $P2$ .

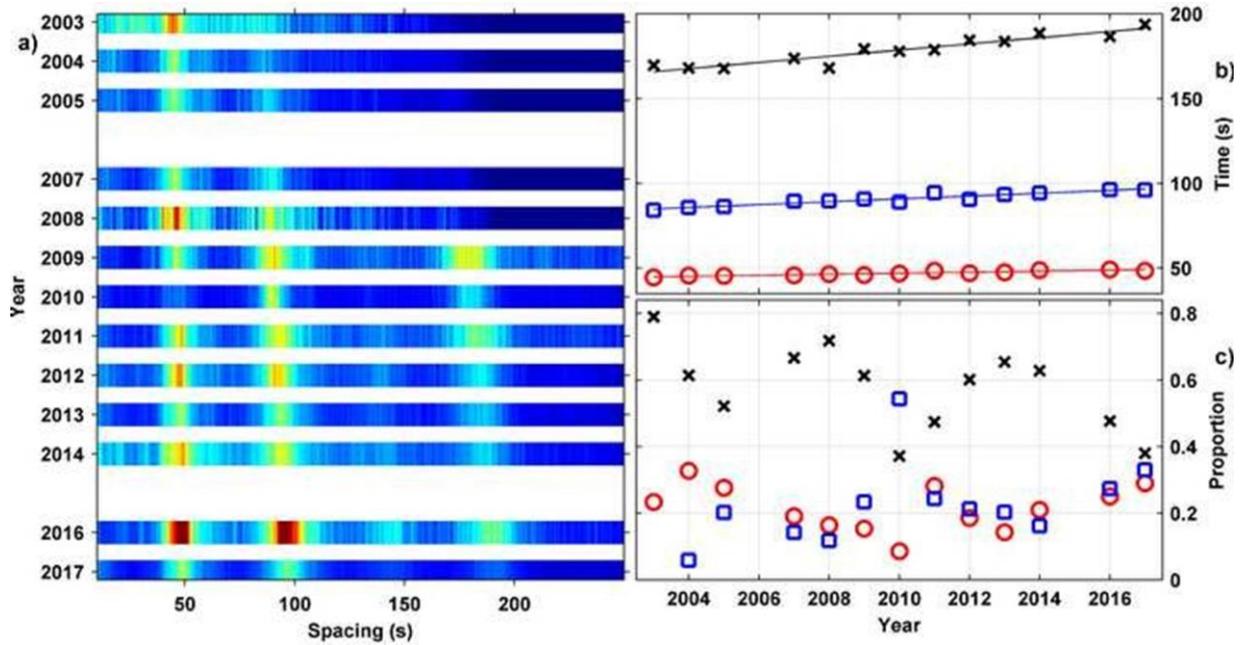


Figure 4.10. ISI-analysis for all seasons. (a) Density distribution of type II repeat interval for all years (normalised each year with the colour scale from 0=blue to 1=red), (b) peak time interval across years over 30-60 s (red circle, P1 song ISI), 70-100 s (blue square, P2 song ISI) and 160-200 s (black cross (P3 song ISI), and c) proportion of song-repeat values with year (same symbols and colours as b). The solid lines on b) are linear fits. The resolution used in a) was 0.1 s and 0.25 dB.

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Table 4.3. Fitted curves to ISI-spacing across seasons for P1, P2 and P3 songs (ISI-curve analysis).

Song-type	Linear Fit <sup>1</sup>	95% CI of coefficient (SE)	Correlation coefficient, $r^2$	F (DF), $p$
P1 Unit II only	$t = 0.305 Y - 565.5$	0.083 (0.038)	0.86	65.9 (1/11), << 0.001
P2 Units II & III	$t = 0.843 Y - 1602.8$	0.185 (0.084)	0.90	100.5 (1 /11), << 0.001
P3 Units I, II & III	$t = 1.826 Y - 3491.5$	0.435 (0.198)	0.86	85.4 (1/11), << 0.001

1. Details of linear fits of song repetition interval for the three pygmy blue whale song-types across seasons from the Perth Canyon. The fit values give  $t$ , the song repetition interval in seconds, for  $Y$ , the year, with fit statistics given.

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Table 4.4. ISI-spacing for the P1, P2 and P3 songs each year (ISI-curve analysis).

Year	II song (P1)	II & III song (P2)	I, II & III song (P3)	P2/P1	P3/P1	P3/P2
2003	44.55	84.15	169.75	1.889	3.810	2.017
2004	45.65	85.75	172.05	1.878	3.769	2.006
2005	45.55	86.25	167.75	1.894	3.683	1.945
2007	45.75	89.45	173.75	1.955	3.798	1.942
2008	46.55	89.65	168.05	1.926	3.610	1.875
2009	46.05	90.75	179.35	1.971	3.895	1.976
2010	46.85	88.95	177.95	1.899	3.798	2.001
2011	48.45	94.45	178.85	1.949	3.691	1.894
2012	47.05	90.55	184.45	1.925	3.920	2.037
2013	47.55	93.35	183.75	1.963	3.864	1.968
2014	48.85	94.25	188.65	1.929	3.862	2.002
2016	49.25	96.35	186.65	1.956	3.790	1.937
2017	48.45	96.15	193.75	1.985	3.999	2.015
Mean, 95% CI				1.932, 1.911 - 1.953	3.807, 3.743 - 3.871	1.970, 1.940 - 2.000

Song to song repeat interval (s) given by feature space analysis and ratios of these for each year, with: year; (P1) time between consecutive type II only songs (s); (P2) time between consecutive type II & III only songs (s); (P3) time between consecutive type I, II & III songs (s); ratio P2/P1; ratio P3/P1; ratio P3/P2.

To calculate the relative proportions of each song-type from the ISI-curve using equations 1-4 (Supp. 1) required the mean length of the type II unit, since at least half a type II unit was required for the search algorithm to locate the unit. Based on the time for 90% of the unit energy to pass this length was 20.9 s (95%CI 20.88-20.92) with a median of 21.0 s derived from 499,193 type II signals. The median value was used in the proportion analysis. The mean ambient sound recording lengths for each season were listed in Table 1. Using these values, the magnitudes of measured ISI-curves each year and the technique described in Supp. 1, the relative proportions of each song-type per year were calculated, assuming only songs of the *P1*, *P2* and *P3* types were present (hybrid song-types were ignored) and correcting for additions of multiples of shorter song-types. The trends calculated across time are presented on Fig 4.10c with statistics listed in **Table 4.5**. While the proportion of song-types has varied across the thirteen years, systematically but not linearly, the range is small and the proportions of different song-types fall within a narrow band. Statistics of song proportions (**Table 4.5**), have the *P1* (type I) only song present on average across the seasons analysed 21.5 % of the time (95%CI 17.30-25.70, all data), the *P2* song (type I & II) present 24.2 % (95%CI 16.39-32.01, 2005 on) and the *P3* song (type I, II & III) present 56.0 % of the time (95%CI 48.81-63.19, 2004 on). Note the earlier years had relatively short ambient sound recording lengths compared to the *P2* and *P3* song length plus fewer whales singing, so early years have been excluded from calculations of statistics of the proportions of *P2* and *P3* songs.

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Table 4.5. Proportions of *P1*, *P2* and *P3* song-types given by ISI-curve analysis.

Song	Min. – max.	Mean, 95% CI, (median)	Years included (N)
<i>P1</i> Type I only	8.6 – 32.7	21.5, 17.30 - 25.70 (21.0)	2003 - 2017 (13)
<i>P2</i> Type I & II	11.8 - 54.3	24.2, 16.39 - 32.01 (21.3)	2005 - 2017 (11)
<i>P3</i> Type I, II & III	37.2 - 71.8	56.0, 48.81 - 63.19 (60.7)	2004 - 2017 (12)

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Statistics on proportions of each song-type as given by the feature space analysis of type II to type II time-level differences.

## 4.5 Discussion

The song structure of Eastern Indian Ocean pygmy blue whale has been shown to be variable and changing across time, while still retaining its uniqueness when compared with the song types of other Southern Hemisphere pygmy blue whale stocks. The fundamental song structure is three units repeated in a phrase (*P3*), but with a further two common variations (*P1* and *P2*) in which not all units are repeated per phrase, sections where phrases combining different combinations of units are repeated and recently, the alteration of units by splitting them into two sections.

The high level of agreement in the classification of different song events by multiple untrained observers provides support for the classification of phrase and song structures outlined in this analysis. The temporal variations of the *P3* song type, delineated from *P3* by a longer or shorter than average phrase repeat interval, proved to be the most difficult for untrained observers to identify. Removal of the temporal element of song event classification resulted in a near perfect agreement between observers. This in part may be due to an inconsistency in the length of sample times which often precludes the recordings of multiple phrases for longer song variants. As such it is recommended that longer recording times are to be utilised in future studies to capture the variability in phrase repeat times. Additionally, further investigation into the temporal variability of song structures may help to better identify temporal song and phrase variants.

The observed changes in song structure were in the form of variations to: 1) the structure of units with broken or broken units observed in recent years; 2) variability in phrase composition where different units were omitted (*P1*, *P2* or *P3*) or where a consecutive song had a different arrangement of units to the previous phrase-type (hybrids); 3) the duration of a phrase cycle; and 4) the interval between consecutive phrases within a song, which increased yearly. In the context of this discussion, the *P1*, *P2* and *P3* phrase type refer to singular sequences of these phrases while the *P1*, *P2* and *P3* song variations refer to repeated sequences of the respective phrase types. Hybrid song types are those which alternate between two different phrase structures. There are a number of adaptive

processes by which song changes can occur and a number of factors that may be driving these changes. Gradual changes to song structure over a long period of time may be attributed to slow evolutionary processes such as genetic or cultural drift (Rendell and Whitehead 2001), whereas rapid changes to characteristic vocalisations may reflect changes in environmental or physical conditions (Helweg et al. 1998). Further short-term shifts in the structure or content of songs may be indicative of the social or behavioural context of the caller (Rekdahl et al. 2013). It must be understood in interpreting song variation that at this point in time, we have no information as to the sex of singers for pygmy blue whales and it would be wrong to automatically assume all singers are males. However, given the large body of information on song production in other species of whale, along with other taxa, it is suspected song may have some function in mate attraction and selection (Gavrilov et al. 2011a; Oleson et al. 2014; Sirovic et al. 2017; Herman 2017).

It is tempting to relate the observed long term, linear decline of the frequency of the type II unit in pygmy blue whale songs (a decrease of 0.12 Hz/year in the call fundamental frequency (Gavrilov et al. 2011a)), with the long term, linear increase in the song repetition interval as found here. There is growing evidence to support a relationship between annual changes in frequency and ISI, particularly in the songs of fin whales (Oleson et al. 2014; Sirovic et al. 2017). However, we could find no simple association between increased ISI values and a decrease in call frequency across time, suggesting further investigation is needed to identify any relationship between the frequency and temporal domains of song production for the pygmy blue whale. Song structure is likely to confound any attempt to relate the two parameters in this study as tonal frequency is measured from the type II song unit and not the overall song, while ISI takes into consideration the repetition interval for the entire phrase sequence. The findings of this study indicate that the rate of change in ISI is variable between song variants with an average increase of  $0.30 \pm 0.083$  s/year,  $0.84 \pm 0.185$  s/year and  $1.73 \pm 0.466$  s/year for the *P1*, *P2* and *P3* songs respectively. How or if the increase in ISI through time observed here and the decrease in call frequency through time observed by (Gavrilov et al. 2011a) relate to each other is not yet clear.

Changes to song repetition interval may result from an increase in background noise, primarily here from the chorus of other pygmy blue whales singing in the same area. In the most recent data sets the largest obstacle to identifying the song structure of vocalising animals in the manual analysis was other vocalising animals which flooded samples with pygmy blue whale signals. As population numbers increase (McCauley et al., 2018 for EIOPB), it may be a natural adaptation for song repetition intervals to increase. Whether

this may be because animals do not have to call as frequently to attract a mate, or the benefit of producing more signals in a shorter time period is outweighed by the energetic cost, or competition due to increases in vocal activity of other animals, would require more investigation. Such density dependent singing dynamics have been studied widely in other taxa such as birds and frogs (Lucas, Howard, and Palmer 1996; Ronald et al. 2015; Ward, Speakman, and Slater 2003; Wiggins et al. 2015). There is also the possibility that changes in the body size of individual whales may have occurred post whaling, with the proportion of larger animals increasing as the population increases. An increase of larger animals may correlate with the observed increase of ISI time separation, but, as we have no data on comparative body size across years this cannot be verified.

The three primary phrase-types defined all contained the type II unit, indicating that this unit seems to underlie song structure of the EIOPB whale population. Intriguingly, the time between consecutive songs seemed to almost double for renditions of each song-type (**Table 4.4**). Given that the resolution used in the analysis to obtain these ISI values was 0.1 s, the ratios of ISI between the three song-types is close to two for *P1* to *P2* and *P2* to *P3*, ISI values respectively. This suggests that inter-song interval may be set by a common oscillator or internal clock, sampled at integer multiples. Further to this, vocal animals displaying the hybrid song structures demonstrated a strict timing conformity with the second phrase of the sequence lasting half the time of the first phrase. For instance, an animal producing a *P3A* song with the first *P3* phrase lasting ~ 180 s was followed by a *P2* phrase of ~ 90 s length, again suggesting a fixed ratio relating to phrase intervals.

The proportion of each song-type calculated from the manual analysis of song events and the ISI-curve analysis technique utilising time and level differences between all type II units in an ambient sound recording, differed significantly (4.3, 52 and 44% for *P1*, *P2* and *P3* song occurrence from manual measures, and 21.5, 24.2 and 56.0% for *P1*, *P2* and *P3* song occurrence respectively from the ISI-curve analysis when averaged across all seasons). The ISI-curve analysis method was largely independent of biases, although: 1) the curves produced for each song-type will be slightly smeared due to different ISI values between song events; and 2) was sensitive to sample length pre 2009 (samples < 300 s). For the samples of shorter length the proportions of the longer song-types which could be detected in that sample length dropped significantly, thus lowering curve peak values and so increasing errors in determining curve peak values and baseline noise levels (since the peak level may have been close to that of background noise or the background noise was sloped downwards for longer ISI times as it approached the sample length). But, the trends in the

ISI-curve analysis technique were largely consistent across seasons which were treated independently, the expected proportion of third multiples of the *P1* ISI were identified correctly by the technique, and the equations used gave the correct ratio of song proportions within < 1% when comparing derived proportions from set proportions using a simulator (Supp. S1). The manual method will be subject to biases, primarily because the songs that were analysed had few background callers present to reduce confusion in following the same vocalising animal. There may also be inherent biases where during periods with multiple singers present, animals are more likely to produce songs similar to the other vocalising animals resulting in a shift towards one particular song structure. The proportions derived from the ISI-curve analysis would be preferred when using the values to manipulate song counts into abundance measures.

Either analysis technique indicates that song occurrence is not a direct reflection of calling whale abundance. The presence of shorter ISI values than the *P3* phrase-type means that simply counting the presence of type II units across time (song/time) will not directly equate to the number of animals present at the time. The ISI-curve analysis shows that while across the 13 years of sampling available the relative proportions of each song-type does not change in any systematic way, suggesting phrase production per unit time may be comparable for relative abundance, the proportions have considerable variation in ranges amongst years of up to  $\pm 8\%$  for the 95% CI of any song-type (Table 4.5). Thus, comparing rates of phrase per unit time as given by the presence of one call unit, may not be directly valid without correcting for changes in ISI values and the relative proportion of song-types. For using song as a measure of abundance in pygmy blue whales then some discrimination of song-type (*P1*, *P2* or *P3*) needs to be made. One technique utilised by the authors is to split an ambient sound recording into time windows less than the *P2*, ISI (96.4 s in 2017, 70 s is a window length commonly used), count the number of type II units within each window and use the maximum value in any window as an estimate of the number of vocalising whales. Using the manual ISI analysis song-type proportions suggest this is correct for 96% of songs, while using the ISI-curve analysis technique for proportions of song-types averaged across seasons suggests this is correct for 80% of songs.

The large degree of variability in ISI values demonstrates that differences exist in timing and phrase production even within similar song structures. This indicates the possibility that variability in phrase structure may be attributed to individual callers and reflects important social information such as identity, sex or size (August and Anderson 1987; Dunlop 2017). The importance of song in individual identification has been explored in bird song as well as

the signature whistles of dolphins and dialects of killer whales (Agafonov and Panova 2017; Deecke, Ford, and Spong 2000; Noad et al. 2000). However, studies of individual variability are more limited in baleen whales. The ability to identify individual animals by their song would likely be beneficial in any population of social animals where the mechanisms and cognition exists to allow this to happen. It is unclear whether individualisation in bird song results from physical or social differences in song learning and production, though studies in cetaceans suggest that individualisation may be a social process (Deecke, Ford, and Spong 2000). The consistency in the proportion of detected vocal animals producing the less common song varieties would suggest that there may be an individual or familial link between the song variant produced and the vocalising animal. Familial linkages can occur through genetic or learned processes, which are often intrinsically entwined in maternal animals that exhibit social behaviour (Deecke, Ford, and Spong 2000; Cantor and Whitehead 2013b; Whitehead and Rendell 2014).

Patterns in the timing of song production and as seen in the ISI analysis are reminiscent of the phonology of speech and song in other species. Phonology, or the arrangement of sounds within a language, allows for the interpretation of different song elements based on a hierarchical context (Lachlan and Nowicki 2015; Kershenbaum et al. 2014). The ability of animals to display elements of complex phonology has been demonstrated previously in studies of song-bird populations (Kershenbaum et al. 2014; Lachlan, Ratmann, and Nowicki 2018; Lachlan and Nowicki 2015). The findings suggest that mechanisms underlying complex phonology likely evolved separately and prior to the human linguistic traits of semantics and syntax (Lachlan and Nowicki 2015). It is therefore likely that these traits will be present in the communicative abilities of other evolutionary lineages such as cetaceans.

For a number of cetaceans, it is nearly impossible to separate genetic linkages on the maternal side and cultural processes as the cause of particular behaviours that are passed from mother to calf (Brunel-Pons, Alem, and Greenfield 2011; McDonald, Hildebrand, and Mesnick 2006; Adi, Johnson, and Osiejuk 2010; McCauley and Jenner 2010b). In baleen whales, song is believed to be a male only phenomenon though it is unclear whether it is learnt or inherited and it must be reiterated that the sex of pygmy blue whale singers has not been confirmed. The existence of a large number of song variants combined with the low genetic diversity of pygmy blue whales (Attard, Beheregaray, Jenner, Gill, Jenner, Morrice, Bannister, LeDuc, and Moller 2010; Attard et al. 2015a), suggests that it is unlikely

that song variants are linked to genetic drivers alone. Genetic processes are slow to act as they occur over the life cycle of an animal. Given the rapid appearance of phrase and unit variations, which seem to appear within a season, it is implausible that genetic processes are responsible for the variability in song production.

Culture is recognised as a driver of behaviour in cetacean species. Culture relies on the social and familial networks of a species and in turn is a driver of social behaviours of a species such as the production of song (Cantor et al. 2015; Cantor and Whitehead 2013b; Galef 2001; Garland, Rendell, Lamoni, et al. 2017; Hammond et al. 2017). The hybrid pygmy blue song patterns, as well as the broken song units that have appeared post 2015, reflect an increase in complexity of song structure setting them apart from the *P1* and *P2* variants of the typical, *P3* phrase song. Increased complexity within songs is thought to be a reflective of cognitive fitness, which may be a favourable trait for sexual selection (Cholewiak, Cerchio, et al. 2018; Creanza, Fogarty, and Feldman 2016; Ward, Speakman, and Slater 2003; Wiggins et al. 2015). Innovation is a cultural process whereby an individual makes a change to the song structure and this change is then copied by other whales and can spread through the population (Cantor et al. 2015; Filatova et al. 2015; Garland, Rendell, Lamoni, et al. 2017; Kershenbaum et al. 2014; Mercado, Herman, and Pack 2005). Vocal learning is the primary mechanism by which changes to song are proliferated throughout the population as well as the means by which juveniles learn the characteristic vocalisations of the population (Deecke, Ford, and Spong 2000; Galef 2001; Janik 2014; Janik and Slater 1997). Similarly, errors in vocal learning can result in variations to song structure, which may then be passed on to others within the population (Filatova et al. 2015; Janik 2014; Deecke, Ford, and Spong 2000). Cultural processes are generally widespread as is seen in humpback populations where changes proliferate through the population [60]. There may be selective pressure for song variation and diversity within the population with females displaying a preference for novel or complex song-types, as is frequently the case with bird song (Lachlan and Nowicki 2015; Mori, Liu, and Wada 2018; Smith 2014; Ward, Speakman, and Slater 2003; Wiggins et al. 2015). Innovation and cultural proliferation would be a more reasonable explanation for the rapid inclusion of unit variations in a significant portion of the pygmy blue whale song phrases post 2015. The fact that broken units represent such a high level of variability suggests a more complex mechanism of song learning and proliferation within the population.

Whilst not energetically costly, singing represents a cost to the animals in terms of the time involved, as it is assumed to preclude other behaviours such as feeding (Oleson,

Calambokidis, Burgess, McDonald, and LeDuc 2007; Dunlop and Noad 2016). As such the time demands of singing must be balanced with any benefits it provides such as increased reproductive output (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Dunlop and Noad 2016). Where male whales dominate singing, song is presumed to have a role in attracting female conspecifics as well as in competing with other males in the area (Dunlop and Noad 2016; Cholewiak, Cerchio, et al. 2018). Sound source level analysis has revealed that the first unit of the P3, EIOPB whale phrase-type is the least intense and thus in high levels of background noise is the hardest to detect (Gavrilov et al. 2012; Gavrilov et al. 2011b; Gavrilov and McCauley 2013; Gavrilov and Parsons 2014). The second unit is the most intense making it the easiest to detect (Gavrilov and Parsons 2014; Samaran et al. 2008; Gavrilov et al. 2012). The Perth Canyon is becoming noisier, largely as a result of the increased number of pygmy blue whale vocalisations (Erbe et al. 2015; McCauley et al. 2017). Thus, focusing time and energy on producing the song units that are best transmitted among high levels of 'noise' and removing the lower level signals could potentially provide a benefit with the individual more likely to be heard by females in the area, as well as by keeping the 'noise' down. Studies of humpback whale calling behaviour suggest that female whales prefer more complex songs (Cholewiak, Cerchio, et al. 2018; Garland, Rendell, Lilley, et al. 2017; Herman 2017; Herman et al. 2013) which is what appears to be happening with the hybrid song-types and unit variations. There have been observations for other mammals of the ability to change song structure dependent on environmental conditions (Lewis and Sirovic 2018; Sirovic et al. 2017). For instance, audience effects (increasing source levels) have been observed in the communication of close range gorilla calls whereby vocalisations were changed dependent on the distance of the caller to the receiving animal (Hedwig et al. 2015). Such a capacity to adapt vocalisations based on target audience and environmental conditions would likely prove beneficial to cetacean species as well, especially as their acoustic environment becomes more complex (Erbe et al. 2015; McCauley et al. 2017). From the data analysed here, it would not appear that there are distinct patterns in the production of particular phrase and song varieties at different times of the year or even within single days as multiple variants were present within one 24 hour period. Whilst this does not negate the potential existence of a relationship between environmental conditions and song production, a more detailed analysis of physical ocean properties, background noise and dominant song varieties would need to be conducted to look for any relationship.

One of the most significant findings of this study is that variability exists in the characteristic song of the EIOPB whale subpopulation. Song structure has previously been used as a diagnostic tool to separate populations of pygmy blue whale (McDonald). Variability in what were previously considered to be static signals raises questions as to the validity of song structure as a diagnostic for sub populations. Consequently, it is recommended that a global study on variability within and between the vocalisations of all sub populations of pygmy blue whale should be conducted.

## 4.6 Conclusion

Through long term passive acoustic monitoring we found three distinct variations of the Eastern Indian Ocean pygmy blue whale phrase structure in the Perth Canyon, Western Australia, and a further three song pattern variations. Within these phrase structures there exist variations in the inter-song interval resulting in two further temporal variations on the three unit phrase structure. Further, the most recent data sets include variations to the units where they are split, or 'broken', within the existing song structures, which adds an additional level of complexity. The mechanisms behind the increase in song diversity are unclear though the rapid appearance of new phrase variants that represent progressive changes to the original phrase structure is consistent with social or cultural evolution. Such rapid change, with new variants appearing within a migratory season, indicates that the levels of variability cannot be attributed to genetic processes. Variability in song and phrase structure is not prolific throughout the population with all the variations present within one year. This sets pygmy blue whales apart from the well-studied humpback whales where changes in song structure are generally propagated through the entire population and supersede earlier song-types. This raises the question as to whether physical environmental conditions may influence song production as has been documented for other baleen whale populations (Cholewiak, Clark, et al. 2018). Peaks in the number of calling animals displaying various phrase-types and the relative stability of the number of detected song events with rare structures across the sample years suggests that song variation may be linked to specific cohorts of animals though further studies are needed to explore this. It is unclear whether physical environmental processes (noise produced by the whales singing) or cultural processes are at play as the concept of culture has only been explored in odontocete and humpback whale populations. There is also the potential for a level of

signal plasticity to exist allowing for context-specific production of vocal cues. Further studies utilising passive acoustic techniques and visual observations, as well as genetic analysis are recommended to elucidate the function of pygmy blue whale song and the driving forces behind changes in phrase structure that are directly translatable to song structure. It is also recommended that a detailed study of fine scale vocal parameters, including temporal variability be conducted to identify the level of variability between vocalising animals. Finally, it is evident that there is a need for comparative studies between pygmy blue whale populations to assess widespread variability in song production.

## 4.7 Supplementary material S1.

### Use of inter-song interval curves to define the proportion of pygmy blue whale song-types

This analysis resulted from calculating the time spacing and sound level difference between all combinations of type II song units found within a sample and appending these pairs together in a matrix for all samples within a season, the resultant matrix became the 'feature space'. These time and level difference pairs were gridded, then summed for all level differences < 2.7 dB to give an "ISI-curve" which displayed peaks at the inter-song-spacing (ISI) for the three major song varieties (*P1*, *P2* and *P3*). All song types had the type II unit and there was only one type II unit within each song type. Obtaining the ISI value for each curve was simply the time values at each of the curve peak's. Obtaining the proportion of a song type was more complex and is described here. The magnitude of peaks in the ISI-curve was dependant on three factors: 1) the noise levels resulting from random spacing of type II to type II units (different individuals singing) or false detections; 2) the prevalence of a song type producing the peak (plus multiples of shorter song types adding to this where applicable); and 3) the expected occurrence of a song length in an ambient sound recording length. Examples of ISI curves for an early season of 2007 with shorter ambient sound recordings (205 s) and a later season (2012) with longer ambient sound recordings (307 s), is shown on Figure 4.11. For a short ambient sound recording length, the curves tail off at the longer ISI values as the expected number of long song types which fit into the available sample length drops rapidly.

It transpired that the shorter song type ISI values produced multiple peaks in the ISI-curve and were an integer multiple of the longer song types, thus adding into the peaks for the longer song-type, ISI-curves. In the methods here we initially define the song proportion analysis by assuming the peaks in the ISI curves are independent or occur at times which are not multiples of each other. The overlapping ISI values, or shorter song types which do have ISI values which are integer multiples of longer song types, are then dealt with.

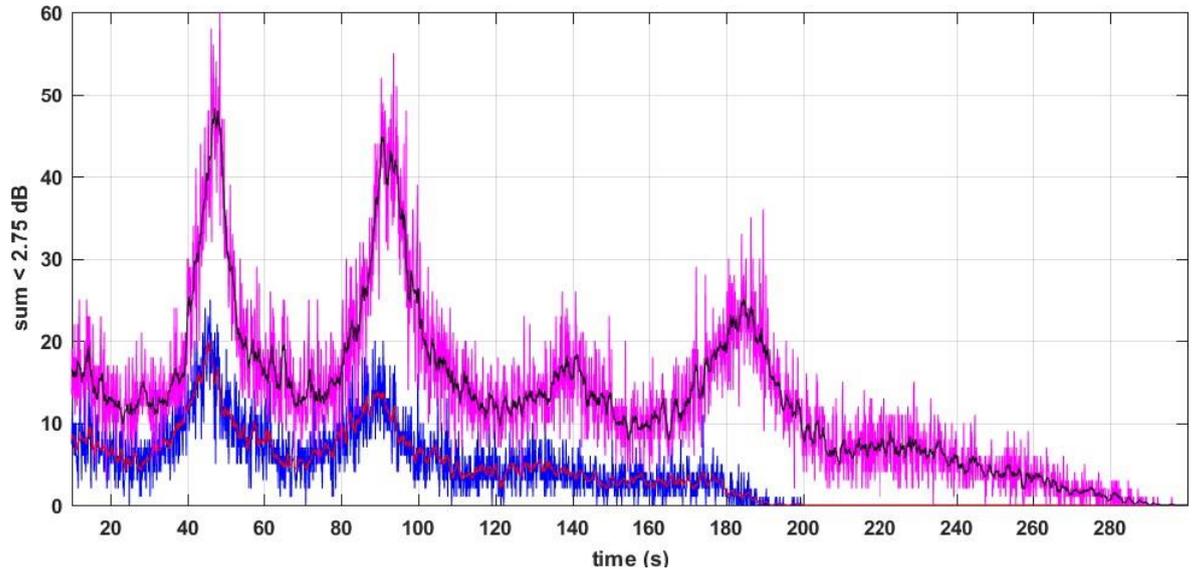


Figure 4.11. Example ISI-curve's for seasons 2007 (blue curve for raw data, red curve for smoothed curve) and 2012 (magenta for raw data, black for smoothed curve).

The first step in analysis was to account for “noise” of a peak in the ISI-curve. Noise levels were calculated by obtaining the base noise level at the centre of the respective ISI peak by interpolating between the low values either side of the peak. In the example shown on Figure 4.4 the noise levels were flat, but for the shorter ambient sound recordings (pre-2009, paper, Table 4.3 or 2007 data Figure 4.11) the base noise levels were sloped downwards for longer song types reflecting the decreasing number of songs of longer length expected in samples of shorter duration. Once noise level values for each respective peak were derived they were subtracted from the maximum value of each peak in the smoothed ISI-curve (smoothed using a running linear fit, 5 points either side of point in question). The integer number of songs ( $N_m$ ) which can be detected in the mean sample length ( $T$  in s, Table 4.5) was then calculated. The search algorithm used to locate type-II units required at least half of the length of the type II unit ( $L$  in s), thus the mean sample length for each deployment was reduced by  $L/2$  to account for this. The maximum number of full song-cycles ( $N_m$ ) which will fit into a sample is:

$$N_m = \text{floor} \left( \frac{T - \frac{L}{2}}{S} \right) \quad (1)$$

where  $S$  is the song repetition interval (s) derived from the type-II to type II, time-level difference analysis described above for the respective song type and *floor* rounds to the lowest integer value. The value  $N_m$  is not the expected number of song cycles, which may be detected within a sample of given length, which is defined by the two equations:

$$c = T - [(N_m - 1) * S] - \frac{L}{2} \quad (2)$$

which gives  $c$ , the available sample length minus the time for  $N_m - 1$  full song cycles. The expected number of song cycles ( $\alpha$ ) which can be detected in the sample of length  $T$  for a song-cycle of length  $S$ , is then:

$$\alpha = (N_m - 1) + \left( \frac{c - S}{c} \right) \quad (3)$$

For the simplest situation where we assume no overlap of multiples of one song type with the ISI of another song type, the value of  $\alpha$  can be used with the peak  $y$ -values derived from ISI-curves (corrected for noise) for all song-types, to give the relative proportions (0-1,  $r_i$  where  $i$  denotes the song type) of each of the three main song types within a season as:

$$r_i = \frac{\frac{Y_i}{\alpha_i}}{\sum_{i=1}^3 \frac{Y_i}{\alpha_i}} \quad (4)$$

where  $Y_i$  is the  $y$ -value, corrected for background noise addition, found at the peak of the ISI-curve from the time-level difference analysis, and  $i$  refers to the song type. As mentioned above, it transpired that multiples of the ISI values for the shorter song types added to the  $Y$  values for the  $P2$  and  $P3$  song ISI values. The ISI of the  $P1$  song was just under half of the ISI of the  $P2$  song and one quarter of the  $P3$  song. This meant that the ISI value for  $P1$  to  $P1$  to  $P1$  songs ( $P1 \times 2$ ) calculated by the ISI-curve technique added into the  $P2$  to  $P2$  ( $P2 \times 1$ ), ISI-curve. To account for this, the value of  $Y_i$  used in Equation 4 for the second song type ( $P2$ ) had to be reduced (to  $Y_2$ ) by the expected proportion of  $P1 \times 2$  songs. The value to reduce it by, was calculated from the expected number ( $\alpha_4$ ) of a song with ISI value of length  $P1 \times 2$  determined using equations 1 & 2, divided by the expected number

of the  $P1$  to  $P1$ , ISI ( $\alpha_1$ ) and to multiply this by the  $Y_1$  value (corrected for noise) used in equation 4, for the  $P1$  to  $P1$  song, i.e.  $Y = \frac{\alpha_1^4 Y_1}{\alpha_1^1}$ , so  $Y = Y_1 - Y_{i(2)}$  (Equations 5 & 6). This

corrected value of  $Y_2$  was then used in equation 4.

Similarly, the  $P1$  to  $P1$  to  $P1$  to  $P1$  to  $P1$ , ( $P1 \times 4$ ) multiple added into the  $P3$  curve peak, as did the  $P2$  to  $P2$  to  $P2$  ( $P2 \times 2$ ) multiple, so these also had to be removed in the same fashion, from the  $P3$  peak value. The magnitude of the  $P2 \times 2$  value which contributed to the  $P3$  curve magnitude used the  $P2 \times 2$  curve peak magnitude after correction for the  $P1 \times 2$  contribution.

As an initial check on the use of the y-values, or magnitudes, in the ISI-curves for calculating relative proportions of song we can compare a multiple of the  $P1$  song ( $P1 \times 3$ ) with the  $P1$  to  $P1$ , ISI. It can be seen that a peak occurred at  $\sim 145$  s on the ISI curve of Figure 4.4b or Figure 4.11 above, which did not overlap any of the other song types or multiples of these. This was the  $P1 \times 3$  peak. If the logic of equations 1-3 were correct then the y-value (noise corrected) of the  $P1 \times 1$  and  $P1 \times 3$  peaks divided by the expected number of each call type should be the same, or if these are divided by each other they should give one, which they did within the error bounds, at  $0.95 \pm 0.17$  ( $\pm 95\%CI$ ) when dividing the  $P1 \times 1$  by the  $P1 \times 3$  result.

As a second check on the validity of Equations 1-6 and to provide error estimates on the proportions of each song type calculated per season using the ISI curve technique, simulated data sets were built and the analysis using equations 1-6 as used on the real data sets applied. The proportions of songs set in the simulated data set were compared with the song proportions derived using the analysis technique. The simulated data used 100 model runs with overlapping ISI values (i.e. the longer song ISI values were multiples of the shorter song-type ISI values). Each run: used 1000 samples each 500 s length; had 3000 songs in total set in ratios of 10.8-29.6% of  $P1$  songs, 10.2-29.7% of  $P2$  or 44.8-77% of  $P3$ , such that the proportions ( $P1 + P2 + P3$ ) added to one for each run, the ratios were randomised within this range for different runs; between 1-3 callers per sample (where callers were present, many samples in a model run had no callers) were allowed such that the correct proportions of song types were maintained; used call ISI values of 45 (repeated  $P1$  song), 90 (repeated  $P2$  song) and 180 s (repeated  $P3$  song) or 50, 100 and 200 s (repeated  $P1$ ,  $P2$  and  $P3$  song, respectively), with the ISI value of each 'individual' varying by  $\pm 0.5$  s in a random fashion; setting the start-point of a song sequence as a random

proportion of the ISI increment for that individual from the start of the sample; and used a level range of from 1-15 dB with consecutive songs of the same individual allowed to randomly vary in level by  $\pm 1$  dB. This analysis gave error estimates (root-squared errors of hard fixed song proportions compared with derived proportions) for all song types combined at 0.8% ( $\pm 0.07\%$  95%CI or SD of 0.67%, N=300), or for the *P1* song proportion at 0.5% ( $\pm 0.11\%$  95%CI or SD = 0.54%, N=100), *P2* song proportion at 0.9% ( $\pm 0.14\%$  95%CI or SD = 0.71%, N=100) and the *P3* song proportion at 1.0% ( $\pm 0.14\%$  95%CI or SD = 0.69%, N=100). The comparatively low error estimates between song proportions set and derived from this analysis plus the correct prediction of a multiple of the *P1* song type (*P1* x 3) in real data sets show the ISI-curve analysis technique to be valid in predicting song proportions.

## Chapter 5 Comparing the acoustic behaviour of the eastern Indian Ocean Pygmy Blue Whale at two Australian aggregation areas

### 5.1 Abstract

*Long term data of underwater passive acoustic monitoring (PAM) collected from two sites of pygmy blue whale presence within Australia, the continental shelf off Portland (38.5° S, 141.2° E) and the Perth Canyon (32° S, 115° E), were analysed to compare acoustic behaviour of eastern Indian Ocean pygmy blue (EIOPB) whales. Pygmy blue whale song detection was consistently higher at the Perth Canyon site than that at the Portland sample site. Statistical analysis found there to be a significant difference in the production of song and phrase variants between sites ( $p < 0.01$ ) with a shorter two unit (P2) variant being more common in the Perth Canyon area, while the traditional three unit (P3) variant was more frequent off Portland. This was supported by manual and feature space analysis techniques. Increasing song complexity was observed in the form of phrases with broken song units, a phenomenon that was first observed at the Portland site on isolated occasions but has occurred and proliferated in the Perth Canyon area from 2016 onwards. Analysis of environmental conditions indicated that increased background noise due to multiple EIOPB whales vocalising, as well as water depth, may influence song length. This was reflected by shorter phrase structures dominating in higher background noise conditions and deeper water, while longer more complex phrase types dominate in quieter, shallower conditions. Further research is recommended to isolate any potential influence of environmental factors on song production.*

### 5.2 Introduction

The ability to predict the distribution and timing of rare species throughout their geographic range has implicit benefits for conservation and management. Understanding habitat selection by whales including any relationship between seasonal changes and resource availability is of importance to scientists for this reason (Gill et al. 2011). With an increase in the demand for marine based industries, including shipping, defence, oil and gas

exploration and production, it is important for there to be an understanding of habitat use by threatened marine mammal species (Nowacek et al. 2016; Thomas, Reeves, and Brownell 2016; Shabangu et al. 2017b).

Pygmy blue whales, *Balaenopterus musculus brevicauda*, are a subspecies of blue whale whose range extends into subtropical oceans around the world. There are five vocally distinct populations in the southern hemisphere all with limited geographical ranges (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Tripovich et al. 2015; Kato, Miyashita, and Shimada 1995; Stafford et al. 2011; Barlow et al. 2018; Branch, Monnahan, and Sirovic 2018; Williams et al. 2011; Buchan et al. 2014; McDonald, Hildebrand, and Mesnick 2006). These populations are the eastern Indian Ocean (EIO) sub population (McCauley et al. 2018; McCauley et al. 2006; Branch, Monnahan, and Sirovic 2018), the Chilean sub population (Williams et al. 2011; Buchan et al. 2014), the Sri Lankan sub population (Stafford et al. 2011), the Madagascan sub population (Samaran et al. 2013; McDonald, Hildebrand, and Mesnick 2006; Branch, Monnahan, and Sirovic 2018; Williams et al. 2011; Buchan et al. 2014; Ljungblad, Clark, and Shimada 1998) and the New Zealand sub population (Barlow et al. 2018; Branch, Monnahan, and Sirovic 2018; Miller et al. 2014). Understanding the behaviour and ecology of these subpopulations is an area of growing research (Stafford et al. 2011; Balcazar et al. 2015; Gedamke et al. 2007; Samaran et al. 2013) with implicit consequences for species conservation and management (Waples and Raudino 2018). The eastern Indian Ocean pygmy blue (EIOPB) whale, characterised by the EIO song type and referred to hereafter in the text as pygmy blue whale, is known to migrate along the West Australian coastline from feeding grounds between 32 °S and 55 °S to breeding grounds in Indonesia (Branch, Abubaker, et al. 2007; McCauley and Jenner 2010b; Double et al. 2014a; McCauley et al. 2018). Two feeding grounds have been identified along the coast of Australia (McCauley et al. 2018; McCauley and Jenner 2010b), although there are likely other feeding areas along the shelf edge. Identified feeding areas are the Perth Canyon off Rottnest, Western Australia and the Bonney Upwelling region off the coast of Portland, Victoria (Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009; Gill et al. 2015; Gill 2002). More recently, feeding pygmy blue whales have also been reported in the subtropical convergence zone (latitude bands 20° - 45°), south of Australia (Garcia-Rojas et al. 2018).

The Perth Canyon is a submarine canyon to the west of Rottnest Island, Western Australia. The Western Australian coastline is generally considered to be oligotrophic; however, a number of factors combine to create favourable conditions for krill to thrive in the Perth

Canyon area, attracting feeding aggregations of pygmy blue whales on their northern migration (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). The head of the canyon is a hot spot for aggregations of krill and other euphausiid species that are distributed at a range of depths most likely due to circulation (Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009; Rennie 2005). Pygmy blue whales are present in the Perth Canyon between November and June each year. However, their behaviour and persistence in the region may be linked to krill abundance. Jenner, Jenner and McCauley (pers. comms) have in some years followed EIOPB whales which have simply traversed the Perth Canyon then headed north in a year of poor krill abundance; whereas, in other years, upwards of 18 EIOPB have been sighted in the Perth Canyon in a single day, some with a resight interval of three weeks (McCauley, Bannister, Burton, Jenner, and Rennie 2004).

The Bonney upwelling is an oceanographic phenomenon that begins every year from around late October to late March. At this time of the year, until up to March following year, the winds blow alongshore from the southeast (Cai and Lennon 1993a). This results in a process of Ekman upwelling where the westward flowing surface waters are nudged to the 90° towards the south by Coriolis forces and so out to sea. The wind driven current results in upwelling of cold, nutrient rich waters from submarine canyons and the deep sea which flow to the surface to replace the displaced water along the coast (Nieblas et al. 2009; Gill 2002; Cai and Lennon 1993a; Middleton and Bye 2007). The upwelling phenomenon primarily occurs between west of Kangaroo Island, and the Victorian town of Portland, a stretch of coastline that is, on average, closer to the continental slope than any other in Australia, with only around 20 km from shoreline to continental slope (Gill 2002; Middleton and Bye 2007). The influx of upwelling water allows phytoplankton and eventually krill (typically *Nyctiphanes spp.*) to flourish. These secondary levels of productivity may not reach sufficient levels to attract feeding whales until several months after the initial upwelling event that supports primary levels of productivity in the form of phytoplankton (Croll et al. 2005). This forms the foundation of the ocean ecosystem and creates a hot spot for marine life from fish and penguins to marine mammals (Gill 2002; Cai and Lennon 1993a; Croll et al. 2005). EIOPB whales are one of the many marine mammal species that are drawn to the Bonney coast which plays host to abundant swarms of krill (Read and Wade 2000; Gill et al. 2011; Gill 2002). Three zones have been identified along the Bonney coast that are utilised by pygmy blue whales, the western, central and eastern zone. The zones have differing environmental and oceanographic conditions including shelf

width and sea surface temperature (Gill et al., 2011). It was found that pygmy blue whales occupied the western and central zones in November and progressed east along the coast in December (Gill et al. 2011). From January through to April they were widely dispersed through the central and eastern zones (Gill et al. 2011). Aerial surveys conducted between 1998 and 2001, sighted 405 EIOPB whales in 261 sighting events (Gill et al. 2011). Whales were sighted within 2 km of krill swarms in 48% of sightings and were observed feeding in 36% of all sightings (Gill et al. 2015; Gill et al. 2011), indicating that the Bonney Upwelling represents an area of ecological significance to migrating pygmy blue whales. The presence and distribution of blue whales has been linked to annual and seasonal patterns of upwelling and primary productivity in a number of publications (McCauley et al. 2018; Munger et al. 2009; Lopez and Methion 2019).

Recent studies have found the vocal behaviour of North Pacific blue whales to vary between inshore and offshore locations (Lewis and Sirovic 2018). The capacity of whales to alter vocal behaviour based on their environmental context has been discussed for humpbacks (Mercado and Frazer 1999) and more recently blue whales (Lewis et al. 2018). Such behavioural plasticity could result in variability in vocal behaviour both temporally and geographically and may reflect not only the physical oceanographic environment but also variability in ambient sound. The impact of anthropogenic noise on cetacean behaviour is a topic of ongoing study, with numerous studies documenting both avoidance behaviours, changes in swimming behaviour and changes in vocal behaviour (Cholewiak, Clark, et al. 2018; Croll et al. 2001; Kvasdheim et al. 2017; Melcon et al. 2012; Nowacek, Johnson, and Tyack 2004). However, it is still unclear whether ambient sound levels may influence the vocal behaviour of whales.

Whilst the Perth Canyon and Portland regions have been identified as areas where EIOPB whales feed, the areas are utilised differently with the Bonney upwelling region believed to be primarily a feeding area with the presence of whales determined by food availability (McCauley et al. 2018; Gill et al. 2011). Upwelling has been found to be a strong predictor for pygmy blue whale presence at the Portland site indicating the presence of animals is linked to prey availability (McCauley et al. 2018). On the other hand, the Perth Canyon is a way stop for EIOPB whales on their northern migration, with a predictable annual presence (Gavrilov and McCauley 2013; McCauley and Jenner 2010a) though the presence of krill likely influences the length of time animals spend in the area (McCauley and Jenner 2010b). Photo identification data of pygmy blue whales from the Perth Canyon and Portland regions have identified individuals that have been previously sighted in the Perth Canyon area,

within the Portland region (McCauley et al. 2018; McCauley and Jenner 2010b). This suggests that the Bonney Upwelling region constitutes part of the range of the eastern Indian Ocean population of pygmy blue whales (Gill et al. 2015; Gill et al. 2011; McCauley et al. 2018; Attard, Beheregaray, Jenner, Gill, Jenner, Morrice, Bannister, LeDuc, and Möller 2010). Population exchange between the two feeding regions is supported by genomic studies concluding that there is no genomic divergence between animals in the Perth Canyon and those in the Portland region (Attard et al. 2018). Additionally, the two sites represent different geographical and bathymetric features, with the Perth Canyon representing an offshore underwater canyon system, and Portland an inshore shelf break. The Perth Canyon and Portland aggregation areas represent biologically important areas for pygmy blue whales requiring a deeper understanding of habitat use and links. The presence of blue whales in the Bonney Upwelling region presents challenges for conservation management with the South coast of Australia being an area of ongoing interest for the oil and gas industries. Further, the proximity of the Portland feeding ground to the coastline makes it an attractive prospect for whale watching tourism (Gill 2002; Gill et al. 2015). Thus, it is important to quantify the use of each region by pygmy blue whales to deconflict human activities and the potential threat they pose to the population.

The pygmy blue whales that utilise the Portland and Perth Canyon feeding grounds produce the same characteristic three unit EIOPB whale song, which along with geographical range is a delineating factor between pygmy blue whale sub-populations. Detailed analysis of recordings from the Perth Canyon area has found this three-unit phrase to be variable with several shortened and hybridised variants to phrase and song structure existing within the population (Jolliffe *et al.* 2019). Currently it is unclear what drives this variability, and a comparison of song production at different areas may provide insights into potential drivers. This study aims to compare EIOPB whale song production between two known aggregation areas using acoustic recordings from the Perth Canyon and Portland sites, to quantify similarities and differences in calling behaviour. It was expected that given the genomic similarities in the two feeding aggregations there would be little difference in observed vocal behaviour between locations.

### 5.3 Methods

Data Collection

Data were collected using the passive acoustic observatories of the Integrated Marine Observing System (IMOS) located off Portland, Victoria and in the Perth Canyon area, Western Australia (Figure 4.1). Each IMOS observatory consisted of one to four Curtin University CMST-DSTO sea noise receivers, referred to here as acoustic receivers (McCauley et al. 2017). These instruments were deployed in a triangular tracking configuration where possible, with one instrument central to three placed in an approximately equilateral triangle. Instruments were deployed on the seabed at depths of between 430 and 490 m in the Perth Canyon area, and around 160 m at the Portland site, with the main mooring and instrument decoupled by a ground line approximately double the length of the deployment depth. The main mooring consisted of a dump weight, an acoustic release (EdgeTech ORE, CART) and subsurface floats. The instrument setup was configured such that to reduce noise artefacts from the mooring lines in the acoustic recordings. Receivers were programmed to sample sea noise by individual recordings of 300 to 500 s length every 900 s, at a sample rate of 6 kHz with a low pass cut off filter at 2.8 kHz. To increase the dynamic range, sea noise spectra were flattened using a low-order high-pass filter with a roll off below 8 Hz. See McCauley et al. (2017) for calibration protocols, which allowed absolute pressure levels to be calculated from 2 Hz to the Nyquist frequency.

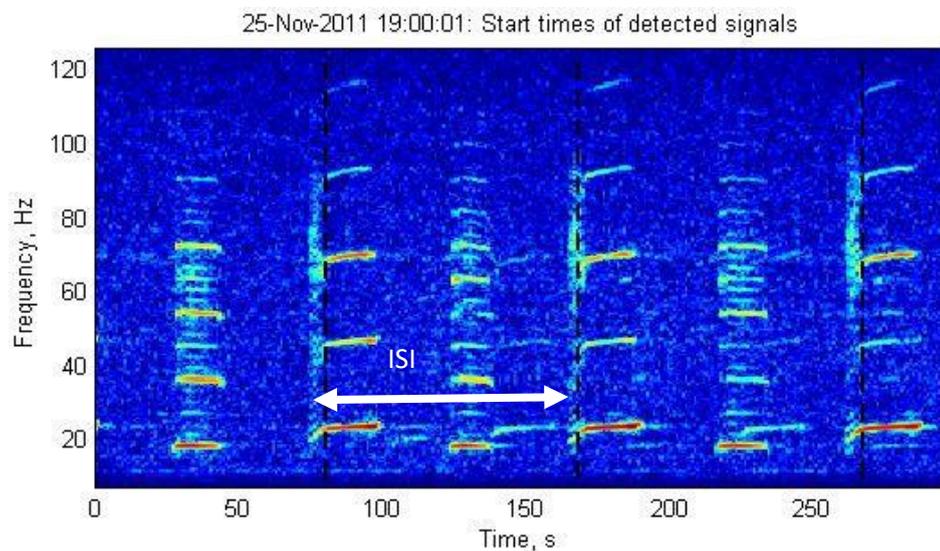
Acoustic recorders were deployed in all years between 2010 and 2017; however, some data sets were unavailable for analysis. Data sets that were used for analysis in this paper are shown in Table 5.1, as indicated by shaded cells. Data were collected and analysed for a total of six years out of eight for the Perth Canyon sample site, and four out of eight years for the Portland sample site.

Table 5.1. Data collection years for Perth Canyon and Portland sample locations. The grey shaded boxes indicate years for which data were included in this analysis.

	2010	2011	2012	2013	2014	2015	2016	2017
CANYON								
PORTLAND								

Data Analysis

Data were loaded into the MATLAB environment and reviewed using the CHORUS GUI software tool for the visualisation and analysis of sea noise data (Gavrilov and Parsons 2014), as well as a signal processing GUI specifically designed for EIOPB whale signals. Song structure was classified using the EIOPB song catalogue (Appendix 1) in accordance with classification established in Jolliffe *et al.* (2019), where the three unit phrase that is repeated to form the EIOPB whale song was found to have two unit and one unit phrase variants. The appearance of further variation in the form of unit breaks, where signal production stopped midway through a song unit, required song types to be further classified for comparative analysis (Figure 5.2). Song parameters, including unit length and inter-unit spacing, were manually measured from spectrograms produced using a 6000 sample Fast Fourier Transform (FFT) as shown on Figure 5.2, by clicking on the spectrograms at desired features. The GUI would then output the frequency and time at those points of the spectrogram. These were appended to a data file and sequential measurements used to calculate ISI and unit lengths. The manual derivation of song features is termed manual analysis (MA) for this chapter.



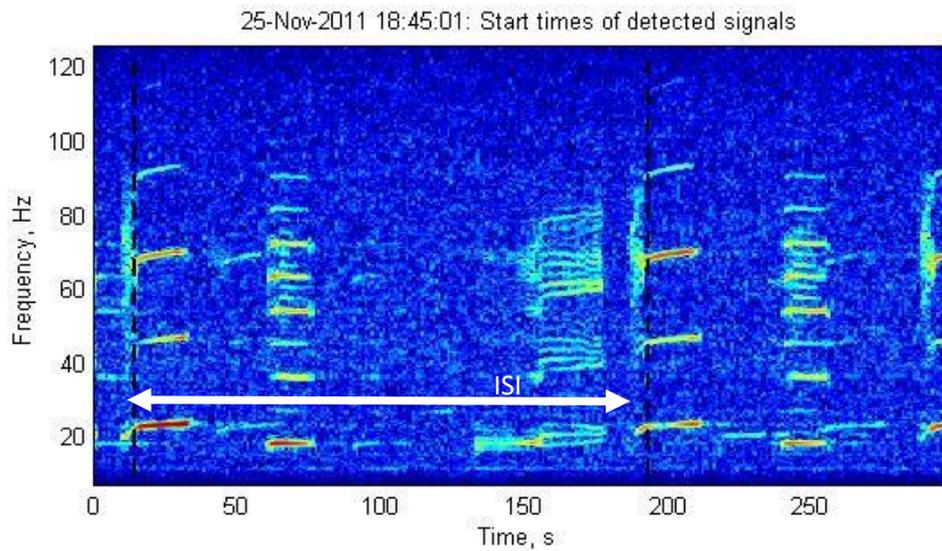


Figure 5.1. Song repetition interval (ISI) as measured for a P2 song (top) and a P3 song (bottom). Spectrograms taken from Perth Canyon 2011 data set and produced using a 6000 point FFT with a Hamming window and 50% overlap.

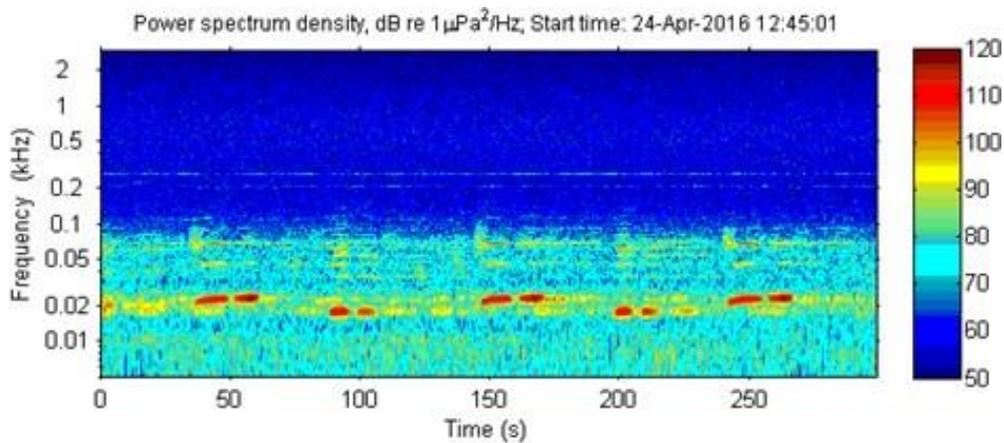


Figure 5.2 Spectrogram showing unit breaks in the unit II and unit III of the P2 EIO phrase type. Spectrogram produced using 6000 point FFT with a Hamming window. Spectrogram is from the Perth Canyon 2016 data set.

A coding system was derived to describe the presence of broken units within the phrase structure of singing animals (Table 5.2). This coding system utilised the numbers one through six to refer to whether a phrase had any unit breaks and which units were broken.

Table 5.2. Coding system to differentiate between phrase structures with broken units. The shaded grey area indicates the unit of the song structure that is split, while the split code refers to the code given to the song for comparative analysis.

Split Code	Unit I	Unit II	Unit III	Description
0				No unit variations
1				Unit break in 1 <sup>st</sup> unit
2				Unit break in 2 <sup>nd</sup> unit
3				Unit break in 3 <sup>rd</sup> unit
4				Unit break in 1 <sup>st</sup> and 2 <sup>nd</sup> unit
5				Unit break in 2 <sup>nd</sup> and 3 <sup>rd</sup> unit
6				Unit breaks in all units

Song events (the repetition of the same phrase structure at a consistent ISI and received level both within a sample and between temporally adjacent samples) were assumed to represent individual vocal animals. Differences in the occurrence of vocalising animals between sample sites and years were explored, with song repetition interval (ISI) used as a metric for song length (see Jolliffe *et al.* 2019). ISI was measured using two methods, MA as described above, and using feature space analysis which is described in detail in Chapter 3, as well as supplementary material for Jolliffe *et al.* 2019 (included in this thesis as 4.7 Supplementary Material S1). The feature space analysis is termed FS for this chapter. Where not specified below, the reporting and discussion of results refers to the outputs of the manual analysis.

A high-density scatterplot was produced to display the long-term changes in ISI for each sample location. This was achieved by binning bivariate data, with location set as either Perth Canyon or Portland, into points to represent a density at each data point. Box and whisker plots were used to explore the variation in ISI between years at each sample site. The occurrence of unit breaks across sample sites was plotted as a histogram for each

location. The annual emergence of broken song units was displayed with a stacked box plot to visualise the difference between sample years and locations.

### *Quantitative Analysis*

Quantitative analysis was carried out in the R statistical environment (R Development Core Team 2010). The relationship between ISI and predictor variables including whether or not a unit was broken, location, average water depth and ambient sound levels were explored using a generalised linear model (GLM) with Quasi-Poisson distribution to account for over-dispersion of data. Repeated F-tests were used to determine the best model selection, which required split code and sample location being removed as explanatory variables in the model. The resultant model utilised sample year and song structure as explanatory variables for ISI. The GLM was validated using a chi squared analysis, and residuals were plotted to ensure equal distribution around the mean.

A binary GLM was used to model the differences in the occurrence of broken units between sample locations and years. Chi squared tests were then used to compare the relevance of explanatory variables within the model, with the resultant model including the variables sample location, year and song structure. Model residuals were plotted to ensure the Gaussian distribution and correct specification of variance structure in conformity with model assumptions.

### *Environmental conditions*

Ambient sound measurements were made in MATLAB using the CHORUS software which accounts for system calibrations (see McCauley et al. 2017 for calibration methods). The median power spectral density (PSD) in frequency bands of 1/12 octave were calculated monthly and used to compare the background noise conditions between sample locations. Background noise was compared between the Perth Canyon and Portland sample sites for the three peak months of pygmy blue whale presence, March, April and May.

The bathymetry of sample sites was retrieved in the qGIS environment for a 20 km radius around the acoustic observatory location. This radius was selected based on the output of tracking analysis (detailed in Chapter 6) which found high quality signals and accurate localisations of animals were concentrated within a 20 km radius from the centre of receivers' array. In addition, receiver deployments at the Portland sample site were

approximately 20 km from the coastline meaning depth analysis outside this range would include coastline, skewing depth measurements. Bathymetry data were taken from the GEBCO\_2014 Grid (version 20130318 available from <http://www.gebco.net>). Receiver locations were overlaid on the base map and the GEBCO\_2014 raster layer was trimmed to a 20 km radius around each IMOS observatory to define a depth sampling area. Sample areas were then randomly sampled at 10,000 points. The point sampling tool was used to calculate basic statistics for the sample areas including mean, range, maximum, minimum and standard deviation. An individual T-test was conducted on 10,000 point samples at each sample location to test for differences in depth within a 20 km radius of Portland and Perth Canyon IMOS observatories.

## 5.4 Results

The MA gave a total of 3,439 song events recorded at the Perth Canyon sample site across six years of data compared to 934 song events across four years from the Portland sample site (Table 5.3). All phrase variations and song structures were observed at each sample site. The greatest difference in the production of song variants was a much higher proportion of traditional *P3* phrase songs in the Portland region (61%) as opposed to the Perth Canyon (36%). Conversely the proportion of *P2* phrase songs was nearly double in the Perth Canyon (46%) compared to the Portland sample site (24%). The output of a two-way ANOVA determined the number of *P3* as opposed to *P2* songs was significantly different between sample locations ( $p < 0.01$ ). The distribution of phrase variations in identified song events was relatively consistent between years at each sample location. The proportion of song types presented in this chapter differ slightly from that presented in Chapter 4 as a result of the inclusion of the 2017 data set in MA and the inclusion of the *P3S* phrase songs as separate from *P3* phrase songs. Where not specified below, the reporting and discussion of results refers to the outputs of the MA.

Table 5.3. Number of song events detected at the Perth Canyon and Portland sample sites across all sample years and breakdown of the proportion of identified song structures from MA.

	<b>CANYON</b>	<b>%</b>	<b>PORTLAND</b>	<b>%</b>
<b>TOTAL</b>	3439	100	934	100

<b>P3</b>	1269	36	566	61
<b>P3S</b>	5	<1	1	<1
<b>P2</b>	1622	46	225	24
<b>P1</b>	145	4	10	1
<b>P3A</b>	147	4	16	2
<b>P2A</b>	47	1	3	<1
<b>P3B</b>	3	<1	1	<1
<b>UNIDENTIFIED</b>	201	6	112	11

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The FS analysis yielded similar results to those of the MA indicating higher proportions of *P3* songs at the Portland sample site and less *P1* songs compared to the Perth Canyon (Figure 5.3). The proportion of *P2* songs appears to be about the same for Portland and the Perth Canyon in the output of the FS (Figure 5.3). The ISI of prominent song structures *P3*, *P2* and *P1* showed a slight increasing trend across sample years at the Perth Canyon location (Figure 5.3c). In comparison, the ISI of *P3* and *P2* songs remained relatively invariable at the Portland location with a slight decrease observed in the ISI of *P1* songs (Figure 5.3c).

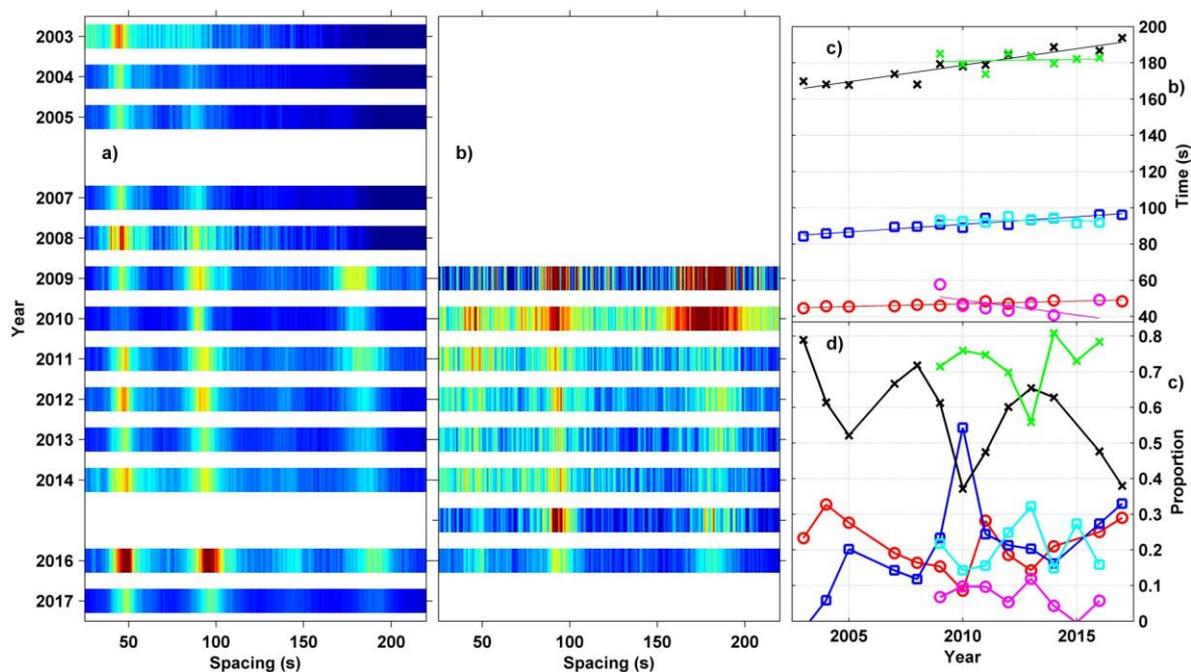


Figure 5.3. Results for whale song feature space analysis: a) feature space of time between unit-II calls for Perth Canyon calculated across the period of northern migration; b) feature space for Portland; c) measured ISI for songs P1 (circles), P2 (squares), P3 (crosses) at Perth Canyon (red, blue and black for P1, P2 and P3 respectively) and Portland (magenta, cyan and green for P1, P2 and P3 respectively); and d) estimated proportions of each song type assuming only P1, P2 and P3 song types (symbols and colours as for c).

When comparing the feature space analysis output with that of the manual ISI analysis, there was a high level of agreement in the proportion of P2 (MA 24%, FS – from fig 5.3c - 21%) and P3 song types (MA 61%, FS 72%) within the Portland data sets. The level of agreement between analysis techniques was not so high for P3 song events in the Perth Canyon (MA 36%, FS 56%). The greatest disparity in the outputs of each technique was for P2 song events in the Perth Canyon (MA 46%, FS 24%). Interestingly the level of disagreement for P1 song events in the Perth Canyon (MA 4%, FS 21%) was also high. It is important to note that the FS analysis does not take into consideration hybrid song patterns which combine multiple phrase structures and so which may confound ISI results. While the MA analysis can only be carried out in low density singing periods due to difficulty in following individual whales in time.

Based on MA results, the variation of song units in the form of breaks first appeared in Portland in 2011, where the second unit of a P3 song appeared to be broken into two parts.

At Portland, this unit variation was detected six times between the 13<sup>th</sup> and 16<sup>th</sup> of March 2011, and then was only observed on another three occasions in 2015. The unit variation was observed on all noise recorders of a tracking grid within one sample year, confirming that it was not simply an effect of destructive interference due to multipath sound propagation to different receivers in the ocean sound channel but actual interruption in signal transmission. Split song units were not seen again until 2016 in the Perth Canyon when nearly 25% of recorded songs had a unit break in the type II song unit (**Error! Reference source not found.**). The number of song events with broken units was considerably higher in the Perth Canyon than Portland (Table 5.4).

Table 5.4. Occurrence of split song unit variations at the Perth Canyon and Portland sample sites across all sample years.

Split Code	Canyon	%	Portland	%
1	202	5.9	2	0.2
2	502	15	9	0.9
3	0	0.0	0	0.0
4	16	0.5	0	0.0
5	57	1.7	0	0.0
6	17	0.5	0	0.0

The 2017 Perth Canyon data set had the highest number and variation of song events with broken units. Unit breaks were observed in all three song units, though not necessarily all units within a phrase were broken. Some phrases contained only one broken unit, some contained two broken units, and in some phrases all song units were broken. Unit breaks could occur in any of the units of a phrase, though were most commonly observed in the type II unit. Roughly 50% of all song events in 2017 in the Perth Canyon had one or more song unit that was broken in two (Table 5.4).

Differences in the occurrence of song unit variations between locations and sample years were modelled using a quasi-Poisson GLM. The final GLM equation looked for variability in ISI with respect to sample year, call structure and location. The occurrence of unit breaks was significantly linked to sample year ( $F$ -test,  $p \ll 0.001$ , degrees of freedom = 2379) which is reflected in the increasing prevalence of broken song units in song events observed in the 2016 and 2017 data sets. Sample location was also found to be linked with the occurrence of unit breaks, with these unit variations more likely to occur in song events recorded in the Perth Canyon ( $p \ll 0.001$ ). Though it is important to note that data were not available for the Portland site in later sample years, it is impossible to say whether similar changes were present at the Portland site. Phrase structure was also included in the GLM model, as it accounted for a significant amount of variation within the data. Unit breaks were found to occur significantly more frequently in  $P3$  ( $p \ll 0.001$ ) than  $P2$  ( $p < 0.005$ ) song variants.

When using ISI values for all song types from the MA, the longest ISI was observed in the Perth Canyon, though it was observed that ISI of lengths greater than 200 s in the Perth Canyon appeared to be outliers, with most song events (primarily  $P2$  and  $P3$  structures) having an ISI of between 100 and 200 s (Figure 5.4). ISI lengths were more evenly distributed in Portland with song events generally exhibiting an ISI between 100 and 250 s (Figure 5.4).

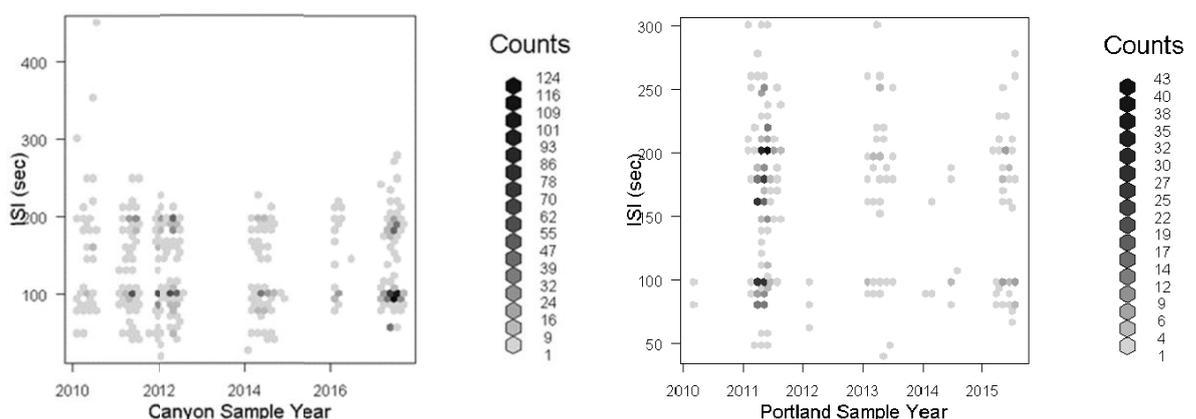


Figure 5.4. Density scatter plot displaying ISI measured using MA for each sample year at Perth Canyon and Portland sample sites.

Comparison of the mean and range of ISI between sample sites across all years in the MA when using all song types, showed a higher level of interannual variability in the Portland data sets (Figure 5.5). Only a small number of song events were sampled at the Portland site in 2014, likely resulting in the observed small ranges and means of around 100 s, while data from 2011, 2013 and 2015 were more widely distributed across the range of ISI (Figure 5.5). The median song length for Portland song events in 2011, 2013 and 2015 was around 180 s, consistent with a P3 song phrase (Figure 5.5). Data from the Perth Canyon was less variable between years with the appearance of a slight decreasing trend in mean ISI (Figure 5.5).

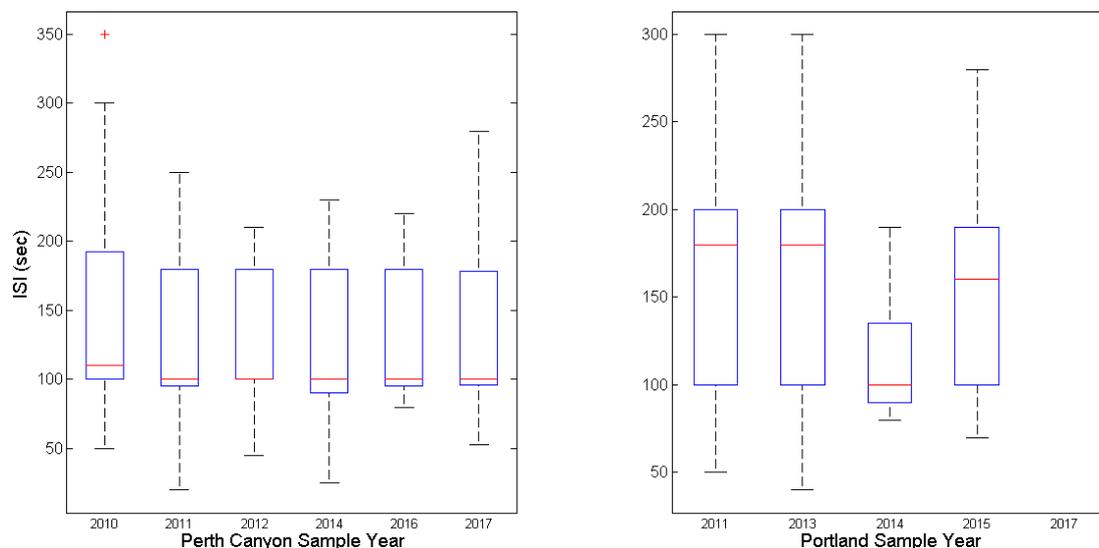


Figure 5.5. Box and whisker plots displaying the median (red line), range and interquartile ranges of lumped ISI values (all song types) for each sample year at Perth Canyon (left) and Portland (right) sample sites

The output of a GLM analysing the effect of sample location, sample year and song structure on ISI found there to be no significant relationship between the location and ISI. Model fit was assessed through the residual deviance of Pearson residuals, to determine the level of variability in the data described by the model. Song structure was the major

driver of changes in ISI, and as such any analysis on differences in ISI is confounded by differences in the prevalence of longer or shorter song structures. Differences in the ISI between sample years were not found to be statistically significant ( $p = 0.116$ ) and there was no significant directional annual trend in ISI at either location when using MA ISI data lumped for all song types.

Table 5.5. Noise levels within the 20 - 21 Hz frequency band from median PSD curves for Perth Canyon and Portland locations across peak months of EIOBP whale presence.

Month	Perth Canyon	Portland
March	89 $\mu P2/Hz$	81 $\mu P2/Hz$
April	96 $\mu P2/Hz$	80 $\mu P2/Hz$
May	88 $\mu P2/Hz$	79 $\mu P2/Hz$

Median PSD curves were used to represent noise levels that are not exceeded 50% of the time. Peaks in the PSD curves represent consistently intense sources of sounds in the environment. Measurements of background noise conditions indicated differences in the intensity of environmental noise at each sample site. The Portland and Perth Canyon PSD curves of sea noise have a similar shape with peaks in the same frequency bands (Figure 5.6). This indicates similar background noise inputs at each location. At frequencies below 100 Hz the PSD level was dominated by peaks in the frequency bands that coincide with pygmy blue whale vocalisations (Figure 5.6) indicating that input from the whales themselves is one of the most persistent sources of environmental noise at each sample location during the peak months of whales' presence. The Portland PSD curve was consistently lower than the Perth Canyon PSD curve in the 10 to 100 Hz frequency range (Figure 5.6). The PSD curve for Portland exceeded Perth Canyon only in May 2016 for noise levels in the frequency range greater than 100 Hz (Figure 5.6). The greatest disparity in the PSD curves of the Portland and Perth Canyon sample sites occurred in April and May (Table 5.5) when the PSD levels of noise in the frequency bands corresponding to the pygmy blue whale sounds was notably, by about 10 dB, higher at the Perth Canyon site (Figure 5.6). Sound levels in these frequency bands were similar at the Portland site from March through to May (Figure 5.6). Noise levels at the Perth Canyon site were consistently high in the frequency bands corresponding to pygmy blue whale vocalisations but peaked in April and

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May (Figure 5.6). It is important to note that the PSD curves in Figure 5.8 show median noise levels in each frequency band and thus do not necessarily reflect high intensity sounds observed in a limited time frame. It was found that the depth within 20 km of receiver array at the Perth Canyon sample site was on average deeper ( $mean = 589.28 m \pm 341.20 m$ ) than the Portland sample site ( $mean = 308.88 m \pm 255.48 m$ ). Based on random samples, the difference between depth at each sample site was found to be statistically significant ( $t = -48.641, p << 0.001$ ).

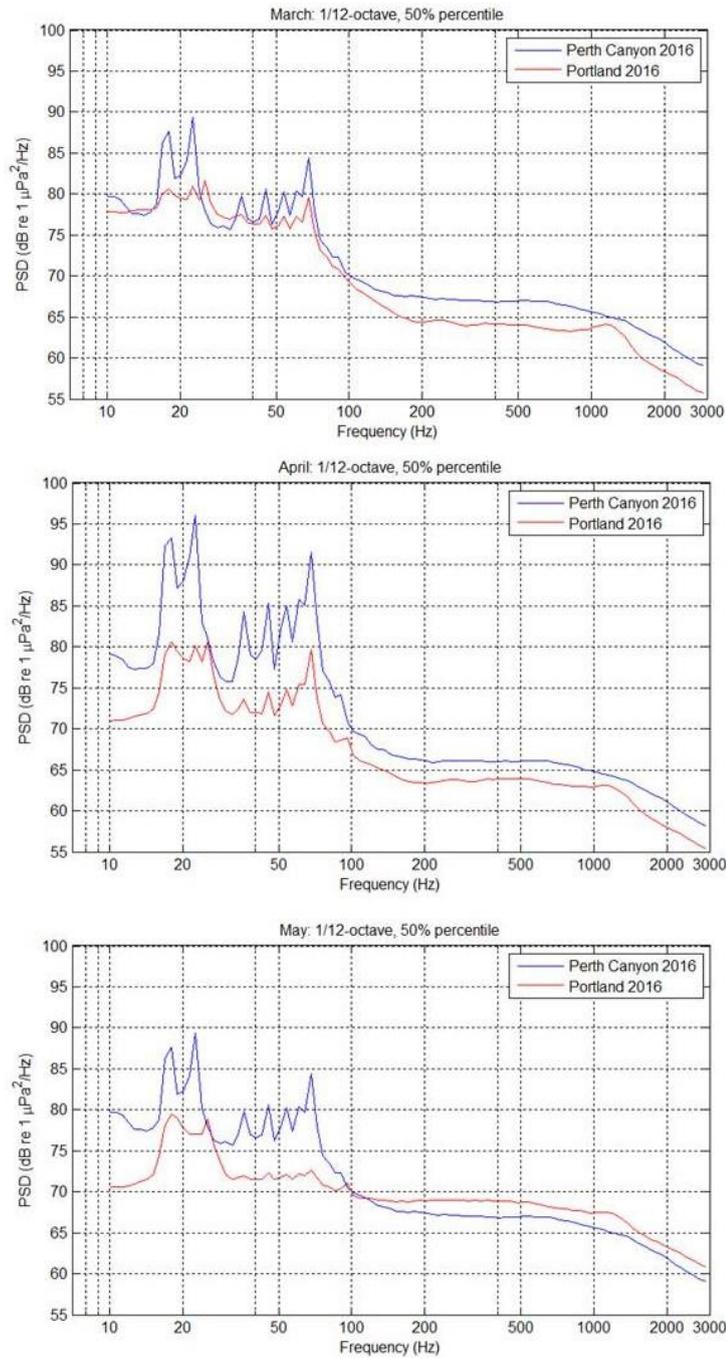


Figure 5.6 Background noise analysis using 50% percentile PSD curves to display the level of noise at each location in March (top), April (middle), and May (bottom) 2016 where systems are calibrated pre and post deployment to account for any differences in gain between recorders

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## 5.5 Discussion

The EIOPB whales utilise the Perth Canyon in Western Australia and the Bonney upwelling region in Victoria as biologically important areas for foraging (McCauley and Jenner 2010a; Gill et al. 2015). The Bonney upwelling is an annual phenomenon that lasts from November through to May, bringing nutrient rich waters from the deep ocean to the photic zone in the upper ocean layers (Cai and Lennon 1993b). In the months following this upwelling event, primary productivity increases resulting in a peak in the availability of secondary productivity in the form of zooplankton several months later (Nieblas et al. 2009). Peaks in EIOPB whale vocal activity occurred from January through to April supporting the findings of other studies that indicate pygmy blue whales remain in the Bonney upwelling region for a number of months after the upwelling event, likely utilising the eastern and central regions from December through to April (Gill et al. 2015; Gill et al. 2011; McCauley et al. 2018). The high level of vocal activity of animals over this period indicates that, whilst resource availability aggregates pygmy blue whales in the area, whales may utilise the opportunity to sing and so potentially find a mate or engage in social behaviour (Gill et al. 2011). Whilst the link between vocalisations and behaviour is still unclear, this is a potential explanation for the peak in vocal activity.

Vocal activity in the Perth Canyon area peaked from November to June in line with what has been found in previous studies (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Gavrilov et al. 2011a; Gavrilov et al. 2012; Branch, Stafford, et al. 2007). Variability in the prevalence of different song structures and ISI was observed between years in the Perth Canyon which may be due to external factors including depth, ambient sound, and density of calling whales resulting in increased background noise levels and a reduced ability to follow an individual whale using manual analysis (McCauley et al. 2018). Note that the probability of detecting the type II unit in the surrounding sea noise is not overly reduced; it is identifying and following a singer through sequential samples that is. The level of variability in phrase and song structure was linked to sample size with higher structural diversity observed in years with a larger number of song events. It is unclear whether this is a result of density dependent vocal behaviours, such as audience effects (Hedwig et al.

2015), or if increased diversity is an artefact of higher population numbers. The number of vocalising whales at each sample location is likely linked to resource availability (Munger et al. 2009), with numbers expected to be more stable in the Perth Canyon area due to its location along a migratory thoroughfare, whereas the Bonney Upwelling is believed to be solely a feeding ground. Interannual variability in the number of detected song events was observed at each location, with 2011 representing a peak in song events for the Portland site, and 2017 a peak for the Perth Canyon area. This may be due to more favourable background noise conditions in those years resulting in increased detectability of vocalising whales.

The most notable disparity between the vocal behaviour of pygmy blue whales at each location was a difference in the prevalence of phrase types. The Perth Canyon site had a higher prevalence of shorter *P2* phrase structures while the Portland site had a higher proportion of *P3* phrase structures. While there was a high level of agreement for the MA and FS ISI measurement techniques used for the Portland location, there were differences in the proportion of song types yielded by the MA and FS for the Perth Canyon location. These disparities are thought to be driven by either the larger presence of hybrid songs in the Perth Canyon which convolute the automatic technique of ISI analysis and are only detectable with manual spectrogram perusal, or by the MA not being able to follow individuals in high density signing periods. This would explain the higher than expected prevalence of *P1* song types and lower than expected prevalence of *P2* song types indicated by the FS analysis. This in part may also be due to the similarities in ISI for *P1* and *P2* song types, with some *P1* phrases lasting around 80 s, similar to some *P2* phrases at around 90s.

While the reason behind this variability in song structure prevalence are unclear, it has been suggested that the song length may be linked to background noise levels with shorter songs being produced in higher background noise level conditions (Fristrup, Hatch, and Clark 2003; Noad, Dunlop, and Mack 2017; Job, Kohler, and Gill 2016). This is supported by background noise analysis with the Perth Canyon having consistently higher 50% percentile PSD levels than Portland in the frequency range of whale vocalisation, indicating that background noise levels were on average higher in the Perth Canyon than those at the Portland site. It is important to note that the highest levels of noise are in the frequency bands of EIOPB whale song production and are caused by the overlap of concurrently singing animals creating a chorus. Overall, higher numbers of vocalising animals in the Perth Canyon appear to be linked with a prevalence of shorter phrase types, suggesting density dependent factors may play a role. However, as the second unit of the EIOPB whale song

type is the most detectable due to a higher source level (Gavrilov et al. 2011b), it can be suggested that production of shorter song structures increases the likelihood an animal will be heard based on the number of type II units produced in a singing bout. This would potentially make it beneficial to sing *P2* phrase songs in areas with higher background noise conditions, such as the Perth Canyon. Another possibility is that variability in phrase types and song structures may be linked to finding a mate whereby certain song structures may be more attractive to the opposite sex than others (Kershenbaum et al. 2014; Garland, Rendell, Lilley, et al. 2017).

Several other scenarios to explain variability exist including that song structure may be linked to behavioural state or communicate important information about the environment or behavioural context of the vocalising animal (Dunlop 2017; Lachlan and Nowicki 2015; Cholewiak, Cerchio, et al. 2018). In this instance, it is possible that *P2* phrase types may be more efficient to produce whilst travelling, while *P3* songs may be favoured whilst feeding. Additionally, there is evidence that whales may preferentially change vocal behaviour based on physical environmental properties, including water depth (Lewis and Sirovic 2018).

## 5.6 Conclusion

This study found that differences exist in the song production of EIOPB whales between two sample locations within their migratory range. Specifically, there was a higher prevalence of songs composed of shorter phrase structures in the Perth Canyon, and a higher prevalence of songs composed of longer phrase structures at the Bonney Upwelling site. It is unclear whether these differences are due to learned behaviours of individual animals, differences in depth between nearshore (Portland) and offshore (Perth Canyon) sample sites, or differences in the background noise environment. The prevalence of shorter songs was linked with higher background noise levels and deeper depths in the Perth Canyon, while the prevalence of longer songs was linked with lower background noise levels and a shallower average depth in the Bonney Upwelling region. A detailed study of the inter-annual variability in song length and phrase structure within one sample location to eliminate the potential influence of site-specific conditions is recommended to identify the driving factors behind song length variability. It is evident that despite belonging to the same breeding and migratory population, singing behaviour of EIOPB is

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variable between the Portland and Perth Canyon sample sites confirming the potential for behavioural plasticity of EIOPB whales.

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## Chapter 6 Tracking pygmy blue whales in the Perth Canyon using passive acoustic observatories

### 6.1 Abstract

*Eastern Indian Ocean pygmy blue (EIOPB) whales were localised and tracked through the Perth Canyon area utilising a passive acoustic tracking array. Vocalising animals were tracked across recordings for an average of 109.3 minutes (95% CI  $\pm$  26.96 minutes), suggesting that animals move slowly through the array area. Comparisons of the distribution of animals between sample years revealed non-uniform distribution of animals suggesting that environmental variables may drive pygmy blue whale spatial location. Analysis of the movement patterns of acoustically tracked animals found that animals tracked between January and early March generally exhibited directional movement while animals tracked between March and May exhibited directional and milling movement patterns indicating that feeding and singing may occur in the same areas. Comparisons of visual and acoustic localisations found animals to be located in about the same area around the passive acoustic observatory on days where survey effort overlapped, though acoustic survey methods returned consistently higher numbers of detections. Further, the persistence of vocalising animals in the Perth Canyon later in the season, when pygmy blue whales were also sighted much further north along their migratory route, indicates that migratory behaviour varies between individuals and may not be obligatory for all animals within the population, with potential variability likely between animals of different age and gender.*

### 6.2 Introduction

The ability to track individuals or groups of animals presents useful applications for the study of cetacean behaviour including: 1) for use as a potential monitoring tool to help identify the exposure of animals to anthropogenic noise and the dangers associated with busy shipping lanes (White et al., 2006), 2) for behavioural studies or 3) understanding the migratory movements and patterns of presence of a species (Gavrilov et al. 2012). A number of studies incorporating the acoustic localisation or tracking of marine mammals have been carried out to date; however, the best methods for doing this are still being

examined (Caudal and Glotin 2009; Macaulay et al. 2017; Kusel et al. 2017; Miller et al. 2013; Whoriskey et al. 2017). The most common method for localising a calling animal relies on the inversion of an acoustical model, relating time delays in signals received by different recorders in a passive acoustic array to the source of the signal, which is the position of the vocalising animal (Caudal and Glotin 2009; White et al. 2006; Warner, Dosso, and Hannay 2017; Clark 1995; Frankel et al. 1995). This process is complicated by sound speed variations in the water column and the multipath transmission of sound signals in the ocean sound channel (Brekhovskikh 1982; White et al. 2006). Reflection of the sound signal at the seabed and sea surface, and refraction in the water column can result in the signal waveform and spectrogram looking dissimilar at each receiver, making it difficult to recognise as the same sound. This leads to a poor correlation of the signal when cross correlating waveforms received at different receivers to get time offsets between received signals, resulting in inaccurate localisation (Wiggins et al. 2013; White et al. 2006). The accuracy of sound speed profiles is important for localising sound sources as it affects the accuracy of TDOA measurements utilising the wrong sound speed profile can also result in failure to account for multipath propagations which may confound TDOA calculations (Brekhovskikh 1982). Additionally, the number of acoustic sensors used to localise the sound source influences the accuracy of the localisation. Animals can be localised with as few as three sensors, though accuracy increases if more acoustic receivers are used (Brekhovskikh 1982; Watkins and Schevill 1972; Thode 2004). The greatest error in the localisation of vocalising animals when using bottom mounted acoustic sensors is often in the vertical plane, rather than the horizontal plane, and is largely influenced by the chosen sound propagation model (White et al. 2006). For a triangular array, such as the one used in this study, localisation errors in the horizontal plane decrease as an animal moves closer to the sensor array and, depending on sound transmission, locations can be very accurate (< 100's m) within a certain distance of the sensors (Gavrilov et al. 2012; White et al. 2006). Background noise also plays a role in the accuracy of localisation, with errors of similar magnitude to those that arise as a result of using the wrong sound speed profile (White et al. 2006), highlighting the importance of in situ measurements of the sound speed profile.

Numerous studies have successfully utilised a similar set of methods to track a variety of marine mammals, from dolphins to sperm and blue whales (Gavrilov et al. 2012; Clark 1995; White et al. 2006; McConnell et al. 2013; Nosal 2013; Wiggins et al. 2013; Miller et al. 2013). These studies involved cross correlation of the sound signal arriving at each of the receivers. Accurate TDOA measurement is inherently dependent on the synchrony of the

clocks of the acoustic receivers, which can be achieved by measuring the relative time offsets of clocks in different receivers.

Depending on the accuracy of localisation methods, it is possible for vocal animals' movements to be tracked, allowing for inference of behavioural state using variations of Markov movement models (Houegnigan et al. 2010; McConnell et al. 2013; Wiggins et al. 2013). Whilst it may be possible to track multiple animals simultaneously with one array, complications arise in identifying individual animals which is challenging for species where the entire population produces a similar vocal cue. There are several approaches for tracking individual and multiple animals, but the one most suited for this study is similar to that used by Nosal (2013), which separates animals by tracking slowly varying bearings. Through utilisation of a model-based TDOA framework, the derived locations were combined with a clustering technique based on average swim speed and track duration to determine likely tracks by looking at the maximum change in TDOA (Nosal 2013). In the study, Nosal (2013) use an average swimming speed of 10 km/h to determine that the corresponding maximum change in TDOA would be 0.002 s. Points satisfying this TDOA criteria are chosen as the next point in the track. If no points exist satisfying the criteria then the track is terminated (Nosal 2013). Similar criteria combined with visual observation of signals have been used by Guazzo *et al.* (2017) in the distinction of localisations for individual animals. In populations where vocal animals are generally separated by some distance and have small group sizes, this approach can be useful in guiding tracking analysis (Guazzo et al. 2017). It is likely that advances in future methods of signal analysis and localisation will have decreased errors and been able to separate individual animals with higher certainty without the need for concurrent visual survey. In recent years there has been a diversity of approaches to acoustic tracking including the use of gliders fitted with acoustic recorders as a method to calculate animal density (Kusel et al. 2017).

A previous study by Gavrilov et al. (2012) successfully observed the movement of eastern Indian Ocean pygmy blue (EIOPB) whales (*Balaenoptera musculus brevicauda*) through the Perth Canyon area using a passive acoustic tracking array. The study observed 170 events of whales moving through the canyon area in the vicinity of the tracking array over the course of the deployment period from November 2009 to July 2010 (Gavrilov et al. 2012). The study refined a set of methods to track vocalising whales using a triangular array of passive acoustic recorders with a high level of accuracy within 10 km of the receiver array centre (error ellipses < 0.5 km). The accuracy of localisations increased the closer the whale approached the passive acoustic observatory (Gavrilov et al. 2012). By tracking back

azimuth angles, Gavrilov et al. (2012a) identified two distinct periods of pygmy blue whale presence around the canyon with most whales moving southward from December to January mainly to the west of the observatory, further offshore. From February to July whales were tracked moving mainly northward inshore and offshore from the observatory (Gavrilov et al. 2012).

Understanding the migratory behaviour of baleen whales is of importance to any study of abundance or population health (Attard, Beheregaray, and Moller 2016; Ramp et al. 2015). Further, knowledge of the triggers of migratory behaviour and diversity in migratory behaviour is important for predicting the presence of whales in areas of interest. While visual surveys are incredibly useful for obtaining behavioural and identity information on migrating animals, they are time consuming and costly, and subject to observer bias. Acoustic receivers have much larger detection ranges, are lower in cost and can operate in any conditions allowing for year round monitoring of animal presence. There are a number of studies that compare the performance of acoustic and visual surveys, and in many cases information on behaviour and movement patterns identified in visual surveys can be used to improve the efficacy of acoustic surveys (Barlow and Taylor 2005; Wiggins et al. 2004) It is commonly accepted that baleen whales migrate from high latitude feeding grounds to low latitude calving grounds, though there is increasing research to suggest that in many species breeding is not constrained to a certain time of year or location (Clark and Clapham 2004; Thomisch et al. 2016). This may mean that the migratory behaviour is not obligatory for baleen whales nor directly related to reproduction success. Migratory behaviour may vary between mature and juvenile whales, and non-reproductive females, especially where wintering grounds have poor resource availability (Payne and McVay 1971). Thus, investigating patterns in the presence, timing and movements of baleen whales is imperative to furthering our understanding of the population. This study aims to investigate the short-term movements of singing pygmy blue whales in the vicinity of a passive acoustic tracking observatory, providing comparisons with visual surveys where possible, in order to guide future acoustic studies and contribute to the understanding of EIOPB whale singing behaviour.

## 6.3 Methods

### Data collection

Passive acoustic observatories were deployed in the Perth Canyon area to the west of Rottnest Island to collect long term acoustic data as part of the Australian Integrated Marine Observing System (Figure 6.1). Passive acoustic observatories were deployed for periods of about 12 months at a time, though pygmy blue whale presence was only observed between December and June. The passive acoustic observatory consisted of three to four Curtin University CMST-DSTO sea noise recorders (see McCauley et al. 2017b for instrument and deployment details) deployed on the seafloor in a triangular tracking configuration with the fourth recorder set in the middle of the array. The passive acoustic observatory was deployed with hydrophones on the seabed placed at depths of 430 to 490 m with a sampling regime of 450 s every 900 s in 2009-2010, and 400 s every 900 s in 2010-2011, at a sample rate of 6 kHz with a low pass anti-aliasing filter at 2.8 kHz. A gentle high-pass roll off was applied below 8 Hz to flatten the sea noise spectra and increase the dynamic range of the recordings. Calibration was carried out using injection of white noise in series with the hydrophone to obtain full system frequency response to be corrected for in post-processing. Instrument clocks were set to UTC time before deployment and calibrated post deployment. See McCauley *et al.* (2017b) for full calibration details.

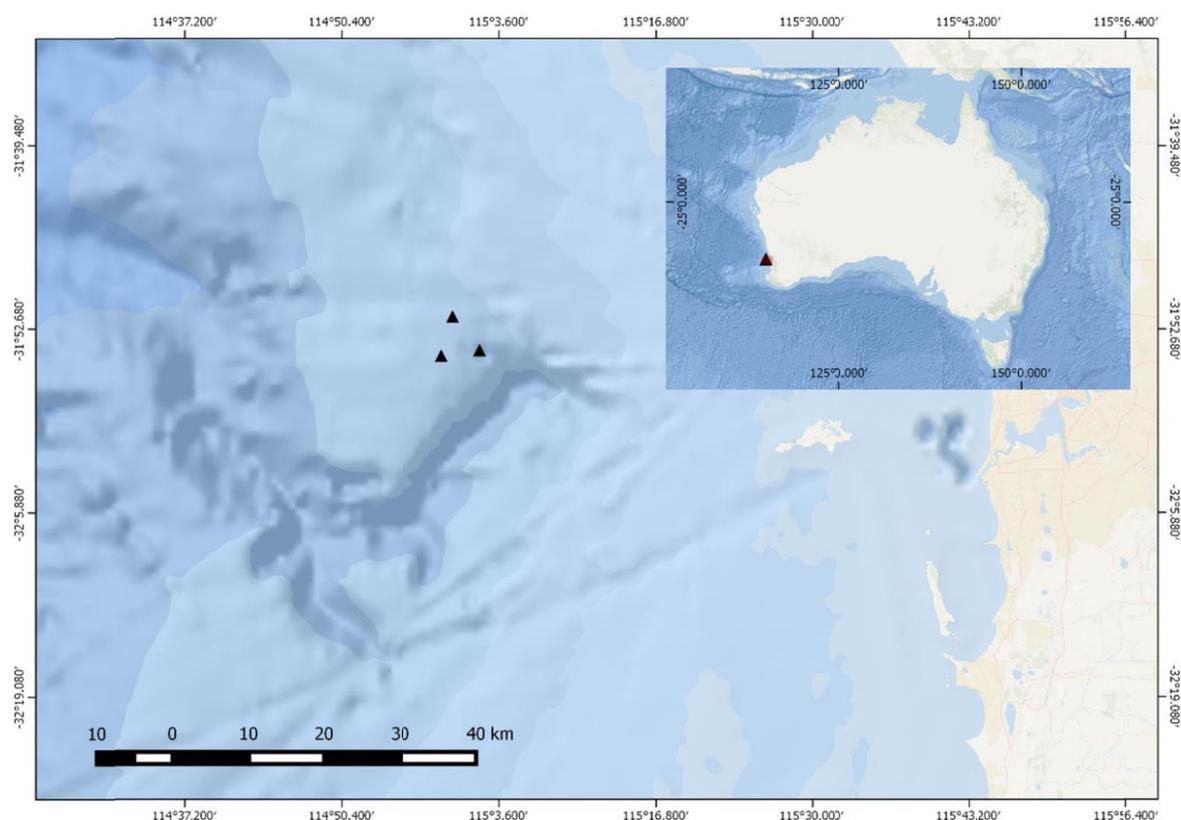


Figure 6.1 Location of Integrated Marine Observing System (IMOS) passive acoustic observatory with relation to Rottnest Island, Western Australia. Inset: Location of the sample site with relation to Australia. Maps produced using ESRI World Ocean Base 2018.

Data sets from three deployments in 2009-2012 were used for tracking of vocal EIOPB whales as they contained simultaneous recordings from three to four recorders in the array for the entirety of the deployment period. Receivers were deployed from November 2009 to August 2010, August 2010 to May 2011, July 2011 to June 2012.

The accuracy of sound source localisation depends largely on the synchronisation of instrument clocks and the accuracy of the receiver positions. This was achieved using a 7.5 kHz pinger attached to one receiver, set to ping on a pre-programmed regime every 20 s for 35 minutes once per day, and recorded by each recorder switched to a 20 kHz sampling rate at the pinger operation time. This allowed us to synchronise the clocks in all recorders relative to the clock of the reference recorder. Detailed information on the methods used for clock synchronisation is outlined above in the methods chapter, and in Gavrilov *et al.* (2012).

Vessel surveys were carried out by the Centre for Whale Research in 2010 and 2011.

#### EIOPB whale signal detection

Pre-processing of acoustic data was carried out in the MATLAB environment to calculate the Power Spectrum Density (PSD) of sea noise for each sample in the CHORUS software package (Gavrilov and Parsons, 2014). PSDs were stacked in time for quick perusal of long time periods of several days. Spectrograms were produced using 6000 point FFT (1 Hz resolution) and Hamming window with no overlap.

Pygmy blue whale vocalisations were detected using an automatic search algorithm as defined in Gavrilov and McCauley (2013). The algorithm searches for the fundamental frequency and third harmonic components (18 to 22 Hz and 60 to 70 Hz respectively) of the type II unit of the three unit EIO song type (see Chapter 4, as defined in McCauley et al. 2000 and McDonald et al. 2006). The energy in the frequency bands of the type II song unit is compared with that in surrounding frequency bands of sea noise to detect the whale sound. The algorithm has missed and false detection rates of less than 5% (Gavrilov and McCauley 2013). Detections were visually verified by spectrograms. Manual perusal of spectrograms allowed for classification of song structure in accordance with phrase and song variations outlined in Jolliffe *et al.* (2019).

#### Tracking Methods

The type II unit of the EIOPB whale song was the target for localisation as it is present in all song variants (Jolliffe et al. 2019). The TDOA of the type II unit at each of the receivers within the array was measured. To discard wrong or erroneous localisations that arise as a result of poor signal-to-noise ratio or multipath propagation, localisations with inconsistent TDOA measurements were omitted from further analysis (see Chapter 3 - Methods). The bearing angle calculated from the array to the source using the TDOA measurements of the signal at each pair of receivers and a plane wave fitting method, was used to track the direction of movement of distant whales. Further details on the framework for localisation can be found in Gavrilov *et al.* (2012).

A set of criteria was used to determine whether successive localisations within individual samples and in successive samples were likely to have been produced by the same vocalising whale. These criteria included some characteristics of the sound spectrogram such as the received sound level, direction of travel – as given by localisation, song

structure, phrase length, calling rate and the SNR of the song units in the spectrogram. The distance and direction to the whale from the previous localisation was also considered with the maximum travel speed of a pygmy blue whale assumed to be around 10 km/h or less. As such, the distance travelled between successive samples (15 minutes) must be less than 2.5 km in a consistent direction for the signal to be attributed to the same animal. Similar criteria were utilised successfully by Guazzo et al. (2017) in the acoustic tracking of grey whales. Each detected signal was assessed against these criteria and either assigned to an existing track if all conditions were satisfied, or designated as the start of a new track if not satisfied (Guazzo et al. 2017). This allowed for manual tracking of multiple whales in any one time period. Whale tracks were numbered chronologically and, where there were lapses in the track between samples, the previous track was terminated. The start and end time of each track, length of vocalising time, song structure and movement patterns were recorded for each track ID. Tracking was only carried out on localisations within a 10 km radius of the central point of the receiver array as localisations outside of this area had too large errors which would make it erroneous to track successive localisations.

#### Data Analysis

Movement behaviour was classified into two categories based on successive localisations in the track. Tracks with successive localisations being very close (< 500 m) to each other and with no directional movement were classified as circular or milling behaviour. Those with consistent directional localisations indicating movement or travel were classified as directional. The number of directional tracks was compared to circular tracks to look for patterns in movement behaviour. Back azimuth bearings of localisations were calculated using a separate method that is described in detail in Gavrilov et al. (2012). The slowly varying back azimuth bearings of localisations were plotted for both sample years to examine seasonal patterns in directional movement, with 0° representing travel in the northern direction, and 180° representing travel in the southern direction. Westerly travel was represented by a bearing of -90°, while easterly travel was represented by a 90° bearing. Whale call localisations within 10 km of the array were removed from bearing angle analysis as bearing estimates were valid only for remote whale calls. A plane wave fitting method was used to measure the bearing angle. The x and y coordinates of localised signals were used to generate a density plot showing the distribution of localised vocalising animals within and around the receiver array area. Statistical and graphical analysis of data was carried out in the MATLAB environment (Mathworks 2000) to better visualise and

compare data from different sample years. Errors presented here represent the 95% confidence interval (CI) for all measurements.

### Visual surveys

Visual surveys in 2010 and 2011 were conducted by the Centre for Whale Research, Western Australia aboard *RV Whale Song* (Jenner, C. and Jenner, M.N., pers. comms). Visual sightings were logged including date, time, GPS coordinates, number of animals and behavioural states. Visual sightings were sorted by date and plotted in qGIS allowing for the sightings for each individual day to be overlaid on a map of the Perth Canyon region. Sighting locations were compared with acoustically derived locations of singing whales on the same day. The number of animals detected visually was compared to the number of whales detected acoustically over the same sample period for the time periods when visual and acoustic surveys overlapped.

## 6.4 Results

A total of 1,461 acoustically localised EIOPB whale signals contributed to 383 localisations or tracks of whales across 2010 and 2011. Many of these consisted of only one whale location, while 121 consisted of four or more successive localisations. The mean number of tracked/localised animals was 3.04 (95% CI  $\pm$  1.89) per day in 2010 and 2.86 (95% CI  $\pm$  1.64) per day in 2011 (Figure 6.2 and Table 6.1). Visual examination of acoustically derived tracks allowed animal movement to be classified into two categories. The number of signals detected by the search algorithm and successfully classified by song variant was compared with the number of localised signals within the same year to establish the efficiency of the acoustic tracking methods, with 81.1% of classified song variants (as opposed to detected signals) attributable to a tracked or localised animal (Table 6.1).

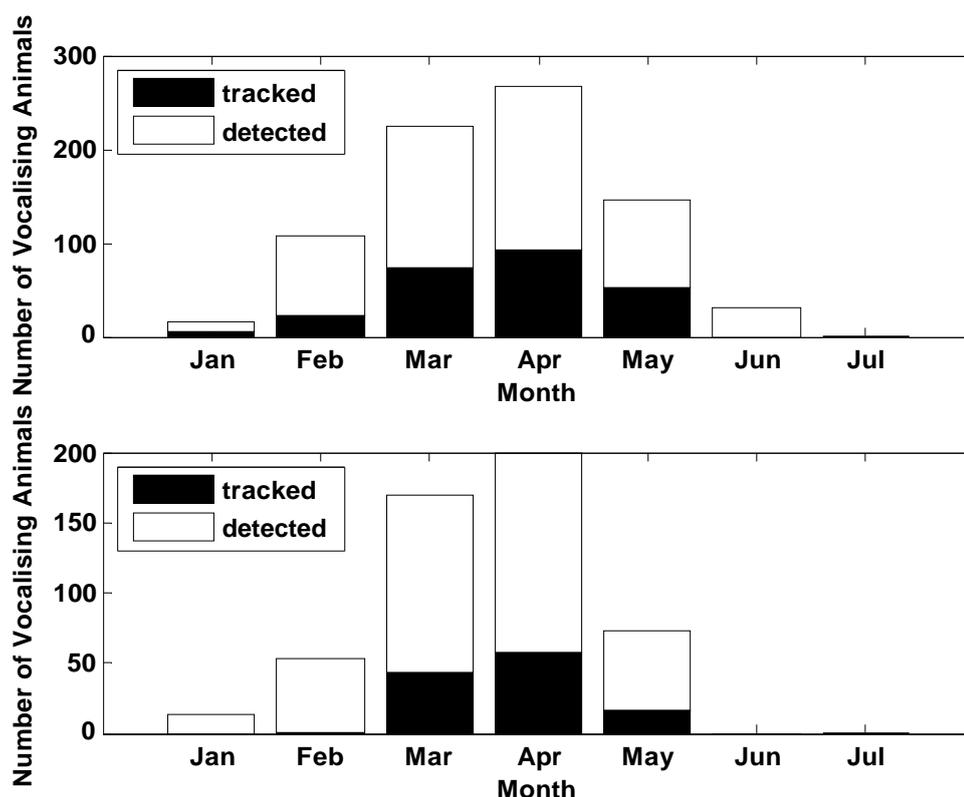


Figure 6.2. Graphical representation of the proportion of tracked to detected vocalising animals for 2010 (top) and 2011 (bottom).

The EIOPB whale song has been found to have three major variations in phrase structure, with additional variations in song composition discussed in Jolliffe *et al.* (2019). The traditional P3 phrase song was the most frequently tracked with 49.6% of tracked animals producing this song variant. This was closely followed by the P2 song variant with 42.3% of tracked animals producing this song (Table 6.1). The P1 songs and hybrid song patterns were less frequently tracked but are also less common song variants in the population. There were also four occasions where a tracked animal appeared to change the vocalisation pattern from a P3A pattern to a P3 song variant. It is important to note it was assumed to be the same animal based on consistent SPL, unit II appearance in spectrogram and location of the animal in tracking grid when there appeared to be no other vocalising animals in the area. However, this was only an assumption without any other proof. See Jolliffe *et al.* (2019), Table 4.2 in this thesis, or figures in Appendix 1 for song definitions.

Table 6.1 Number of tracked vocalisations of each song structure as a proportion of the whole data set.

<b>Song Variant / Pattern</b>	<b>Number of Tracks</b>	<b>% Tracking Sample</b>	<b>% Detections</b>
<b>P3</b>	190	49.6	42.1
<b>P2</b>	162	42.3	30.8
<b>P1</b>	10	2.6	3.2
<b>P3A</b>	17	4.4	4.3
<b>P2A</b>	2	0.5	0.5
<b>P3B</b>	2	0.5	0.3
<b>Total</b>	383	100	81.1
<b>Alternating P3A to P3</b>	4	0.1	n/a

Previous research demonstrates that the pygmy blue whales aggregate in the Perth Canyon between late November and late June and then continue their northward migration (Gavrilov et al. 2012; McCauley, Bannister, Burton, Jenner, and Rennie 2004; McCauley and Jenner 2010b; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). Localisations tapered off slowly from mid-May to June, with no detections from late July to late October and small numbers of detections through November and December. Southward migration of pygmy blue whales occurs from late October through to February; however, there were very few localisations for this period. This may be a result of variability between the northern and southern migratory routes with most of the whales likely be travelling much further from the acoustic array during their southern migration and hence too far away to be localised (Gavrilov et al. 2012)

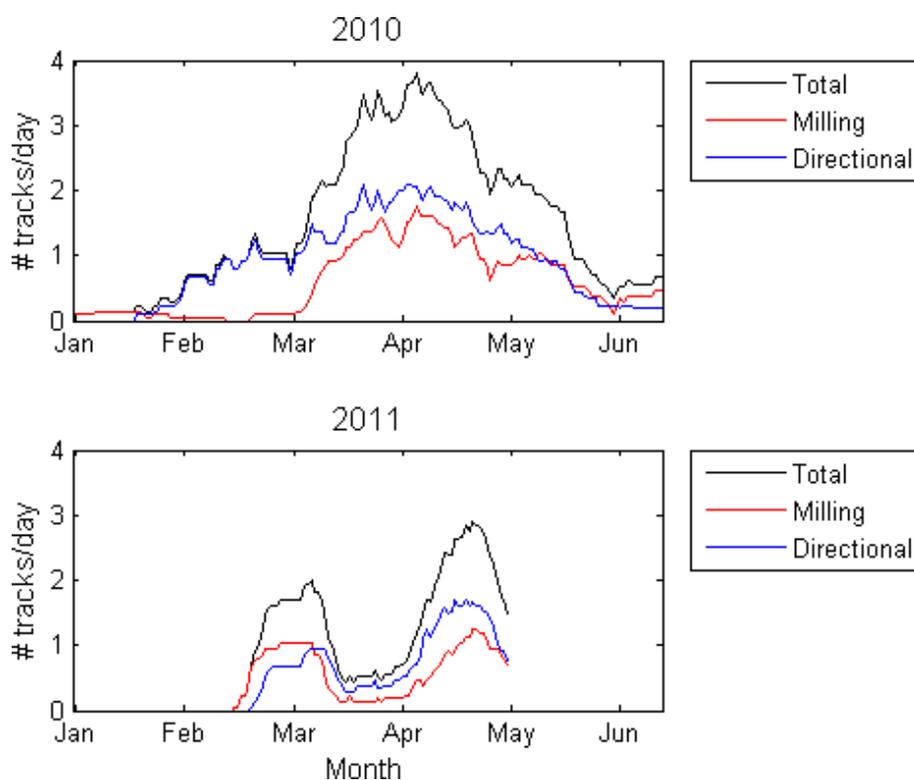


Figure 6.3. Average daily number of vocal animals successfully tracked throughout the sample period with a 10 day moving average for 2010 sample year (top) and 2011 sample year (bottom). The total line represents all tracked animals, while the milling and directional lines indicate the movement patterns of vocalising animals based on track appearance. The x ticks represent the first day of the labelled month.

The highest number of animals were tracked in March and April which is consistent with the peak in pygmy blue whale presence within the Perth Canyon area (Figure 6.3). Ratios of detected vocalisations to vocalisations that were localised and attributed to a track (Figure 6.2) show that the number of animals localised and tracked is a relatively consistent proportion of the total number of detected vocal animals for those producing *P2* and *P3* songs. February had the lowest proportion of localised to detected animals in 2010, with no detections and localisations in 2011. There was no consistent between-year trend in the movement patterns of tracked animals. In 2010, directional tracks dominated from January through to March, while from mid-March to June, milling behaviour became nearly as common (Figure 6.3). In 2011, milling behaviour was most common from mid-February to early March, at which point directional tracks became more common. Directional tracks remained more common through to the end of May (Figure 6.3). Overall in 2011 there was a much earlier peak in milling behaviour which did not occur in 2010 until the start of

March. The movement patterns in 2011 follow a similar pattern to the overall number of tracked animals with a dip in both directional and milling tracks mid-season from mid-March to April. Conversely, the 2010 data shows a peak in the number of tracked animals from mid-March to April with a notable early dominance of directional tracks (Figure 6.3).

Monthly trends in the whale distribution are indicated by the localisations of calling whales, with animals being primarily spread to the northwest of the receiver array in February, while in March they were more evenly dispersed around the receiver array (Figure 6.4). This reflects long-term trends identified by Gavrilov *et al.* (2012a) with a distinction in the bearings of localisations between migratory legs (Figure 6.6). The directionality and distribution of localisations compared between the southern and northern migratory legs also indicates that movement shows more directionality over the southern migratory pulse whereas vocalising animals tended to mill in smaller areas during the northern migratory pulse.

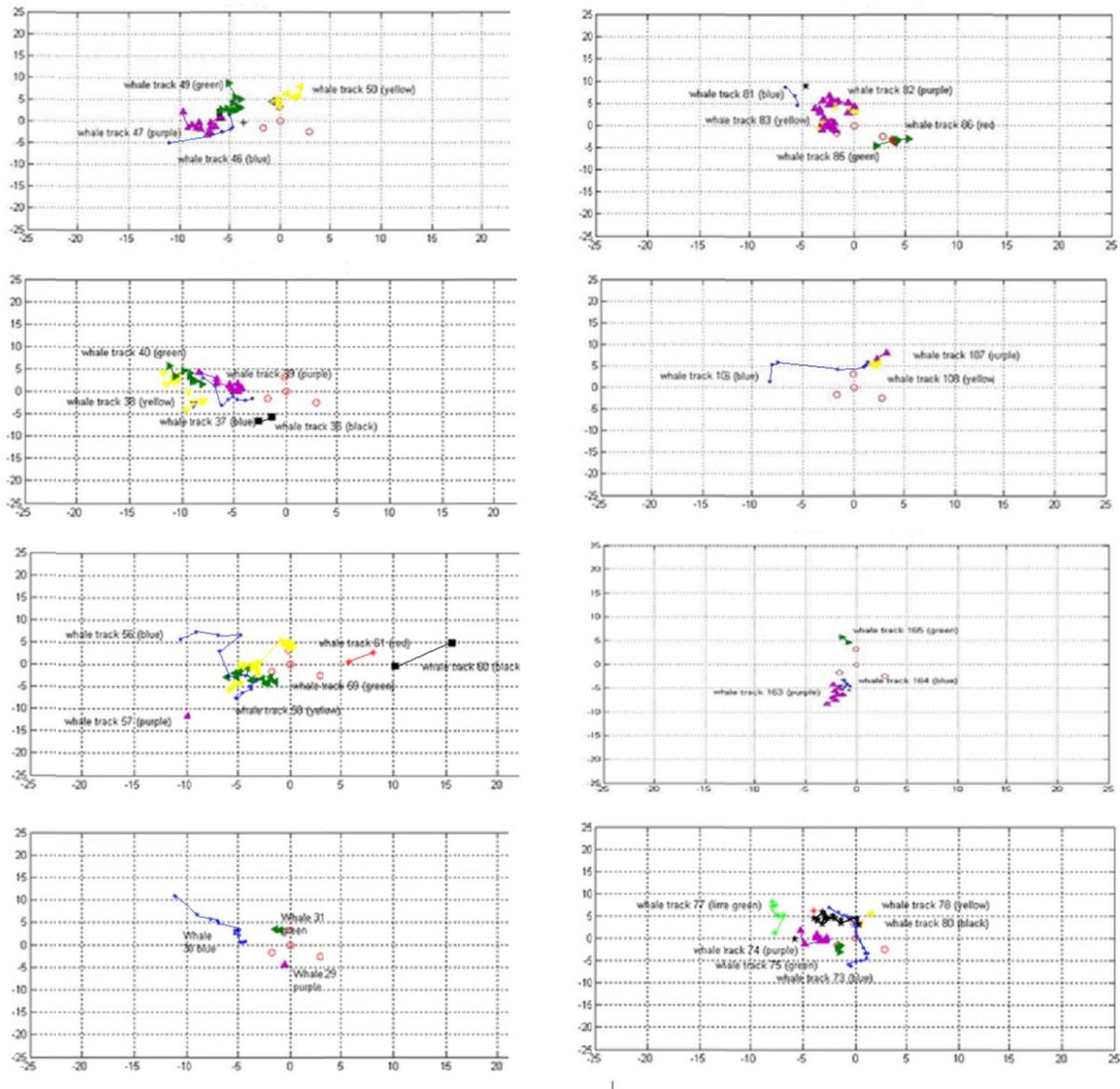


Figure 6.4 Tracks of vocalising animals within the vicinity of the acoustic observatory where each grid square represents 25 km<sup>2</sup> and the x and y axis represent distance from the central point of the receiver array. Red circles show receivers' position. Left column from top: 14<sup>th</sup> February 2010, 11<sup>th</sup> February 2010, 20<sup>th</sup> February 2010 and 4<sup>th</sup> February 2010. Right column: 3<sup>rd</sup> March 2010, 11<sup>th</sup> March 2010, 22<sup>nd</sup> March 2010 and 2<sup>nd</sup> March 2010.

Manual analysis of the location of vocalising whales with simultaneous visual analysis of signal spectrograms and the tracking criteria outlined above, allowed animals to be followed with a high degree of certainty as to the continuity of the track and the likelihood that the vocalisations were produced by one animal. Observations gathered during the tracking analysis indicated several occasions where multiple whales were localised simultaneously calling from within the observation area with different song structures.

These whale localisations often came from different areas around the passive acoustic observatory, though there were occasions where a vocalising animal followed a similar path to another concurrently vocalising animal. It is however possible that this is an artefact of only being able to localise animals in close proximity to the array. It was also observed that animals appeared to utilise similar areas around the array at similar times (Figure 6.4). On many occasions, animals were observed milling in a very limited area around the receiver array. There also appeared to be patterns in the tracks on any given days with animals often congregating in one area or following similar paths through the receiver area at different times (Figure 6.4).

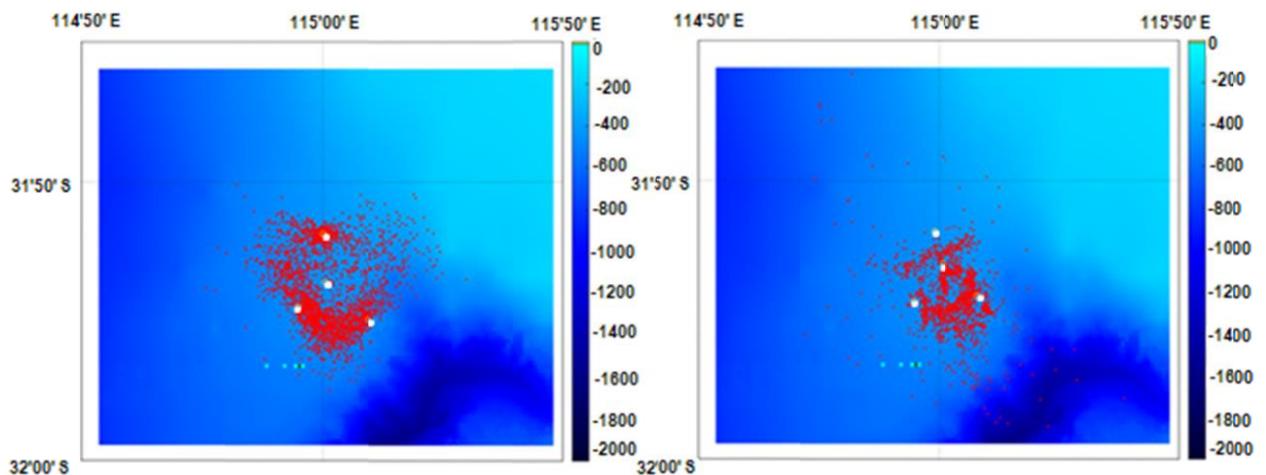
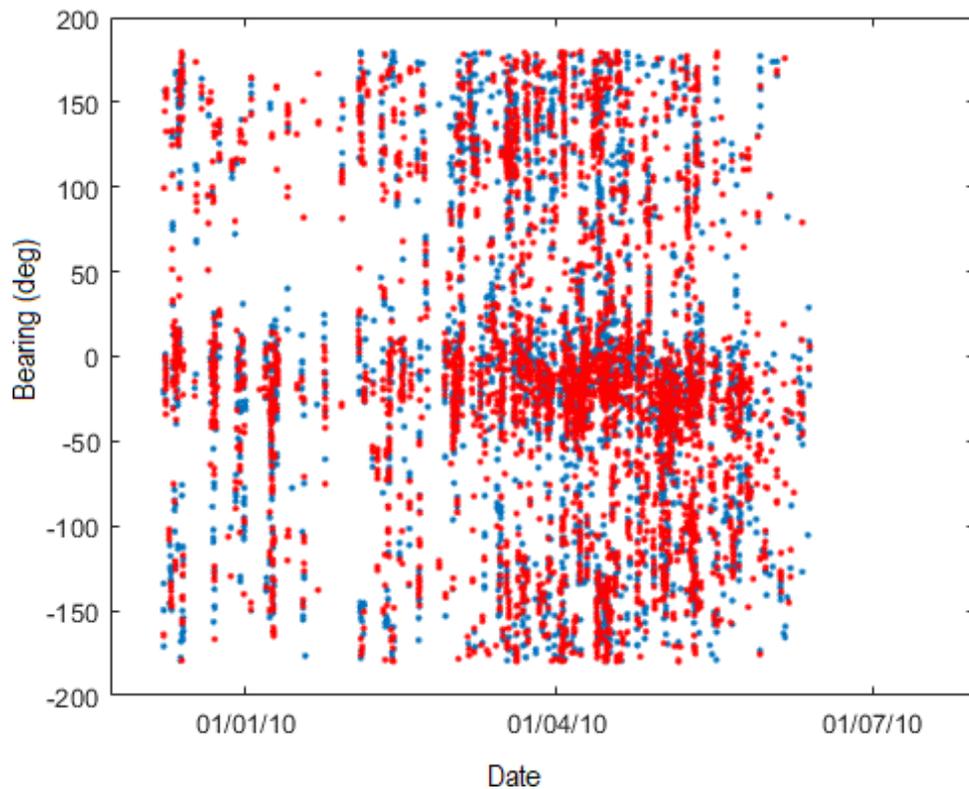


Figure 6.5 Distribution of localised vocal events around the acoustic observatory in the 2010 sample year (left) and 2011 sample year (right). These plots include all data for each sample year

The spatial distributions of all localisation of vocalising whales in 2010 and 2011 are shown Figure 6.5, indicating that most localisations were limited to within 10 km of the array. Data from 2010 and 2011 have areas of higher concentrations of whale locations, with differences in distribution patterns between the two years (Figure 6.5). The 2010 localisations display a concentration of animals around the northernmost instrument and a band of higher concentration along the southern side of the passive acoustic observatory (Figure 6.5). By contrast, the 2011 data set shows a concentration of animals around the central receiver and a band of animals along the south eastern area of the passive acoustic

observatory (Figure 6.5). It appears that there are areas of higher occupancy within the receiver array which may indicate a preference for these areas or alternatively could be the result of sweet spots for signal localisation based on differences in sound transmission between years.



*Figure 6.6. Bearings to localised vocalising animals for 2010 data set (red) and 2011 (blue). 0 degree bearing corresponds to North. Values between 0 and 180 represent the eastern directions between North and South while negative values between 0 and -180 represent the western directions between South and North.*

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A plot of the bearings to localised animals shows that animals were located primarily to the north of the receiver throughout the sample period, with a higher density located to the northwest (between 0 and -50) as the season progressed (Figure 6.6). The 2010 data show that most whales tracked in January and February were moving towards the south, whereas from March they tended to stay north of the array and move in the northern direction (Figure 6.6).

The length of time an animal was tracked varied from a single localisation in time, to tracks that spanned multiple samples over the course of several hours. The average length of time an animal was tracked was  $\sim 109$  minutes (95% CI  $\pm \sim 27$  minutes). Only those signals with particularly distinctive spectrograms or unusual song structure that were isolated from other animals in their localisations were possible to be tracked for longer than a few samples.

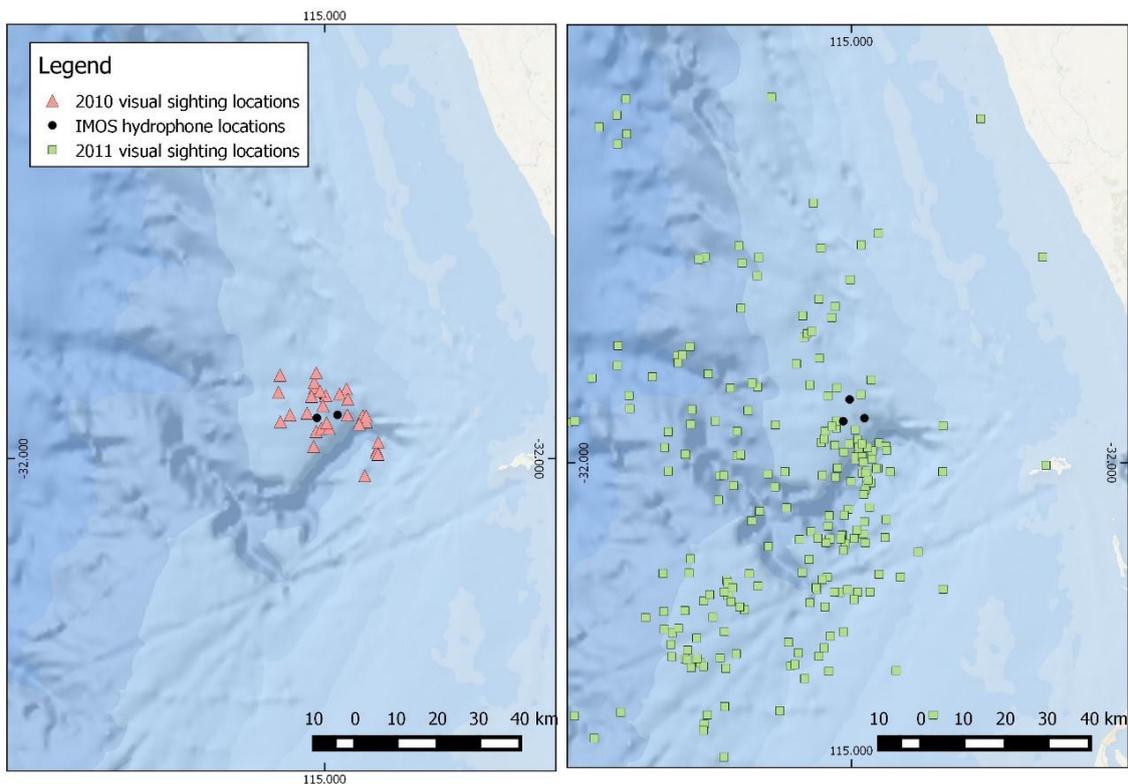


Figure 6.7. Visual sighting locations with respect to the passive acoustic observatory for 2010 (left) and 2011 (right). Maps produced using ESRI World Ocean Base 2018. Visual surveys conducted by J. Bannister, C. Burton, C. Jenner and M. Jenner.

The first vessel based visual sighting in 2010 occurred on the 21<sup>st</sup> of March with the last on the 28<sup>th</sup> of April. Within this period there were 15 days on which pods were sighted, with the number of pods ranging from 0 to 2 a day (mean =  $0.77 \pm 1.37$ ). The first sighting of the 2011 visual survey was on the 12<sup>th</sup> of March with the final sighting on the 28<sup>th</sup> of May. Sightings occurred on 47 days in this time, with the number of pods sighted per day in this

time period ranging from 0 to 4 (mean =  $1.63 \pm 1.89$ ). Visual observations of sighted animals confirmed that most animals were travelling alone, with an average pod size of 1.1 animals. The visual survey effort in 2010 was focused around the passive acoustic observatory (Figure 6.7), while the visual survey effort in 2011 was spread along the lower west WA coast following the migratory route of the EIOPB whale (Figure 6.7).

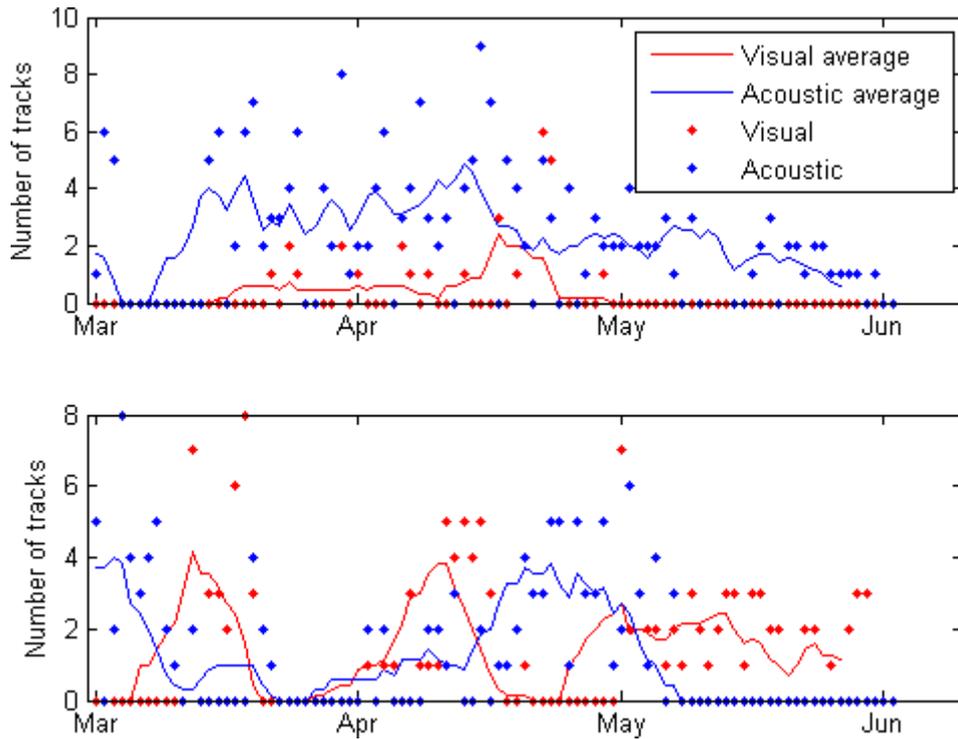


Figure 6.8. Number of visual and acoustic tracks per day with 3-day moving average for 2010 (top) and 2011 (bottom).

A comparison of daily visual and acoustic tracks found there were a much larger number of animals tracked acoustically than visually in 2010, with the peak in visual tracks occurring in late April when acoustic tracks start to drop (Figure 6.8). However, the number of animals tracked acoustically in 2011 was similar to the number of animals tracked visually (Figure 6.8). There appeared to be little to no correlation in the timing of visual and acoustic tracks, aside from a period of no presence at the end of March 2011 (Figure 6.8). This is to be expected given the significantly larger survey area covered by the visual survey in 2011 when compared to the acoustic survey, as well as the transient nature of visual surveys

where only a small area can be sampled instantaneously, before the vessel moves on across the wider survey area.

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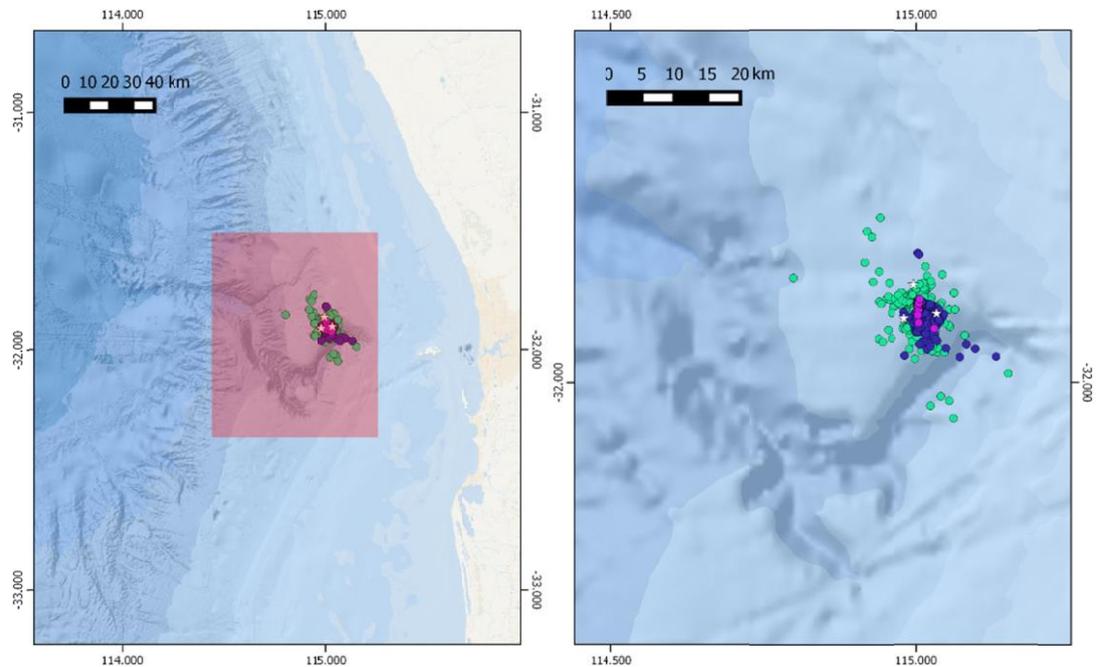


Figure 6.9. Locations of visual sightings in 2010 and 2011 (left) and acoustically derived locations (right). The overlay in the left map indicates the area depicted in the right map. White stars indicate the location of the acoustic receivers, green dots represent March locations, blue represents April locations, and magenta represents May. Maps produced using ESRI World Ocean Base 2018.

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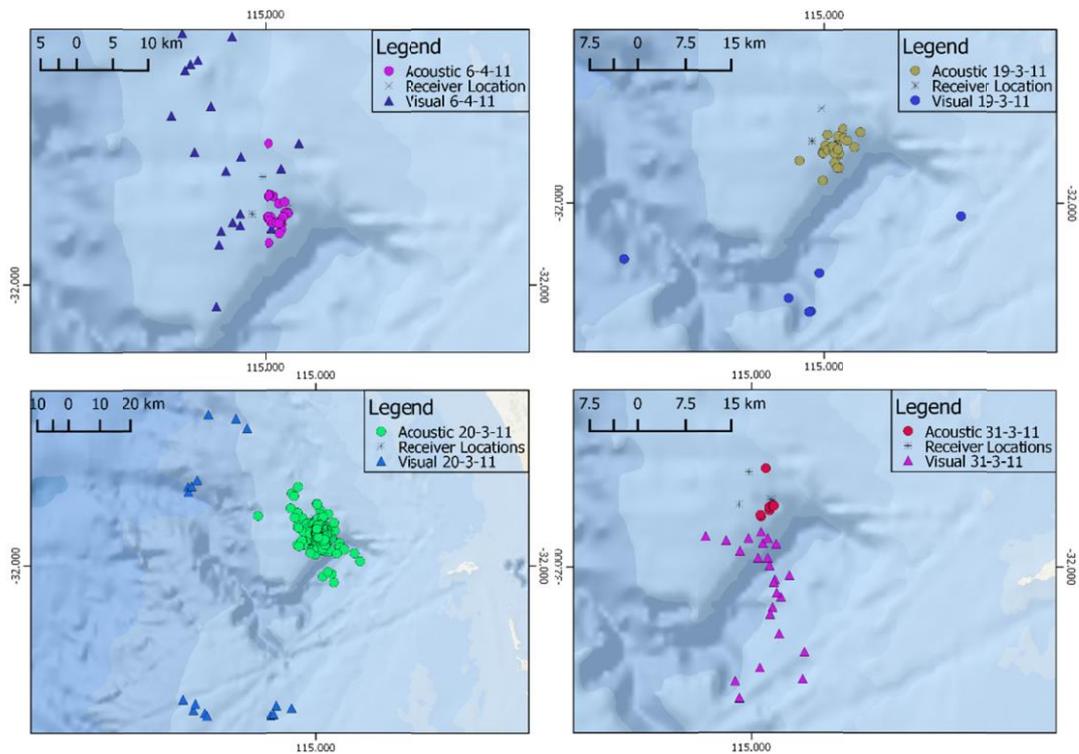


Figure 6.10. Comparison of visual and acoustic locations of EIOPB whales in vicinity of the passive acoustic observatory on the same day. Localisations are shown for the 6th April 2011 (top left), the 19<sup>th</sup> March 2011 (top right), the 20<sup>th</sup> March 2011 (bottom left), and the 31<sup>st</sup> March 2011 (bottom right). Maps produced using ESRI World Ocean Base 2018.

Comparisons of acoustic and visual sighting locations were only possible for three days in March 2011 and one day in April 2011 (Figure 6.10). This was due to the distribution of acoustic localisations in the immediate vicinity of the acoustic observatory, while the survey effort of the single vessel was considerably more spread out resulting in a wider distribution of sightings. Visual and acoustic sightings were found to overlap on two occasions, the 6<sup>th</sup> April 2011 and the 31<sup>st</sup> March 2011 (Figure 6.10). A comparison of visual and acoustic localisations on these days indicates that visually surveyed animals were not in the same location as acoustically surveyed animals.

## 6.5 Discussion

Utilising passive acoustic observatories for the localisation of vocalising whales presents a wealth of possibilities for the management and study of cetacean species. Through the definition of a set of tracking criteria, successive localisations of vocalising pygmy blue whales were joined together into tracks allowing for the movement of vocalising animals through the receiver area to be estimated. Patterns in the movement and occupancy of certain areas around the receiver array were observed across two sample years with vocalising animals often following similar routes or milling in similar areas on a given day. Differences in distribution were observed between migratory legs with the animals favouring the western side of the receiver array on their southward migration and remaining more central and to the east on their northern migration. Given that blue whales are opportunistic feeders, it is possible that they choose to migrate along the edge of the continental shelf on their northern migration to make the most of potentially productive areas where upwelling may occur, such as the Perth Canyon (Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). On their southern migration to their summer feeding grounds, whales may travel further offshore to lessen encounters with predators such as killer whales (Avgar, Street, and Fryxell 2013; Ford and Reeves 2008; Clapham 2001; Reeves, Berger, and Clapham 2006).

Patterns in the localisation of successive song units indicated that vocalising animals were engaged in either milling or directional movement behaviour. This indicates that the animals may be engaged in feeding or socialising behaviour and directional travel. This was particularly the case for the early part of the 2010 season where directional travel dominated, while from mid-March onwards in both 2010 and 2011 milling tracks were as common, indicating that the early season behaviour may reflect migratory or travel, while from mid-March resource availability around the canyon may peak resulting in the prevalence of movement behaviour reflective of feeding (Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009; Bailey et al. 2009; Wilson et al. 2007). Previous studies focusing on other baleen whales have found movement patterns to vary between animals, though the reasons behind this are not clear. This was evidenced by a study of the movement of humpback whales in the south Atlantic Ocean that demonstrated that some whales switched between transiting and localised behaviours regularly whereas others would travel rapidly to an area and engage in localised behaviour (Rosenbaum et al. 2014). The results of this study reflect highly variable movement patterns between tracked

animals. The observation of circular movement patterns that are consistent with area restricted search behaviour (Irvine et al. 2014) reiterates the importance of the Perth Canyon area as a region of ecological significance for the EIOPB whale population (McCauley, Bannister, Burton, Jenner, and Rennie 2004; Gavrilov et al. 2012; McCauley et al. 2006). Whilst it has been suggested that blue whales sing whilst travelling in straight line (Oleson et al. 2007), these findings suggest that whales may engage in singing behaviour whilst milling on feeding grounds. Recent studies by Lewis and Sirovic (2018) indicate that singing behaviour is not conducive with feeding based on the dive profiles of singing animals. Given that singing and feeding are mutually exclusive behaviours, the milling behaviour of localised singing whales supports the idea that whales that engage in singing behaviour in feeding areas likely do so at the cost of feeding exhibiting their fitness to potential mates (Lewis et al. 2018; Lewis and Sirovic 2018). Visual and acoustic detections only overlapped on a handful of days in this study, and monthly comparisons found that the number of visual and acoustic tracks per day peaked in different months, this may be indicative of short-term variability in animal behaviour with animals partitioning their time on the feeding ground between vocalising, which would make them more acoustically detectable, and feeding which may make them more visually detectable during their surfacing. For an animal that is generally solitary, the opportunity to attract a mate, or need to mediate interactions with conspecifics whilst aggregating in feeding areas may require the animal to balance time between vocalising and feeding (Cholewiak, Cerchio, et al. 2018; Darling, Jones, and Nicklin 2006; Herman 2017). The differences observed in this study in the timing of acoustic and visual tracks, and the tracking of vocally active animals engaged in milling behaviour suggests that pygmy blue whales may balance their time in areas of high productivity between vocalising and feeding behaviours.

Comparison of visual and acoustic localisations demonstrates the increased detectability of animals acoustically than visually, though acoustic localisations were limited to within close proximity of the receiver array, whereas visual sighting locations were more spread out reflecting the path of the survey vessel. This indicates that acoustic surveys, while more effective at detecting vocal animals, are limited by their ability to accurately localise animals within a certain proximity of the receivers, though this can be overcome by adding sub arrays and increasing the number of receivers (White et al. 2006; Skarsoulis et al. 2018).

An additional finding of this study is the ability to follow individual vocalising whales to confirm the production of combination song patterns. The first instance of a combination song structure was found by localising successive type II units of the *P3A* song pattern

(Jolliffe et al. 2019) to confirm that it would have been produced by the same vocalising animal. At that time, there were no other vocalising whales in the area and the continuity of the spectrogram appearance (i.e. Phrase structure and presence of unit breaks), the frequency curve of the unit II, and the ISI were consistent with the signals coming from an individual animal. It is possible that combination song structures have been missed in past studies of pygmy blue whales that has focused on the presence and density of singing animals due to automatic classification and detection algorithms. By localising the successive type II units and comparison of the spectrograms, it was possible for an individual whale to be pinpointed as the source of the combination call structure.

## 6.6 Conclusion

This study utilised TDOA measurements and triangulation to track pygmy blue whales based on a number of criteria, including the maximum travel speed and song characteristics. Based on the movement patterns of acoustically tracked animals, and the locations of visually sighted animals, this study suggests animals may balance their time in areas of high productivity between vocalising and feeding, two behaviours that have previously been demonstrated to be mutually exclusive, but both provide a fitness benefit to the animal.

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## Chapter 7 Variability in the temporal characteristics of the eastern Indian Ocean pygmy blue whale song

### 7.1 Abstract

*Temporal structure is an important element of cetacean song. The song of the Eastern Indian Ocean pygmy blue whale (EIOPB) has an Inter-Song Interval (ISI) that has been shown to be highly variable. Whilst ISI appeared to remain consistent within a song event, it was found to be variable within sample years with no observable monthly patterns. Detailed analysis indicated variability in ISI arises from changes in phrase structure, variability in the length of song units and pauses between successive song units. The EIOPB produce three primary song types, one containing three units repeated, one containing units II and III repeated, and one with only unit II repeated. The three unit phrase of the EIOPB whale song has the longest song repetition interval of around 200 s, double that of songs composed of the two unit phrase at 100 s ISI. This extra length was found to come from the inclusion of the type I song unit which was highly variable in length, ranging from 20 to 60 s in duration, and variability in length of other units within the phrase. The second unit was observed to be longer, though not significantly, in three unit songs (mean 24.74 s 95% CI  $\pm$  1.44 s) than that in two unit songs (mean 23.66 s 95% CI  $\pm$  1.69 s), and differences in the spacing between units were observed. Song structure was a confounding factor in the analysis of variability in song repetition interval. Annual comparisons of noise conditions indicate that the variability in ISI cannot be explained by background noise conditions alone. The results of this study suggest that song repetition interval may vary between individual whales and locations, possibly as a result of behaviour and is most influenced by phrase structure.*

### 7.2 Introduction

Whilst music is accepted as a cultural art form unique to humanity, there are elements of whale song that appear to share similar characteristics (Kello et al. 2017). Strict rules appear to govern whale song structural conformity and repetition times, much like human music (Guinee and Payne 1988; Marler 1997; Handel, Todd, and Zoidis 2009; Wiggins et al.

2015). Similarly, long term changes in characteristic song are common across several species of whale and include changes to structure, frequency and duration.

The songs of the humpback whale (*Megaptera novaeangliae*) have been well studied and are among the most intricate and complex vocalisations produced by mysticete whales. Within the songs of humpback whales, phrase duration has the lowest level of variability between singing animals and within an animal's song (Cholewiak, Sousa-Lima, and Cerchio 2013). Significant differences have been found in the average length of song from an individual singer, as well as a high degree of variability between vocalising animals. Variability in the singing behaviour of an individual whale has been linked to acoustic disturbances, including low frequency sonar and vessel noise (Cholewiak, Clark, et al. 2018; Fristrup, Hatch, and Clark 2003). Changes in humpback surface behaviour have also been observed in response to acoustic disturbances such as low frequency sonar (Fristrup, Hatch, and Clark 2003; Cholewiak, Sousa-Lima, and Cerchio 2013). It is possible therefore, that behaviour and song length are linked, with song length in humpback whales found to increase in response to acoustic disturbances (Cholewiak, Sousa-Lima, and Cerchio 2013; Fristrup, Hatch, and Clark 2003). Similar effects have been observed for blue whales with an increase in vocalisation rate for D calls, believed to be contact or social calls, reported in the presence of ship noise (Melcon et al. 2012). Low frequency sonar has also been found to influence whale behaviour with blue whales ceasing to vocalise (Melcon et al. 2012), humpbacks altering their spatial distribution relative to sonar (Fristrup, Hatch, and Clark 2003; Cerchio, Jacobsen, and Norris 2001). Additionally, there are several studies demonstrating changes in bowhead whale calling rates and dive behaviour in response to seismic sound (Blackwell et al. 2015; Blackwell et al. 2017; Robertson et al. 2013).

Ambient sound conditions may also have the potential to influence the acoustic behaviour of whales. In a long term study of the short and long term behavioural response of northern and southern right whales (*Eubalaena spp.*) to increases in background noise, it was found that right whales alter their calling rate and frequency based on background noise conditions with lower calling rates associated with higher levels of background noise (Parks, Clark, and Tyack 2008). This has been found to be a variable response indicating it is not a result of selection pressure but a behavioural response to increased levels of anthropogenic noise (Parks, Clark, and Tyack 2008). Gray whales (*Eschrichtius robustus*) have also been found to exhibit behavioural plasticity in song production depending on the background noise environment (Au and Hastings 2008; Dahlheim and Castellote 2016). Comparative studies of gray whale vocal behaviour on feeding grounds and along migratory

routes have found variability in song production to be greatest between behavioural states, indicating a link between song variability and behaviour (Au and Hastings 2008; Rannankari, Burnham, and Duffus 2018). In addition to behaviour driving song variability, 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 and McVay 1971). Inter note interval was found to transition from a short to long duration over the course of a season without reverting back to a short duration (Morano et al. 2012; Weirathmueller et al. 2017). The short duration inter note interval coincided with the breeding season when the caller density was at its highest (Morano et al. 2012), highlighting the potential for caller density to influence song intervals. Whilst at odds with the temporal variations observed in the songs of other whales, shortening of vocalisation intervals in response to increased noise parallels what has been observed in terrestrial ecosystems, where birds such as red-throated ant-tanagers (*Habia fuscicauda*) have been observed to increase their song rate in noisier environments (Simpson and McGraw 2018).

While evidence for variations in song structure including song duration and repetition interval in mysticete whale song continues to grow, the cause of such variation is harder to define (Fristrup, Hatch, and Clark 2003; Kershenbaum and Garland 2015; Ronald et al. 2015). It is not understood whether the drivers of this variability are background noise conditions, changes in behavioural state, or changes in some other aspect of the singer's situation or environment (Cazau et al. 2016; Dunlop 2017). There is evidence to support the notion that whales can communicate information through vocal displays (Dunlop 2017; Cazau et al. 2016). This information has the potential to be communicated through changes in the frequency or duration of calling whales vocalisations (Cazau et al. 2016). Using long term data collected from the Perth Canyon, Western Australia, the variability in song repetition interval will be investigated for the Eastern Indian Ocean pygmy blue (EIOPB) whale. Understanding the song repetition rate as well as the driving factors behind changes to this element of call structure will be essential for the long-term use of acoustics as a population monitoring tool.

The EIOPB whale has several distinct song and phrase variations with songs composed of one, two or three units (Chapter 4). Variability in the structure of the EIOPB whale song is explained in detail in Chapter 4, though can be summarised as repeated three unit (*P3*), two unit (*P2*) or one unit (*P1*) phrases. There are also a further three variations which represent variation in the composition of songs, combining multiple phrase structures, termed *P3A*, *P3B* and *P2A* songs (Chapter 4). Understanding the level of variability that exists in different

elements of song, as well as any directional changes will contribute to an overall understanding of song variability. Further, quantifying the level of variation in song repetition interval within the population is necessary to improve the efficacy of acoustic monitoring methods. 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 (ISI).

### 7.3 Methods

#### Data Collection

Long term data were collected from the Perth Canyon, Western Australia (Figure 7.1), located to the west of Rottnest Island. The Perth Canyon is a submarine canyon that supports a hot spot of productivity on a largely oligotrophic coastline (Rennie 2005; Rennie, Hanson, McCauley, Pattiaratchi, Burton, and al. 2009). 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.

Data collection and processing are described in the Methods chapter of this thesis. A total of five sample years from the Perth Canyon were included in this analysis between 2011 and 2016 as per Table 7.1.

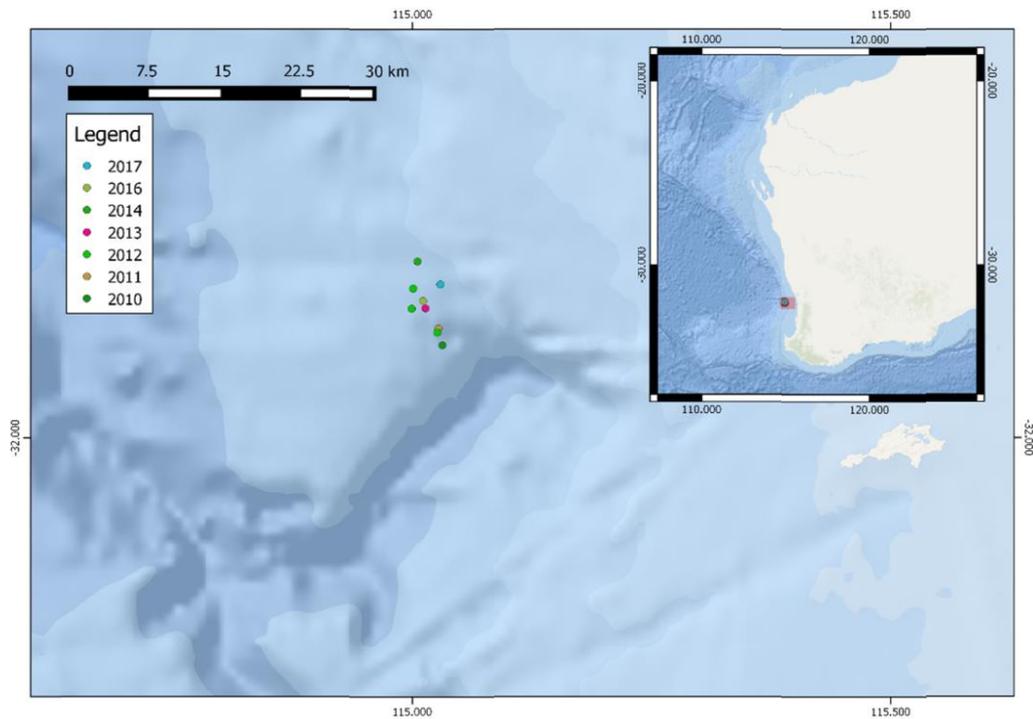


Figure 7.1 Location of noise receiver deployments in the Perth Canyon, Western Australia, with three logger deployments in 2012 and 2014, and one in all other years, none of the sample years used in this study had four deployments. Chart not to be used for navigation purposes.

Table 7.1 Data collection years, sample regime and recording equipment for the Perth Canyon data set.

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

### 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 analysed 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 Kruskal-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.

A total of 1,812 song events were used in this analysis. Spectrograms were produced with a 2048 point fast Fourier transform (FFT), with an 80% overlap using a 1 kHz sample rate (0.488 Hz and 0.41 s frequency and time resolution, respectively). The introduction of broken song units (see Figures in Appendix 1) in later sample years provided the opportunity for further comparison of temporal characteristics. Further analysis of broken song units was carried out on a subset of 240 song events across the two major song variants (120 *P3* songs and 120 *P2* songs). The above subset of 1,812 suitable song events, defined as those with a high enough signal noise ratio for accurate manual measurements, and those for which one entire song repetition was captured within the sample window, was sorted by song type. Randomised sampling was then used to randomly select 120 of the *P2* and 120 of the *P3* song events for further analysis. The length of each song unit was measured as well as the time between the end of one unit and the start of the next, defined as an inter-unit interval (IUI), and the song repetition interval (ISI), as defined in Figure 7.2. The starting and maximum frequency of the 60-70 Hz 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 7.2). 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 chapter uses data manually derived from spectrograms of complete song phrases.

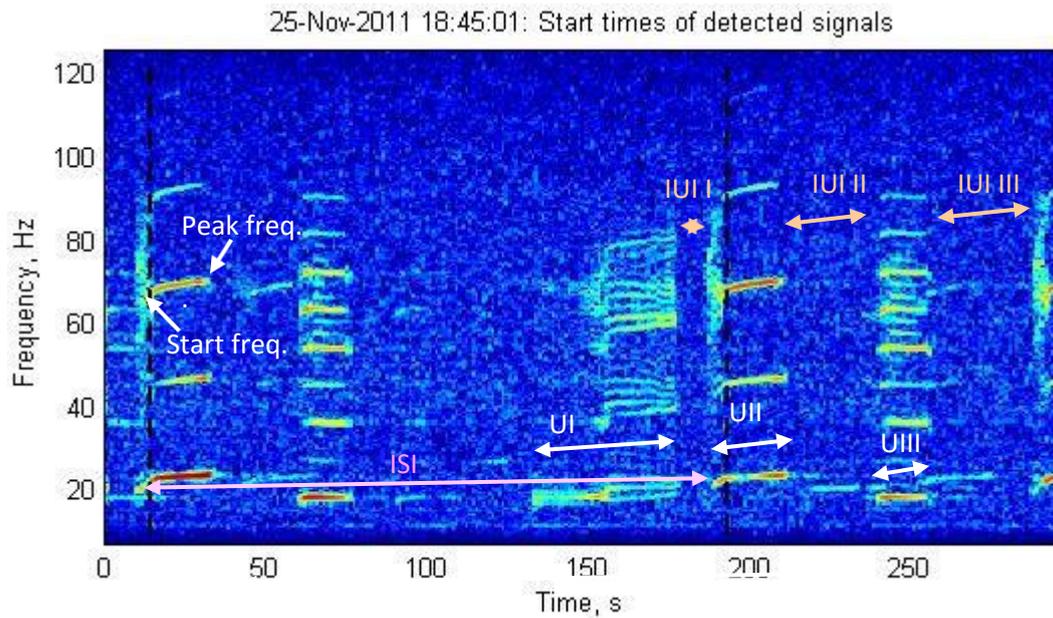


Figure 7.2. Definition of IUI, ISI, start frequency and peak frequency measurements for a full three unit song phrase. The start and peak frequency are measured on both the fundamental and third harmonic, though are only labelled on the third harmonic in this figure for clarity.

### 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 50% percentile value using the CHORUS software which corrects for the frequency characteristic of receivers using calibration data (McCauley et al. 2017). 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.

## 7.4 Results

A total of 1,812 song events were recorded and classified for use in this analysis. ISI were averaged across all song types and plotted across sample years showing an overall decreasing trend in ISI when all song variants were included in the same analysis (**Error! Reference source not found.**). The range in ISI varied between years, with the presence of

longer phrase structures resulting in higher mean ISI's in those years (**Error! Reference source not found.**). Separation of song events by song type revealed 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 7.3). ISI was consistently lower with less variability in 2016 and 2012 (Figure 7.3). While there are no clear monthly 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 both P3 and P2 songs (Figure 7.3). Mean ISI appears 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 7.3).

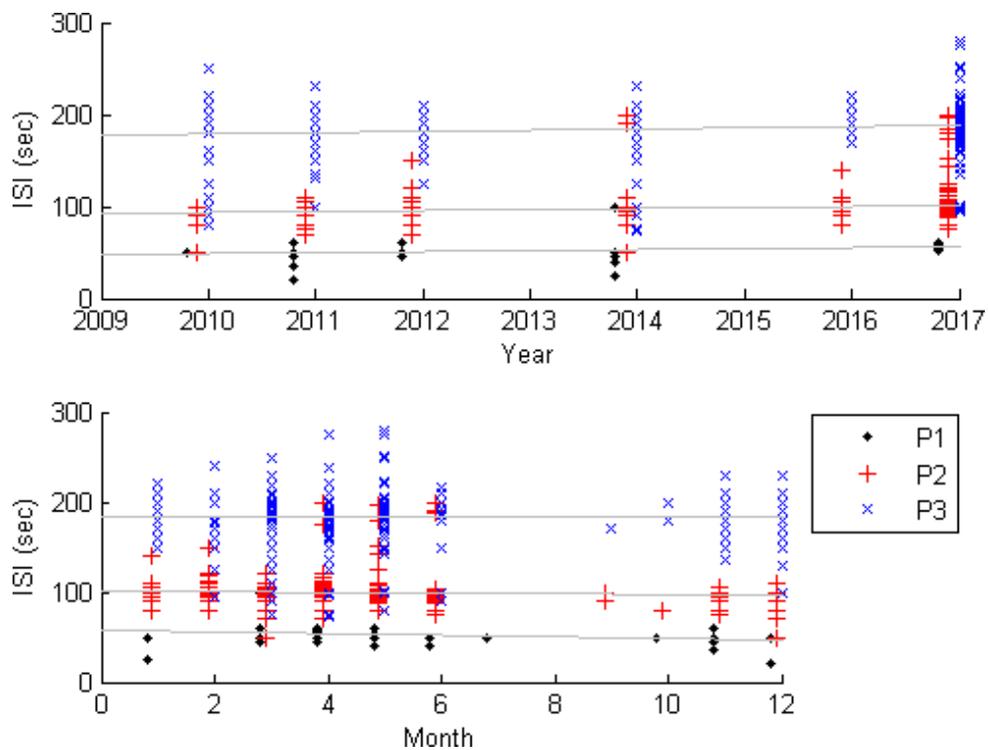


Figure 7.3. Top; ISI (seconds) measured from EIOPB whale song events in the Perth Canyon separated by song structure across all sample years. Bottom; ISI (seconds) from EIOPB whale song events across sample months. Data points are clustered by sample year (top) and month (bottom), grey lines represent a linear fit to assess seasonal and annual trends in ISI.

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  $\pm$  3.87%),

Chapter 7. Variability in the temporal characteristics of the EIOPB song

while *P3* songs on average represented 38.8% (95% CI  $\pm$  3.77%) of all songs analysed, with a peak of 45.2% in 2016 where they were the dominant song type (Table 7.2). The less common song variants 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 *P3S* (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 7.2). The longer song variants, *P3* and *P3A*, were prevalent in 2016 representing 45.2% and 8.4% of all songs respectively (Table 7.2).

Table 7.2. 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.

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

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 ( $p \ll 0.001$ ,  $K^2 = 26.426$ ) violating the standard assumption of a normalised distribution. Consequently, a Kruskal-Wallis test determined that there was a statistically significant difference in the proportions of song structure between years ( $p \ll 0.001$ ). 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 ( $p = 0.036$ ). 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 ( $p = 0.025$  and  $\ll 0.001$  respectively).

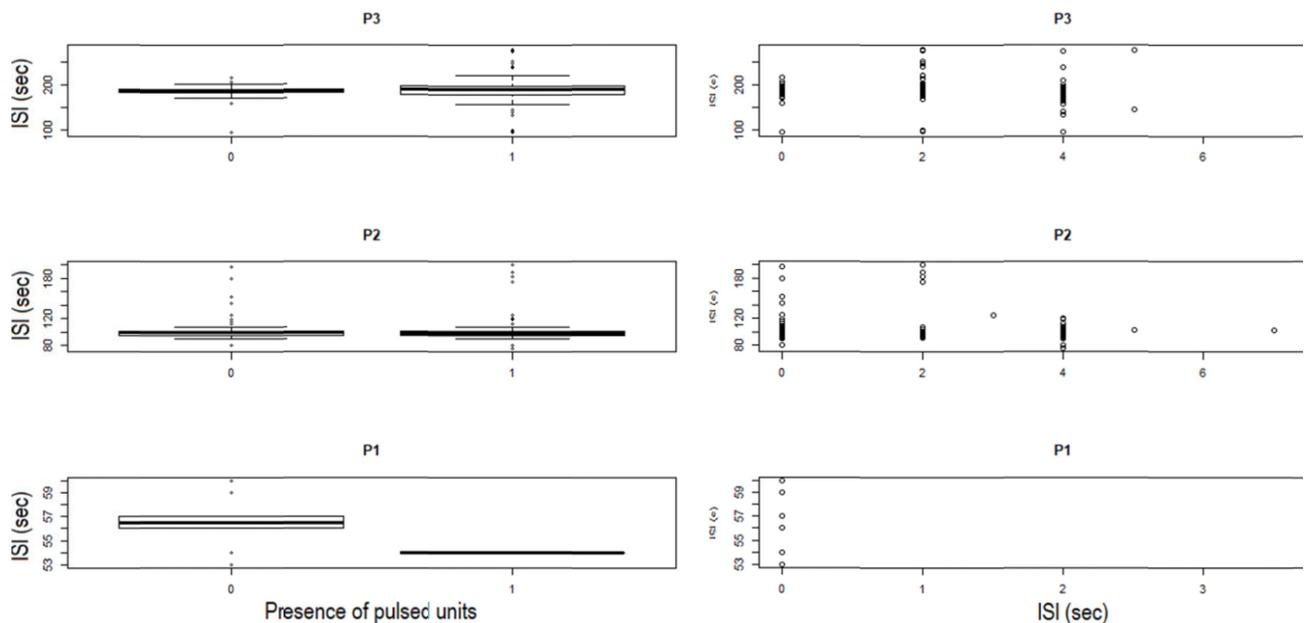


Figure 7.4. The influence of broken song units on ISI (seconds) for each of the three main song structures (P3-top, P2-middle and P1-bottom). Left: Mean ISI between normal (0) and song with broken units (1). Right: ISI for song units with breaks of varying lengths (seconds) in one or more song units.

Investigation of the influence of broken song units on ISI provided conflicting results with broken units contributing to a slight increase in mean ISI in P3 songs and P2 songs (Figure 7.4). However, a slight decrease in ISI was seen for P1 songs potentially due to the low number of P1 song events with broken units (Figure 7.4). There was no indication of a relationship between break length and ISI for any song type (Figure 7.4). Statistical testing indicated that the apparent relationship between ISI in songs with broken and unbroken song units was statistically significant for P3 ( $p = 0.012$ ), but not P2 ( $p = 0.381$ ) song types. A statistically significant relationship also existed for P1 songs ( $p = 0.039$ ), though the direction of the relationship was opposite to what was expected with P1 songs with broken units having a shorter ISI than those without. This is likely due to the rarer occurrence of this song variant.

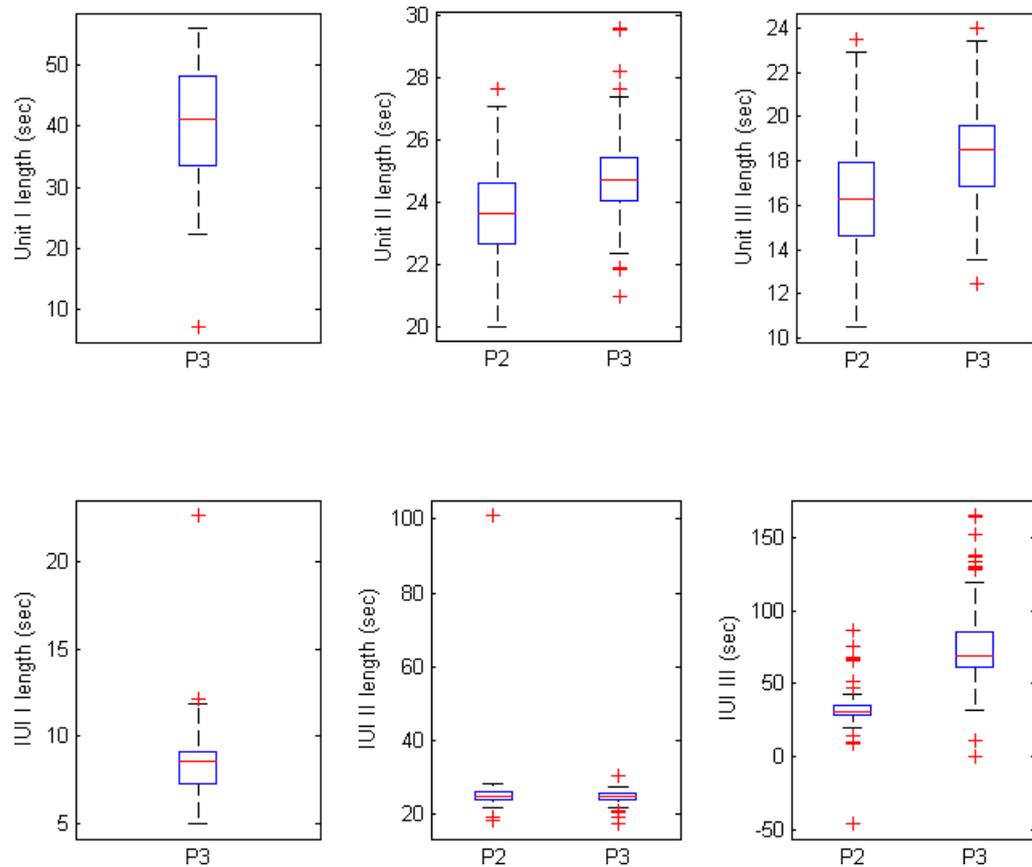


Figure 7.5. Box plots showing the median, interquartile range, and range of song units and inter-unit intervals for the subset of P3 and P2 songs that were used for further analysis. Top row, from left: Length of unit I (P3 songs only), inter unit interval I (P3 songs only), length of unit II. Bottom 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).

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, 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 7.5). 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 7.5).

Table 7.3. 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
<b><i>P2</i></b>	Mean	23.66 s	24.59 s	16.25 s	32.37 s
	95% CI	± 1.69 s	± 1.72 s	± 2.42 s	± 13.05 s
<b><i>P3</i></b>	Mean	24.74 s	25.61 s	18.18 s	75.39 s
	95% CI	± 1.44 s	± 7.12 s	± 2.11 s	± 27.81 s
<b>Ratio</b>	<i>P2</i> / <i>P3</i>	0.96	0.96	0.89	0.43

The length of the IUI between unit I and unit II in *P3* songs was variable, with unit II found to be generally longer in *P3* songs than that in *P2* songs (Table 7.3). The length of IUI between unit II and unit III was the most consistent (Figure 7.5), though was more variable in *P3* songs as opposed to *P2* songs (Table 7.3). Unit III length was highly variable though was on average shorter in *P2* songs as opposed to *P3* songs (Table 7.3). 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 7.3), and within song structures (Figure 7.5). Measurements of the length of the individual elements of song structure indicate a high level of variability in unit and IUI length between songs, with some elements more variable than others (Figure 7.5). In particular, for *P3* songs the length of unit I and IUI-III contribute 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 pauses between units are also comparatively shorter than for *P3* songs (Table 7.3).

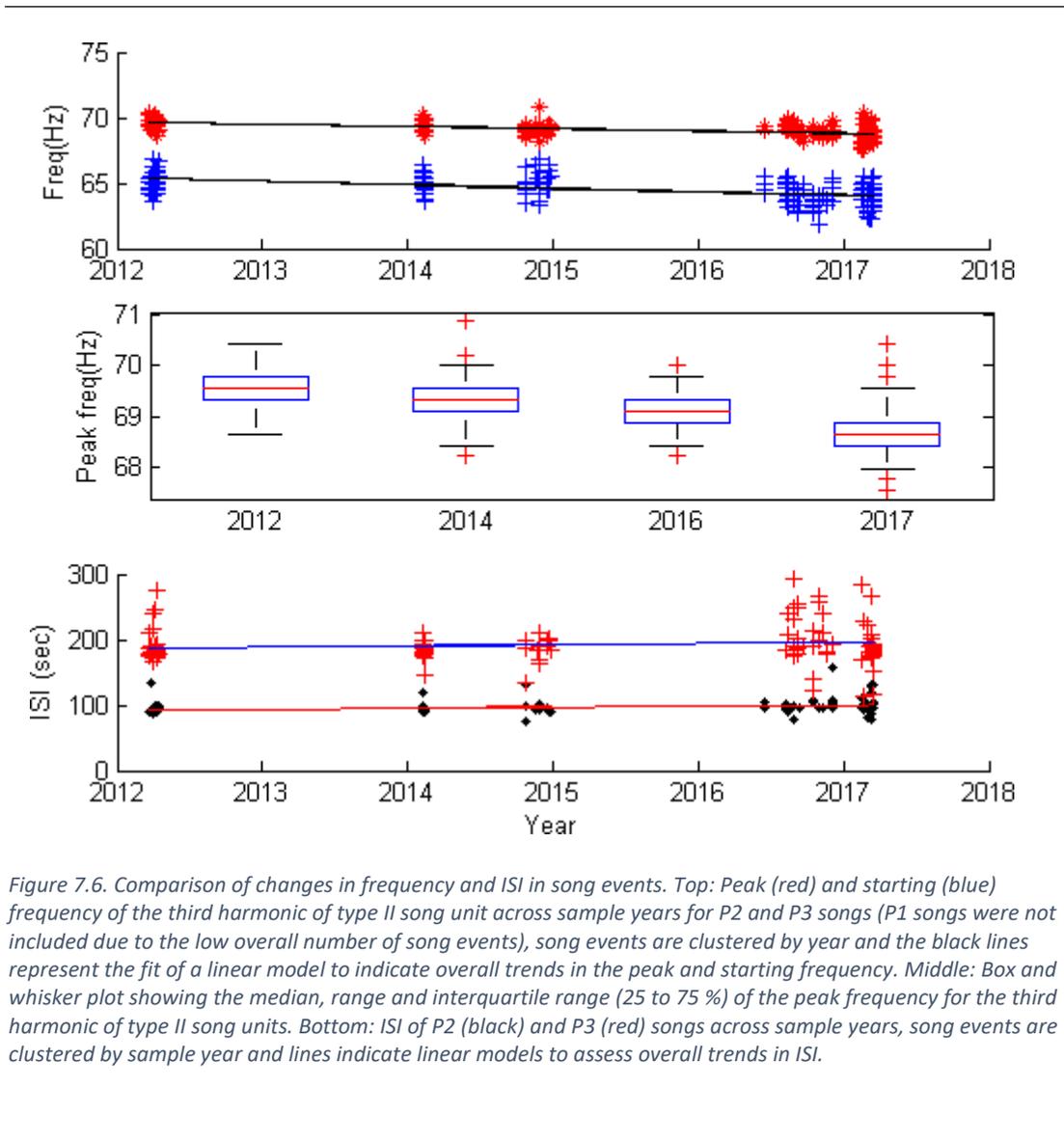


Figure 7.6. Comparison of changes in frequency and ISI in song events. Top: Peak (red) and starting (blue) frequency of the third harmonic of type II song unit across sample years for P2 and P3 songs (P1 songs were not included due to the low overall number of song events), song events are clustered 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. 2011b) of declining tonal frequency (Figure 7.6). 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 7.6). Comparison of ISI across sample years indicates an increase in maximum ISI, though no clear trend in mean ISI, as well as higher ISI in the sample months of March, April and May (Figure 7.3). 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 ( $p = << 0.001$ ,  $F = 125.0659$ ), however there was no significant effect of ISI on frequency change ( $p = 0.4275$ ,  $F = 0.6368$ ). The residuals of the ANOVA model were normally distributed indicating an appropriate fit of the statistical model.

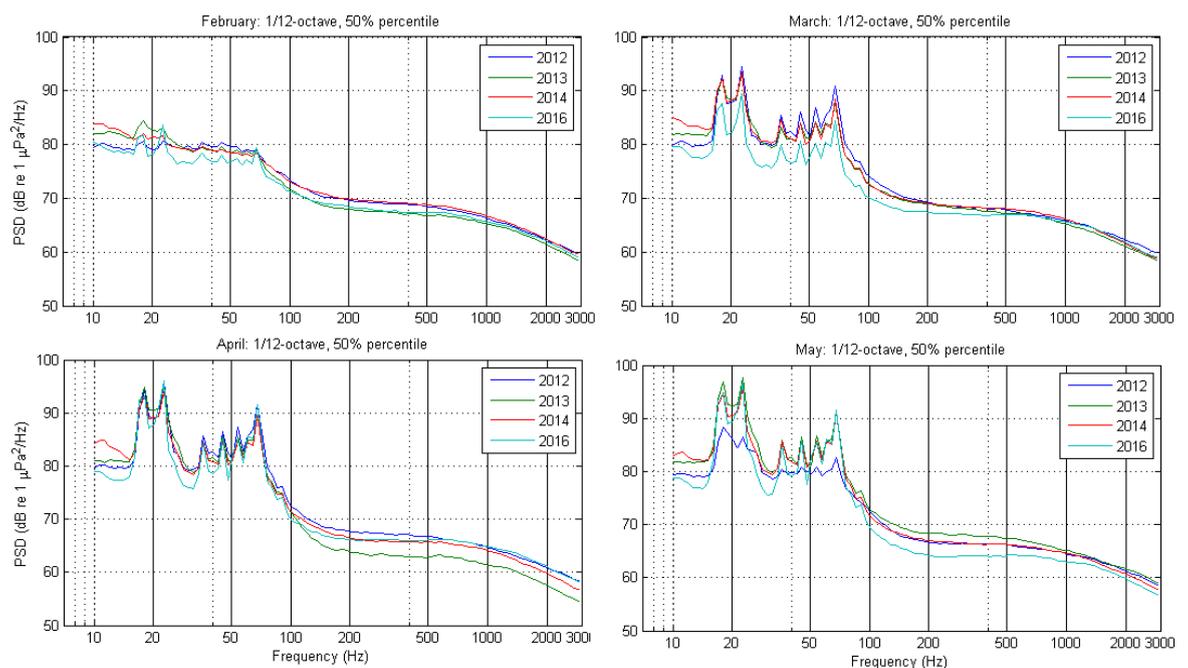


Figure 7.7. PSD of 50th percentile of sea noise spectrum level in 1/12-octave bands for months of peak pygmy blue whale presence in the Perth Canyon area across four sample years.

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 =  $82 \pm 1.25$  dB re  $1\mu\text{Pa}^2/\text{Hz}$  at 20-21 Hz, Mar =  $93 \pm 2.35$  dB re  $1\mu\text{Pa}^2/\text{Hz}$  at 20-21 Hz, Apr =  $96 \pm 0.63$  dB re  $1\mu\text{Pa}^2/\text{Hz}$  at 20-21 Hz, May =  $95 \pm 5.01$  dB re  $1\mu\text{Pa}^2/\text{Hz}$  at 20-21 Hz). Environmental noise between 20 and 70 Hz is dominated by pygmy blue whale vocalisations (Figure 7.7). Higher occupancy of the Perth Canyon by pygmy blue whales from March to May is reflected in the peaks of the 50<sup>th</sup> percentile PSD curves in all years (Figure 7.7). 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 7.7).

## 7.5 Discussion

There is evidence that inter-annual variability in song production is common for many species (Lewis and Sirovic 2018; Sirovic et al. 2017; Garland, Rendell, Lamon, et al. 2017; Garland, Rendell, Lilley, et al. 2017). Timing is an important structural element of song, though little research has been conducted to date on the variability in the ISI or phrase length for the pygmy blue whale subspecies. Song repetition intervals for the EIOPB whale, defined as the time between successive type II song units (inter song increment or ISI), were found in this study to be highly variable. The ISI appeared to remain consistent within song events but varied considerably between song events of the same structure. With an overall decreasing trend in ISI observed when all song types were combined, but an increasing trend observed when considering the song types in isolation. Consequently, it is unclear whether the overall decrease in ISI is driven by the song repetition interval of individual animals' songs, or by the prevalence of songs of shorter phrase structures, which appear to dominate in later sample years. Based on the results of the feature space analysis in Chapter 4 which showed ISI values for the *P3*, *P2* and *P1* songs slightly increasing annually, this reduction in ISI observed is likely due to shorter phrase songs increasing in prevalence.

Longer phrase structures were most susceptible to variation in temporal structure with more units and IUI's for variability to occur, while shorter phrase structures had the lowest level of temporal variability. Within the phrase structure, some units and IUIs were more temporally stable than others. The greatest variability for *P2* and *P3* songs come from the IUI between the end of unit III and the start of the next phrase (unit I for *P3* songs and 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. Units II and III are common to *P2* and *P3* songs yet were distinctly shorter in *P2* songs as opposed to *P3* songs (ratio *P2/P3* length 0.96 and 0.89, units II and III respectively; Table 7.3), contributing to the overall shorter ISI in *P2* songs compared to *P3* songs. Variability in the temporal structure of unit II and III was greatest between song events with different phrase structures, rather than song events of the same phrase structure. This indicates that, 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. Further, the higher than expected level of variability in all song units and IUIs supports the notion that individual animals may have distinguishable vocal characteristics. 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 from 2016 onwards, 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 have a role in communicating information about the singers themselves or their environment, as has been documented for other whale and bird populations (Dunlop 2017; Job, Kohler, and Gill 2016).

Overall, this study found that, 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. 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 the song repetition interval for the sample year as well as having a significant influence on the mean ISI. Consequently, statistical methods used for analysing song repetition intervals need to take song structure diversity into consideration. By separating the data by song type, it is evident that ISI is more variable within some song types than others. The longer song types, such as *P3* and hybrid variations, have greater scope for variability with an extra one or two units in the phrase, and thus more units and inter unit intervals for variability to occur. Long term comparison of *P3* ISI identified a slight increasing trend across all sample years, which was also seen in the ISI of *P2* songs. This is in agreement with the increase shown by the feature space analysis in Chapter 4. Contrary to what was expected, a relationship between range in ISI and sample size was not observed,

and the absence of such a relationship may be due to links between behavioural state and singing, or could be a reflection of short term changes to background noise in the environment (Frstrup, Hatch, and Clark 2003; Cholewiak, Sousa-Lima, and Cerchio 2013). This could potentially explain the large range of song repetition intervals in the relatively small 2010 data set; perhaps environmental factors in that sample year caused whales to alter their song repetition interval (Parks, Clark, and Tyack 2008; Melcon et al. 2012). The consistency of song repetition interval within song events may indicate that individual whales have a 'signature' song repetition interval which, along with differences in phrase structure, helps to identify them or make them stand out from other singing whales (Galef 2001; Herman 2002; Janik and Slater 1997; Cazau et al. 2016; Johnson et al. 2015; Mercado, Herman, and Pack 2005). The mechanisms behind changes in song structure are not well enough understood to determine how or why variability occurs. However, if variability was the result of errors in song learning, or communication of individual information, variation between sample years and locations could reflect the migratory habits and timing of individual whales.

Song variability over time showed an increased occurrence of *P1* song events while the percentage of *P3* and *P2* events remained relatively consistent (Chapter 4 and 5). 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 *P3S*, *P2A* (a *P2* and *P1* phrase combination) and *P1* which all occurred in the highest proportions for that sample year, while *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 *P3S*) 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 SST 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.

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 and higher mean ISI values. Further, ISI was seen to increase in March, April and May corresponding with higher PSD levels in these months. Notably these peaks in background noise correspond with the frequency bands of EIOPB song and are caused by an increased density of vocalising EIOPB whales. This indicates that EIOPB may increase their song length in response to increasing levels of background noise, with long duration repetitions of shorter song types (i.e. *P2* and *P1* songs) preferred 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, Zollinger, and Brumm 2018; Job, Kohler, and Gill 2016; Fristrup, Hatch, and Clark 2003), 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.

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 Chapter 4. A number of studies have described the worldwide decline in frequencies of whale sounds (Gavrilov, McCauley, and Gedamke 2012; Leroy et al. 2018; Oleson et al. 2014), and this phenomenon has been documented for the type II EIOPB whale sound (Gavrilov et al. 2011b). 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 Chapter as well as Chapter 4. This would suggest that there may be a trend towards increasing ISI if song frequency continues to decline inter-annually, as observed in the feature space analysis, despite the intra-annual variability observed in ISI. Though a larger sample size with respect to the number of song events analysed 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 Chapter 4.

## 7.6 Conclusion

The results of this study identify that there is a distinct level of variability in the temporal characteristics of EIOPB whale song with preliminary findings suggesting a relationship between the increased density of vocalising animals (as shown by higher background noise levels) and the temporal structure of individual song types. Further, this study 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 of shorter phrase types being shorter in duration. Such a finding confirms that variability in song production is deliberate and not just a result of errors in song learning. It is hypothesised that these changes could be the result of individual differences within the population, or changes in environmental conditions including background noise. In order to elucidate any links that may exist between behavioural state, environmental factors 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 behaviour of whales. Further, photo identification of singing animals would allow for confirmation of whether variability in songs can be linked to individual animals.

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## Chapter 8 Investigating fine scale variability in the Eastern Indian Ocean pygmy blue whale song type

### 8.1 Abstract

*Acoustic data from the Perth Canyon, Western Australia were collected for the 2017 northern migration allowing for detailed acoustic analysis of eastern Indian Ocean pygmy blue (EIOPB) whale songs within a migratory season. A weak negative linear relationship was observed between the length and frequency of the type II song unit ( $p < 0.001$ ) suggesting that long term declines in frequency may be linked with temporal shifts in unit production. An algorithm was used to follow the unit II signal in time, tracking the change in frequency over the duration of the signal. The results of this analysis indicate that variability between the song production in singing bouts may exist and thus it is possible that individual whales may have distinct characteristics. Spectrograms of sea noise were viewed individually allowing for classification of song structure and measurements of signals. The presence of breaks within a unit was identified as a significant level of variability in song production within the 2017 data set and was seen to increase throughout the season. It is hypothesised that unit breaks may play a role in intra species communication, as well as represent a novel variation to song production that may increase individual fitness. Overall, the level of variability in song structure was high throughout the 2017 season with all but one song structure identified up to 2016, present in 2017 across peak occupancy months, indicating song structure is not linked to separate cohorts of individuals, but rather that animals may have the capacity to change between song structures.*

### 8.2 Introduction

Outside of humans, cetaceans demonstrate some of the richest vocal and evolutionary cultures known, that mirror the behaviour and capabilities of some species of bird and ape (Cantor et al. 2015; Cantor and Whitehead 2013b; Creanza, Fogarty, and Feldman 2016; Deecke, Ford, and Spong 2000; Filatova et al. 2015; Galef 2001; Kopps et al. 2014; Krützen et al. 2005). These include vocal transmission, social learning, gene-culture coevolution and

tool use (Garland et al. 2015; Garland, Rendell, Lamoni, et al. 2017; Rendell and Whitehead 2001; Cantor et al. 2015; Kopps et al. 2014; Krützen et al. 2005; Mann et al. 2000). Transmission of vocal culture can be seen in the rapid change of song between seasons and across geographic scales in humpback whales (Cerchio, Jacobsen, and Norris 2001; Garland et al. 2015; Garland, Rendell, Lamoni, et al. 2017; Helweg et al. 1998; Rekdahl et al. 2013). Song change can take time however, and it may take years for the song to spread through an entire population, alternatively it can happen relatively quickly and be more of a revolution, depending on the population and mechanism of transfer (Garland, Rendell, Lamoni, et al. 2017; Noad et al. 2000). The novelty threshold hypothesis recognises that once novelties reach a certain prevalence in the population, they will be adopted by all singers (Garland, Rendell, Lamoni, et al. 2017; Campbell and Hauber 2010). This implies that song revolution only takes place when a new song is heard multiple times (Garland, Rendell, Lamoni, et al. 2017). Humpbacks have been shown to be able to distinguish between novel and common songs, and it is hypothesised that they can recall songs from past years as they do not revert back to old songs, but exhibit continual directional change (Garland, Rendell, Lamoni, et al. 2017).

Culture is difficult to quantify in cetacean species, as it is impossible to assess natural levels of cognition and neural pathways in wild animals, and those kept in captivity are living in conditions inherently devoid of culture (Mann 2017). Some animals are simply too large to study under laboratory conditions, and thus our understanding of their behaviour and cognition is limited to what can be gathered from visual and acoustic studies of wild animals (Mann 2017). Where these animals are widespread, migratory and elusive, comprehensive behavioural studies are challenging at best. Acoustic analysis of vocal cues is one of many ways that researchers can gain an insight into the behaviour and cognitive capacity of these animals (Boisseau 2005; Garland, Rendell, Lilley, et al. 2017; Galef 2001; Rendell and Whitehead 2001). Quantifying change and variability in vocal behaviour is an important step in understanding the function and complexity of calling behaviour in species.

Humpback whales (*Megaptera novaeangelia*) and killer whales (*Orcinus orca*) are the best known examples of cultural species in the cetacean world. Humpbacks demonstrate many 'cultural' behaviours including maternally directed site fidelity, feeding behaviours and vocal signals. Killer whales have distinct dialects and life histories and have learned to depredate long line fisheries, while bottlenose dolphins use tools to forage in sediments for their food as can be seen in the sponge use of Shark Bay dolphins (Mann et al. 2000; Mann

2017; Deecke, Ford, and Spong 2000; Kopps et al. 2014; Krützen et al. 2005; Yano and Dahlheim 1995). Humpback song is an example of a nested hierarchy where single sounds or units are grouped into phrases, which are repeated in themes and joined together in a song (Garland, Rendell, Lamoni, et al. 2017; Payne and McVay 1971; Payne and Payne 1985; Guinee and Payne 1988; Handel, Todd, and Zoidis 2012; Cholewiak, Sousa-Lima, and Cerchio 2013). Studies of blue whale song worldwide have identified variability in the frequency, length and structure of songs (Jolliffe et al. 2019; Lewis and Sirovic 2018; Lewis et al. 2018; Miksis-Olds, Nieukirk, and Harris 2018). A number of drivers of this variability have been suggested, including that song length may vary depending on the environmental context of the caller, including whether they are in inshore or offshore waters (Lewis et al. 2018). Analysis of the songs of Sri Lankan blue whales found decreases in frequency that were inconsistent between song units and it was postulated that these changes were not a result of the Lombard effect but rather that each unit of the song contains information about the caller and thus is subject to selection pressures (Miksis-Olds, Nieukirk, and Harris 2018). Other studies have used song length to assign song to individual animals, suggesting an individual level of variability in song production (Sirovic, Hildebrand, and Wiggins 2007). The ability of blue whales to alter their behaviour in response to their environment is a recurrent theme across a number of studies, including depth dependent changes in singing behaviour to maximise efficiency (Lewis et al. 2018), potential changes in source level in response to higher ambient noise conditions (Sirovic, Hildebrand, and Wiggins 2007), and changes in foraging behaviour in response to prey availability (Hazen, Friedlaender, and Goldbogen 2015). The songs of the eastern Indian Ocean pygmy blue (EIOPB) whale (*Balaenoptera musculus brevicauda*) are not as complex but are comprised of a similar hierarchical structure with individual song units combined in phrases and repeated in songs which comprise one or two repeated phrases (Chapter 4). Despite varying levels of complexity, it has become apparent that there is variability in the production of song within blue whale populations (Sirovic et al. 2017; Lewis and Sirovic 2018). Given that this variability occurs over shorter timescales than would be possible for genetic drivers to act, it is likely song learning is under cognitive control (Galef 2001).

The neural pathways involved in song production and vocal learning in cetaceans have not been mapped as they have in birds and humans so we can only hypothesise based on what we know of other animals and human language (Garland, Rendell, Lamoni, et al. 2017; Webb and Zhang 2005). Vocal learning has been described for many taxa of animals, with studies demonstrating this ability in gibbons, bats, birds, hyraxes, mice, birds, bats,

elephants, humans, cetaceans and pinnipeds (Garland, Rendell, Lamoni, et al. 2017; Janik and Slater 1997; Janik and Slater 2000; Galef 2001; Rendell and Whitehead 2001; Webb and Zhang 2005; Mori, Liu, and Wada 2018; Koren and Geffen 2009, 2011). Rapid change in vocal behaviour including changes in song structure and phrase composition indicates that song production in blue whales is a behavioural rather than genetic trait that requires the ability to vocally learn (Sirovic et al. 2017; Lewis and Sirovic 2018). In addition, it is possible that vocal behaviour may vary between animals of different age/sex/class and contain biological information about the singer as has been observed in rock hyraxes (Koren, Mokady, and Geffen 2008; Koren and Geffen 2009, 2011; Demartsev et al. 2014). The processes that govern EIOPB blue whale song production are poorly understood, therefore an in-depth analysis of fine scale song variability may contribute to the overall understanding of song production in this population. Based on the large degree of variability in the EIOPB song type, including variable temporal structure and phrase structure, it is suspected that song production may be variable at the individual level. This paper will investigate song parameters of the EIOPB in depth across one sample year to look for fine-scale differences in signal production between song events. Further, variability in the prevalence of song structures, temporal structure and unit breaks will be looked at across the sample year to investigate whether it is plausible that EIOPB may exhibit behavioural plasticity in song production with the ability to shift between song structures rather than being constrained to producing one song variant based on the timing and occurrence of song variability.

### 8.3 Methods

#### Data Collection

Data were collected from the Perth Canyon, a submarine canyon off the west coast of Rottnest Island, Western Australia (Figure 8.1). The Perth Canyon is a hot spot of productivity that is known to support an annual feeding aggregation of pygmy blue whales between the months of March and June (Rennie et al. 2009a). In 2017, a Curtin University CMST-DSTO sea noise logger, or acoustic receiver (McCauley et al. 2017) was deployed at a depth of 430 m on the seabed with a decoupling from the main mooring by a ground line twice the water depth. The receivers were retrieved through use of an acoustic release attached to a dump weight. Sample rate was set at 6 kHz, roll off applied below 8 Hz, and a

low pass cut off filter at 2.8 kHz. The sampling regime was programmed to record 500 s of sea noise every 900 s.

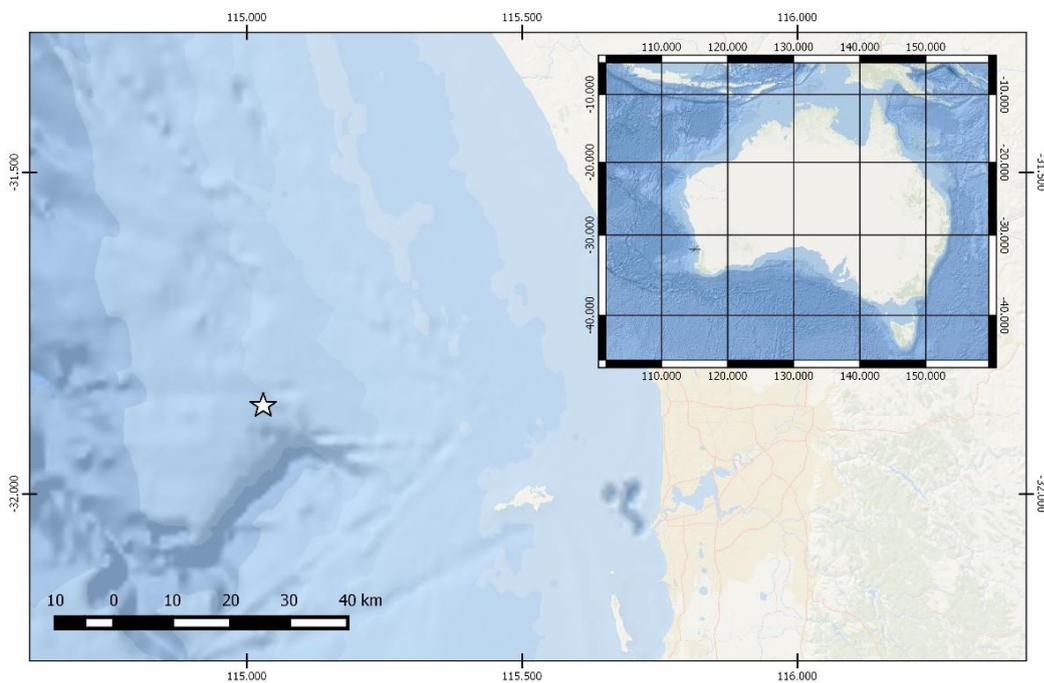


Figure 8.1 Data collection location for 2017 from the Perth Canyon, Western Australia. Inset; Location of the Perth Canyon with respect to Western Australia. Map produced using ESRI world ocean base map 2018.

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### Data Processing

Pre-processing of data was carried out in the MATLAB environment with a specialised GUI to manually view ambient sound recordings. Spectrograms were produced with a 16,384 point fast Fourier transform (FFT) and a 0.8 overlapping Hanning window, giving a frequency and time resolution of 0.342 Hz and 0.5865 s, respectively. EIOPB songs events were classified in accordance with the classification system described in Chapter 4 and song catalogue provided in Appendix 1.

### Data Analysis

Data were analysed in MATLAB to assess the variability in temporal structure and frequency of songs. Song units from the same song sequence, indicative of an individual vocalising animal, were measured where possible (see Chapter 7 for details of how these measurements were taken). Follow line analyses were carried out to identify individual variability in the production of the second unit of the characteristic EIOPB song type. An algorithm was used to follow individual signals in a spectrogram named “follow line analysis”. The algorithm uses a predefined set of parameters to follow the signal in frequency and time dimensions. The first of these parameters, distance X is set at four to five times the spectrogram time resolution, and the second, distance Y is set at four times the spectrogram frequency resolution. The algorithm uses the square root of the sum of these values to compute the maximum ‘distance’ it can look forward from a manually defined starting point in the spectrogram. Parameters of angles to look in are specified to limit the rate of frequency change allowed. The angles used are specific to the call type and uses a compass rose (where 0° is vertical in the spectrogram) to define the minimum and maximum angle in the change of signal frequency that the algorithm will look for. For EIOPB songs this was set at 30° and 95° respectively. The final value to be entered is a dB value (5 dB was used in this study). The routine asks for an area definition, encompassing the time and frequency range of the entire signal, plus a small amount of surrounding background noise. The median spectral level within the box is found and any points which fall within the specified angle bounds and ‘distance’ forward in time, which exceed the dB value are scored as 1. If any such values are found the algorithm moves to the next point in time found, following the first time point found at the lowest frequency with a score of 1, and repeats the search, until no more suitable points are found. The points located thus ‘follow’ the spectral line in time and frequency.

Follow line analysis were used to assess the frequency modulation in the upper and lower primary harmonics of the second unit of the EIOPB song type.

For broken song units, the length of the break or pause in song units was measured, as well as the frequency change in the broken units. Songs with broken units were classified into one of six categories to quantify variability in song unit production (Table 8.1).

Table 8.1 Song classification codes for song structures with broken units.

Phrase Code	Type I unit	Type II unit	Type III unit	Description
0				No broken units
1				1 <sup>st</sup> unit broken only
2				2 <sup>nd</sup> unit broken only
3				3 <sup>rd</sup> unit broken only
4				1 <sup>st</sup> & 2 <sup>nd</sup> unit broken
5				2 <sup>nd</sup> & 3 <sup>rd</sup> unit broken
6				All 3 song units split

The length, starting and peak frequency of the type II song unit were manually extracted from the spectrogram, along with the song repetition interval (ISI), defined as the time between successive type II song units within a song sequence. Song units were selected from within and between song sequences in order to compare similarities and differences in unit production. Song units were only classified as being from within a song sequence if they were within the same sample to avoid making assumptions regarding the continuity of singing across samples. It is important to note that signals from adjacent samples may be produced by the same animal however they were not assumed to be for this analysis. Each song unit within the spectrogram was assigned to a category based on its appearance in the spectrogram. There were four categories, N/A meaning not present, *n* meaning normal, *s* meaning unit split, and *b* meaning unit break. The *s* and *b* categories were defined to distinguish between song units that had a short pause of less than 4 s, classified as a unit split (*s*), and those that had a longer pause of 5 to 8 s classified as a unit break (*b*). An

additional variable, break frequency (Hz), was also used for songs with unit breaks/splits to describe the variability in frequency within the song unit. Unit breaks/splits where the unit frequency remained constant when signal production resumed were classified as 1, while those whose frequency post unit break/split decreased, returning to the starting frequency of the unit were classified as 0. This element of unit breaks/splits was deemed important to measure as it appears to represent a progression in the song variations from previous years and appeared on first observation to delineate between splits and breaks, along with the length of the break.

Follow line analyses were plotted to visualise frequency change over time for the first and third harmonic. This was compared to ISI and the length of the second song unit to look for patterns in timing and frequency of song production. The frequency curves from follow line analysis output were sampled at constant time spacing between 24 and 57 digital sample points. The variance in frequency was compared at each of these points between successive signals from the same animal and signals from random samples. The variance across a signal was averaged and a paired, two sample t-test conducted in R to determine whether there was any statistical difference between signals from song assumed to be produced by the same, and different animals.

## 8.4 Results

A total of 933 song events were analysed and classified to song structure in this study. Song events suitable for analysis were detected between March and June for the 2017 season and were classified to one of five song structures. All three common song variations, *P3*, *P2* and *P1* were present in the data set (Figure 8.2). Combination or 'hybrid' songs, where two phrase types were repeated were also present, with many *P3A* songs and fewer numbers of *P2A* songs. No *P3B* pattern songs were detected in this sample year (see Appendix 1 for description of hybrid song types). The shortest song variant, *P1*, was only detected in April and May, the two months when pygmy blue whale songs are most commonly recorded. February, March and June had the highest relative numbers of *P2* songs compared to other sample months. The presence of combination song patterns was linked to months with the highest number of song events which as expected, had the highest levels of song diversity (Figure 8.2). The number of song events with unit breaks was highly variable through the sample year. The most common patterns observed were a unit break in the first unit of a *P3*

song, which was most commonly seen in April, or a break in the second unit of the song, which was most common in June (Figure 8.2). Unit breaks in the second and third units of the same song were also relatively common and observed in February, April and May (Figure 8.2). Song events with unit breaks in all three song units were rare and occurred only in May and June. Almost no song events contained unit breaks in March, as opposed to June in which approximately 70% of all song events had a unit break. The pattern of unit breaks varied between months with no more than three variations occurring in any one month (Figure 8.2).

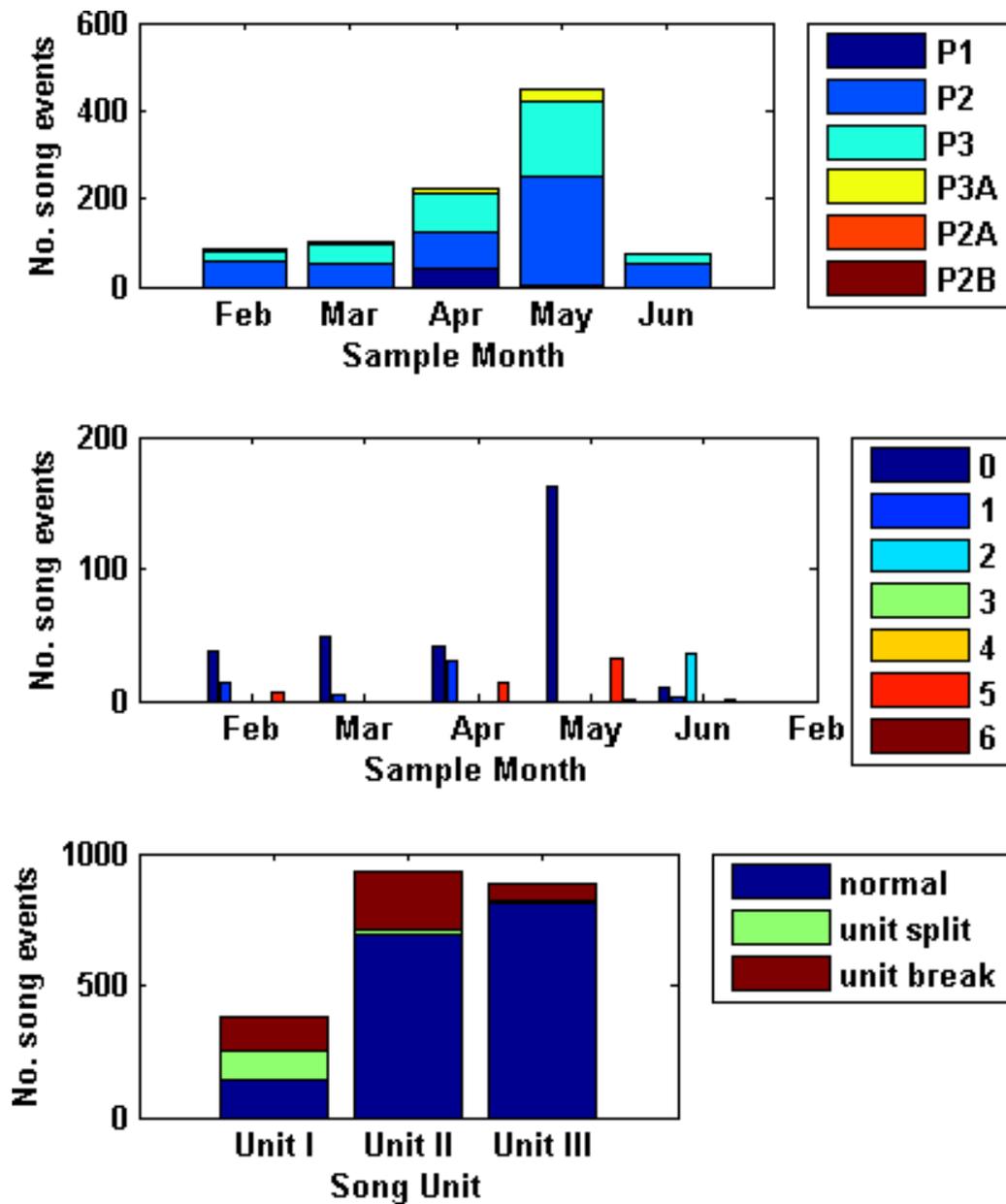


Figure 8.2. Top: Detected song events by song type for each month of the 2017 pygmy blue whale season. Centre: Occurrence of broken song variants, separated by pulse code across the sample months of the 2017 pygmy blue whale season. Bottom: Appearance of each song unit, classified as normal, split, or with a unit break for each song unit in all classified song events.

The appearance of each unit within the signal spectrogram was described as normal, split (pause of  $\leq 4$  s) or broken (pause of  $\geq 5$  s). The first unit of the EIOPB song type, whilst the least common unit across all song events was the most susceptible to unit splits and breaks (Figure 8.2). The second unit was the most common as it is a part of the structure of all song variants and was also subject to a reasonable degree of variability, though more often contained unit breaks as opposed to unit splits (Figure 8.2). The third unit was the least variable and only contained unit breaks or splits on rare occasion, and only when other units of the same song event also contained unit breaks or splits (Figure 8.2).

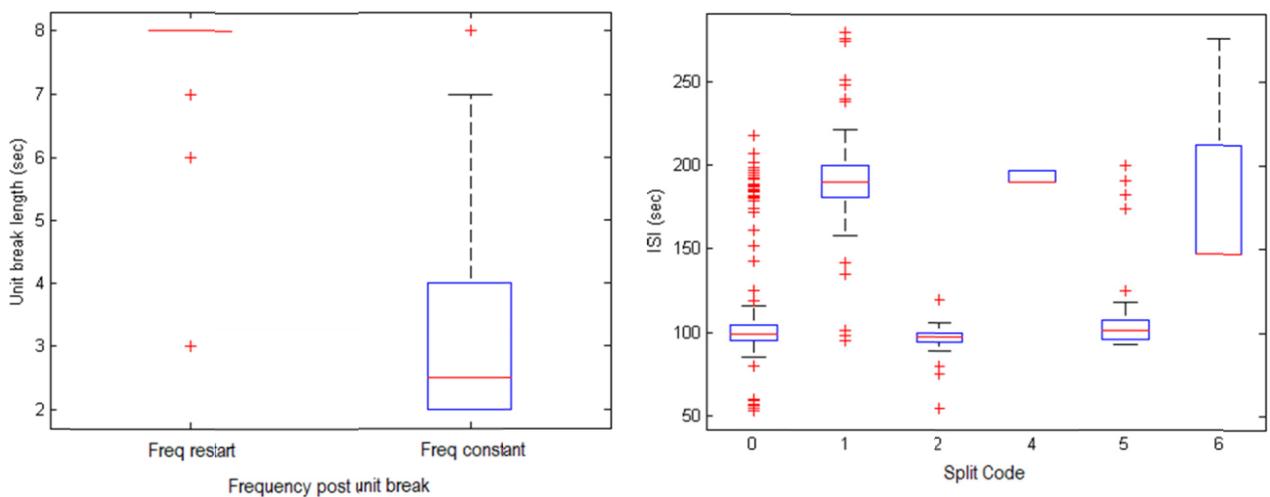


Figure 8.3. Left: Length of unit break for song units where frequency is maintained after the unit break ( $N=225$ ), or frequency restarts at unit start frequency after break ( $N=28$ ). Right: Influence of unit breaks on ISI, for split code 0 ( $n=493$ ), 1 ( $n=197$ ), 2 (151), 4 (16), 5 (57) and 6 (17).

Song length has been found to be variable within the EIOPB whale song type and unit breaks add an additional level of complexity to the temporal structure of songs. The length of the unit break was observed to have a relationship with the appearance of unit II in the frequency domain (Figure 8.3). Unit breaks less than 7 s generally had a constant frequency (Figure 8.3) so that the second unit appeared normal aside from a pause in the signal. On the contrary where the unit break lasted for 8 s, the frequency of the signal when it resumed generally dipped to the starting frequency of the unit (Figure 8.3), giving the impression of two short unit IIs in sequence (Figure 8.4). When assessing the impact of unit breaks on the overall song length (ISI), it is evident that the location of the unit break within

the song plays a large role. Songs with a unit split or break in the first song unit, which includes those with pulse codes 1, 4 and 6, were on average longer than those with no unit breaks (Figure 8.3). Conversely, where unit breaks occurred only in the second and/or third song units (pulse code of 2 or 5), there was minimal effect on the overall song length as compared to songs with no breaks (Figure 8.3).

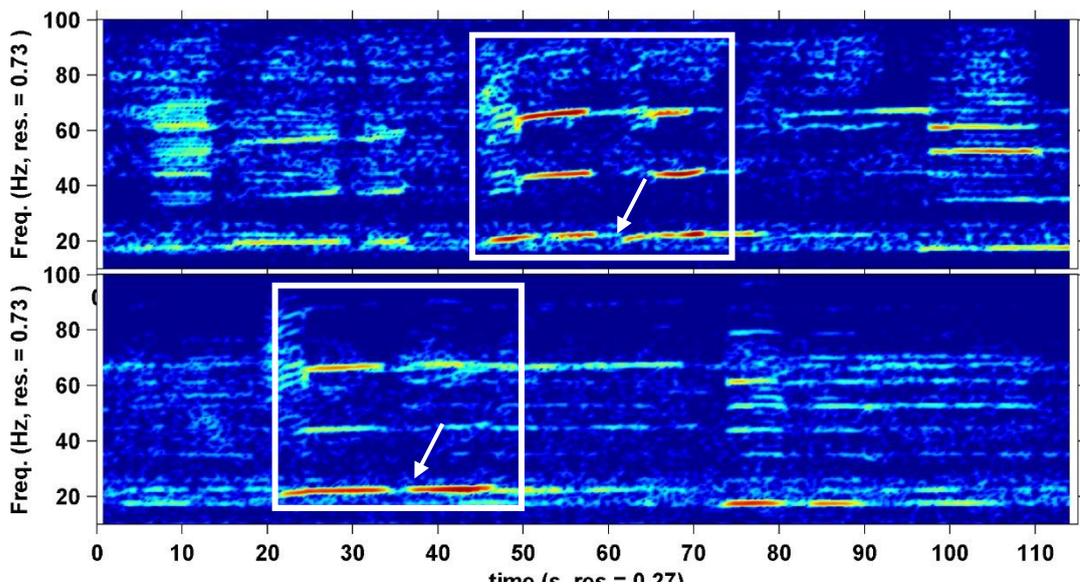


Figure 8.4. Spectrograms showing frequency restarting after the unit break to the start frequency of the unit constant (top) and constant frequency after a break in the second song unit (bottom). Both spectrograms from the 2017 Perth Canyon dataset. Spectrograms produced with a frequency resolution of 0.73 Hz.

The relationship between the length and peak frequency of unit II was investigated using linear regression. Despite there being a weak negative linear relationship, there was a significant correlation (Spearman's  $R^2=0.18$ ,  $n=932$ ,  $p < 0.001$ ) between the length of unit II and the frequency of unit II (Figure 8.5).

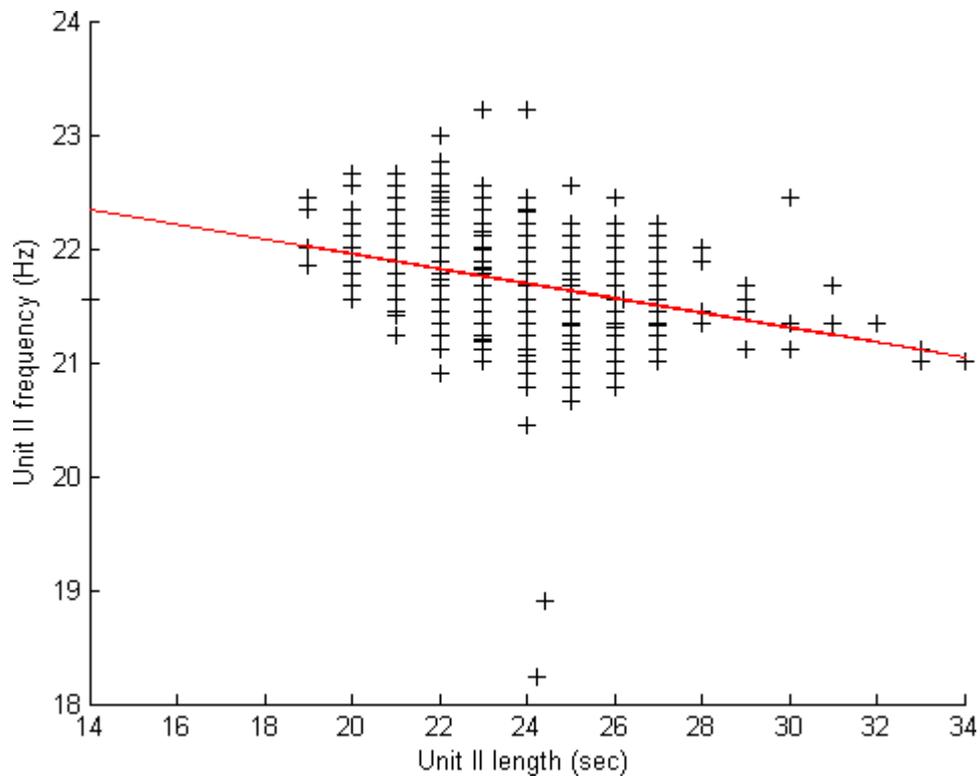


Figure 8.5. Relationship between the length and frequency of unit II signal (N = 932)

Follow line analysis allowed for a comparison of the variability in the production of individual unit IIs. Follow line analyses were conducted on a total of 211 type II song units. It is evident that a great degree of variability exists in the production of song units, aside from length and frequency (Figure 8.6). This includes the rate of change for frequency, measured as the angle of the line, as well as the curvature of the line itself (Figure 8.6). Such variability indicated that there may be the potential for future analyses to identify individual animals from their signal production (Figure 8.6).

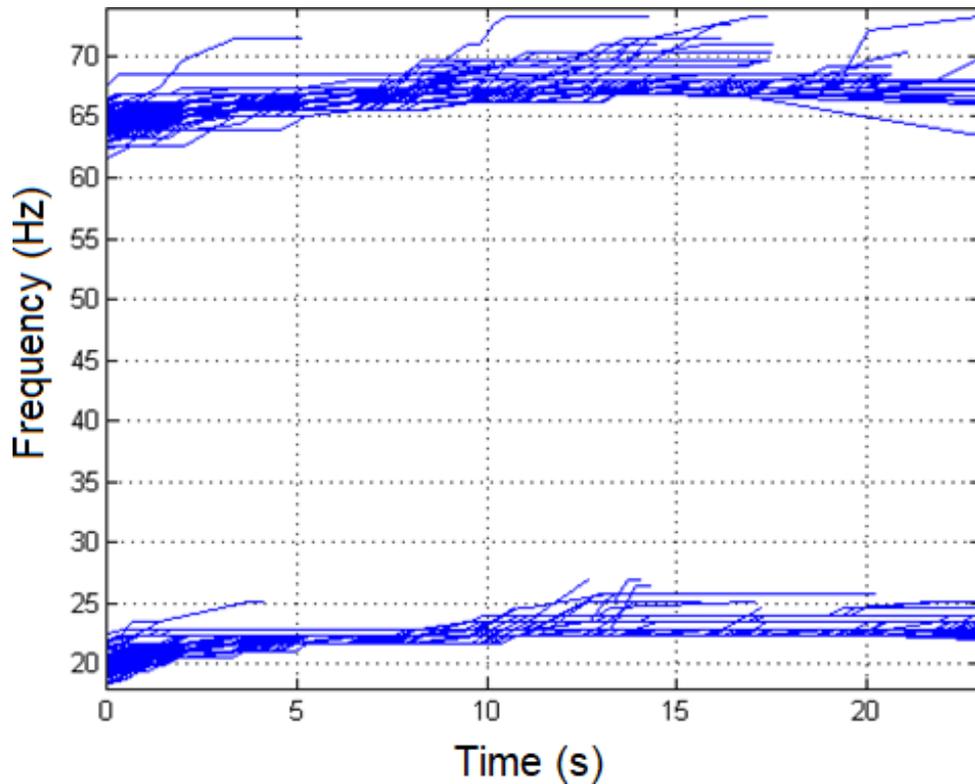


Figure 8.6. Follow line analysis for unit II of the EIOPB song type ( $N = 211$ ), lines represent unit II spectrogram contour for signals within and between singing bouts. The frequency curve of the upper harmonic ( $\sim 70$  Hz) and fundamental frequency ( $\sim 20$  Hz) harmonic are plotted for the duration of the signal showing variability in individual signal production. The time scales for all signals have been zeroed to the starting point selected. Lines represent individual signals to demonstrate that there is variability in the production of unit II.

A comparison of the follow line analysis for signals believed to be from the same vocalising animal based on spectrogram appearance and occurrence within the same sample were plotted (Figure 8.7). Unit breaks were found to confound the analysis by causing jumps in the spectrogram contour line reflecting limitations of the follow line algorithm that could not follow a spectrogram where there was a break in the signal production. There appears to be less variability in the frequency curves of signals that are likely from the same animal (Figure 8.7), than those that are from different animals, as is shown by the variability in lines in Figure 8.6. This is visually indicated by a comparison of Figure 8.6 and Figure 8.7, where the former shows the difference in curves from all signals, including those from signals within and between singing bouts, and the latter shows the similarity in signal frequency and time curves for signals from the same song event assumed to be the same individual.

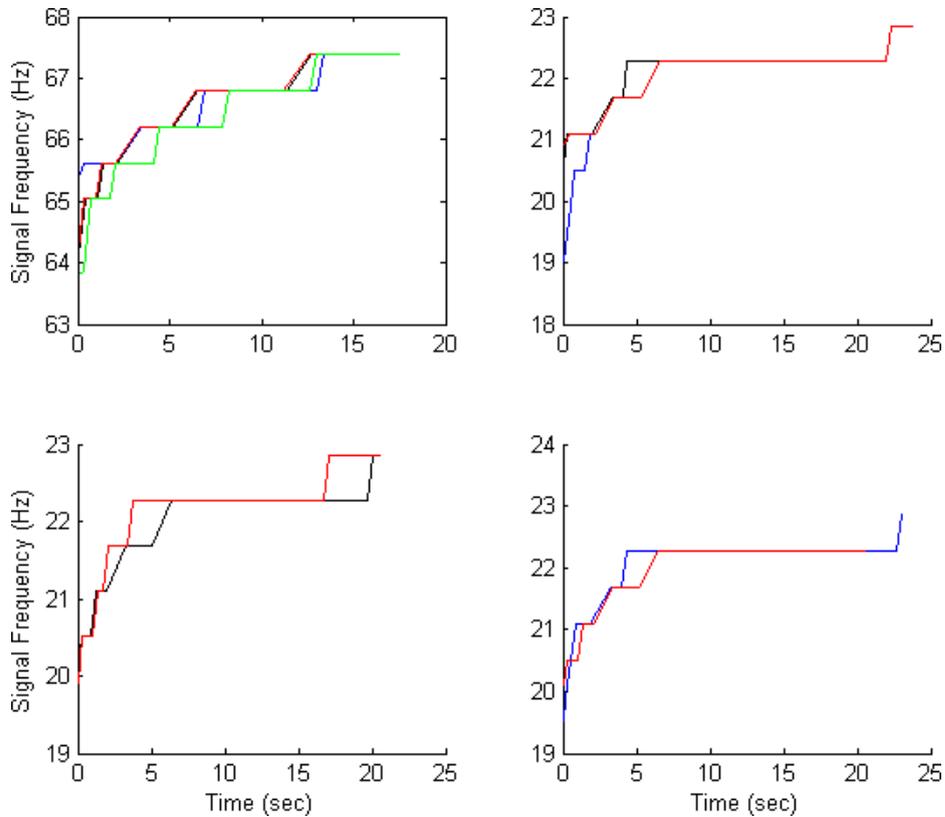


Figure 8.7. Follow line analysis of the unit II signal showing the fundamental frequency ( $\sim 20$  Hz) of type II unit. Each panel represents what is suspected to be a different vocalising animal with each coloured line representing a signal from the same song sequence (Top left  $N = 4$ , top right  $N = 3$ , bottom left  $N = 3$ , bottom right  $N = 3$ ). The time scales have been zeroed for the fundamental frequency and harmonic signals.

Statistical analysis of the frequency change across a signal revealed that signals from what was believed to be the same singing animal varied by an average of 0.182 Hz ( $SD \pm 0.165$  Hz,  $N=76$ ) at any point in time, while signals from random samples at any point in time varied by an average of 0.365 Hz ( $SD \pm 0.160$  Hz,  $N = 259$ ). The frequency difference at a point in time between signals assumed to be produced by the same animal and signals from random samples was highly statistically significant ( $p \ll 0.001$ ).

## 8.5 Discussion

### Individual variability in songs

Detailed analysis of the variability in song production within one season indicates that differences in song production may exist at the individual level within the EIOPB whale sub population. Follow line analysis conducted on the type II song unit of the EIOPB song type, revealed discrete differences in the frequency and temporal domains of unit production. Further, comparison of signals from within a single song sequence indicates a more consistent frequency curve than is seen between signals from all song sequences. Individuality in song production has been observed in rock hyraxes whose songs contain information about their own status and identity (Koren, Mokady, and Geffen 2008; Koren and Geffen 2009, 2011). Individual differences in signal production would represent the potential for individual templates to be used to identify animals acoustically. However, a better understanding of the potential for individual song production to vary over time is needed. Given long term trends in frequency decline, the stability of these curves with regards to starting frequencies is unlikely, although the rate of change within the unit (Hz/s) may be consistent across sample years. The conduct of studies utilising short duration acoustic tags across multiple seasons would be necessary to confirm whether individual unit production remains stable over time.

It cannot be discounted that each unit of a song may contain information about different aspects of the animal's behaviour, condition or physical/cognitive attributes, as is believed to be the case in humpback and North Pacific blue whales (Lewis and Sirovic 2018; Dunlop 2017). The high level of variability in phrase structure, such as the regular absence of unit I, suggests that different units may contain different information or be essential for different purposes. It is commonly suggested that increased song complexity may indicate a higher quality signaller (Galef 2001; Rendell and Whitehead 2001; Smith 2014). This is thought to be the case for humpback whale populations, where song is known to function as a mating display, with females proposed to favour high levels of complexity as an indicator of cognition and favourable genetics (Herman 2017) and song also serves a purpose in mediating male-male interactions (Cholewiak, Cerchio, et al. 2018). This may explain the appearance of shortened type I and III units within song phrases, as an attempt to maintain complexity while increasing signal production efficiency. Variability in the production of unit I has the largest impact on song variability in the temporal domain. Variability in unit

breaks influences the appearance of type II units in the frequency domain and represents a progression towards what may in the future represent a change in song structure with unit II signals repeated in sequence mid song. The second song unit appears to be the most fundamental, appearing in all song variations and being the most transmissible in poor noise conditions. This is of particular importance as background noise levels continue to increase, largely as a result of increased density of vocalising animals (McCauley et al. 2018 and Chapter 7). Given that unit II is the most easily detectable unit (McCauley, Bannister, Burton, Jenner, and Rennie 2004), it likely holds importance for intraspecies communication, thus it is possible that splitting the type II unit is an energetically efficient way of increasing the chance of being heard by conspecifics.

It is not only the units of a song themselves that have the potential to convey important information about an animal. Temporal variability, influenced by unit breaks within and between units, also has the potential to communicate information about an individual or group of animals. This may relate to environmental conditions (Lewis and Sirovic 2018; Morano et al. 2012) or portray something about the animal such as social status or quality (Dunlop 2017; Ronald et al. 2015; Koren, Mokady, and Geffen 2008; Koren and Geffen 2009, 2011; Ilany et al. 2013). However, if changes in unit break, song length and song production reflected changes in environmental conditions, then there would likely be differences in song production observed between sample months due to seasonal fluctuations in environmental conditions. Unit breaks, measured through the comparison of song pulse codes across sample months were found to be variable between sample months, indicating that the splitting of any song unit into two could be used to portray something about the environment at the time. However, interpretations of variability in any element of song production over time are confounded by the likelihood that different groups of animals will be moving through the area of the receiver array at that time. Given the proposed social context of song, as a means of attracting mates and mediating interactions with conspecifics, it is likely that songs may vary between cohorts of animals passing through the area. This may include variability between the age/sex/class of animals utilising the region at different times.

Variability in the temporal structure of songs has been observed in a number of cetacean populations, including humpback and fin whales (Sirovic et al. 2017; Oleson et al. 2014; Kello et al. 2017). Alongside the worldwide decline in the tonal frequencies of blue and fin whale song, there has also been notable change in song length for many species (Leroy et al. 2018; Gavrilov, McCauley, and Gedamke 2012; Miksis-Olds, Nieukirk, and Harris 2018).

The findings of this study indicate that there may be a link between the temporal and frequency domains of signal production in the EIOPB whale song regardless of song structure. Similarly, a long-term increase in inter-pulse-interval (IPI) for fin whales has been observed that persists despite distinct changes to song type (Morano et al. 2012; Sirovic et al. 2017; Weirathmueller et al. 2017). Further, variability in song and song length has been linked to changes in environmental context, including water depth, as seen in population of blue whales off southern California (Lewis and Sirovic 2018). The potential for water depth to influence song production or potentially the physical mechanisms underlying it, suggests that factors underlying song transmission provide a stimulus for song variability. Based on models for sound production in baleen whales, it is possible that dive depth and time, as well as physical properties of the water column including temperature and pressure may influence song production (Reidenberg and Laitman 2018; Adam et al. 2013; Tervo et al. 2011).

#### Cultural and social context

Singing behaviour in whales is traditionally considered to be a mating signal, used by male animals to attract females (Herman 2017; Herman et al. 2013), though is increasingly being demonstrated to have a role in mediating male-male interactions (Darling, Jones, and Nicklin 2006; Herman 2017; Cholewiak, Cerchio, et al. 2018). It is postulated that song has an important role in what may be a lekking system of mate selection, with females choosing prospective mates based on the quality of the attributes singing portray (Herman 2017; Wiggins et al. 2015). For widespread, long-ranging vocal animals in an underwater world, song is the most likely trait upon which female selection may act. Numerous studies across a number of taxa, particularly songbirds, indicate that females generally show a preference for more complicated and intricate mating displays, and it is likely a similar preference extends to song (Benedict and Warning 2017; Herman 2017; Wiggins et al. 2015; Janik 2014; Smith 2014; Lachlan and Nowicki 2015; Lachlan, Ratmann, and Nowicki 2018; Creanza, Fogarty, and Feldman 2016; Osiejuk 2014; Ward, Speakman, and Slater 2003; Kello et al. 2017). The ability to remember and repeat complex songs indicates cognitive fitness which would be a favourable trait for animals that live in a highly variable environment.

Studies on the singing behaviour of humpback whales have proposed that long term stability in song types is achieved through the desire of animals to conform to the dominant song type (Rekdahl et al. 2013; Lachlan, Ratmann, and Nowicki 2018). Termed the

conformity bias, this would suggest that animals are more likely to copy the majority, which leads to wide scale song changes (Lachlan, Ratmann, and Nowicki 2018; Rekdahl et al. 2013). Over time, this leads to stability within a population (Lachlan, Ratmann, and Nowicki 2018; Lachlan, Janik, and Slater 2004; Rekdahl et al. 2013). This bias towards conformity also drives highly precise learning which leads to a stability in song units that rivals the stability of human cultural traditions (Lachlan, Ratmann, and Nowicki 2018). Conformity bias however does not explain the high levels of variability that are maintained in the EIOPB whale population. Should blue whales exhibit vocal plasticity, the ability to switch between complex three unit phrase songs in times of favourable background noise conditions, would present a benefit for mate attraction. Conversely, in times of poorer background noise conditions, such as when there is a lot of 'vocal traffic' from competing whales, it is possible that switching to a simpler two unit or one unit phrase song may provide an energetic benefit. Combination song structures may represent a trade-off between the benefits of longer more complex phrase types and shorter phrases that are more likely to be heard. In vocally busy times it is unlikely that the sound signal of the first unit of the phrase would be received by other animals, so it would be more energy efficient to produce as many type II units, the 'loudest' and most effectively transmitted unit, as possible in the hopes of being heard above other animals. This phenomenon has been observed in bird species that will preferentially choose signals that are transmitted over longer distances in periods of higher background noise (Benedict and Warning 2017). This may also explain the rapid proliferation of broken song units which are present in the highest proportions in times of peak pygmy blue whale presence. Splitting the type II unit in half may add favourable complexity to a song, while maximising the chance of the signal being transmitted. In cases where halves of the broken song unit appear to follow the same frequency curve as the whole unit over a compressed time frame, this may have the effect of being interpreted as two type II units. This may have implicit benefits for out competing other animals, attracting more potential mates, or warning away potential adversaries (Brunel-Pons, Alem, and Greenfield 2011; Cholewiak, Cerchio, et al. 2018). Further, should song units contain discrete information about the individual, the production of different song variants may be dependent on who is listening. Recent studies on humpback breeding grounds have shown that physical interaction and the proximity of male whales to other males has a significant impact on singing behaviour (Cholewiak, Cerchio, et al. 2018), a factor which is well studied in song birds (Creanza, Fogarty, and Feldman 2016; Moser-Purdy and Mennill 2016; Ronald et al. 2015; Lachlan and Nowicki 2015; Osiejuk 2014). Competition between whales often results in one animal ceasing singing behaviour or changing the sequence of the song

(Cholewiak, Cerchio, et al. 2018), indicating that social factors, including who else is 'listening', drive song production. Within the context of the EIOPB, it is suggested that increased levels of variability in song production, both temporal and structural, may be the result of competition between singing males, with song not only functioning as a mating display but communicating information about the quality of the animal itself.

## 8.6 Conclusion

Blue whales are generally not considered to be social animals, though male and female breeding pairs have been observed on breeding grounds (Oleson, Calambokidis, Burgess, McDonald, and LeDuc 2007; Oleson, Calambokidis, Barlow, et al. 2007). It is believed that males compete for females, so it is likely that females exert a selection pressure on males, which may influence social behaviours such as singing (Janik 2014; Wiggins et al. 2015; Cholewiak, Cerchio, et al. 2018). While large numbers of animals may aggregate in feeding areas, they usually travel at a distance to each other (Lomac-MacNair and Smultea 2016). For animals that disperse over such great distances, and are so often solitary, long range communication signals are of vital importance, not only for attracting mates but likely for assessing who is in the area. Further, what we consider to be solitary may not be so in the context of animals that can communicate over such great distances (Payne and McVay 1971), and thus songs may represent a form of communication with a purpose beyond solely attracting a mate. As seen in other cetacean species, birds and frogs, songs can be used to mediate interactions between conspecifics, which may be useful for avoiding conflict, or improving chances at reproductive success (Lucas, Howard, and Palmer 1996; Creanza, Fogarty, and Feldman 2016; Garland, Rendell, Lilley, et al. 2017; Kalas, Fiske, and Saether 1995; Wiggins et al. 2015; Dunlop and Noad 2016; Cholewiak, Cerchio, et al. 2018). Further, songs may contain information about the quality of an individual, from their size, to their cognitive capacity (Wiggins et al. 2015). In the EIOPB, the inclusion of unit I, and variability within unit I has the greatest influence on song length, though adds additional complexity to songs, suggesting a trade-off between favourable song production and energy efficiency. The high level of variability in song production that is maintained within the EIOPB population may suggest that the purpose of song is not solely for mate attraction, given it goes against theories of conformity bias for vocal populations. Consistent levels of variability across sample months indicates that animals may have the vocal plasticity to switch between song types under varying circumstances, rather than song type being solely linked to groups of passing animals. The continued evolution of the

EIOPB song type, seen most recently in the inclusion of unit breaks and splits. Unit breaks may represent a novel way to increase song complexity and improve the chance of unit II signals being heard over long distances in increasingly noisy conditions, without additional energy expenditure. The variability in signal production seen within one song unit indicates that animals may have distinct 'voices', though further analysis will need to include some form of visual or genetic identification to confirm this. Further, decreases in tonal frequency appear to be correlated to unit length, with the possibility that changes in time and frequency domains may be adaptations to a changing environment.

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## Chapter 9 General Discussion

### 9.1 Understanding the vocal behaviour of the EIOPB whale

#### The pygmy blue whale

Throughout the nineteenth century, populations of blue whale were decimated by the whaling industry. Their enormous size made blue whales a prized target for whalers who could yield large amounts of oil and meat from one animal (Thomas, Reeves, and Brownell 2016; Tulloch et al. 2018). Unlike other species, such as the humpback whale, whose populations have rebounded to near pre-exploitation levels under the protection of the International Whaling Commissions 1982 moratorium on whaling, the recovery of blue whale populations is believed to be slow (Attard, Beheregaray, and Moller 2016; Thomas, Reeves, and Brownell 2016; Tulloch et al. 2018). For many sub populations of pygmy blue whale, which were only identified as a sub population at the end of the whaling era, population status remains largely unassessed (Ichihara 1966; Thomas, Reeves, and Brownell 2016; Reilly et al. 2008). Further, given that throughout the whaling era most pygmy blue whales were assumed to be the same as Antarctic, or 'true' blue whales, there exists little data on the pre-exploitation population levels (Branch, Stafford, et al. 2007; Zemsky and Sazhinov 1982). Although recently Branch (2018), has attempted to split catch data amongst sub populations in order to provide population specific information on the effect of whaling on blue whale sub-populations (Branch, Monnahan, and Sirovic 2018).

The paucity of knowledge on pygmy blue whale population numbers makes their current population status and health difficult to assess, which has led to a listing of 'data deficient' on the IUCN red list (Reilly et al. 2008), while the Antarctic blue whale is listed as critically endangered (Thomas, Reeves, and Brownell 2016). As recently as 2012, it was believed that global blue whale stocks remained 98 % depleted, with potentially fewer than 10,000 animals world wide (Thomas, Reeves, and Brownell 2016; Tulloch et al. 2018). Assessment of blue whale abundance is complicated by their broad distribution, preference for deep offshore waters, and cryptic nature, making them difficult to survey visually. Acoustic surveys have led to the discovery of several distinct sub populations of blue whale, including Antarctic blue whales, and four populations of pygmy blue whale separated by song type (Samaran et al. 2013; Stafford et al. 2011; Samaran et al. 2008; Ljungblad, Clark,

and Shimada 1998; McDonald, Hildebrand, and Mesnick 2006). The song types, termed Australian, Madagascan, New Zealand and Sri Lankan (McDonald, Hildebrand, and Mesnick 2006; Samaran et al. 2013; Buchan et al. 2014; Balcazar et al. 2015) have been used to identify the distribution of sub populations (Stafford et al. 2011; Samaran et al. 2008; Barlow et al. 2018; McDonald, Hildebrand, and Mesnick 2006). There appears to be little overlap between sub populations of pygmy blue whale leading to geographically isolated, and largely genetically restricted breeding populations (Attard et al. 2015b). While interbreeding between Antarctic and EIOPB whales has been identified (Attard and Moller 2013), a low level of genetic diversity has been observed within the EIOPB whale population (Attard, Beheregaray, and Moller 2016; Attard et al. 2015b), leaving this population potentially vulnerable to long term environmental change as we would expect less genetic diversity for natural selection and adaptation to act upon. It is likely that other populations of pygmy blue whale also exhibit low levels of genetic diversity, making them vulnerable to environmental change (Attard, Beheregaray, and Moller 2016). Given the potential lack of genetically adaptive capacity within the population, the importance of effective management and conservation for the EIOPB whale population is of critical importance. There is a need for the abundance of EIOPB whales to be quantified, allowing for some form of assessment of the conservation status of pygmy blue whales. Visual surveys are expensive, time consuming and challenging for open ocean species highlighting the importance for the development of acoustic techniques to assess populations.

#### The role of acoustics

Traditionally, methods for assessing abundance with acoustic techniques involve counting the number of acoustic cues, defined as a focal element of a song or signal, within a set period of time to count the number of animals present (Marques et al. 2013). These methods require a detailed understanding of the production of vocal cues and rely on consistency in cue production across a population. Further, unless such methods include tracking, then they assume that animals pass through the focal area rather than lingering (Caillat, Thomas, and Gillespie 2013; Marques et al. 2013). The fundamental objective of this thesis was to contribute to a greater understanding of the vocal behaviour and movement of the EIOPB whale on two feeding grounds off the coast of Australia, to improve the efficacy of future acoustic population assessment. The primary focus was on the behaviour of whales in the Perth Canyon, Western Australia, where they are known to aggregate to feed from late February through to June (Double et al. 2014a; Gavrilov and

McCauley 2013; Rennie, Hanson, McCauley, Pattiaratchi, Burton, Bannister, et al. 2009). A second feeding ground, off the coast of Portland, Victoria, provided a secondary area of interest to investigate the vocal behaviour of this population (Tripovich et al. 2015).

Initial assessment of acoustic data revealed a high level of variability in the song type of the EIOPB whale (Chapter 4). Rather than solely producing a song of repeated three unit phrases, a number of variations, including a two unit and one unit phrase were identified along with combination song patterns (Chapter 4). However, the second song unit (unit II) was found to be common to all phrases of the EIOPB song type. The description of these new phrase and song structures represented a new understanding of the level of variability in the song production of blue whales that until now have been considered to produce only stereotyped song structures. Such a discovery raises questions about the vocal behaviour of other sub populations of blue whales around the globe, suggesting future research directions for other populations. The discovery of variable song structures has implications for existing acoustic assessments of abundance, though builds on the existing understanding of EIOPB song structure providing information to better inform future acoustic abundance estimates.

### Variable vocal behaviour

Based on the level of variability in song structure that was uncovered, analysis was undertaken to quantify whether differences existed in vocal behaviour between geographically separated sample sites. Similar levels in song variability were found at each sample location, confirming that animals at different feeding grounds belong to the same breeding population of pygmy blue whales. This behavioural assessment supports the findings of recent genomic analysis indicating that animals from the same population spread across the two feeding grounds (Attard et al. 2018). Further, such a finding would suggest that variability in vocal behaviour does not have a genetic basis, which is supported by the rapid occurrence of new unit and phrase variations. There was however found to be a difference in the prevalence of major song types between sample sites. The Perth Canyon, which plays host to a larger number of whales at a given point in time, had an overall dominance of shorter *P2* songs, while the Portland feeding ground had a higher proportion of longer *P3* songs. This finding indicates that population density or environmental variables may have some influence on song structure. A depth analysis for 20 km around each sample location found the Perth Canyon sample site to be on average

deeper than Portland, indicating a relationship may exist between water depth and song length, as has been observed elsewhere (Lewis and Sirovic 2018). Potentially there may be a behavioural link with song production, with the Bonney region of Portland known to be primarily a feeding ground for blue whales (Gill et al. 2011; Gill 2002), while the Perth Canyon may serve an additional social purpose as a way point on the northern migration (Gill et al. 2011; Gill 2002).

One of the most variable elements of song structure observed was song repetition interval (ISI). Measured as the time between successive type II units within a song, ISI was confounded by phrase and song structure, though appeared to adhere to formal rhythmic constraints. The length of a one unit phrase was half that of a two unit phrase, and the length of a two unit phrase was half that of a three unit phrase. Temporal rhythms are believed to be an inherent component of language, though only a few species of animal are believed to be capable of rhythmic perception (Handel, Todd, and Zoidis 2012; Tessmar-Raible, Raible, and Arboleda 2011). The conformity of the various song structures to what appears to be inherent temporal rules indicates that blue whales may be one of these species, and rhythm may be an important aspect in song variability (Kershenbaum et al. 2014). It has been hypothesised that song units and the spaces between them could potentially play a role in intra-species communication, conveying some sort of information regarding the quality or identity of an animal (Cholewiak, Cerchio, et al. 2018; Kello et al. 2017; Herman 2017; Koren and Geffen 2009, 2011). This was observed in the high variability of ISI between song events, as well as the variability in the temporal structure of type II song units between song events. While this variability was not found to be consistent with any monthly trends, indicating it is not relevant to specific cohorts of individuals or local environmental changes (Cholewiak, Cerchio, et al. 2018; Garland, Rendell, Lamoni, et al. 2017), annual trends in ISI were detected. When separated into song types, it appears that ISI is increasing within the individual phrase structures, while overall there is a shift towards the shorter two-unit song. The mechanisms behind these changes are not understood. However, increasing song length has been observed as a response to increased levels of background noise in other taxa (Hedwig et al. 2015; Benedict and Warning 2017; Job, Kohler, and Gill 2016). Levels of background noise were measured at the Perth Canyon and Portland sample sites in an attempt to explain the dominance of longer phrase types at Portland (*P3* song), and shorter phrase types in the Perth Canyon (*P2* song). A consistently higher level of background noise, due to a higher density of vocalising

EIOPB, was measured in the Perth Canyon than at Portland indicating that background noise is a plausible driver of the observed differences in song length.

Further investigation into the fine scale changes of song found a high degree of variability in the length of individual song units with trends in the length of song unit II within a sample year. These trends indicate that the length of unit II is increasing, while the frequency of the third harmonic of unit II is decreasing, with some correlation between the two. This same trend was observed within a sample year as well as over many sample years. This trend suggests a physical link between the temporal and frequency domains of song production. Whilst it has been proposed that the global decline in tonal frequencies of whale song is an adaptive response to increased anthropogenic noise, this hypothesis is an illogical conclusion for low frequency singers such as blue whales. For blue whales, a decrease in song frequency would put their songs further into the band of sea noise produced by increasing ship traffic.

One of many proposed alternative hypotheses for changes in song structure including declining frequency and song variability is increased population density. Increased population density would result in increased competition for mates, and likely result in a change in singing strategy, as has been observed in the behaviour of various species of frogs and birds (Herman 2017; Lucas, Howard, and Palmer 1996; Cholewiak, Cerchio, et al. 2018; Creanza, Fogarty, and Feldman 2016; Moser-Purdy and Mennill 2016; Ronald et al. 2015; Lachlan and Nowicki 2015; Sockman and Lyons 2017) Whale song is believed to have a reproductive function and females likely exert selective pressure through their selection in mates. Decreasing the frequency of song may portray the animal to be of a larger size than it is, portraying a high level of fitness and increasing their attractiveness as a potential mate (Kalas, Fiske, and Saether 1995; Brunel-Pons, Alem, and Greenfield 2011). Increased unit length may be a physical side effect of decreasing frequency. Alternatively, as has been observed in rock hyraxes, song length may vary depending on who is listening, with singing bout length and rate increasing in the presence of attentive listeners (Demartsev et al. 2014). The ability to alter the syntactical structure and complexity of songs in rock hyraxes in response to their environmental context and who is listening (Demartsev et al. 2014; Kershenbaum et al. 2012) suggests this capacity may have evolved in other species as well. While the order of EIOPB whale song units remains the same, in what appears to be a grammar like structure (Kershenbaum et al. 2014), the complexity of the song and rate of singing appears to be variable suggesting they too may demonstrate syntactic flexibility. Further research is needed to establish whether these variations occur in response to

audience effects or environmental context. It is possible that song units may portray other important information about the quality of an animal including cognitive fitness (Dunlop 2017; Ronald et al. 2015; Demartsev et al. 2014). Based on several studies across a number of vocal taxa, it is believed that females prefer complex vocal displays, potentially as they may indicate an animal with greater cognitive capacity (Herman 2017; Demartsev et al. 2014). Cognitive capacity could be an important quality for individual fitness, especially in migratory animals and those that live in highly variable environments (Mann 2017; Mitchell 2016; Sewall 2015). Further, genetic sequencing of cetacean brains indicates that the brains of mysticete whales are much more complex and recently evolved than previously expected (Webb and Zhang 2005; Ridgway and Van Alstyne 2017; Mitchell 2016; Marino 2002; Duffield, Haldiman, and Henk 1992). The presence of key vocal learning genes, such as the *foxP2* gene, indicates that mysticete whales are capable of vocal learning, like their odontocete counter parts (Li et al. 2007; Webb and Zhang 2005). If complex songs were preferred by females, then we would expect there to be an increase in three unit songs, yet there is a relatively stable proportion of song variations within the population (Creanza, Fogarty, and Feldman 2016; Wiggins et al. 2015; Janik 2014). Given that the second song unit has the best transmission in poor noise conditions, it is suspected that there is some sort of trade-off between producing longer, more complex phrase types and producing as many type II units as possible in an energetically effective way, with less complex and shorter phrase types. It is postulated that this balancing act between complexity and maximising effective signal propagation may explain the appearance of combination song patterns, shortened song units, and unit breaks within existing phrase structures. In the most recent sample years, a rapidly increasing number of songs with unit breaks were observed, where the type II unit is split into two, and at times resembles two shortened type II units instead of one. The rapid (within a season) appearance of new variations in phrase and song structure, as well as unit production provide further evidence that variable singing behaviour in blue whales does not have a genetic basis. Rather, it is more likely that blue whales are capable of vocal learning and exhibit vocal plasticity. This would suggest blue whales can alter their song production to suit the background noise conditions, as well as the present company. For example, in times of high vocal traffic, the focus may shift to producing songs that allow for more unit II's to be produced within a singing bout. In quieter times, the focus may be on singing more complex, longer three unit songs. Until now, the capacity for open ended vocal learning and vocal plasticity has been limited to humans, a small number of birds, dolphins, orcas and humpback whales (Dorado-Correa, Zollinger, and Brumm 2018; Filatova et al. 2015; Janik 2014; Mercado, Herman, and Pack

2005; Webb and Zhang 2005; Galef 2001; Rendell and Whitehead 2001). It is proposed that this ability may be wider spread than previously expected and given the well-defined singing and learning abilities of humpback whales (Garland, Rendell, Lamoni, et al. 2017; Kershenbaum et al. 2016; Cantor and Whitehead 2013b; Rendell and Whitehead 2001), it is highly likely that similar capacities exist in other mysticete whales, including blue whales.

## 9.2 Limitations

One of the major limitations in any study focused on the vocal behaviour of blue whales is a lack of understanding of the cue rates and behavioural context of vocalisations. The lack of information on the physiological (e.g. age/sex/maturity) and behavioural context of vocalising whales is a limiting factor in understanding how variability in vocal behaviour arises. In addition, tracking analyses of vocal pygmy blue whales relied on a set of assumptions that were used to define track criteria. These assumptions were based on sound biological knowledge garnered from previous studies of pygmy blue whales, and the methods of other similar studies. All attempts have been made throughout this thesis to limit assumptions in order to make sound scientific conclusions regarding the findings of the data. All findings from this thesis are directly applicable only to the eastern Indian Ocean sub population of pygmy blue whales and associated characteristic EIOPB song type. However, the findings may be indirectly applicable to other sub populations of blue whale by raising questions about the cognitive capacity and behavioural variability of the wider blue whale species complex.

## 9.3 Future directions

It is envisioned that the themes of this thesis will continue to be developed, with the intention of developing a robust acoustic method of assessing the abundance of the EIOPB whale sub population. Devising such a method on acoustic analysis alone is fraught with many uncertainties and consequently it is intended that the findings of this thesis will be combined with visual surveys in an attempt to accurately quantify the variability in vocal behaviour and census the population. The following recommendations represent the future

directions for this research that will allow for better assessment and management of this, and other populations of blue whales.

- Joint visual and acoustic study of pygmy blue whales in the Perth Canyon attempting to link visual and acoustic identification of individuals.
- Development of individual song templates based on spectrogram contours to identify individual animals from their songs, allowing for an assessment of the residency time of an individual animal in the canyon area.
- Cataloguing of song templates and photo identifications for future population assessment.
- Conversion of individual song templates into an acoustic mark-recapture model to measure abundance based on individual song templates, and modelling of detection range, population migratory range, and accounting for silent animals.
- In situ measurements of oceanographic properties in conjunction with acoustic studies to determine any possible influence of changing environmental variables on unit II length and frequency.

#### 9.4 Conclusion

This thesis has made an original and substantial contribution to the understanding of whale communication and vocal behaviour. Through the work contained within this thesis, it has become evident that blue whale songs exhibit a much greater level of complexity than previously believed. The findings of this thesis have been instrumental in highlighting variability in unit production, phrase and song structure, as well as potential relationships between the frequency and temporal domains of song production. It is postulated that these changes represent vocal plasticity in response to changing conditions in the physical environment, including increased background noise. Though notably, it would appear that it is the increase in background noise produced by many singing EIOPB, that most affects individual EIOPB singing behaviour. These findings are of critical importance to the assessment of acoustic abundance estimation techniques and will be useful for guiding future acoustic abundance studies. Future studies need to incorporate varied data including in situ oceanographic measurements and visual observations of behaviour to shed light on the blue whale communication system that goes beyond describing levels of variability and long-term change. Consequently, it is recommended that similar acoustic studies be carried

out on blue whale populations worldwide, as it is likely that similar levels of acoustic variability exist elsewhere impacting attempts for acoustic abundance estimation. Further, future studies on the eastern Indian Ocean population of blue whale should include concurrent visual surveys in order to visually and acoustically identify individual animals.

With continued focus on the instability of global climate, the health of small, genetically isolated populations of animals is of increasing concern. Genetic isolation in small populations decreases the capacity for species to adapt to environmental changes (Attard, Beheregaray, and Moller 2016). For an animal such as the blue whale, whose survival depends on the consumption of massive quantities of small krill, this instability is even more concerning. Zooplankton abundance and distribution is directly linked to primary productivity and the health of the oceans (Willis 2014; Munger et al. 2009). Oceanographic warming and calcium carbonate deficiencies threaten the ongoing productivity of these primary levels of the trophic cascade, which in turn support the largest animals in the world (Koelmans et al. 2017; Thorne 2005). Like all environmental cycles, the presence of blue whales is important for the health of ocean systems as their waste products recycle massive quantities of nutrients from the deep ocean to the photic zone, which feeds directly back into the system that supports them, and us (Willis 2014; Nicol et al. 2010). While forests are commonly believed to produce the oxygen that sustains terrestrial ecosystems and their inhabitants, it has been shown that photosynthesis by planktonic species is the largest contributor to oxygen production (Willis 2014; Nicol et al. 2010). Without oceans, the world cannot survive, and without whales, the systems upon which these oceans depend will fail. Thus, in the face of climatic uncertainty, it is more important than ever to derive accurate and thorough population assessment methods for these ecosystem engineers.

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Appendix 1

Signal Catalogue for the 'Australian' Song Type  
of the Eastern Indian Ocean Pygmy Blue Whale



Capri Beck

Robert McCauley

Alexander Gavrilov

Curt Jenner

Micheline Jenner

***Centre for Marine Science and Technology***

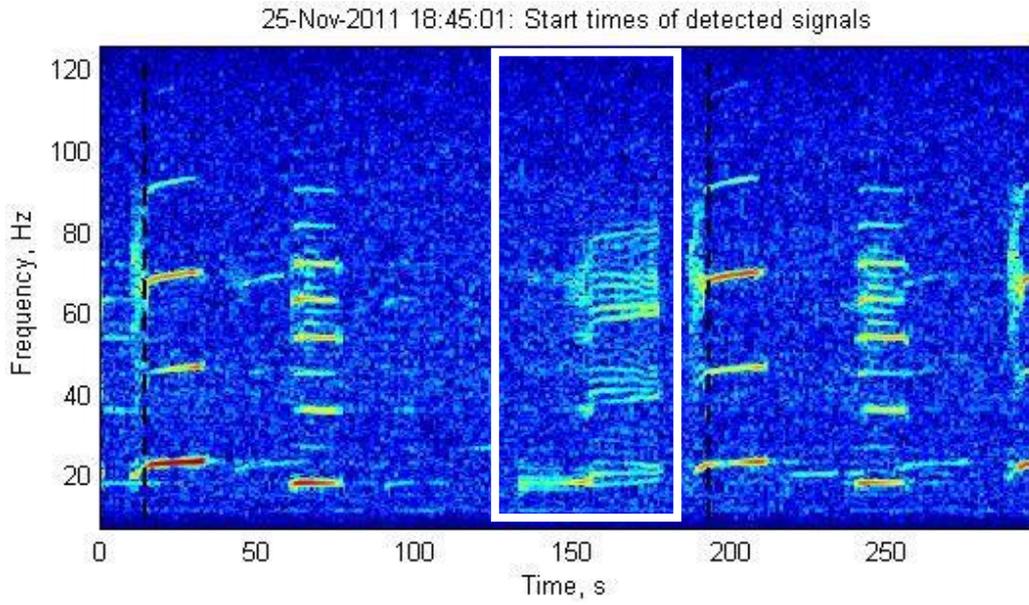
***Curtin University***

**August 2018**

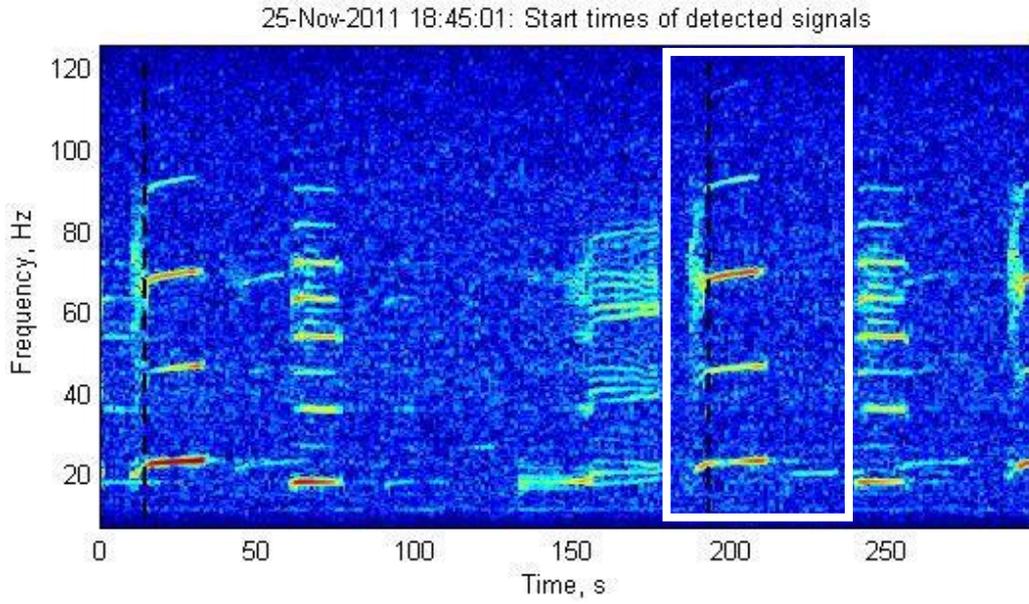
Appendix 1

Unit Types

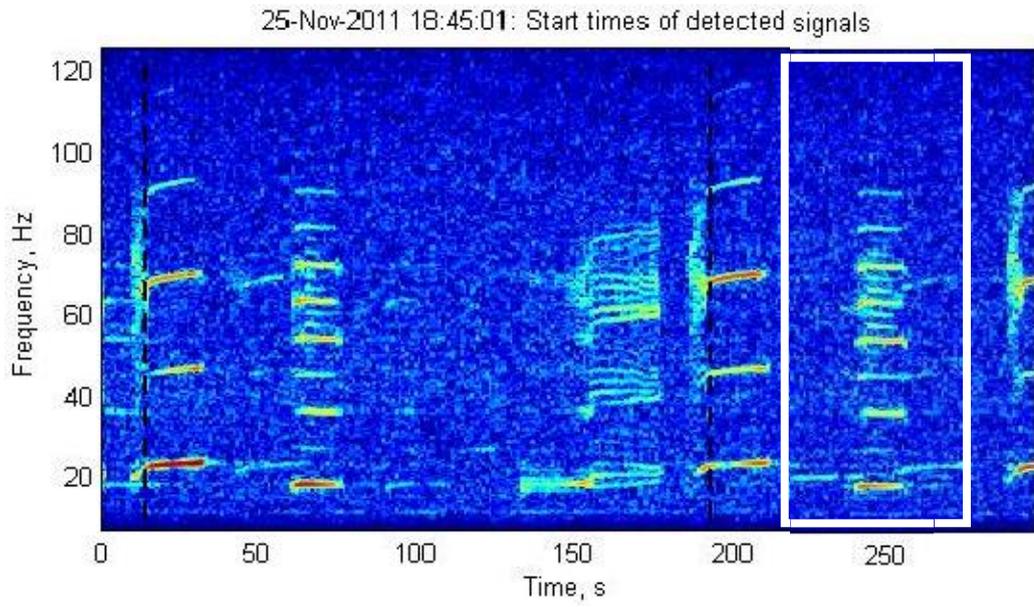
**Unit I**



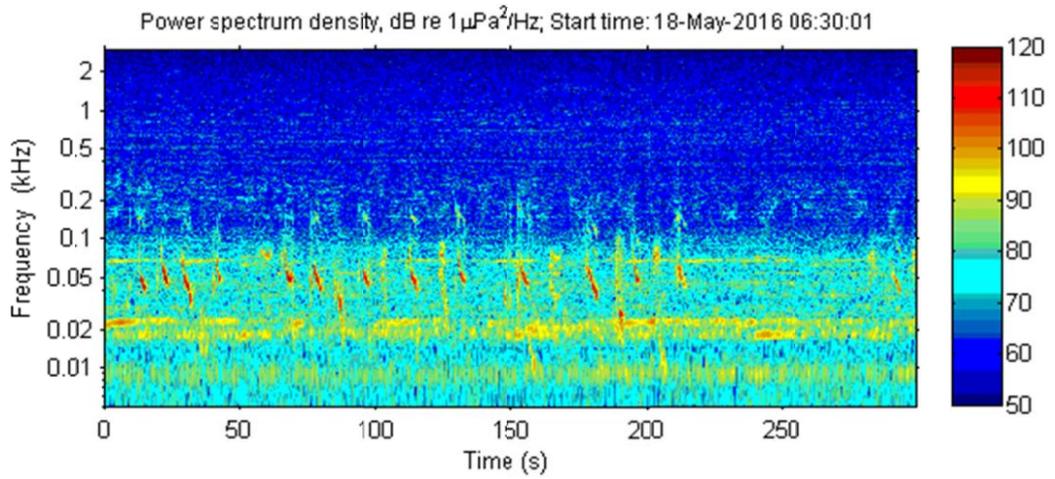
**Unit II**



Unit 3

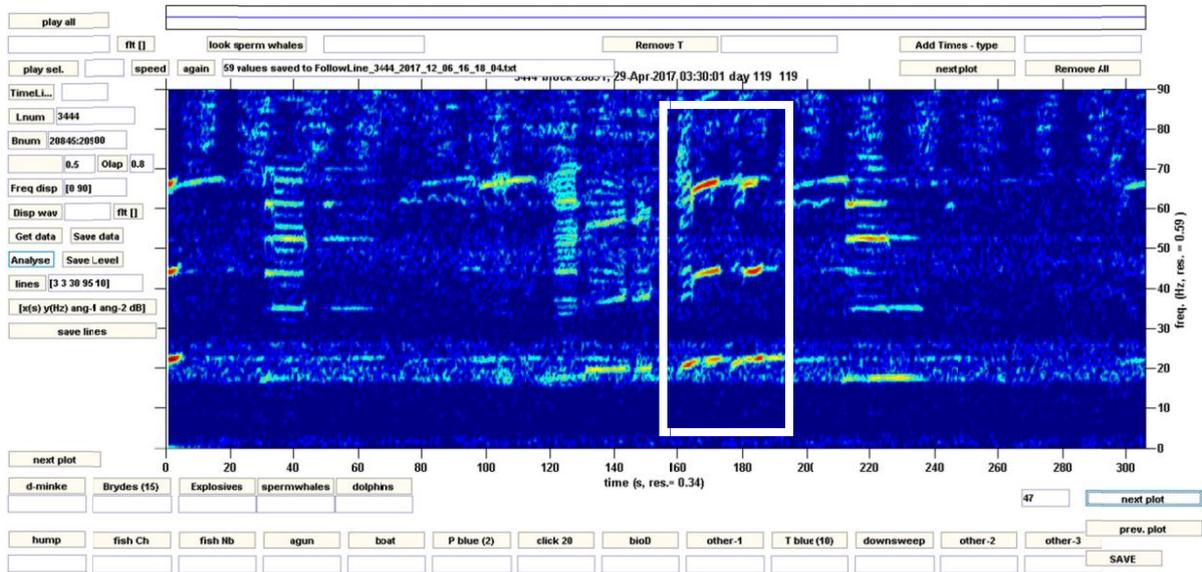


**Down sweeps – often called D calls or social sounds**

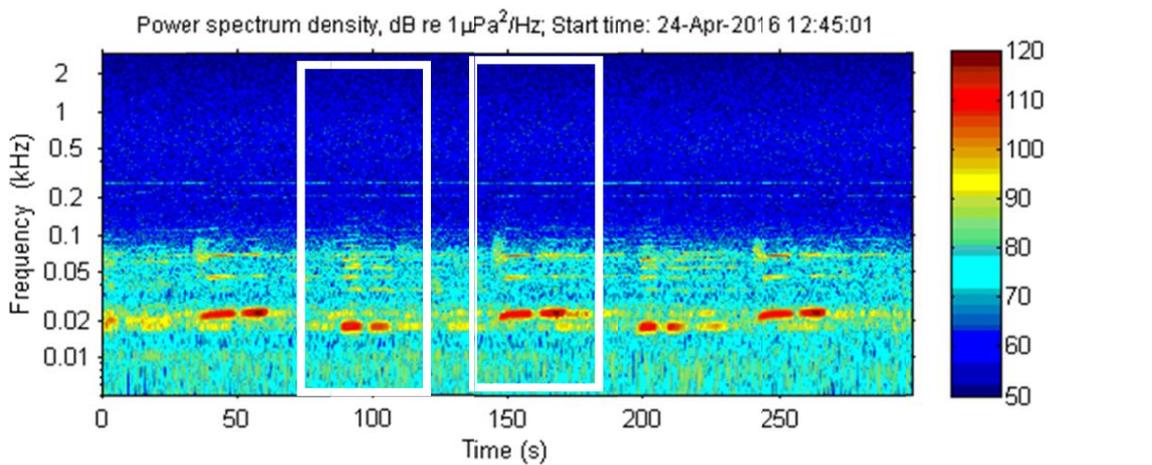


Appendix 1

**Unit Break** – pause of greater than 4 seconds in the middle of any song unit where the signal dips in frequency after the break



**Unit Split** – pause of less than 4 seconds in the middle of any song unit where frequency remains constant

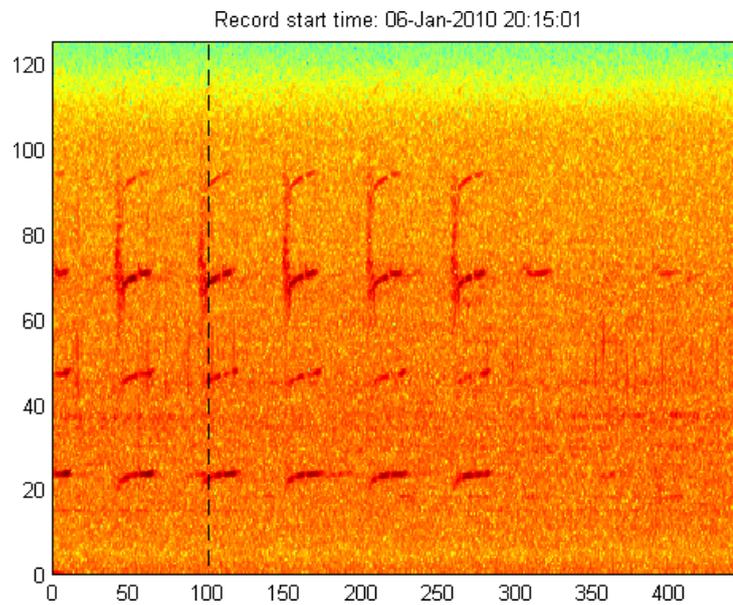


## Appendix 1

### Phrase Types

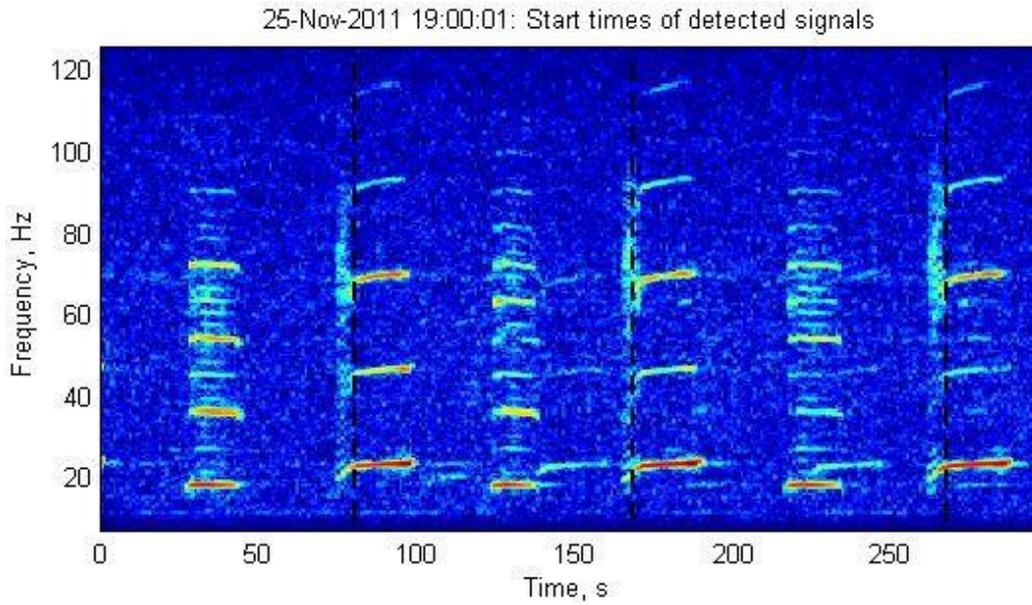
When repeated form a song. A single phrase is one repetition of the unit sequence. In some of the following spectrograms more than one phrase will be visible. Where more than one phrase is repeated in succession this represents the song of the same name.

**P1** – defined as a solitary type II unit repeated at intervals of 40 to 80 seconds.

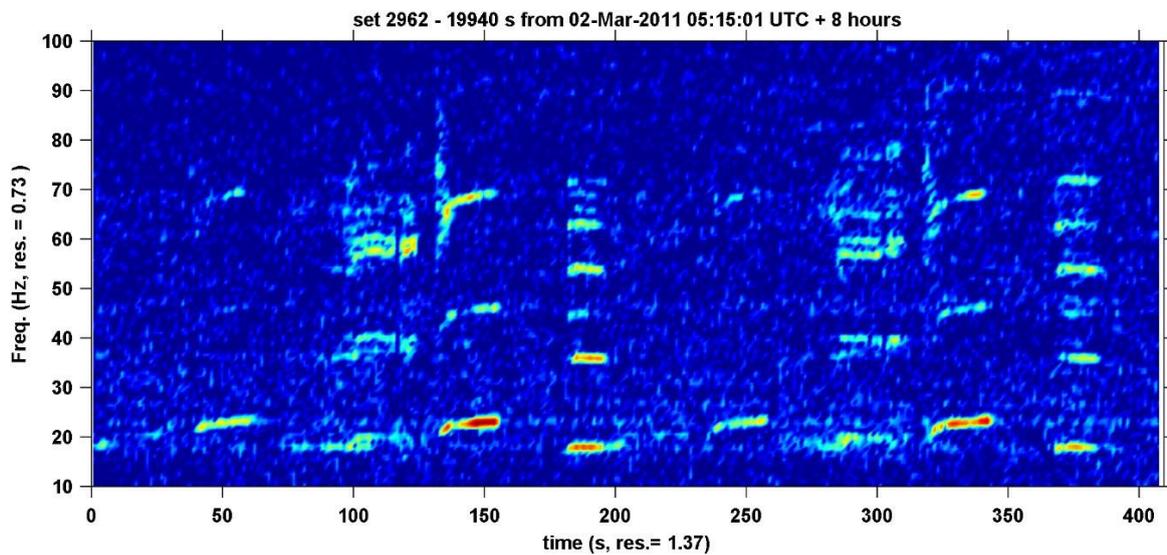


Appendix 1

**P2** – unit I and unit II comprise the *P2* phrase. They are repeated in a song sequence at intervals of between 80 and 120 seconds.

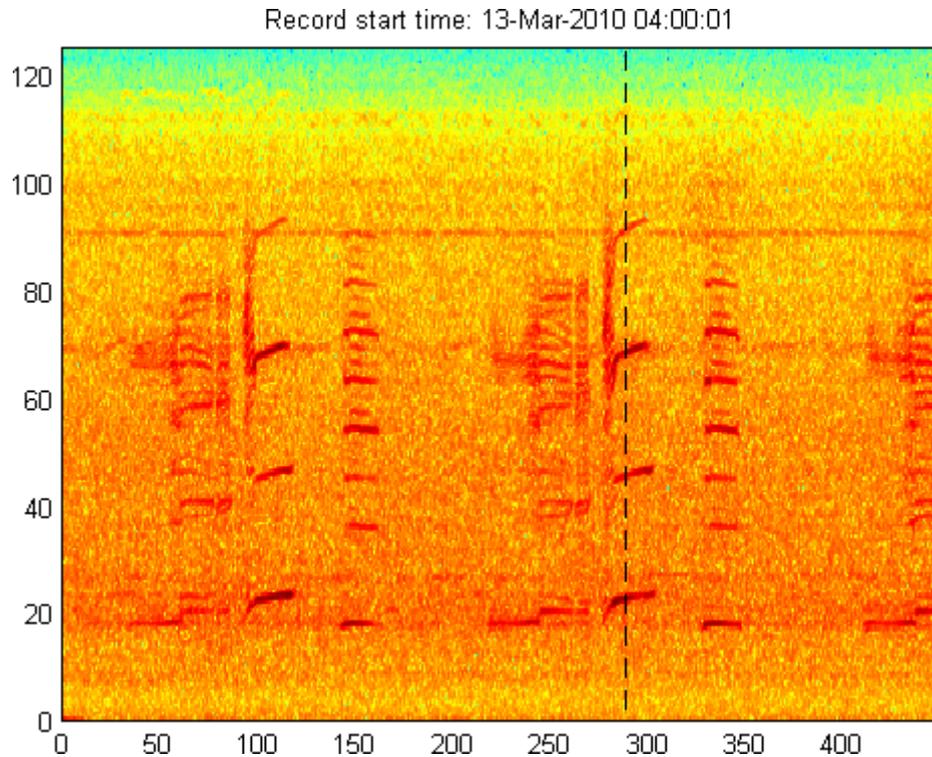


**P3** – phrase consists of a unit I, unit II and unit III in that order. Repeated in song sequences at intervals of between 160 and 220 seconds.

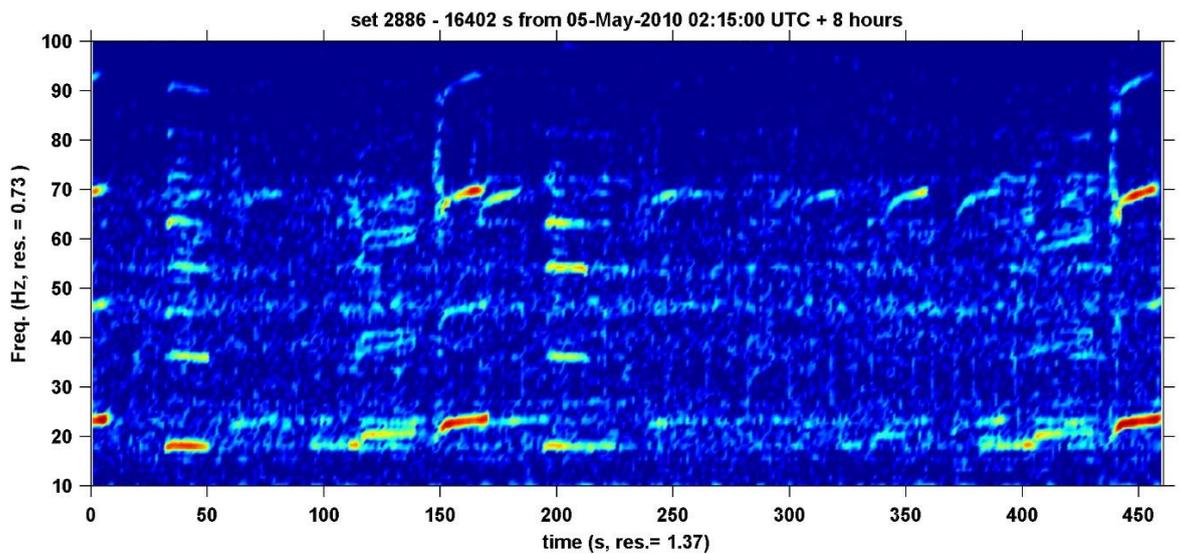


Appendix 1

**P3S** – the same as the *P3* song sequence but repeated at a shorter interval of less than 160 seconds. Generally has a shortened unit I and a very short break between unit I and unit II.



**P3L** – same sequence as a *P3* phrase but repeated at longer intervals of greater than 220 seconds. Often has an elongated unit I.

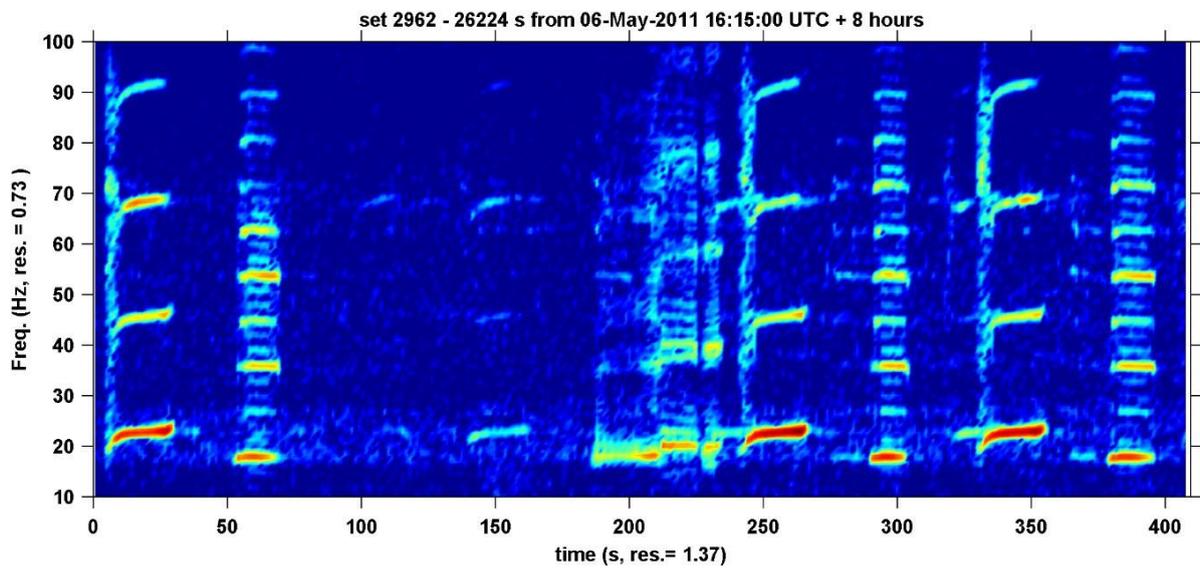


Appendix 1

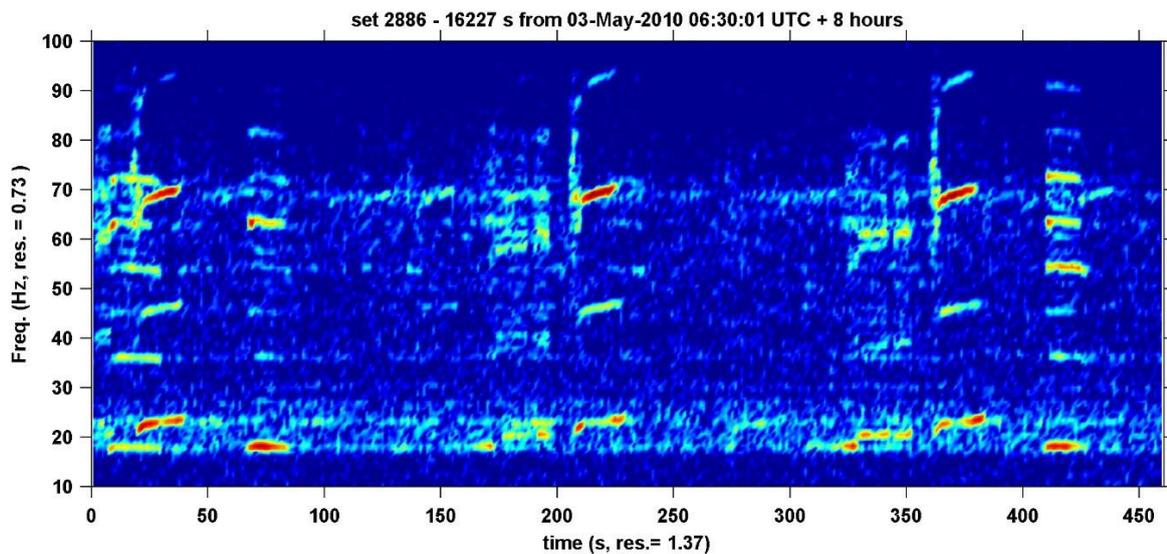
*P3L* (same as *P3* but with a longer repetition interval of >220s, generally has an elongated unit I)

Song Combinations

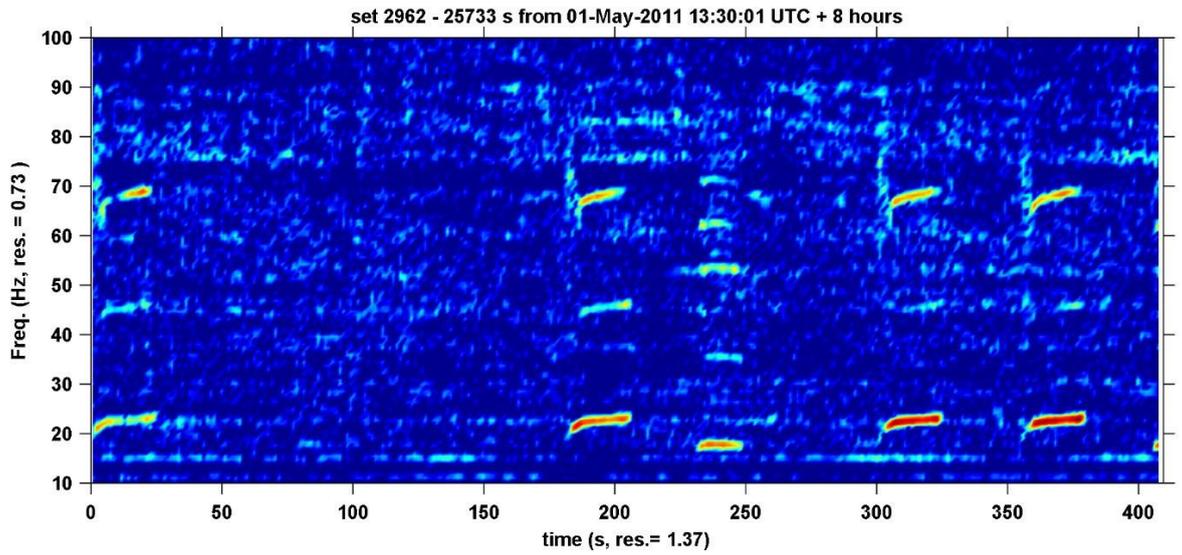
***P3A*** – a *P3* and *P2* phrase repeated in sequence. The time for the entire sequence is a multiplier of the *P3* and *P2* phrase types with the *P2* phrase being half the length of the *P2*. Generally repeated at intervals of 240 to 300 seconds.



***P3B*** – A combination of the *P3* phrase type followed by a unit I and unit II.



**P2A** – A combination of the *P2* phrase type and a *P1* phrase. There may be one or more type II units following the *P2* phrase. The repeat interval is a combination of the *P2* and *P1* phrase times with the *P1* segment half the length of the *P2*.



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Appendix 2

Co-author contribution statements

By signing below, co-authors agree to the listed publication being included in the candidate's thesis and acknowledge that the candidate is the primary author, i.e. contributed greater than 50% of the content and was primarily responsible for the planning, execution and preparation of the work for publication, unless otherwise indicated.

**Publication title:** Song variation of the Eastern Indian Ocean pygmy blue whale population

**Co-authors:**



**Professor Robert McCauley**



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**Dr Alec Duncan**



**Curt Jenner**



**Micheline Jenner**